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Anaïs Bompard, Coline C Jaworski, Nicolas Desneux, Philippe Bearez. Sharing a predator: can an invasive alien pest affect the predation on a local pest?. *Population Ecology*, 2013, 55 (3), pp.433-440. 10.1007/s10144-013-0371-8 . hal-02107771

HAL Id: hal-02107771

<https://hal.science/hal-02107771>

Submitted on 23 Apr 2019

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Sharing a predator: can an invasive alien pest affect the predation on a local pest?

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Received: 7 August 2012 / Accepted: 12 March 2013
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Abstract Invasive species can strongly affect biotic interactions in ecosystems, interacting both directly and indirectly with local species. In European tomato greenhouses, the invasive alien pest *Tuta absoluta* may impact the population dynamics of other pests like whiteflies. Besides inducing damages to the host plant and competing for resources with local pests, this alien species may exert a predator-mediated interaction on local pests sharing common natural enemies. Biocontrol agents usually used against whiteflies may also prey upon *T. absoluta* and this could alter the dynamics of local pest populations. We evaluated possible resource competition and predator-mediated interactions in a system involving one mirid predator *Macrolophus pygmaeus* and two pests, *T. absoluta* and a local whitefly, *Bemisia tabaci*, on greenhouse tomatoes. Results showed that both resource competition

and predator-mediated interactions occurred simultaneously. In the presence of the shared predator, there was a short-term positive effect of *T. absoluta* on *B. tabaci* [up to 5.9-fold increase of *B. tabaci* juveniles (egg + larvae) after four weeks]. However, in the long-term there was a negative predator-mediated interaction of *T. absoluta* on *B. tabaci*, i.e., after ten weeks the density of *B. tabaci* was 7.3-fold lower in the presence of the invasive pest. We emphasize the critical role of generalist predators in managing both local and invasive alien pest populations and that the strength and direction of predator-mediated indirect interactions can depend on the time scale considered.

Keywords Apparent competition · Apparent mutualism · *Bemisia tabaci* · *Macrolophus pygmaeus* · Resource competition · *Tuta absoluta*

A. Bompard and C. C. Jaworski contributed equally to the study.

Electronic supplementary material The online version of this article (doi:10.1007/s10144-013-0371-8) contains supplementary material, which is available to authorized users.

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Introduction

The economic and ecological negative effects of invasive arthropod species are widely recognized (Mack et al. 2000; Desneux et al. 2010, 2011; Ragsdale et al. 2011). Invading alien species may strongly affect species interactions notably in greenhouse crops which are simplified agroecosystems with low levels of biodiversity (Enkegaard and Brodsgaard 2006). In these agro-ecosystems there is only one resource plant (the cultivated crop) supporting generally few pest species and natural enemies (e.g., predators and parasitoids). Invasive alien pests may destabilize these ecosystems via various interactions including resource competition (Mack et al. 2000) and plant- or predator-mediated indirect interactions with other herbivores (Holt 1977; Abrams et al. 1998; Stout et al. 2006). Resource competition may arise when an alien species has higher

functional and/or numerical responses than an indigenous species (notably owing to higher food uptake capacity) (Shea and Chesson 2002). Plant-mediated indirect interactions between two pests can occur when infestation by a first pest changes the shared plant (e.g., synthesis of secondary metabolites) in a way that affects a second pest (Stout et al. 2006; Mouttet et al. 2011). Predator-mediated indirect interactions occur, for example, when a shared predator feeds preferentially on one given prey type and decreases predation pressure on a second prey (Settle and Wilson 1990).

