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# Apparent competition between major pests reduces pest population densities on tomato crop, but not yield loss

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**Abstract** Increased pest control by generalist predators has been successfully achieved in several cases by promoting apparent competition, which is the reciprocal negative interactions between prey mediated by their shared predator. However, the presence of alternative prey does not always result in an improved control of the target pest species, due to the complexity and specificity of biotic interactions. To increase the effectiveness of IPM programs, a fine understanding of the interactions among co-occurring pest species and their biocontrol agents is necessary. We tested the occurrence of apparent competition between the major tomato pests *Tuta absoluta* and *Bemisia tabaci* when preyed on by a generalist mirid bug *Macrolophus pygmaeus*, by monitoring pest and predator population dynamics in a greenhouse experiment. We also measured the cascading effect of the shared predator on plant and fruit damage due to pests. We observed higher predator population growth and reduced population densities of both prey in treatments

with two prey, as compared to treatments with one prey, showing that apparent competition occurred. Plant and fruit damage caused by *B. tabaci* was reduced in the presence of *T. absoluta*, but damage due to *T. absoluta*, which accounted for the major part, was not reduced in the presence of *B. tabaci*, resulting in similar levels of total damage when pests co-occurred. This study demonstrates that, even if promoting apparent competition leads to actual reduction in pest densities, yield loss may not be reduced when this strategy is applied to major pests such as *T. absoluta*.

**Keywords** *Bemisia tabaci* · Indirect interaction · *Macrolophus pygmaeus* · Plant damage · Predator-mediated interaction · *Tuta absoluta*

## Key message

- Efficiency of apparent competition to control pests is rarely assessed, its impact on yield even less.
- We measured predator-mediated apparent competition between key agricultural pests.
- *Tuta absoluta* poorly supported population growth of the predator *Macrolophus pygmaeus*.
- The presence of *T. absoluta* lowered damage by *Bemisia tabaci*; reverse was not observed.
- Apparent competition resulted in lower pest densities, but not in reduced yield loss.

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## Introduction

There has been an increasing interest in pest management methods that maximize biological control services provided by pests' natural enemies. Generalist predators are

widely used as biocontrol agents for their ability to regulate populations of herbivorous arthropod species (Symondson et al. 2002; Desneux et al. 2006; Lu et al. 2012). They may attack several pest species that co-occur in agro-ecosystems and induce indirect interactions among them (Holt and Lawton 1994; Abrams and Matsuda 1996). These pest–pest interactions are classified indirect because they necessarily involve a third mediating species, as opposed to direct biotic interactions such as predation and resource competition (Holt 1977; Wootton 1994). Multiple direct and indirect interactions may occur simultaneously and strongly affect population dynamics in agro-ecosystems, thus they may impact the efficiency of pest management methods (Holt and Lawton 1994; Tack et al. 2011; Bompard et al. 2013).

The nature and strength of predator-mediated interactions between prey depend on species characteristics such as prey capacity to escape predation (e.g., through refuge; Lind and Cresswell 2005), predator prey preference (Eubanks and Denno 2000; Desneux and O’Neil 2008; Jaworski et al. 2013), and predator foraging behavior (Oaten and Murdoch 1975; Holt and Kotler 1987; Abrams and Matsuda 1996; Evans and Toler 2007; Jaworski et al. 2013). Predator-mediated interactions between prey may also change through time due to predator population dynamics (Bompard et al. 2013). Such interactions are predicted to be generally positive at time scales shorter than the predator generation time due to a shared predation pressure between prey (Holt and Lawton 1994; Abrams and Matsuda 1996), and may become negative at longer time scales, if predator population growth is enhanced by the increased prey availability (Harmon and Andow 2004; Chailleux et al. 2014). Indirect interactions mediated by shared natural enemies are known as *apparent competition*, if negative interactions are reciprocal, or *apparent amensalism*, if one prey suffers from the presence of the other prey (Holt 1977; Holt and Lawton 1994).

The promotion of indirect interactions for improving biocontrol has been tested at various spatial scales (Chailleux et al. 2014). At large scales, maintaining a high biodiversity level has been shown to enhance the population growth of pests’ natural enemies, improving the control of target pests (Settle et al. 1996; Huang et al. 2011). Similarly, Harwood et al. (2007) showed that the control of a target pest species by naturally occurring generalist predators in soybean fields was sometimes improved by the presence of alternative prey. Smaller-scale experiments have shown that polyphagous predators benefit from a mixed diet, either through an alternative prey (Liu et al. 2006; Messelink et al. 2008, 2010; Calvo et al. 2011) or an alternative plant resource (Evans et al. 1999; Van Rijn et al. 2002; Nomikou et al. 2010; Vandekerckhove and De Clercq 2010). However, both positive and negative enemy-

mediated indirect interactions have been reported between co-occurring prey or host species (Prasad and Snyder 2006; Kuusk and Ekbohm 2010; Tack et al. 2011). Further, enemy-mediated interactions may be asymmetric, and the evidence of a negative indirect effect of one pest species upon another does not always imply the occurrence of a reciprocal effect. Many studies showing apparent competition between two prey sharing a predator do not fully test the reciprocity of the indirect interaction. An asymmetric interaction may reduce the potential contribution of apparent competition to efficient biocontrol (Müller and Godfray 1997; Chaneton and Bonsall 2000; Dangremond et al. 2000; Van Veen et al. 2006). The possibility of increasing biocontrol on two pests sharing a common natural enemy through apparent competition needs to be experimentally tested at an appropriate scale for each combination of pests and shared natural enemy. Especially, the net effect of the shared predator on pest abundances, as well as on crop damage, is seldom assessed.

