Impact of a shared sugar food source on biological control of *Tuta absoluta* by the parasitoid *Necremnus tutae*

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Abstract

Honeydew is a sugar-rich food source produced by sap-feeding insects, notably by major pests such as aphids and whiteflies. It is an important alternative food source for the adult stage of various key natural enemies (e.g., parasitoids), but it may be used also as food by agricultural pests. *Necremnus tutae* is an idiobiont parasitoid, and it is the most abundant larval parasitoid associated with the South American tomato pinworm, *Tuta absoluta*, in recently invaded European areas. The impact of *N. tutae* on *T. absoluta* populations was evaluated under greenhouse conditions with and without the presence of a honeydew producer, the aphid *Macrosiphum euphorbiae*. In addition, laboratory experiments were performed to evaluate the longevity of *N. tutae* and *T. absoluta* adults when fed with water, honey or honeydew produced by the aphid. In the greenhouse, *N. tutae* effectively reduced *T. absoluta* population by the end of the experiment, and this independently of the presence of the aphid; still the presence of *M. euphorbiae* led to delayed and reduced *T. absoluta* population peak when controlled by the parasitoid (there was a fourfold increase in parasitoid density in presence of aphid). The longevity of both *N. tutae* and *T. absoluta* females increased in the presence of honeydew (when compared to water only) under laboratory conditions; it hinted that honeydew could be used by an herbivore as *T. absoluta*. The interactions between the two phytophagous species showed contrasting effects, and this mostly independently of parasitoid presence. *Tuta absoluta* had no impact on aphid population dynamics. By contrast, the production of *T. absoluta* larvae was higher in the first part of the experiment as the adults lived longer (feeding on aphid honeydew) and produced more larvae. In the second part of the experiment, there were fewer *T. absoluta* larvae in the presence of the aphid, likely owing to resource competition and/or negative plant-mediated indirect interactions. We demonstrated that honeydew producers could impact parasitoid-host population dynamics both through direct and indirect interactions and that potential positive effects of a sugar food source toward a pest can be nullified in the long term by other negative effects occurring simultaneously.

Keywords  Eulophidae · Biological control · Solanaceae · Gelechiidae · Honeydew

Key messages

- The parasitoid *Necremnus tutae* suppressed *T. absoluta* population growth with and without aphid under greenhouse conditions.
- Honeydew increased *N. tutae* and *T. absoluta* adult longevity both under laboratory and greenhouse conditions.
- Aphid presence led to delayed and reduced *T. absoluta* population peak when controlled by *N. tutae*.
- *Necremnus tutae* had no impact on aphid population growth despite effective biological control of the other herbivore (*T. absoluta*).
- Honeydew producer could impact parasitoid-host population dynamics through direct and indirect interactions.
Introduction

The South American tomato pinworm, Tuta absoluta Meyrick (Lepidoptera: Gelechiidae), is considered one of the main agricultural threats to world tomato production (Desneux et al. 2010, 2011; Biondi et al. 2018). Tuta absoluta was first observed outside South America in Eastern Europe in 2006 and spread rapidly throughout Africa, the Middle East and parts of Asia (Campos et al. 2017; Sankarganesh et al. 2017; Han et al. 2018, 2019; Mansour et al. 2018; McNitt et al. 2019), as well as in central America in a lesser extent (Biondi et al. 2018; Verheggen and Fontus 2019). Chemical control is the method used most to prevent the outbreaks of T. absoluta in newly invaded areas due to the lack of effective alternatives (Biondi et al. 2018). However, insecticide efficiency may be compromised due to the cryptic nature behavior of the larvae that mine leaves, and occasionally stems, flowers and tomatoes (Guedes and Picanço 2012). Moreover, wide use of insecticides can cause extensive side effects, such as the development of resistance to insecticides in T. absoluta populations (Campos et al. 2015; Roditakis et al. 2018; and see Guedes et al. 2019) as well as a detrimental impact on non-target organisms such as natural enemies (Lu et al. 2012; Biondi et al. 2015; Jam and Saber 2018; Mohammed et al. 2018; Passos et al. 2018; Soares et al. 2019a, b) through multiple potential sublethal effects (Desneux et al. 2007). Indeed, an alternative to conventional pest control is to increase the activity of naturally occurring enemies within integrated pest management (IPM) programs (Ragsdale et al. 2011; Biondi et al. 2018; Perovic et al. 2018; Jacquel et al. 2019).

Several predators and parasitoids spontaneously attacking T. absoluta in tomato crops in Europe have been identified (Castañé et al. 2011; Mollá et al. 2011; Zappalà et al. 2013). However, in tomato systems, T. absoluta coexist with a large number of pests including aphids, whiteflies and fruit worms (Kennedy 2003), that may indirectly interact with potential biological control agents in complex food webs. Indirect interaction is an important force driving insect communities, species density and diversity, including direct and indirect effects inside and outside the agroecosystem (van Veen et al. 2005). Indirect interactions may occur (i) between two prey or host species sharing the same natural enemy through predation or parasitization, and (ii) between two species separated in time or space and interacting in different ways with natural enemies (Chailleur et al. 2014b). Among the other pests present in the tomato systems, aphids such as Macrosiphum euphorbiae Thomas (Hemiptera: Aphididae: Macrosiphini) have been described as pests able to produce honeydew (Hullé et al. 2019). Honeydew is a carbohydrate-rich source that may be used as a food source by adults of natural enemies and phytophagous pests to enhance their fitness (Wäckers et al. 2008). Hence, the availability of suitable food sources (e.g., intrinsic plant quality in terms of nutritional status, and other alternative food sources) could affect the outcome of pest-natural enemy interactions and may be critical for the efficiency of biological pest control (Bomard et al. 2013, Chailleux et al. 2014b; Jaworski et al. 2015; Biondi et al. 2016; Desneux et al. 2019). The study of the multitrophic interactions among natural enemies and invasive pests is required to design effective biological control within the framework of the tomato management program.