Among other factors (for review see Liebhold and Tobin 2008), an alien pest has potential for being invasive because it may be released from predation pressure in the invaded area (Shea and Chesson 2002), i.e., *enemy release hypothesis* (Colautti et al. 2004). Indeed, local natural enemies present in the invaded area may not efficiently control the alien pest if the latter shows distinct key characteristics from local pests, e.g., size, moving or sheltering behaviors (Sih et al. 2010; Li et al. 2011). However generalist predators are known for their capacity to regulate herbivore arthropod populations in various ecosystems (Symondson et al. 2002; Desneux et al. 2006; Lu et al. 2012). They can rapidly establish populations in highly disturbed ecosystems, e.g., annual cropping systems, by using alternative prey (Harwood et al. 2007; Desneux and O'Neil 2008; Juen et al. 2012) and plants (Evans et al. 1999; Van Rijn et al. 2002; Vandekerckhove and De Clercq 2010) as food resources. The occurrence of such natural enemies can contribute to the biotic resistance of ecosystems, i.e., a local ecosystem could be resilient to invasion by evolutionary naive species (Shea and Chesson 2002; Juliano et al. 2010; Sih et al. 2010). If natural enemies of local pests can prey upon an invasive pest, then this latter may exert enemy-mediated effects on the local pests, i.e., natural enemy-mediated indirect interactions (Wootton 1994). Indirect interactions may vary in nature and time (Holt and Lawton 1994) and mathematical models predict that they would be generally positive (apparent mutualism or commensalism) at time scales shorter than the predator generation time, owing to shared predation pressure on multiple pests. They would be negative at longer time scales owing to a higher predator numerical response to increased prey availability in comparison with unique prey systems (apparent competition or amensalism, Holt 1977). Theoretical conditions to predict outcomes of enemy-mediated interactions have been largely studied (Holt and Lawton 1994; Abrams and Matsuda 1996; Abrams et al. 1998; Ito and Kondo 2012). However, conditions strongly depend on the characteristics of the pests involved, hence experiments are needed to characterize these types of interactions (Tack et al. 2011).

Resource competition and enemy-mediated interactions are likely to occur simultaneously (Holt et al. 1994), and it is difficult to predict the impact of an invasive species arriving in an ecosystem. For example, the arrival of *Erythroneura variabilis*, a new pest of the Californian vineyards of the San Joaquin Valley led to a drastic decline of the native leafhopper species *Erythroneura elegantula* abundances (Settle and Wilson 1990). In this case, the invasive leafhopper served as an alternative host resource for the shared parasitoid, increasing the parasitoid populations even though the native leafhopper was the preferred host prey. This resulted in apparent amensalism from the invasive leafhopper on the indigenous leafhopper. Conversely, a study from Jones et al. (2009) showed a higher impact of resource competition than apparent competition in shaping aphid communities. The aphid species *Acyrtosiphon pisum* led to the extinction of the aphid species *Megoura viciae* Buckton via competition for the plant resource *Vicia fabae*, even in presence of a shared parasitoid; *Praon dorsale*. The recent invasion of Afro-Eurasia by the South American tomato pinworm *Tuta absoluta* Meyrick (Desneux et al. 2010, 2011) offers an opportunity for assessing the impact of an invasive alien pest on species interactions in a greenhouse crop. The alien pest may affect biological control programs used to manage local tomato pests, e.g., via positive predator-mediated indirect interactions on these pests.

We studied the impact of *T. absoluta* on the local pest *Bemisia tabaci* Gennadius (the tobacco whitefly, biotype Q) controlled by the mirid predator *Macrolophus pygmaeus* Rambur in greenhouse experiments on tomato crops. We evaluated the effect of the invasive alien pest, either via resource competition or predator-mediated interactions, on the local pest population dynamics. *Tuta absoluta* is a major pest for tomato crops causing losses up to 100 % by mining in tomato leaves, stems and fruits. *Bemisia tabaci* (biotype Q) is a widespread European indigenous species (Qiu et al. 2011; McKenzie et al. 2012; Parrella et al. 2012; Saleh et al. 2012) responsible for major damages in tomato crops; as a sap-feeding insect, it causes both direct and indirect (e.g., vectoring viruses) damages to plants (Oliveira et al. 2001; Jiao et al. 2012). *Macrolophus pygmaeus* is one of the most used biocontrol agent against *B. tabaci* and other whiteflies. This generalist predator can also feed on a wide variety of prey such as thrips, aphids, mites, and eggs and larvae of Lepidoptera (Fauvel et al. 1987), notably on those of *T. absoluta* (Urbaneja et al. 2009; Desneux et al. 2010). The study reveals the occurrence of consecutive short- and long-term predator-mediated indirect interactions between an invasive and a local pest. We also discuss the relative importance of resource competition vs. predator-mediated interactions between two pests sharing both the host plant and a predator.