In the present study, we explore the possibility of apparent competition between two major pest species in tomato crops, *Tuta absoluta* and *Bemisia tabaci*, mediated by a shared predator, *Macrolophus pygmaeus*, and whether it results in reduced pest population densities and reduced yield loss. *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) is a tomato pinworm causing crop losses up to 100 % by mining in tomato leaves, stems, and fruits (Urbaneja et al. 2009; Desneux et al. 2010). Its recent and rapid invasion of Afro-Eurasia from South America (Desneux et al. 2010, 2011) has highlighted the need to search for new IPM practices, or to readjust the already-existing biological control programs (Chailleux et al. 2012, 2013). This invasive alien pest frequently co-occurs in European tomato crops with another major tomato pest, the whitefly *B. tabaci* (Gennadius; biotype Q; Hemiptera: Aleyrodidae), which is a widespread European indigenous species (Parella et al. 2012; Saleh et al. 2012). This sap-feeding insect causes direct damage and vector viruses to plants (Oliveira et al. 2001; Jiao et al. 2012). *Macrolophus pygmaeus* is one of the most commonly used biocontrol agents against *B. tabaci* and other whiteflies. This generalist predator can feed on a variety of other prey such as thrips, aphids, mites, and eggs and larvae of Lepidoptera and notably those of *T. absoluta* (Bompard et al. 2013; Zappalà et al. 2013). It can also feed on plant resources (Perdikis and Lykouressis 2000; Castané et al. 2011). In a previous greenhouse experiment, we showed that *T. absoluta* negatively affected *B. tabaci* in tomato crops through resource competition, but also through predator-mediated indirect interactions in the longer term (Bompard et al. 2013). We also showed that the population of the predator *M. pygmaeus* grew faster in the presence of both *T. absoluta* and *B. tabaci* than with *B. tabaci* alone. Another study at

laboratory scale highlighted that *M. pygmaeus* preferentially attacked the most abundant prey when faced with various proportions of *B. tabaci* and *T. absoluta* (Jaworski et al. 2013), a phenomenon known as *prey switching* (Murdoch 1969). In the present study, we focused on predator-mediated effects only, and we explicitly tested the occurrence of apparent competition between the two pest species. We conducted a greenhouse experiment designed to measure short-term and long-term reciprocal predator-mediated indirect interactions between prey by monitoring predator and pest population dynamics, and simultaneously assessing damage to tomato leaves and fruits. Our results provide an experimental demonstration of apparent competition between prey sharing a predator: we measured a higher predator abundance in the presence of both pests and reduced pest abundances in the presence of the other pest, yet it did not result in reduced plant and fruit damage.

## Materials and methods

### Biological materials

Tomato plants (*Solanum lycopersicum* L. cv. Marmande) were grown in climatic chambers ( $23 \pm 1$  °C,  $65 \pm 5$  % RH, 16L:8D). The prey *B. tabaci* and *T. absoluta* were reared on tobacco and tomato plants, respectively, in separate cages, in a climatic chamber ( $23 \pm 1$  °C,  $65 \pm 5$  % RH, 16L:8D). The predator *M. pygmaeus* was provided by Biotop© (In Vivo AgroSolutions), reared on tomato plants complemented with *Ephestia kuehniella* [Lepidoptera: Pyralidae] eggs, and maintained in growth chambers ( $23 \pm 1$  °C,  $65 \pm 5$  % RH, 16L:8D). Thus, predators had no previous experience of predation on *B. tabaci* or on *T. absoluta*, i.e., they were naive on these two prey.

### Experimental design

We investigated the possible apparent competition (reciprocal indirect negative interactions) between the pests *T. absoluta* and *B. tabaci* on a tomato crop in a greenhouse, using a  $2 \times 2$  factorial design. The predator *M. pygmaeus* was present in all treatments. The first two-level treatment varied the presence of *B. tabaci*, and the second two-level treatment varied the presence of *T. absoluta*. Although this design does not allow to dissociate predator-mediated effects from resource competition between pests as addressed in Bompard et al. (2013), it allows to assess the impact of the presence of multiple prey on predator population densities.