Augmentative biological control relies on periodic releases of natural enemies that mainly attack eggs and other small arthropod instars (Desneux et al. 2010; Chailleux et al. 2013; Zappalà et al. 2013). However, other biological control agents that impact different pest stages, mainly in T. absoluta, as well as in different phenological stage and architecture of tomato plants have to be implemented (Perdikis et al. 2014; Mirhosseini et al. 2019). The eulophid parasitoid Necremnus tutae Ribes & Bernardo (Hymenoptera: Eulophidae) has been observed and is widespread in Europe and Africa parasitizing T. absoluta (Gebiola et al. 2015). It has been identified as a promising biological control agent on T. absoluta (Biondi et al. 2013a; Chailleux et al. 2014a; Naselli et al. 2017; Bodino et al. 2019). Previous laboratory trials showed that N. tutae reproductive and longevity outcomes were enhanced by the simultaneous presence of the sap feeder Bemisia tabaci Gennadius (Hemiptera: Aleyrodidae), a honeydew producer (Dong et al. 2018). However, more field studies are needed to test the ability to control pest population.

In this context, we assessed the effect of the aphid presence on both T. absoluta and N. tutae population dynamics in a greenhouse experiment (i) to confirm the potential role of N. tutae as biological control agent of T. absoluta; and (ii) to test the impact of the presence of the honeydew, as a sugar food source, on parasitoid longevity and its ability to control the pest population. In addition, we tested the impact of honeydew as a food source for these two insects on the parasitoid longevity in a laboratory experiment.

Materials and methods

Biological material

Tomato plants cv. Nano were grown in a climate chamber until the seedlings emerged (25 ± 3 °C, 65 ± 5% relative humidity [RH] and a photoperiod of 16:08 [L:D] h) in cubic plastic pots (7 × 7 × 6.5 cm). After emergence, the tomato seedlings were placed under greenhouse conditions (20 ± 2 °C, 65 ± 5% RH and a photoperiod of 10:14 [L:D]...
h). At 6 days after seeding (DAS), the tomato seedlings were washed to remove soil and then transferred to new pots containing inert substrate (Perlite Italiana srl, Corsico, Italy) (see schedule Table 1). At DAS 24, the plants were transferred to larger pots (diameter: 10 cm, height: 9 cm) filled with the same substrate and placed in four separate compartments in the greenhouse. All the plants were watered using nutrient solution, and the latter was adapted for all the treatments to pH 6.0 ± 0.2 by using H$_2$SO$_4$ (0.2 M) according to the compartment.

The *T. absoluta* colony was maintained in cages (55 × 75 × 80 cm), in regular chambers using pesticide free potted tomato plants (Biondi et al. 2013b). A solution containing 10% honey was provided ad libitum to adults in rearing cages. The *N. tutae* parasitoids originated from field-collected material and were reared in cages (45 × 45 × 55 cm) on *T. absoluta* kept on tomato plants in a climatic chamber. The *M. euphorbiae* aphid colony was maintained in a cage (90 × 50 × 60 cm) placed in the greenhouse using tomato plants as host (22 ± 5 °C, 60 ± 10% [RH] and during a photoperiod of 15:09 [L:D] h).

### Greenhouse experiment

The experiment was performed at the French National Institute for Agricultural Research (INRA), Sophia Antipolis, France, in 2016 and 2017. The performance of *N. tutae* was checked with and without the honeydew produced by *M. euphorbiae* in semi-field. The experiment was carried out in the greenhouse in four separated glass compartments. Each compartment had eight rows, and every row was composed of eight tomato plants (Fig. 1). Four tunnels were created for the treatments and consisted in 16 tomato plants that were covered with slim nylon mesh (5 × 1 × 2 m). The following four treatments were set up: (i) *T. absoluta* (negative control), (ii) *T. absoluta* + *M. euphorbiae*, (iii) *T. absoluta* + *N. tutae* (iv) *T. absoluta* + *M. euphorbiae* + *N. tutae* (Fig. 1). The treatments described above were replicated four times in each greenhouse compartment. A general overview of the experiment design is shown in Table 1. The first release was performed with 20 couples of *T. absoluta* in 30 DAS in all treatments (i–iv). 34 DAS, five *M. euphorbiae* were placed on top of each tomato plant in treatments (iii) and (iv). 44

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**Table 1** Sampling protocol schedule including plant growth (S = plant seeding; T1/T2 = plant handling events), and plant sampling events (A = assessment)

| Species                        | Days after seeding (DAS) |
|--------------------------------|--------------------------|
|                                | 0 6 23 30 34 44 45 64 71 78 85 92 99 106 113 |
| Solanum lycopersicum           | S T1 T2 A A A A A A A A A |
| *Tuta absoluta*               | R R R R R R R R R R R R R |
| *Macrosiphum euphorbiae*      | R R R R R R R R R R R R R |
| *Necremnus tutae*             | R R R R R R R R R R R R R |

* *T. absoluta* adults (n = 20 couples), *M. euphorbiae* adults (n = 5 aphids/tomato plant) and *N. tutae* adults (25 couples) infestation (R: release time) and development throughout the plant development stages. The assessment started 71 days after seeding (DAS) to DAS 113.
DAS, 25 couples of *N. tutae* were released in treatments (ii) and (iv). Likewise, in the second release, 20 couples of *T. absoluta* were again released at 45 DAS. The second parasitoid release was performed at 64 DAS with 25 couples of *N. tutae* in treatments (ii) and (iv). The assessments started one week after the second release at 71 DAS. The assessments were carried out randomly on four tomato plants for each treatment, on 16 tomato plants weekly. Two tomato leaves were surveyed on the top, middle and at the bottom of tomato plants. The number of *T. absoluta* larvae and adults, *N. tutae* adults and *M. euphorbiae* (nymphs and adults) was counted.

**Laboratory experiment**

*Honeydew collection*. The honeydew was collected using parafilm (plastic packaging, Chicago, IL) strips in the *M. euphorbiae* colony reared on tomato plant. The parafilm was exposed for 24 h under the tomato leaves with high *M. euphorbiae* density. Once the parafilm strips were removed, the abundance of honeydew was checked using a stereo microscope (20x), and thereafter placed inside Petri dishes for storage at −12 °C until needed.