Materials and methods

Insects

The prey *B. tabaci* and *T. absoluta* were reared on tobacco and tomato plants respectively, in separate cages, in a climatic chamber (day/night = 12 h/12 h; T = 23 ± 1 °C, RH = 65 %). The predator *M. pygmaeus*, was provided by the company Biotop[®], and reared on tomato leaves complemented with *Ephestia kuehniella* eggs under controlled conditions (day/night: 16 h/8 h; T = 23 ± 1 °C; RH = 70 %).

Experimental design

We evaluated possible resource competition and predator-mediated indirect interactions of *T. absoluta* on *B. tabaci* in tomato crop in greenhouse. Therefore, we used a 2 × 2 factorial design in which *B. tabaci* was present in all treatments. The first two-level factor consisted of the presence or absence of *T. absoluta*. The second two-level factor consisted of the presence or absence of the predator (*M. pygmaeus*).

Each of the four treatments was replicated four times in 40 m² distinct compartments of an environment-controlled greenhouse, with identical climatic conditions (T = 25 ± 2 °C; RH = 60 %). The greenhouse was located at Sophia Antipolis INRA center (South-Eastern France) and the study was carried out during summer 2010. To prevent insect transfer between treatments inside a given compartment, they were isolated from one another by fine mesh material, which formed tunnels (height: 1.2 m, width: 1 m, length: 5 m). Tomato plants were grown on rock wool slabs and each tunnel contained eight tomato plants [*Solanum lycopersicon* (L.), CV. Marmande] grown on double rows. Plants were coated so as to create a continuous vegetation cover, and watered automatically with a nutrient solution to avoid any abiotic stress. Pesticide applications were strictly avoided. The local prey *B. tabaci* was released first in all tunnels, with 20 adults per plant (160 per tunnel), on the 7-week old tomato plants. A week later, the invasive species *T. absoluta* was released, at a level of 2 adults per plant (16 per tunnel). The following week, the predators *M. pygmaeus* were released at the density of 2 females, 1 male and 4 nymphs (L4/L5) per plant.

Sampling

Population dynamics of the pest species were monitored weekly in each treatment during ten weeks (sampling started one week after the predator release). *Bemisia tabaci* adults were counted on eight leaves (four young and four

old) per tunnel. For each leaf sampled, one leaflet was collected for additional observations in the laboratory. We counted juveniles of *B. tabaci* (i.e., eggs and larvae) and juveniles of *T. absoluta* (i.e., eggs and young larvae: L1–L2 stage) using a binocular microscope. These stages were chosen because they are those attacked by *M. pygmaeus* (Bonato et al. 2006; Desneux et al. 2010).

In a lesser extent (i.e., the main focus was to study the effects of *T. absoluta* on *B. tabaci*), we surveyed predator population dynamics to estimate the effect of adding the invasive alien prey on the predator populations. We recorded *M. pygmaeus* adults and nymphs every two weeks on the same leaves selected for monitoring *B. tabaci* adults (see above).