Each of the four treatments was replicated four times in 40 m<sup>2</sup> distinct compartments of an environment-controlled greenhouse, with identical climatic conditions ( $T = 25$  °C; RH = 60 %). The greenhouse was located at Sophia

Antipolis INRA center (South-Eastern France), and the study was carried out during summer 2011. To prevent insect transfer between treatments inside a given compartment, they were isolated from one another by fine mesh material, which formed tunnels (height: 2 m, width: 1 m, length: 5 m). Tomato plants were grown on rock wool slabs, and each tunnel contained two rows of eight plants. Plants were automatically supplied with water and nutrients that prevented any abiotic stress. Pesticide applications were strictly avoided. Plants were vertically tied up and secondary shoots were systematically cut off and left in the tunnels, to allow potential predator eggs inserted in these shoots to hatch after cutting (Fauvel et al. 1987). Prey were released on 4-week-old plants (8–11 leaves/plant), at a rate of 20 adults of *B. tabaci* and two adults of *T. absoluta* per plant. Predators were released one week later at a rate of two females, one male, and four nymphs (L4/L5) per plant.

### Sampling

Population dynamics of the three insect species were monitored during the 10 weeks following predator introduction. Four plants per tunnel were randomly chosen, and adults and nymphs of *M. pygmaeus*, adults of *B. tabaci*, and larvae of *T. absoluta* were counted on all leaves. For each plant sampled, eight leaflets equally distributed on the plant were collected for additional observations in the laboratory. They were observed under a binocular microscope to count the number of eggs and nymphs (i.e., juveniles) of *B. tabaci*.

Leaf damage due to sooty mold by nymphs of *B. tabaci* or to chewing by larvae of *T. absoluta* was also measured on the collected leaflets. Leaflets were classified as “healthy,” when <50 % of the leaf area was damaged, and were otherwise classified as “damaged.” In the two-prey system, the type of damage was also recorded as ‘*T. absoluta* only’ when galleries were visible but sooty mold absent, ‘*B. tabaci* only’ when sooty mold was present but galleries absent, or ‘*T. absoluta* and *B. tabaci*’ when both types of damage were visible.

Mature tomato fruits were harvested and weighed once a week in each tunnel. Fruits were either classified as “healthy” or “damaged” as soon as sooty mold or a gallery was observed on the fruit, and the type of damage was also recorded (*T. absoluta* only/*B. tabaci* only/*T. absoluta* and *B. tabaci*), and the different groups of fruits were weighed separately. This allowed to assess yield loss due to pests because, from an applied perspective, any damaged fruit cannot be sold.

### Statistical analyses

All statistical analyses were performed using the R software program (R Development Core Team 2015, version

3.2.1). We used either linear mixed models or non-linear mixed models (library lme4) in which error structures were chosen to best account for data distribution, based on the AIC/BIC criteria. The significance of fixed effects in the models was estimated through a type-II comparison of models, based on  $\chi^2$  tests. The fixed effects were the *B. tabaci* and *T. absoluta* treatments (presence or absence of prey species), as well as the interaction between these simple effects for statistical tests including all treatments. The random effect was plant tunnel (unless otherwise specified) and accounted for temporal pseudo-replication of measures. When fixed effects were significant, we evaluated their direction and relative intensity using the parameter estimates of the most complete model including significant effects only.

We tested the impacts of the *B. tabaci* and *T. absoluta* treatments on the three insect population dynamics (*M. pygmaeus*, *B. tabaci*, and *T. absoluta*) using non-linear mixed models with a negative binomial error structure. To differentiate long-term from short-term predator-mediated indirect interactions between prey, the data were divided into three time periods. Long-term interactions were assessed on weeks 1–10, and short-term interactions on weeks 1–7. To better highlight differences in insect densities due to long-term interactions, we also included an analysis at weeks 8–10. These periods were chosen based on the development time of the predator and associated predation activities (Bompard et al. 2013). Temperature inside the greenhouse reached about 1086 cumulated degree days (CDD) at week 7 and about 1593 CDD at week 10. We assumed the entire development cycle of the predator *M. pygmaeus* to be about 940 CDD (Bompard et al. 2013). Consequently, one predator cycle was achieved at the end of the first period (week 7) for eggs laid by the adult predators introduced at the beginning of the experiment. At the end of the second period (week 10), the descendants of the introduced juvenile predators had completed their development.

We tested the impact of *B. tabaci* and *T. absoluta* on plant growth, estimated by the number of leaves per plant, using linear mixed models on the log-transformed number of leaves. Plant tunnel and plant nested within plant tunnel were specified as random factors. We tested the impact of *B. tabaci* and *T. absoluta* on the weekly tomato production using non-linear mixed models with a negative binomial error structure.

We analyzed the impact of the presence of multiple pest species on fruit damage using three endpoints: (i) the total proportion of damaged fruits, i.e., the mass of damaged fruits over the total mass of fruits; (ii) proportion of fruits damaged by *B. tabaci*, i.e., the mass of fruits damaged exclusively or partially by *B. tabaci* over the total mass of fruits; and (iii) the proportion of fruits damaged by *T. absoluta*, i.e., the mass of fruits damaged exclusively or