*Necremmus tutae* and *T. absoluta* survival. The experiment was performed to verify *N. tutae* female parasitoid survival. Three treatments were designed: (i) *N. tutae* + water (control), (ii) *N. tutae* + honey and (iii) *N. tutae* + honeydew. The same procedure was carried out with *T. absoluta* females. The parafilm was cut into strips (1 cm × 5 cm) containing honeydew, honey or water. For each treatment, a parafilm strip was inserted into a glass tube (3 cm diameter × 10 cm height) and the latter was closed using moistened cotton. Then, a 24-h-old female *N. tutae* or *T. absoluta* was introduced into this tube which was placed in the thermostatic cabinet (25 ± 1 °C, 60 ± 10% [RH] for a photoperiod of 16:08 [L:D] h), and checked daily to determine insect survival.

**Statistical analysis**

The statistical analyses were performed using R version 3.4.0. The impact of the treatments (with or without *N. tutae*) and of the time period (number of days after seeding) on the number of *M. euphorbiae* was analyzed using a linear mixed model with the treatments and the time as fixed effects and the compartment number as a random effect (the dependent variable follows a normal distribution confirmed by a Shapiro–Wilk test). Moreover, the impact of the treatments on each sampling day on the number of aphids was analyzed using the same method as described above. The impact of the treatments (T, TM, TMN, TN) and of the time period (number of days after seeding) on the number of *T. absoluta* larvae and adults, as well as the number of *N. tutae* adults, was analyzed using a generalized linear mixed model following a Poisson distribution. This model was built using the treatments and the time as fixed effects and the compartment number as a random effect. The impact of the treatments on each sampling day on the number of *T. absoluta* larvae and adults and *N. tutae* was analyzed using the same method as described above. Whenever necessary, a multicomparison test was done, using the package multcomp. A log-rank test and the Holm–Sidak multiple comparison procedure were used to identify significant differences among the survival curves of *T. absoluta* and *N. tutae* adults fed with water, honeydew produced by *M. euphorbiae* or honey. The figures were obtained using SigmaPlot v.12.5 (SYSTAT Software Inc. 2011).

**Results**

**Greenhouse experiment**

The number of *T. absoluta* larvae depended on the different treatments ($\chi_3^2 = 67.2, P < 0.001$) and the sampling day ($\chi_6^2 = 162.9, P < 0.001$) (Fig. 2). The number of *T. absoluta* larvae was stable the first 85 DAS and in the assessments of 99–106 DAS; it increased between the 92 and 99 DAS; and it finally decreased between the 106 and 113 DAS. Taking into consideration each sampling day, the number of larvae in the treatment with *T. absoluta* only was the lowest until 92 DAS. Then, the number of *T. absoluta* larvae increased until 113 DAS, with a population peak at the 106 DAS (Table 2, Fig. 2). In the treatment with *M. euphorbiae*, the number of *T. absoluta* larvae was higher at the beginning of the assessments and decreased after 78 DAS. However, after 85 DAS the number of *T. absoluta* larvae increased gradually until the end of the assessments, reaching a density almost twofold lower than when *T. absoluta* was alone. The treatment with only the parasitoid *N. tutae* showed a population peak of *T. absoluta* larvae at 92 DAS and then a decrease until 113 DAS, reaching a very low level by the end of the experiment. In the treatment with the three species, the population dynamic of *T. absoluta* was similar but showed lower and delayed population peak density (at 99 DAS) as well as lower larvae densities by the end of the experiment (106–113 DAS) (Fig. 2).

The number of *T. absoluta* adults depended on the various treatments ($\chi_3^2 = 56.6, P < 0.001$) and the sampling day ($\chi_6^2 = 391.9, P < 0.001$) (Fig. 3). The numbers of *T. absoluta* adults were similar the two first weeks (71 and 78 DAS). Then they increased slightly between 85 and 92 DAS and then increase steadily by the end of the experiment. The number of *T. absoluta* adults was not statistically different
among the treatments at 71 to 78 DAS and at 106 DAS (Table 2 and Fig. 3). The number of *T. absoluta* adults in the treatments with only *M. euphorbiae* + *T. absoluta* was higher than in the treatment *T. absoluta* alone (i.e., without *M. euphorbiae*) and with the three species at 99 DAS. Nevertheless, at 113 DAS in the end of the experiment, the number of *T. absoluta* adults was highest in the treatment with *M. euphorbiae* (Fig. 3).

The number of the parasitoid *N. tutae* depended on the presence of *M. euphorbiae* (\( \chi^2 = 12.7, P < 0.001 \)) and on the sampling day (\( \chi^2 = 37.5, P < 0.001 \)) (Fig. 4). The number of *N. tutae* adults was stable the first 85 DAS and between 106 and 113 DAS; it increased between 85 and 92 DAS and at 99–106 DAS; and then it finally decreased between 92 and 99 DAS. The number of *N. tutae* was not statistically different in the first three assessments at 71–85 DAS (Table 2 and Fig. 4). However, in the treatment with *M. euphorbiae* the number of *N. tutae* was threefold–fourfold higher than the treatment without *M. euphorbiae* at 85–113 DAS (Fig. 4).

The number of *M. euphorbiae* was not strongly impacted on the presence of *N. tutae*, although marginally significantly with slightly higher aphid number by the end of the experiment when the parasitoid was present (\( F_{1214} = 3.5, P = 0.065 \)). The main factor was impacting aphid density was sampling day (\( F_{1214} = 30.3, P < 0.001 \)) (Table 2, Fig. 5).

The number of aphids increased on 85–99 DAS, and it was similar to the assessments at 71–85 DAS as well as those at 99–113 DAS.

### Laboratory experiment

*Tuta absoluta* adult survival was impacted by the food source provided (log-rank test: \( \chi^2 = 1462.424, df = 2, P < 0.001 \)) (Fig. 6a). All the survival curves were significantly different.