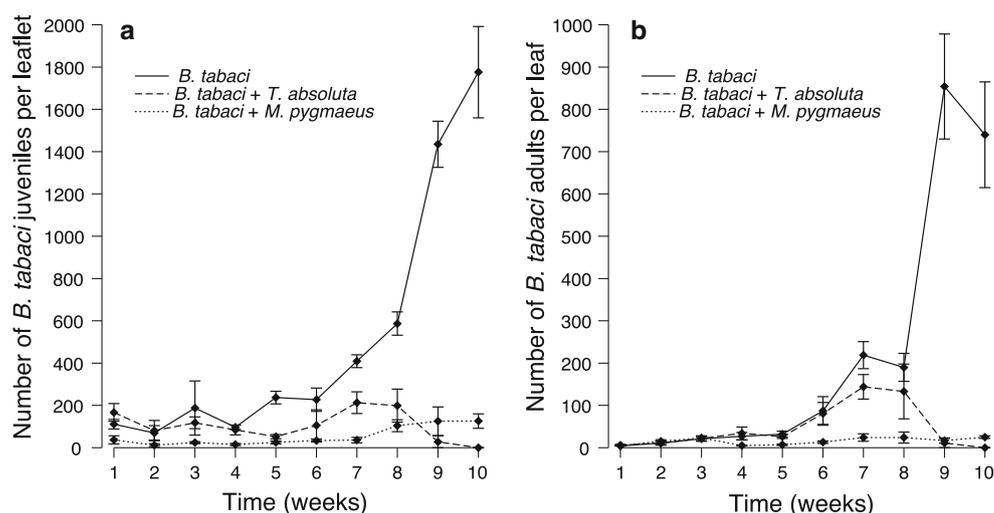
Data analysis

Bemisia tabaci and *T. absoluta* data sets were normally distributed, which was confirmed by a Shapiro–Wilk test. Linear models (ANOVAs) on repeated measurements were used to compare the pest population dynamics among treatments. All statistical analysis was carried out with the software R version 2.12.2 (R Development Core Team).

Predation on the whitefly was tested by comparing *B. tabaci* populations (juveniles and adults) with or without the predator (all without *T. absoluta*). Predation on *T. absoluta* was analyzed by comparing *T. absoluta* populations with or without the predator. Resource competition of *T. absoluta* on *B. tabaci* was assessed by comparing *B. tabaci* populations with or without *T. absoluta* (all without predator). The predator-mediated indirect impact of *T. absoluta* on *B. tabaci* was tested by comparing *B. tabaci* populations (juveniles and adults) with and without *T. absoluta* (all with predator). This last analysis was supplemented by comparing predator populations with *B. tabaci* alone vs. *B. tabaci* + *T. absoluta* because predator-mediated indirect interactions may occur through faster predator population growth with increased prey availability (Holt 1977). Predator data set was analyzed using a linear mixed model (with random effect) because it followed a Poisson distribution (library LME4).

Short-term versus long-term indirect interaction: to depict possible short-term from long-term predator-mediated indirect interactions of *T. absoluta* on *B. tabaci*, data were divided into three periods before further analysis: weeks 1–4, weeks 5–7 and weeks 8–10. These periods were chosen according to the development time of the predator, as documented in the literature (Fauvel et al. 1987; Perdikis and Lykouressis 2000, 2002) and considering the temperatures recorded daily in the greenhouse [Fig. S1 and Table S1 in Electronic Supplementary Material (ESM)]. For weeks 1–4 after release, the prey consumption was expected to be primarily restricted to the released predator

Fig. 1 Impacts of predation by *M. pygmaeus*, and of resource competition with *T. absoluta* on *B. tabaci* population dynamic. Mean number (\pm SEM) of **a** *B. tabaci* juveniles (egg + larvae) per leaflet and **b** *B. tabaci* adults per leaf when *B. tabaci* was alone, together with *T. absoluta*, or together with the predator *M. pygmaeus*



individuals; i.e., the offspring from these predators had not reached the L4-stage yet (the stage when they start actively preying on prey) and their prey consumption should remain negligible (Fauvel et al. 1987; Perdakis and Lykouressis 2000, 2002). Predator-mediated indirect interactions (if any) between prey over this first time period correspond to short-term interactions. Prey consumption should increase from week 4 to week 7 as the offspring individuals were progressively reaching L4-stage and adulthood. After week 8, all offspring that had emerged during the first two weeks had reached adulthood and had optimal prey consumption (Fauvel et al. 1987; Perdakis and Lykouressis 2000, 2002). During both of these periods (weeks 4–7 and weeks 8–10), long-term indirect interactions could be expected.