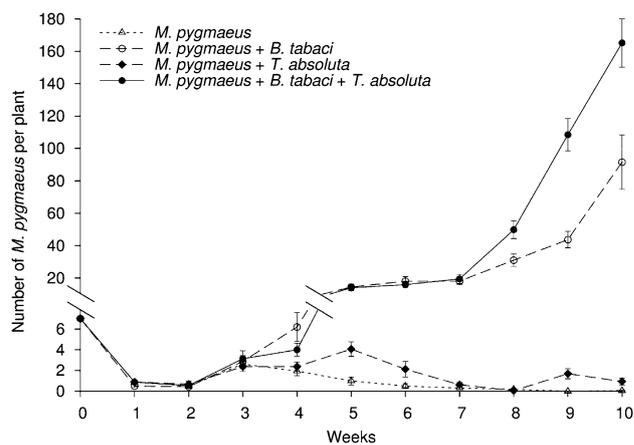
partially by *T. absoluta* over the total mass of fruits. In the *B. tabaci* systems, we analyzed the impact of *T. absoluta* on the total proportion of damaged fruits, and on the proportion of fruits damaged by *B. tabaci* independently, using non-linear mixed models with a binomial error structure. We analyzed the impact of *B. tabaci* in the *T. absoluta* systems in a similar way.

To analyze the impact of the presence of multiple pest species on leaf damage, we used the same method as for fruit damage on the following three quantities: (i) the total proportion of damaged leaflets, i.e., the number of damaged leaflets divided by eight (the number of leaflets collected per sampled plant); (ii) the proportion of leaflets damaged by *B. tabaci*, i.e., the number of leaflets damaged exclusively or partially by *B. tabaci* divided by eight; and (iii) the proportion of leaflets damaged by *T. absoluta*, i.e., the number of leaflets damaged exclusively or partially by *T. absoluta* divided by eight.

## Results

### Insect population dynamics

The statistical results on population dynamics are summarized in Table 1. Populations of adult and nymph predators showed similar dynamics (Fig. A in Supplementary Material), and therefore all individuals were pooled. The presence of both prey *B. tabaci* and *T. absoluta* positively affected predator populations (Fig. 1). The interaction between treatments (simultaneous presence of both prey) had a negative impact on predator populations both at weeks 1–7 and at weeks 8–10 but not on the whole period: predator densities were predicted to be smaller in the presence of both prey than expected if the impact of prey would be purely



**Fig. 1** Impacts of the presence of the prey species *B. tabaci* and *T. absoluta* (alone or together) on the population dynamic of the predator *M. pygmaeus*. Mean number ( $\pm$ SE;  $N = 16$ ) of predators (adults and juveniles) per plant

**Table 1** Statistics from the generalized linear models used to analyze the impact of the *B. tabaci* and *T. absoluta* treatments on the population dynamics of *M. pygmaeus*, *B. tabaci*, and *T. absoluta*

Data set	Time period (weeks)	Source of variation	Degrees of freedom	$\chi^2$	P value	Parameter estimate
<i>M. pygmaeus</i> (juveniles + adults)	1–10	<i>B. tabaci</i> × <i>T. absoluta</i>	1	0.681	0.41	–
		<i>B. tabaci</i>	1	59.3	<0.001***	0.61
		<i>T. absoluta</i>	1	14.8	<0.001***	3.23
	1–7	<i>B. tabaci</i> × <i>T. absoluta</i>	1	5.17	0.023*	–0.57
		<i>B. tabaci</i>	1	44.4	<0.001***	2.06
		<i>T. absoluta</i>	1	2.43	0.12	0.53
	8–10	<i>B. tabaci</i> × <i>T. absoluta</i>	1	9.39	0.0022**	–1.94
		<i>B. tabaci</i>	1	43.0	<0.001***	6.48
		<i>T. absoluta</i>	1	14.1	<0.001***	2.66
<i>B. tabaci</i> juveniles (eggs + nymphs)	1–10	<i>T. absoluta</i>	1	3.66	0.056	–
	1–7	<i>T. absoluta</i>	1	0.754	0.39	–
	8–10	<i>T. absoluta</i>	1	6.07	0.014*	–1.20
<i>T. absoluta</i> larvae	1–10	<i>B. tabaci</i>	1	1.05	0.31	–
	1–7	<i>B. tabaci</i>	1	0.968	0.33	–
	8–10	<i>B. tabaci</i>	1	4.93	0.026*	–0.52

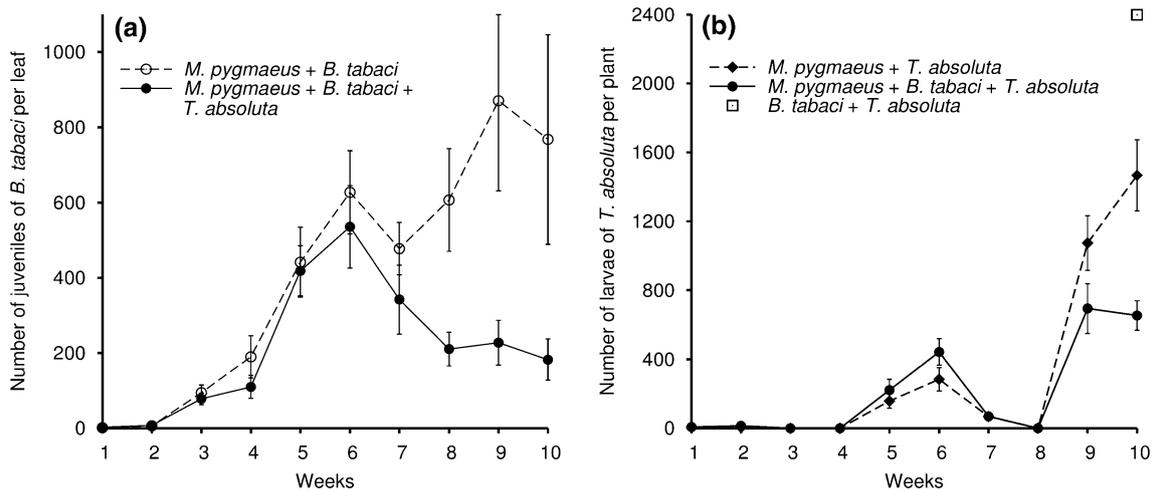
\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