![Mean number (± SEM) of *Tuta absoluta* larvae per tomato leaf per week in four different treatments (*T. absoluta* only, *N. tutae* + *T. absoluta*, *M. euphorbiae* + *T. absoluta* and *N. tutae* + *T. absoluta* + *M. euphorbiae*). GLM following a Poisson distribution was used to compare the number of *T. absoluta* larvae among treatments at each sampling date. Mean number under the same small letters is not significantly different at each sampling day among treatments.](image-url)
Fig. 3  Mean (± SEM) number of *Tuta absoluta* adults per tomato leaf per week in four different treatments (*T. absoluta* only, *N. tutae* + *T. absoluta*, *M. euphorbiae* + *T. absoluta* and *N. tutae* + *T. absoluta* + *M. euphorbiae*). GLM following a Poisson distribution was used to compare the number of *T. absoluta* adults among treatments at each sampling date. Mean number under the same small letters is not significantly different at each sampling day among treatments.

Fig. 4  Means (± SEM) number of *Necremnus tutae* adults per tomato leaf per week in four different treatments per week in two different treatments (with and without *M. euphorbiae*). GLM following a Poisson distribution was used to compare the number of *N. tutae* adults among treatments at each sampling date. Mean number under the same small letters is not significantly different at each sampling day among treatments.
with the Holm–Sidak test ($P > 0.05$). The survival of the parasitoid $N. tutae$ females was also impacted by the food source provided (log-rank test: $\chi^2 = 1222.04, df = 2, P < 0.001$) (Fig. 6b). All the survival curves were significantly different with Holm–Sidak test ($P > 0.05$).

**Discussion**

The importance of sugar food sources in biological control program has been largely reported in light of their positive effects on biocontrol agents (Wäckers et al. 2008; Tena...
et al. 2018; Heimpel 2019; Picciau et al. 2019; Monticelli et al. 2019); still the impact that such food sources may have on herbivorous pests has been scarcely documented (Wäckers et al. 2007; Winkler et al. 2009). Honeydew is the most commonly available sugar food source in agricultural systems (Wäckers et al. 2008) and is produced by sap-feeding insects, including by pests such as aphids and whiteflies (Hendrix et al. 1992; Hullé et al. 2019). In tomato crops, the biological control of the major pest \( T. \) \( \text{absoluta} \) by the parasitoid \( N. \) \( \text{tutae} \) may be modulated by honeydew presences as tomato plants are often infested by whiteflies and/or aphids. The \( N. \) \( \text{tutae} \) parasitoid provided effective biological control of \( T. \) \( \text{absoluta} \), and this regardless of aphid presence (\( M. \) \( \text{euphorbiae} \)). However, the aphid presence had various effects on the system (i) the peak population of \( T. \) \( \text{absoluta} \) was both delayed and reduced when controlled by the parasitoid, (ii) \( T. \) \( \text{absoluta} \) adults fed with aphid honeydew lived longer, stressing that honeydew food source could be used positively by an herbivore, and more larvae were produced in first part of greenhouse experiment, (iii) in the second part, there were fewer \( T. \) \( \text{absoluta} \) larvae potentially owing to occurrence of resource competition and/or plant-mediated indirect interactions with the aphid. The present study hinted that honeydew producers may impact parasitoid-host population dynamics both through direct and indirect interactions and that potential positive effects of a sugar food source toward a pest can be nullified in the long term by other negative effects occurring simultaneously. Analyzing these interactions may provide data on the potential role of biological control agents on key pests in the framework of IPM in greenhouse tomato crops.

**Impact of honeydew**

\( \text{Necremnus tutae} \) is a synovigenic parasitoid species, i.e., females continuously mature eggs throughout their lifespan relying both on their own nutritional reserves and on additional nutrients acquired, for example, through host feeding (Jervis et al. 2001; Balzan and Wäckers 2013). In addition to feeding on host hemolymph, parasitoid females require sugar food sources such as floral nectar and/or honeydew in order to sustain biological traits linked to actual parasitoid fitness (Jervis et al. 2001; Wäckers et al. 2008; Benelli et al. 2017). Honeydew consumption has been shown to increase parasitoid longevity (Hogervorst et al. 2007; Hagenbucher et al. 2014; Tena et al. 2018) and may be involved in parasitoid performance, e.g., by increasing offspring production (Lahiri et al. 2017; Dong et al. 2018; Picciau et al. 2019); this has notably been reported for \( N. \) \( \text{artynes} \) feeding on floral nectar (Balzan and Wäckers 2013) as well as for \( N. \) \( \text{tutae} \) feeding on whitefly honeydew (Dong et al. 2018). We demonstrate further that tomato aphid honeydew enhances \( N. \) \( \text{tutae} \) adult longevity under laboratory conditions (Fig. 6b); the presence of honeydew producers in greenhouse however provided positive effects on parasitoid longevity, although this effect was confounded with potential positive impact on parasitoid fecundity (Fig. 4. DAS 92–113).

In addition to its impact on parasitoid, honeydew also proved as a potential reliable sugar food source for \( T. \) \( \text{absoluta} \) adults notably increasing their longevity under laboratory conditions (Fig. 6a); it was also suggested by the greenhouse experiment when comparing \( T. \) \( \text{absoluta} \) alone vs. \( T. \) \( \text{absoluta} \) + aphid (significantly higher \( T. \) \( \text{absoluta} \) density in DAS 85, 99 and 113, Fig. 3). Still this positive effect of aphid honeydew on adults was offset in the long term by the multiple negative effects that pulling aphids have on \( T. \) \( \text{absoluta} \) larvae (see below). In addition, it is known that lifespan increase does not cascade directly to fitness increase in lepidopterans (Jervis et al. 2007), as demonstrated for \( T. \) \( \text{absoluta} \) for which 97% of realized fecundity occurs in first 17 days (Lee et al. 2014). As honeydew led to an increase in \( T. \) \( \text{absoluta} \) longevity from 17 days (water only) to 26 days (honeydew), such increase could only provide marginal increase in fecundity. Honeydew still may provide other benefits to \( T. \) \( \text{absoluta} \) adults as rich-sugar food sources could enhance lepidopterans mobility and thus dispersion (Jervis et al. 2007).