Results

In the absence of other insect populations, *B. tabaci* populations grew exponentially until the end of the experiment (Fig. 1a, b). In the absence of the predator *M. pygmaeus*, *T. absoluta* populations also grew exponentially at first, and then went extinct by week 9 when all tomato plants were destroyed (Fig. 2). The destruction of the tomato plants led to the extinction of *B. tabaci* populations too (Fig. 1a, b). As a consequence of plant destruction and insect extinction, treatments containing both prey but no predators were removed from analyses after week 8. Over weeks 1–8, the presence of *T. absoluta* without predator induced a marginally significant reduction in the populations of juveniles of *B. tabaci* ($F_1 = 3.86$, $P = 0.097$). Over weeks 5–8, the presence of *T. absoluta* induced a significant reduction in *B. tabaci* populations for both juvenile stages ($F_1 = 134.93$, $P < 0.001$) and adults ($F_1 = 79.140$, $P < 0.001$), resulting in a 2.9-fold decrease for juveniles

(Fig. 1a) and a 1.4-fold decrease for adults (Fig. 1b) at week 8.

In the presence of the predator, both prey populations remained at lower levels, and plants survived during the whole experimental period. The predator significantly reduced *B. tabaci* populations either with or without *T. absoluta* [without *T. absoluta*: Fig. 1a (juveniles), $F_1 = 767.76$, $P < 0.001$ and Fig. 1b (adults), $F_1 = 51.01$, $P < 0.001$; with *T. absoluta*: Fig. 3 (juveniles), $F_1 = 10.68$, $P = 0.017$ and Fig. S2 in ESM (adults), $F_1 = 25.99$, $P = 0.002$]. By week 10, in the absence of the

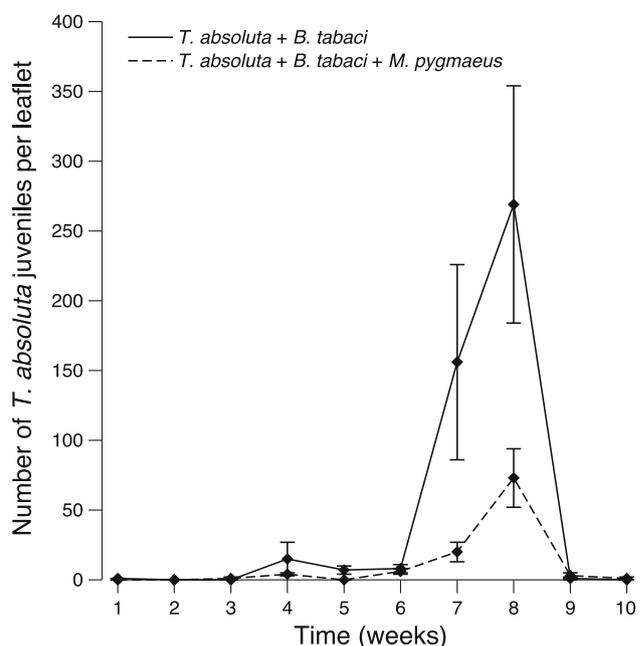
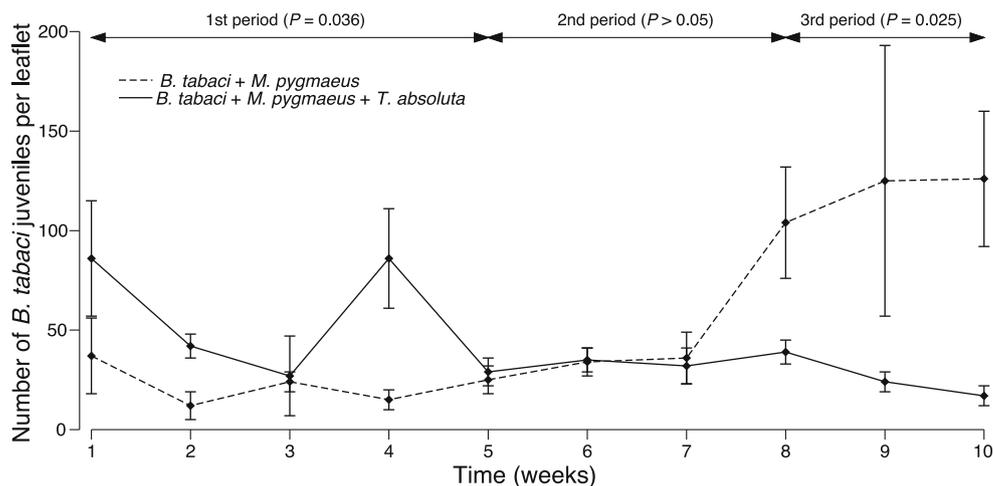