additive, counterbalancing the positive impact of the presence of *T. absoluta* at weeks 1–7 only. At week 10, the predator densities were 1.8 times and 175 times higher in the *B. tabaci*–*T. absoluta* system than in the *B. tabaci* system and the *T. absoluta* system, respectively.

Populations of eggs and nymphs of *B. tabaci* showed similar dynamics (Fig. Bb–c in S1 File), and therefore all individuals were gathered in a pool of juveniles. Populations of adults of *B. tabaci* also showed a similar dynamic to populations of *B. tabaci* juveniles (Fig. Ba in Supplementary Material). The *T. absoluta* treatment

induced a negative impact on *B. tabaci* populations at weeks 8–10. At week 10, there was a 4.2-fold decrease in the population densities of *B. tabaci* juveniles between the *B. tabaci* system and the *B. tabaci*–*T. absoluta* system (Fig. 2a).

Populations of *T. absoluta* larvae were very variable over time, with cyclic drops to very low densities, possibly due to the absence of overlapping generations (Fig. 2b). The *B. tabaci* treatment induced a negative impact on *T. absoluta* populations during weeks 8–10. At week 10, there was a 2.2-fold decrease in the population densities of



**Fig. 2** Reciprocal impacts between prey on their population dynamics. (a) Mean number ( $\pm$ SE;  $N = 16$ ) of *B. tabaci* juveniles (eggs and larvae) per leaf. (b) Mean number ( $\pm$ SE;  $N = 16$ ) of *T. absoluta*

larvae per plant. The squared point “*B. tabaci* + *T. absoluta*” is a rough estimate extrapolated from Bompard et al. (2013)

**Table 2** Statistics from the generalized linear models used to analyze the impact of the *B. tabaci* and *T. absoluta* treatments on plant growth (number of leaves per plant) and on the weekly tomato production

Data set	Time period (weeks)	Source of variation	Degrees of freedom	$\chi^2$	P value	Parameter estimate
Number of leaves per plant	1–10	<i>B. tabaci</i> × <i>T. absoluta</i>	1	0.0649	0.80	–
		<i>B. tabaci</i>	1	0.633	0.43	–
		<i>T. absoluta</i>	1	2.57	0.11	–
	1–7	<i>B. tabaci</i> × <i>T. absoluta</i>	1	0.133	0.72	–
		<i>B. tabaci</i>	1	0.0483	0.83	–
		<i>T. absoluta</i>	1	0.0744	0.79	–
	8–10	<i>B. tabaci</i> × <i>T. absoluta</i>	1	0.719	0.40	–
		<i>B. tabaci</i>	1	1.95	0.16	–
		<i>T. absoluta</i>	1	6.22	0.013*	–0.13
Weekly tomato production	6–11	<i>B. tabaci</i> × <i>T. absoluta</i>	1	0.130	0.72	–
		<i>B. tabaci</i>	1	0.218	0.64	–
		<i>T. absoluta</i>	1	0.146	0.70	–
	6–8	<i>B. tabaci</i> × <i>T. absoluta</i>	1	1.43	0.23	–
		<i>B. tabaci</i>	1	7.33	0.0068**	–0.41
		<i>T. absoluta</i>	1	2.95	0.086	–
	9–11	<i>B. tabaci</i> × <i>T. absoluta</i>	1	0.101	0.75	–
		<i>B. tabaci</i>	1	0.132	0.72	–
		<i>T. absoluta</i>	1	4.45	0.035*	–0.38

\*  $P < 0.05$ ; \*\*  $P < 0.01$

*T. absoluta* larvae between the *T. absoluta* system and the *B. tabaci*–*T. absoluta* system.

### Plant growth and tomato production

The presence of *T. absoluta* had a small negative impact on the number of leaves per plant, at weeks 8–10 (means 37 vs. 35 at week 10 for the no-prey system and *T. absoluta* system, respectively, Table 2). The *B. tabaci* treatment did not affect plant growth, nor the interaction between the *B. tabaci* and *T. absoluta* treatments.

The *B. tabaci* treatment had a small negative impact on the weekly tomato production at weeks 6–8 only, whereas the *T. absoluta* treatment had a small negative impact on the weekly tomato production at weeks 9–11 only (Table 2 and Fig. 3a). The interaction between the *B. tabaci* and *T. absoluta* treatments did not affect tomato production.