**Effects of the secondary pest on biotic interactions at play in the system**

Various biotic interactions are usually at play in complex agroecosystems involving multiple arthropod pests and natural enemies, thus identifying potential mechanisms underneath and the demographic consequences of such key interactions is crucial for increasing both applied and fundamental knowledge (Chailleux et al. 2014b; Naselli et al. 2017). In our system, aphid may have affected biotic interactions through three main non-excluding effects on \( T. \) \( \text{absoluta} \): (i) parasitoid-mediated interactions, (ii) resource competition, and (iii) plant-mediated indirect interactions.

The aphid did provide food source (honeydew) benefiting to the parasitoid \( N. \) \( \text{tutae} \) (at least increasing its longevity), and so, a negative indirect interaction toward \( T. \) \( \text{absoluta} \) occurred through increased parasitoid-induced mortality in the leafminer. Therefore, such effect could be classified as apparent amensalism (\( –, 0 \)) (Chailleux et al. 2014b) as there was no parasitoid-mediated obvious effect of \( T. \) \( \text{absoluta} \) toward the aphid (Fig. 5). Indeed, albeit \( T. \) \( \text{absoluta} \) larvae density was strongly reduced by parasitoid \( N. \) \( \text{tutae} \), there was no change in the \( M. \) \( \text{euphorbiae} \) population growth; therefore, any positive effect of \( N. \) \( \text{tutae} \) on aphid population growth (e.g., preventing leaf being destroyed by \( T. \) \( \text{absoluta} \) and reducing the resource competition between the two pests) might have been nullified by the occurrence
of other effect(s) (e.g., intraspecific competition could be a main driver in aphid population dynamic, Dixon et al. 1993; Mooney et al. 2008; Mohammed et al. 2019).

Resource competition between the two herbivores showed unilateral effects, with mostly *T. absoluta* being affected by aphids. The production of *T. absoluta* larvae was higher in the first part of the experiment, suggesting that no resource competition from aphid was occurring toward the leafminer larvae. However, this increase could be attributed to the positive effect that honeydew had on *T. absoluta* adults (i.e., increased longevity); living longer they produced more larvae. By contrast, in the second part of the experiment (when most adults from the first released cohort had died) there were fewer *T. absoluta* larvae in the presence of the aphid, independently of parasitoid presence. Thus, negative effects may have occurred through resource competition between leafminer larvae and aphids, notably owing to pullulating aphids on the plants. Tomato leaves heavily infested by aphids may be unsuitable for the leafminer (e.g., food quality and/or availability is decreased, Villemereuil and Lopez-Sepulcre 2011; Barabas et al. 2016). In addition, potential physical impairment in *T. absoluta* larvae may result from aphid presence, i.e., a leafminer larvae outgoing from a leaf mine could not dig a new mine owing to overcrowding aphids on the leaf. By contrast to the impact of aphid on *T. absoluta* through resource competition, the lack of effect of the leafminer toward aphid is somehow surprising as *T. absoluta* is known to have a major impact on tomato plants (being a defoliator herbivore). For example, previous studies reported that *T. absoluta* negatively affected biological traits and population dynamic of the whitefly *Bemisia tabaci*, another major sap-feeder insect on tomato (Bompard et al. 2013; Jaworski et al. 2015; Dong et al. 2018). Such discordant results may be linked to the mobility habits of the two pests (aphid and whitefly) which differ drastically and could have its importance in their survival when competing with a defoliating insect. Despite being both sap feeders, mobility of whiteflies is quite limited in non-imaginal stages: only the first nymph stage can move (and barely), the other nymph stages are totally immobile and they die if the hosting leaf is destroyed. By contrast, all aphid stages are well mobile and the destruction of leaves by *T. absoluta* larvae does not lead to aphid death; they can move and start feeding on another part of the plant. Finally, *T. absoluta* may simply not have reached densities able to negatively impact aphid population through resource competition in our present study.

Aphids can also be involved in plant-mediated indirect interactions (Stout et al. 2006; Mouttet et al. 2011; Moreira et al. 2018) through triggering salicylic acid-pathway and subsequent plant chemical defenses (Wallig 2000). Through this mechanism, *M. euphorbiae* may have negatively affected leafminer population dynamic (by lowering down population growth rate). Multiple studies documented that sap feeders could affect negatively the performance of leaf chewers (Zhang et al. 2005; Inbar and Gerling 2007; Soler et al. 2012; Mouttet et al. 2013) and our study is in concordance with these data. In addition, the lack of impact of *T. absoluta* on aphids also matched with results of a previous study from Mouttet et al. (2013) which demonstrated lack of plant-mediated effect of *T. absoluta* to another sap feeder (*B. tabaci*). Finally, because our experimental design did not separate spatially both herbivores on the plants, it was not possible to distinguish between direct and plant-mediated indirect interactions between *T. absoluta* and aphid, although both interactions are likely confounded in realistic conditions.

**Implication in biological control**

Under microcosm and laboratory conditions, the ectoparasitoid *N. tutae* has proved to be a potential biological control agent of *T. absoluta*, targeting the larvae stage (Chailleux et al. 2014a; Biondi et al. 2018; Dong et al. 2018). In the present study we demonstrated that *N. tutae* can provide effective biological control of *T. absoluta* in tomato greenhouse, keeping the population at relatively low densities during the course of the experiment. Alternative food sources (e.g., honeydew produced by aphid) can help keeping parasitoids close to crops, in addition to providing and impacting the performance and longevity of parasitoids (Wäckers et al. 2008; Benelli et al. 2017) and this without promoting pest population growth (despite positive effect on the adult stage of the pest). However, aphids are pests that are targeted also by pest management program(s) and controlling their populations may compromise any benefits associated with their presence in the framework of *N. tutae*-based biological control. Other research has been carried out to select plant flowers, as alternative food sources, facilitating the establishment of *N. tutae* parasitoids and to improve biological control of *T. absoluta* (Balzan and Wäckers 2013; Arnó et al. 2018). Other alternatives such as the use of banker plants has been subjected to great interest as a means of biological control of invasive and/or key pests (Bodino et al. 2018; Kruytwagen et al. 2018; Wang et al. 2018). Banker plant systems are based on the use of non-commercial plants infested with non-pest herbivores serving as alternative host-prey for predators or parasitoids (Frank 2010; Parolin et al. 2012; Li et al. 2015; Zhao et al. 2017; Jaworski et al. 2019). When such plant banker systems are infested by aphids (or more generally by sap feeders), they may serve as sources of alternative foods, notably honeydew. Studies determining the factors limiting or potentially optimizing the biological control through manipulating honeydew producers are still needed to develop further biological control and IPM programs.
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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights This article does not contain any studies with human participants or animals (others than insects) performed by any of the authors.