Fig. 2 Impact of predation on *T. absoluta* populations in presence of the local prey *B. tabaci*. Mean number (\pm SEM) of juveniles (egg + larvae) of *T. absoluta* per leaflet with or without the predator *M. pygmaeus* (all treatments were with *B. tabaci*)

Fig. 3 Short- and long-term predator-mediated indirect impact of *T. absoluta* on population dynamics of the local pest *B. tabaci*. Mean number (\pm SEM) of juveniles (eggs + larvae) of *B. tabaci* per leaflet with or without the invasive alien pest *T. absoluta* (all treatments were with *M. pygmaeus*) during 3 temporal periods. *P* values indicate statistical results when comparing *B. tabaci* population dynamics with vs. without *T. absoluta* for each temporal period (ANOVA on repeated measures)



invasive alien species *T. absoluta*, predators reduced *B. tabaci* populations causing a 14- and 30-fold decrease for juvenile (Fig. 1a) and adult stages (Fig. 1b), respectively. The presence of *M. pygmaeus* also induced a significant reduction in the population size of *T. absoluta* (juveniles) during weeks 1–8 ($F_1 = 34.38$, $P = 0.001$), resulting in a 3.7-fold reduction by week 8 (Fig. 2).

In the *B. tabaci*–*M. pygmaeus* groups, the presence of *T. absoluta* had a significant positive impact on the population levels of *B. tabaci* juveniles (Fig. 3) during weeks 1–4 ($F_1 = 7.24$, $P = 0.036$) resulting in a 5.9-fold increase for juveniles by week 4. During the same period,

M. pygmaeus population size did not show any significant difference in presence vs. absence of *T. absoluta* ($z = 0.602$, $P > 0.05$) (Fig. 4). During weeks 5–7, populations of juveniles of *B. tabaci* in the presence vs. absence of *T. absoluta* did not differ significantly ($F_1 = 0.0027$, $P > 0.05$), nor did *M. pygmaeus* populations (weeks 6–8, $z = 0.336$, $P > 0.05$). However, during weeks 8–10 the presence of *T. absoluta* significantly reduced the populations of juveniles of *B. tabaci* ($F_1 = 8.81$, $P = 0.025$) resulting in a 7.3-fold decrease by week 10 (Fig. 3). The population dynamics of *B. tabaci* adults showed similar trends (Fig. S2 in ESM). On the last sampling date (week 10) the presence of *T. absoluta* induced a marginally significant increase in *M. pygmaeus* populations (t test on the data collected on week 10: $t = 2.038$, $P = 0.08$).