### Fruit damage and leaf damage

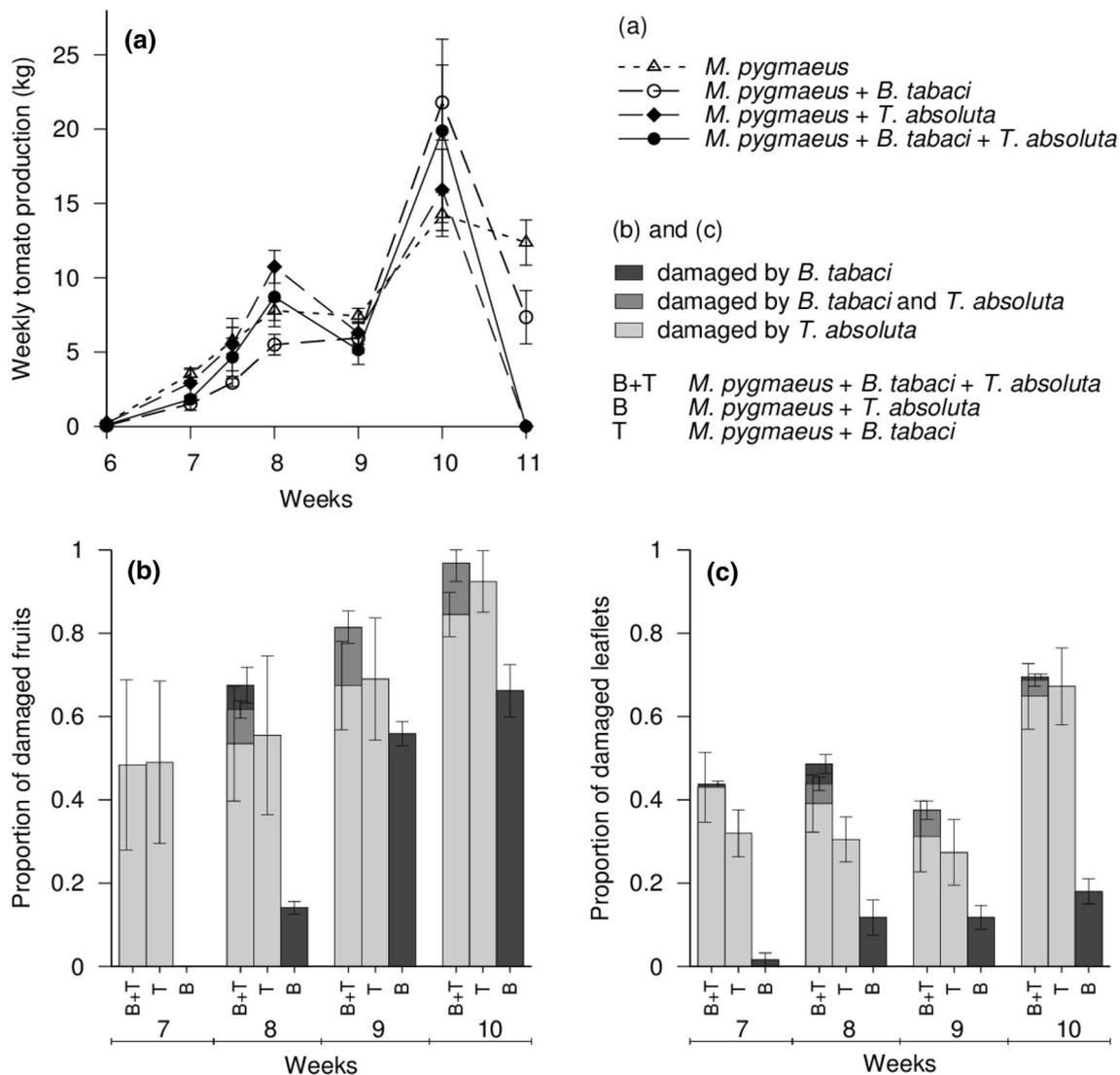
Both the *B. tabaci* and *T. absoluta* treatments induced high levels of fruit damage (Fig. 3b). In the *B. tabaci* systems, the presence of *T. absoluta* resulted in an increased total proportion of damaged fruits and a decreased proportion of fruits damaged by *B. tabaci* (Table 3a). At week 10, this resulted in a 5.4-fold reduction in the proportion of fruits damaged by *B. tabaci* in the *B. tabaci*–*T. absoluta* system, as compared to the *B. tabaci* system. Conversely, in the *T. absoluta*

systems, the total proportion of damaged fruits was similar in the presence of *B. tabaci* and the proportion of fruits damaged by *T. absoluta* was not reduced. The impacts of the *B. tabaci* and *T. absoluta* treatments on leaf damage were very similar to those on fruit damage (Fig. 3c, Table 3b).