References

Arnó J, Oveja MF, Gabarra R (2018) Selection of flowering plants to enhance the biological control of Tuta absoluta using parasitoids. Biol Control 122:41–50
Balzan MV, Wäckers FL (2013) Flowers to selectively enhance the fitness of a host-feeding parasitoid: adult feeding by Tuta absoluta and its parasitoid Necremnus arynes. Biol Control 67:21–31
Barabás G, Michalska-Smith MJ, Allesina S (2016) The effect of intraspecific and interspecific competition on coexistence in multispecies communities. Am Nat 188:E1–E12
Benelli G, Giunti G, Tena A, Desneux N et al (2017) The impact of adult diet on parasitoid reproductive performance. J Pest Sci 90:807–823
Biondi A, Chailleux A, Lambion J, Han P et al (2013a) Indigenous natural enemies attacking Tuta absoluta (Lepidoptera: Gelechiidae) in South France. Egypt J Biol Pest Co 23:117–121
Biondi A, Desneux N, Amiens-Desneux E, Siscaro G et al (2013b) Biology and developmental strategies of the Palaearctic parasitoid Bracon nigricans (Hymenoptera: Braconidae) on the Neotropical moth Tuta absoluta (Lepidoptera: Gelechiidae). J Econ Entomol 106:1638–1647
Biondi A, Campolo O, Desneux N, Siscaro G, Palmeri V, Zappalà L (2015) Life stage-dependent susceptibility of Aphytis melinus DeBach (Hymenoptera: Aphelinidae) to two pesticides commonly used in citrus orchards. Chemosphere 128:142–147
Biondi A, Zappala L, Di Mauro A, Tropea Garzia G, Russo A et al (2016) Can alternative host plant and prey affect phytophagy and biological control by the zoophytophagous mirid Nesidiocoris tenuis? Biocontrol 61:79–90
Biondi A, Guedes RNC, Wan FH, Desneux N (2018) Ecology, worldwide spread, and management of the invasive South American Tomato Pinworm, Tuta absoluta: past, present, and future. Annu Rev Entomol 63:239–258