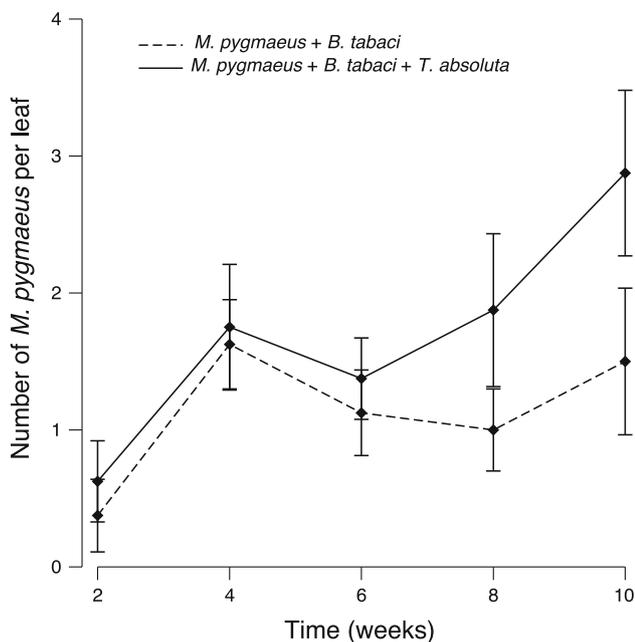


Fig. 4 Impact of *T. absoluta* on the population dynamic of the predator *M. pygmaeus* in presence of the local pest *B. tabaci*. Mean number (\pm SEM) of the predator *M. pygmaeus* per leaf with or without *T. absoluta*

Discussion

Tuta absoluta proved to be a very damaging pest on tomato crops, i.e. it led to 100 % plant destruction at week 9 in the predator-free treatments. Through destruction of tomato leaves, *T. absoluta* likely induced resource competition on *B. tabaci* in several ways: first through a reduction in available oviposition substrate for *B. tabaci* adults, and second through general decrease of available food for *B. tabaci* larvae. Resource competition began to negatively affect *B. tabaci* populations from week 5. At that time, whiteflies had completed an entire development cycle (Bonato et al. 2007), so the reduced offspring production of *B. tabaci* recorded in the presence of *T. absoluta* likely corresponded to a higher larval mortality rather than reduced whitefly oviposition. Whiteflies may also have suffered from an induced plant response to the chewing activity of *T. absoluta* larvae (Stout et al. 2006), but this indirect plant-mediated interaction could not be discriminated from a direct food competition. The impact of

resource competition culminated on 9th week, when plant destruction caused the extinction of both pest populations. By contrast, in absence of other insects, intra-specific resource competition in *B. tabaci* populations was likely low, as they displayed continuous growth until the end of the experiment, i.e., they did not reach the carrying capacity of their environment.

Treatments with predators were more sustainable, as pest populations were maintained at lower levels, and plants remained healthy until the end of the experiment. The predation capacity of *M. pygmaeus* on *T. absoluta* has been previously reported in laboratory conditions (Urbanaja et al. 2009), our study further demonstrates the capacity of this predator to control the invasive alien pest in situ.

The predator-mediated indirect interactions of *T. absoluta* on *B. tabaci* changed over time. At a short time scale (weeks 1–4) the invasive alien species caused a disruption of the control of *B. tabaci* by *M. pygmaeus*, resulting in increased densities of *B. tabaci*. This positive interaction may be the result of a sharing of the predation pressure over this period (Holt 1977; Abrams and Matsuda 1996; Desneux and O’Neil 2008). Predator population densities were identical in treatments with one or two prey during weeks 1–4 (Fig. 4). Since (1) prey availability was higher in treatments with *T. absoluta*, and (2) predation on *B. tabaci* increased (reduction in *B. tabaci* populations from week 3 to week 4, see Fig. 3), we infer that prey availability exceeded predator consumption rate during that time span. This positive, short-term, indirect interaction might be regarded as apparent mutualism. However, to conclude that this interaction is true apparent mutualism (i.e., bi-directional), we would need to test the reciprocal indirect effect of *B. tabaci* on *T. absoluta*.

At a longer time scale (weeks 8–10) a negative indirect effect exerted by the invasive alien prey on the local prey took over the short-term, indirect positive interaction, as predicted by several theoretical models (Gleeson and Wilson 1986; Holt and Lawton 1994; Abrams et al. 1998). The strong reduction in *B. tabaci* populations in the presence of *T. absoluta* could be due to an increased number of predators in response to higher prey availability (Holt 1977; Holt and Lawton 1994). Indeed, predator densities tend to be higher in the presence of both prey from week 8 (Fig. 4). At that time, the offspring of the predators introduced at the beginning of the experiment would have theoretically reached adulthood (Fig. S1 and Table S1 in ESM). Several previous studies support the idea that the numerical response of *M. pygmaeus* depends on the number of available prey (Fauvel et al. 1987; Alomar et al. 2002). This long-term indirect negative effect of *T. absoluta* on *B. tabaci* could be regarded as true apparent competition if (1) *B. tabaci* also exerts a long-term

negative predator-mediated effect on *T. absoluta*, and (2) the predator densities are higher in the presence of both prey. The sampling method may not have been optimal for highlighting the differences in predator population densities among treatments (though it was appropriate for sampling the pest populations).