### Discussion

The present study suggests that a negative predator-mediated indirect interaction occurring between two pests failed to reduce plant damage and yield loss. As expected, we observed an apparent competition between the pests *B. tabaci* and *T. absoluta* when they shared the predator *M. pygmaeus*: there was stronger predator population growth and smaller pest population densities in the two-prey system as compared to both single-prey systems. The numerical response of the predator to *T. absoluta* was weak, whereas the predator response to *B. tabaci* was strong. Finally, leaf and fruit damage by *B. tabaci* was reduced in the presence of *T. absoluta*, but damage by the most damaging pest *T. absoluta* was not reduced in the presence of *B. tabaci*. The total yield loss was similar in the two-prey system than in the *T. absoluta* system.

*Tuta absoluta* and *B. tabaci* are two major pests on tomato crops that are frequently co-occurring in the Mediterranean region (Desneux et al. 2010, 2011; Parrella et al. 2012; Saleh et al. 2012). Therefore, it appears essential to develop pest management strategies aimed at



**Fig. 3** Plant and fruit damage due to pests. Impacts of the presence of the prey species *B. tabaci* and *T. absoluta* (alone or together) on (a) the weekly tomato production (mean production per 16

plants ± SE; *N* = 4); (b) the proportion of damaged fruits (mean ± SE; *N* = 4); and (c) the proportion of damaged leaflets (mean ± SE; *N* = 16)

simultaneously regulating both pest species, but also to increase our understanding of both direct and indirect interactions that are likely occurring between them. In a previous study, we showed that *T. absoluta* negatively affects *B. tabaci* population dynamics through both plant resource competition and predator-mediated indirect interactions (Bompard et al. 2013). Systems containing *T. absoluta* but no natural enemies are hardly manageable due to rapid plant destruction by *T. absoluta* larvae (Bompard et al. 2013), and thus we focused on predator-mediated interactions only in the present study. However, resource competition is likely to have occurred together with predator-mediated interactions given the high level of leaf damage at the end of the experiment (Fig. 3c), and the decrease in pest

population densities in the two-prey system may be the result of the cumulated effects of predator-mediated apparent competition and resource competition (Fig. 2). These combined effects lead to a cascading trophic effect on crop, as shown by the absence of increase in yield loss and plant damage in the two-prey system as compared to the *T. absoluta* system and by the decrease in fruit and leaf damage due to *B. tabaci* in the presence of *T. absoluta* (Fig. 3b–c). Although the reduction in yield loss is typically the aim of pest management, the impact of increased pest control at the plant level is seldom assessed (but see Cardinale et al. 2003; Costamagna et al. 2007; Liere et al. 2015).

Although resource competition may have partly hidden the negative impact of apparent competition on pest

**Table 3** Statistics from the generalized linear models used to analyze the impact of the *B. tabaci* and *T. absoluta* treatments on fruit and leaf damage

Data set and source of variation	Time period (weeks)	Degrees of freedom	$\chi^2$	<i>P</i> value	Parameter estimate
<b>(a) Fruit damage</b>					
Impact of <i>T. absoluta</i> in the <i>B. tabaci</i> systems					
On the total proportion of damaged fruits	6–10	1	8.31	0.0039**	2.09
	9–10	1	4.27	0.039*	3.56
On the proportion of fruits damaged by <i>B. tabaci</i>	6–10	1	14.2	<0.001***	–1.93
	9–10	1	15.4	<0.001***	–2.69
Impact of <i>B. tabaci</i> in the <i>T. absoluta</i> systems					
On the total proportion of damaged fruits	6–10	1	1.18	0.28	–
	9–10	1	1.21	0.27	–
On the proportion of fruits damaged by <i>T. absoluta</i>	6–10	1	0.935	0.33	–
	9–10	1	1.21	0.27	–
<b>(b) Leaf damage</b>					
Impact of <i>T. absoluta</i> in the <i>B. tabaci</i> systems					
On the total proportion of damaged leaflets	6–10	1	9.33	0.0023**	2.20
	9–10	1	7.05	0.0079**	2.05
On the proportion of leaflets damaged by <i>B. tabaci</i>	6–10	1	3.17	0.075	–
	9–10	1	5.72	0.017*	–1.13
Impact of <i>B. tabaci</i> in the <i>T. absoluta</i> systems					
On the total proportion of damaged leaflets	6–10	1	0.584	0.44	–
	9–10	1	0.176	0.67	–
On the proportion of leaflets damaged by <i>T. absoluta</i>	6–10	1	0.424	0.51	–
	9–10	1	0.158	0.69	–

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

population densities in our experiment, the higher population growth of the predator when both prey were present shows that apparent competition occurred on the long term. Apparent competition may have become more obvious if we had observed more than two predator generations, but we had to stop the experiment due to the high levels of plant damage. Predator population growth was likely enhanced by the benefits of a mixed diet on *M. pygmaeus*, something which has been reported for other generalist arthropod predators (Eubanks and Denno 2000; Messelink et al. 2008, 2010). Higher prey density is unlikely the cause of higher predator population growth, as the total prey density was not higher in the two-prey system than in the single-prey systems, due to negative interactions between prey.