Bodino N, Ferracini C, Tavella L (2018) Functional response and age-specific foraging behaviour of Necremnus tutae and N. cosmopterix, native natural enemies of the invasive pest Tuta absoluta in Mediterranean area. J Pest Sci 92:1–12
Bodino N, Ferracini C, Tavella L (2019) Functional response and age-specific foraging behaviour of Necremnus tutae and N. cosmopterix, native natural enemies of the invasive pest Tuta absoluta in Mediterranean area. J Pest Sci 92:1467–1478
Bompard A, Jaworski CC, Bearez P, Desneux N (2013) Sharing a predator: can an alien invasive pest affect the predation on a local pest? Pop Ecol 55:433–440
Campos MR, Silva TBM, Silva WM, Silva JE et al (2015) Spinosyn resistance in the tomato borer Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae). J Pest Sci 88:405–412
Campos MR, Biondi A, Adiga A, Guedes RNC et al (2017) From the Western Palaearctic region to beyond: Tuta absoluta 10 years after invading Europe. J Pest Sci 90:787–796
Castañé C, Arnó J, Gabarra R, Alomar O (2011) Plant damage to vegetable crops by zoophytophagous mirid predators. Biol Control 59:22–29
Chailleux A, Bearez P, Pizzol J, Amiens-Desneux E et al (2013) Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest Tuta absoluta. J Pest Sci 86:533–541
Chailleux A, Desneux N, Arnó J, Gabarra R (2014a) Biology of two key Palaearctic larval ectoparasitoids when parasitizing the invasive pest Tuta absoluta. J Pest Sci 87:441–448
Chailleux A, Mohl EK, Teixeira Alves M, Messeлинk GJ et al (2014b) Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. Pest. Manage Sci 70:1769–1779
Desneux N, Decourtye A, Delpueyo JM (2007) The sublethal effects of pesticides on beneficial arthropods. Annu Rev Entomol 52:81–106
Desneux N, Wajnberg E, Wyckhuys KAG, Burgio G et al (2010) Biological invasion of European tomato crops by Tuta absoluta: ecology, geographic expansion and prospects for biological control. J Pest Sci 83:197–215
Desneux N, Luna MG, Guillemaud T, Urbaneja A (2011) The invasive South American tomato pinworm, Tuta absoluta, continues to spread in Afro-Eurasia and beyond: the new threat to tomato world production. J Pest Sci 84:403–408
Desneux N, Kapilan I, Yoo HJS, Wang S, O’Neil RJ (2019) Temporal synchrony mediates the outcome of indirect effects between prey via a shared predator. Entomol Gen 39:127–136. https://doi.org/10.1121/entomologica/2019/0824
Dixon AF, Kundru R, Kindlmann P (1993) Reproductive effort and maternal age in iteroparous insects using aphids as a model group. Funct Ecol 7:267–272
Dong Y-C, Han P, Niu C-Y, Zappalà L et al (2018) Nitrogen and water inputs to tomato plant do not trigger bottom-up effects on a leafminer parasitoid through host and non-host exposures Pest. Manage Sci 74:516–522
Frank SD (2010) Biological control of arthropod pests using banker plant systems: past progress and future directions. Biol Control 52:8–16
Gebiola M, Bernardo U, Ribes A, Gibson GAP (2015) An integrative study of Necremnus Thomson (Hymenoptera: Eulophidae) associated with invasive pests in Europe and North America: taxonomic and ecological implications. Zool J Linn Soc 173:352–423
Guedes RNC, Picanço MC (2012) The tomato borer Tuta absoluta in South America: Pest status management and insecticide resistance. EPPO Bulletin 42:211–216
Guedes RNC, Roditakis E, Campos MR, Haddi K, Bielza P et al (2019) Insecticide resistance in the tomato pinworm Tuta absoluta: patterns, spread, mechanisms, management and outlook. J Pest Sci 92:1329–1342
Hagenbuecher S, Wackerl FL, Romeis J (2014) Aphid honeydew quality as a food source for parasitoids is maintained in Bt cotton. PloS ONE 9:e107806
Han P, Zhang YN, Lu ZZ, Wang S, Ma DY et al (2018) Are we ready for the invasion of Tuta absoluta? Unanswered key questions for elaborating an Integrated Pest Management package in Xinjiang, China. Entomol Generals 38:113–125
Han P, Bayram Y, Shaltiel-Harpaz L, Sohrabi F, Saji A et al (2019) Tuta absoluta continues to disperse in Asia: damage, ongoing management and future challenges. J Pest Sci 92:1317–1327
Heimpel GE (2019) Linking parasitoid nectar feeding and dispersal in conservation biological control. Biol Control 132:36–41
Hendrix DL, Wei Y, Leggett JE (1992) Homopteran honeydew sugar composition is determined by both the insect and plant species. Comp Biochem Physiol B 101:23–27
Hogervorst PAM, Wackerl FL, Romeis J (2007) Effects of honeydew sugar composition on the longevity of Aphidius ervi. Entomol Exp Appl 122:223–232
Hullè M, Chaubet B, Turpeau E, Simon JC (2019) Encylop’Aphid: a website on aphids and their natural enemies. Entomol Gen. https://doi.org/10.1127/entomologia/2019/0867
Inbar M, Gerling D (2007) Plant-mediated interactions between whiteflies, herbivores, and natural enemies. Ann Rev Entomol 53:431–448
Jactel H, Verheggen F, Thierry D, Escobar-Gutierrez AJ, Thybaut E et al (2019) Alternatives to neonicotinoids. Environ Int 129:423–429
Jam NA, Saber M (2018) Sublethal effects of imidacloprid and pymetrozine on the functional response of the aphid parasitoid, Lysiphlebus fabarum. Entomol Gen 38:173–190
Jaworski CC, Chailleux A, Bearez P, Desneux N (2015) Predator-mediated apparent competition between pests fails to prevent yield loss despite actual pest populations decrease. J Pest Sci 88:793–803
Jaworski CC, Xiao D, Xu QX, Ramirez-Romero R, Guo XJ et al (2019) Varying the spatial arrangement of synthetic herbivore-induced plant volatiles and companion plants to improve conservation biological control. J Appl Ecol 56:1176–1188
Jervis MA, Heimpel GE, Ferns PN, Harvey JA et al (2001) Life-history strategies in parasitoid wasps: a comparative analysis of ‘ovigeny.’ J Anim Ecol 70:442–458
Jervis MA, Boggs CL, Ferns PN (2007) Egg maturation strategy and survival trade-offs in holometabolous insects: a comparative approach. Biol J Linn Soc 90:293–302
Kennedy GG (2003) Tomato, pest, parasitoids, and predators: tritrophic interactions involving the Genus Lycopersicon. Ann Rev Entomol 48:51–72
Kruitwagen A, Beukeboom LW, Wertheim B (2018) Optimization of native biocontrol agents, with parasites of the invasive pest Drosophila suzukii as an example. Evolut Appl 11:1473–1497
Lahiri S, Orr D, Cardoza YJ, Sorenson C (2017) Longevity and fecundity of the egg parasitoid Telenomus podisi provided with different carbohydrate diets. Entomologia Exp et Applicata 162:178–187
Lee MS, Albajes R, Eizaguirre M (2014) Mating behaviour of female Tuta absoluta (Lepidoptera: Gelechiidae): Polyandry increases reproductive output. J Pest Sci 87:429–439
Li S, Tan XL, Desneux N, Benelli G, Zhao J et al (2015) Innate positive chemotaxis to pollen from crops and banker plants in predaceous biological control agents: towards new field lures? Scientific Reports 5:12729