In our study, prey shared simultaneously a predator and a resource plant. No experimental design can strictly determine the respective impacts of apparent vs. resource competition, as both are likely to occur simultaneously, and even interact in the majority of situations. In our system, resource competition was very strong in predator-free treatments. However, resource competition is known to be a density-dependent interaction (Murdoch et al. 2003), and when present, predators caused a strong reduction in the abundance of pest populations. Thus, the intensity of resource competition in the treatments with predators is expected to be lower than in the predator-free treatments. Still some resource competition may occur and might be partly responsible for the long-term, negative impact of *T. absoluta* on *B. tabaci*. In similar insect experiments where species shared a common resource and predator, the outcome of the interaction of one pest on another was also negative on the long-term (Messelink et al. 2008, 2010; Calvo et al. 2012). Conversely, no negative indirect interactions could be observed in a semi-natural forest experiment on oak leaf-miners (Tack et al. 2011). They manipulated the population densities of three co-occurring oak leaf-miners parasitized by a common parasitoid species and found neutral or positive long-term interactions. The parasitoid numerical response may have been limited by other factors than prey densities, hence preventing the occurrence of apparent competition. In addition, prey densities may have been too low for resource competition to occur. The modeling work of Noonburg and Byers (2005) suggested that the negative, competing impact of invasive species on native species is more likely to be apparent competition rather than resource competition. Contrasting this conclusion, Jones et al. (2009) found a higher impact of resource competition than apparent competition. The most likely hypothesis in our study is that both predator-mediated interaction and resource competition are responsible for the observed long-term, negative impact of *T. absoluta* on *B. tabaci* populations. The outcomes of interactions may depend on intrinsic characteristic of the system, such as the capacity of the invasive species to be a strong competitor for resource, or the preference of the shared predator to either one or the other prey.

Scientists, extension specialists and farmers look forward to determining how destructive the arrival of *T. absoluta* may be on tomato crops yields (Desneux et al. 2010, 2011) and whether the alien pest may threaten integrated pest

management (IPM) practices directed against local tomato pests (notably through ecological effects or insecticide-related negative effects on natural enemies, e.g. Desneux et al. 2007; Arno and Gabarra 2011; Biondi et al. 2012). Our results show that *T. absoluta* disrupted only temporarily the control of *B. tabaci* by the predator: the reduction of the predation pressure was moderate and time-limited. Furthermore, the arrival of *T. absoluta* increased the efficiency of predation against *B. tabaci* on the long-term. A symmetrical experimental design could test for the long-term impact of *B. tabaci* on *T. absoluta* populations, so as to suggest possible apparent competition between both species. The possibility for apparent competition could facilitate optimization of IPM programs, e.g., an agroecosystem maintaining simultaneously low levels of several pest populations would be more sustainable than agroecosystems aimed at excluding particular pest species. Generalist predators are often favored by high prey diversity (Symondson et al. 2002; Messelink et al. 2010; Miyashita et al. 2012) and if settled in crops before the arrival of a new invasive prey, they could offer an opportunity to control them, acting as a form of biotic resistance for the greenhouse crop.

Acknowledgments We thank Antonio Biondi (University of Catania, Italy), George Heimpel, Emily Mohl and James Eckberg (University of Minnesota, USA) for helpful comments on an earlier version of the manuscript, Anaïs Chailleux, H el ene Kazuro and C ecile Thomas for their assistance throughout the experiments and Jacques Frandon (Biotop, InVivo AgroSolutions) for providing some biological materials. This work was supported by funds from *Plant Health and Environment and Environment and Agronomy* Departments of INRA and from the French ministry of agriculture (CAS-DAR Project 10063) to ND.

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