The small predator population growth on the isolated prey *T. absoluta* was likely due to a weak numerical response of the predator to this prey, as recently documented. Molla et al. (2013) measured a 15-fold lower reproductive rate of *M. pygmaeus* when preying on *T. absoluta* eggs than on *E. kuehniella* eggs, which are the common prey used for mass rearing of *M. pygmaeus*.

Similarly, Jaworski et al. (2013) measured a similar daily fertility of *M. pygmaeus* preying on *T. absoluta* eggs when fed on tomato plants in the absence of prey, but which was 3.6 times lower than its daily fertility when preying on *B. tabaci* nymphs. These effects may be due to a low nutritive value of *T. absoluta* for *M. pygmaeus*, which seems quite sensitive to prey nutritive quality (Foglar et al. 1990; Hamdan 2006). Another possible explanation for the small predator population growth on the isolated prey *T. absoluta* is the non-regular prey population dynamics. We observed cyclic drops of *T. absoluta* populations to very low densities (Fig. 2b), possibly due to the absence of overlapping generations. Predators may have suffered from the highly variable quantity of available prey over time. Such cyclic, large fluctuations in the population density of *T. absoluta* may also affect interactions between prey and hence the intensity of apparent competition (Abrams et al. 1998; Brassil 2006).

This greenhouse experiment provides a new demonstration that *T. absoluta* is a very damaging pest on tomato crops (Desneux et al. 2010, 2011; Bompard et al. 2013). To estimate the intensity of predation (by *M. pygmaeus*) on

*T. absoluta* population densities, we extrapolated the expected density of *T. absoluta* larvae at week 10 in the presence of the alternative prey *B. tabaci* but without predator, by multiplying the mean measured density of *T. absoluta* larvae in the two-prey system at week 10 by a coefficient obtained from Bompard et al. (2013). This coefficient was calculated as the ratio of the density of *T. absoluta* juveniles in the *B. tabaci*–*T. absoluta* treatment over the density of *T. absoluta* juveniles in the *B. tabaci*–*T. absoluta*–*M. pygmaeus* treatment at week 8, i.e., before population collapse. This very rough estimate is rather uncertain, especially due to the differences in environmental conditions between both experiments, but it suggests a strong negative impact of predation on *T. absoluta* populations (white square on Fig. 2b). Despite the combined effects of predation and negative interactions between *B. tabaci* and *T. absoluta*, the control of *T. absoluta* populations in our experiment was insufficient and plant damage and yield loss due to *T. absoluta* remained particularly high. A tomato fruit contaminated with a single *T. absoluta* larvae cannot be sold, and thus economically acceptable *T. absoluta* population densities in tomato crops are extremely low.

In a previous laboratory-scale experiment, we showed that *M. pygmaeus* had a switching predation behavior between *T. absoluta* and *B. tabaci* (Jaworski et al. 2013). At greenhouse scale, prey switching may contribute to maintaining too high population densities of *T. absoluta* to prevent fruit damage, as the predator would move to patches with higher prey density after having partially depleted *T. absoluta* patches so as to maximize food uptake (Murdoch et al. 2003). In practice, we observed that *Bemisia tabaci* patches were generally denser (around 800 juveniles per leaf, Fig. 2a), whereas *T. absoluta* prey (eggs and larvae) were at densities less than one hundred per leaf in high-density patches. Moreover, the prey stages most preferred by *M. pygmaeus*, i.e., nymphs of *B. tabaci* and eggs of *T. absoluta* (Jaworski et al. 2013), were rarely present in the same patches, as *B. tabaci* nymphs are more often encountered on old tomato leaves (i.e., at the bottom of plants), whereas *T. absoluta* adults lay their eggs on fresh young tomato leaves or stems (i.e., on top of plants; authors' observations). Prey switching may cause *M. pygmaeus* to increase foraging time in *B. tabaci* patches, spatially distant from *T. absoluta* patches (Holt and Kotler 1987). Because the predator is able to move among prey patches, landscape structure is likely to affect pest management also in the field or in a large greenhouse.

Although promoting indirect interactions has been reported to efficiently reduce pest population densities in some cases (Doutt and Nakata 1973; Karban et al. 1994; Evans and England 1996; Settle et al. 1996; Messelink et al. 2008, 2010; Chailleux et al. 2014), apparent

competition between *B. tabaci* and *T. absoluta* mediated by *M. pygmaeus* appears not strong enough to prevent tomato infestation by *T. absoluta*, resulting in strong yield loss. In this situation, the value of employing *M. pygmaeus* as a unique biocontrol agent for both *T. absoluta* and *B. tabaci* is uncertain. Using another biocontrol agent in addition to *M. pygmaeus*, such as a parasitoid (Chailleux et al. 2012, 2013), may result in better control of these two frequently co-occurring tomato pests. Moreover, favoring co-occurring lepidopteran species other than *T. absoluta*, which feed on non-crop plants, may help improve the control of *B. tabaci* by the generalist predator *M. pygmaeus* and reduce crop damage by *B. tabaci*.

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**Author contribution** ND, CJ, and PB conceived and designed the experiment. CJ, PB, and AC performed the experiment. CJ and ND analyzed the data. ND contributed reagents/materials/analysis tools. CJ, ND, and AC wrote the manuscript.

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