Lu YH, Wu KM, Jiang Y, Guo Y, Desneux N (2012) Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. Nature 487:362–365
Mansour R, Bréault T, Chailleux A, Cherif A, Grissa-Lebdi K et al (2018) Occurrence, biology, natural enemies and management of Tuta absoluta in Africa. Entomologia Generals 38:83–112
McNitt J, Chungbaek YY, Mortveit H, Marathe M, Campos MR et al. (2019) Assessing the multi-pathway threat from an invasive agricultural pest: Tuta absoluta in Asia. Proc Royal Soc B 286(1913):20191159
Mirdosseini MA, Fathipour Y, Holst N, Soufabe M, Michaud JP (2019) An egg parasitoid interferes with biological control of tomato leafminer by augmentation of Nesidiocoris tenuis (Hemiptera: Miridae). Biol Control 133:34–40
Mohammed AAH, Desneux N, Fan YJ, Han P, Ali A et al (2018) Impact of imidacloprid and natural enemies on cereal aphids: integration or ecosystem service disruption? Entomol Gen 37:47–61
Mohammed AAH, Monticelli LS, Desneux N, Fan YY, Shi YY et al (2019) Potential for insecticide-mediated shift in ecological dominance between two competing aphid species. Chemosphere 226:651–658
Molla O, González-Cabrera J, Urbaneja A (2011) The combined use of Bacillus thuringiensis and Nesidiocoris tenuis against the tomato borer Tuta absoluta. Biocontrol 56:883–891
Monticelli LS, Tena A, Idier M, Amiens-Desneux E, Desneux N (2019) Quality of aphid honeydew for a parasitoid varies as a function of both aphid species and host plant. Biol Control. https://doi.org/10.1016/j.biocontrol.2019.104099
Mooney K, Jones P, Agrawal A (2008) Coexisting congeners: demography, competition, and interactions with cardenolides for two milkweed-feeding aphids. Oikos 117:3(450–458
Moreira X, Abdala-Roberts L, Castagneyrol B (2018) Interactions between plant defence signalling pathways: evidence from bioassays with insect herbivores and plant pathogens. J Ecol 106:2353–2364
Mouttet R, Bearez P, Thomas C, Desneux N (2011) Phytophagous arthropods and a pathogen sharing a host plant: evidence for indirect plant-mediated interactions. PloS ONE 6:e18840
Mouttet R, Kaplan I, Bearez P, Amiens-Desneux E et al (2013) Spatiotemporal patterns of induced resistance and susceptibility linking diverse plant parasites. Oecologia 173:1379–1386
Nselli M, Biondi A, Tropea Garzia G, Desneux N et al (2017) Insights into food webs associated with the South American tomato pinworm Pest. Manage Sci 73:1352–1357
Parolin P, Bresch C, Poncet C, Desneux N (2012) Functional characteristics of secondary plants for increased pest management. Int J Pest Manag 58:369–377
Passos LC, Soares MA, Collares LJ, Malagoli I, Desneux N, Carvalho GA (2018) Lethal, sublethal and transgenerational effects caused by insecticides on Macrolophus baccinum, predator of Tuta absoluta. Entomol Gen 38:127–143
Perdikis D, Lucas E, Garantonakis N, Giatropoulos A et al (2014) Intraguild predation and sublethal interactions between two zoo-phytophagous mirids, Macrolophus pygmaeus and Nesidiocoris tenuis. Biol Control 70:35–41
Perovic DJ, Gamez-Virues S, Landis DA, Wäckers F, Gurr GM et al (2018) Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales. Biol Rev 93:306–321
Picciau L, Alma A, Ferracini C (2019) Effect of different feeding sources on lifespan and fecundity in the biocontrol agent Torymus sinensis. Biol Control 134:45–52
Roditakis E, Vassakis E, García-Vidal L, del Rosario Martínez-Aguirre M et al (2018) A four-year survey on insecticide resistance and likelihood of chemical control failure for tomato leaf miner Tuta absoluta in the European/Asian region. J Pest Sci 91:421–435
Ragsdale DW, Landis DA, Brodeur J, Heimpel GE, Desneux N (2011) Ecology and management of the soybean aphid in North America. Ann Rev Entomol 56:375–399
Sankarganesh E, Firake DM, Sharma B, Verma VK et al (2017) Invasion of the South American Tomato Pinworm, Tuta absoluta, in...
northeastern India: a new challenge and biosecurity concerns. Entomol Gen 36:335–345
Soares MA, Passos LC, Campos MR, Collares LJ, Desneux N, Carvalho GA (2019a) Side effects of insecticides commonly used against Tuta absoluta on predator Macrolophus basicornis. J Pest Sci 92:1447–1456
Soares MA, Campos MR, Passos LC, Haro MM, Carvalho GA et al (2019b) Botanical insecticides against Tuta absoluta, potential for pest management through combination with natural enemies. J Pest Sci 92:1433–1443
Soler R, Van der Putten WH, Harvey JA, Vet LEM et al (2012) Root herbivore effects on aboveground multitrophic interactions: patterns; processes and mechanisms. J Chem Ecol 38:755–767
Stout MJ, Thaler JS, Thomma BPHJ (2006) Plant-mediated interactions between pathogenic microorganisms and herbivorous arthropods. Annu Rev Entomol 51:663–689
Tena A, Senft M, Desneux N, Dregni J, Heimpel GE (2018) The influence of aphid-produced honeydew on parasitoid fitness and nutritional state: a comparative study. Basic Appl Ecol 29:55–68
van Veen FJ, Morris RJ, Godfray HCJ (2005) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. Annu Rev Entomol 51:187–208
Verheggen F, Fontus RB (2019) First record of Tuta absoluta in Haiti. Entomologia Generalis 38(4):349–353
Villemereuil PB, Lopez-Sepulcre A (2011) Consumer functional responses under intra- and inter-specific interference competition. Ecol Model 222:419–426
Wäckers FL, Romeis J, van Rijn P (2007) Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. Annu Rev Entomol 52:301–323
Wäckers FL, van Rijn PCJ, Heimpel GE (2008) Honeydew as a food source for natural enemies: making the best of a bad meal? Biol Control 45:176–184
Walling LL (2000) The myriad plant responses to herbivores. J Plant Growth Reg 19:195–216
Wang S-x, Di N, Chen X, Zhang F et al (2018) Life history and functional response to prey density of the flower bug Orius sauteri attacking the fungivorous sciarid fly Lycomilla pleuroti. J Pest Sci 92:1–8
Winkler K, Wäckers FL, Kaufman LV, Larraz V, van Lenteren JC (2009) Nectar exploitation by herbivores and their parasitoids is a function of flower species and relative humidity. Biol Control 50:299–306
Zappalà L, Biondi A, Alma A, Al-Jboory II et al (2013) Natural enemies of the South American moth, Tuta absoluta, in Europe, North Africa and Middle East, and their potential use in pest control strategies. J Pest Sci 86:635–647
Zhang LP, Zhang GY, Zhang YJ, Zhang WJ et al (2005) Interspecific interactions between Bemisia tabaci (Hem., Aleyrodidae) and Liriomyza sativae (Dipt., Agromyzidae). J Appl Entomol 129:443–446
Zhao J, Guo X, Tan X, Desneux N, Zappala L et al (2017) Using Calendula officinalis as a floral resource to enhance aphid and thrips suppression by the flower bug Orius sauteri (Hemiptera: Anthocoridae). Pest Manag Sci 73:515–520

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