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Trophic web associated with the South American tomato moth *Tuta absoluta*: implications for its conservation biological control in Argentina

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Abstract

1 The South American tomato moth *Tuta absoluta* is a major pest targeted for biological control by entomophagous insects. Trophic interactions among parasitoids of *T. absoluta* and other gelechiids feeding on crop and spontaneous wild solanaceous were investigated in north-eastern Buenos Aires (Argentina), with the aim of assisting in the design of conservation biological control strategies.

2 A quantitative parasitoid trophic web was constructed that included five gelechiid leafminers, five solanaceous species and a complex of 18 parasitoid species.

3 The relative abundance of *T. absoluta* was highest in the *Solanum melongena* crop, followed by the wild plants *Nicotiana glauca*, *Solanum americanum*, *Solanum sisymbriifolium* and *Salpichroa origanifolia*. Greater parasitoid species richness associated with *T. absoluta* was found in the wild plants *N. glauca* and *S. americanum*.

4 *Pseudapanteles dignus* was the main parasitoid of *T. absoluta* and co-occurred with this pest in four plant species.

5 Parasitism of *T. absoluta* by *P. dignus* was observed throughout the year in *S. melongena*, reaching values up to 33%, whereas it was sporadic and exhibited lower parasitism rates in the noncrop *S. sisymbriifolium*, *N. glauca* and *S. americanum*.

6 The presence of some wild solanaceous plants should be promoted to maintain the *T. absoluta*– *P. dignus* interaction in horticultural farms.

Keywords Agroecosystem, biocontrol, community, leafminer, parasitic Hymenoptera, Solanaceae, trophic interactions.

Introduction

Ecological interactions between plants, insect herbivores and entomophagous natural enemies in agroecosystems occur at population and community levels, linking species within and between functional groups, as well as through crop fields and semi-natural habitats in the landscape (Bohan *et al.*, 2013). However, the conventional approach to pest management still relies heavily on linear associations that consider only the crop, the target pest and its natural enemies. Knowledge of species richness at different trophic levels, the number and the relative magnitude of the interactions between them, the distribution of resources, and the outcome of competition provides meaningful information for our understanding of the complexity of the web. Moreover, these studies allow predictions to be made about how different factors and processes affect the services provided by the agroecosystem (Briand & Cohen, 1987; Pimm *et al.*, 1991). Recently, applied ecology to pest control has started to acknowledge that information gathered in a community context can provide important clues regarding biological control and pest management (Valladares & Salvo, 1999). Top-down effects as a result of naturally occurring parasitoid species, combined with bottom-up effects of some plants supplying food and shelter, may promote the persistence of pest–parasitoid interactions, providing a valuable ecosystem service (Tilman *et al.*, 2002).

Use of the quantitative food web approach helps to assess the occurrence of common enemies shared by herbivorous insects (Memmott & Godfray, 1994; Derocles *et al.*, 2014). Parasitoid food webs focus on interactions between plants, herbivorous insects, their parasitoids and their hyperparasitoids (Rott &

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Godfray, 2000). Food web analyses can be used to determine the parasitoid species richness, host range, information on species interactions and the processes involved in network organization (Valladares & Salvo, 1999; Lewinsohn *et al.*, 2006; Cagnolo *et al.*, 2011).

Conservation biological control is a holistic pest management technique founded in the protection of natural enemy populations through different methods of habitat manipulation. This technique requires theoretical and applied ecological knowledge at the population and community levels, aiming to improve the abundance and diversity of the natural enemies in agroecosystems (Barbosa, 1998; Landis *et al.*, 2000; Messelink *et al.*, 2014).

The tomato (*Solanum lycopersicum* L.) crops in Central and South America have a major native pest: the South American tomato moth *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Luna *et al.*, 2012). Neurotoxic and insect growth regulator pesticides are extensively applied during the cropping season to control this pest. To avoid nontargeted effects of pesticides on natural enemies, other plant protection techniques, such as the use of new generation insecticides, the selection of tomato resistant genotypes, pheromone trapping and the release of sterile males, have been assayed (Polack, 2007; Cagnotti *et al.*, 2012).

This pest has invaded and became established in Afro-Eurasian continents during the last decade, threatening worldwide tomato production (Desneux *et al.*, 2011). In these newly-invaded areas, different plant protection methods, including biological control, are also being investigated (Desneux *et al.*, 2010; Urbaneja *et al.*, 2012; Chailleux *et al.*, 2013; Zappalà *et al.*, 2013).

In its region of origin, *T. absoluta* is associated with many indigenous parasitoids on tomato plants (Vargas, 1970; Colomo *et al.*, 2002; Luna *et al.*, 2015). Among them, the native larval endoparasitoid *Pseudapanteles dignus* (Muesebeck) (Hymenoptera, Braconidae) is a promising candidate for use in augmentative releases for *T. absoluta* control. Several traits of *P. dignus* are beneficial for pest control: seasonal synchronization with host populations, aggregative response to host density, instantaneous attack rate greater than the intrinsic growth rate of the host and high field parasitism rates (Luna *et al.*, 2007; Sánchez *et al.*, 2009; Nieves *et al.*, 2015).

Although *T. absoluta* prefers and exhibits a higher performance on *S. lycopersicum*, it also attacks other cultivated and wild solanaceous plants (Cordo *et al.*, 2004; Pereyra & Sánchez, 2006; Desneux *et al.*, 2010; Zappalà *et al.*, 2013; Bawin *et al.*, 2015). However, there are limited studies on the parasitoid complex attacking *T. absoluta* when it feeds on other crop and noncrop plants, and particularly on the gelechiid host range of *P. dignus.* Natural enemies inhabiting wild plants adjacent to greenhouses may move into crops providing a natural parasitism, which can also benefit the implementation of biological control through augmentative releases (Messelink *et al.*, 2014).

We hypothesed that, in horticultural farms where tomatoes are grown, the interaction of *T. absoluta* and *P. dignus* comprises part of a complex food web consisting of other cultivated and wild solanaceous, many of which are attacked by *T. absoluta* and other gelechiids, which in turn are hosts of *P. dignus* and other larval parasitoids.

To test this hypothesis, we explored the annual abundance of gelechiid leafminers in cultivated and wild solanaceous species and their larval parasitoids in the north-eastern Buenos Aires province, a main horticultural region of Argentina. Our aim was to depict a quantitative trophic web centered on *T. absoluta* to gain understanding about the interspecific relationships established by this pest, the parasitoids, and the crop and wild host plants, laying the basis for the conservation-based biological control of *T. absoluta*.

Materials and methods

Study area, sampling and insect rearing

The study site was located at La Plata Horticultural Belt (34°56′S, 57°59′W), Buenos Aires province, Argentina. This region comprises approximately 5000 cultivated hectares characterized by a mosaic of intensive agricultural farms (Argerich & Troilo, 2010). Half of the national greenhouse production takes place in this region (Desneux *et al.*, 2011). The dominant crops are leafy greens, tomato, sweet pepper, eggplant, squash, cabbage, broccoli, corn, cauliflower and strawberry.

Seven farms were chosen for sampling gelechiid species and their larval parasitoids. In each farm, a list of crop and wild solanaceous plants was developed for sampling, in accordance with the weed phylogenetic centrifugal method proposed by Wapshere (1974). Wild solanaceous plants usually grow near the crops within the horticultural field.

Monthly samplings (from January 2013 to January 2015) were carried out in each farm, involving the inspection of leaves, fruits and stems of selected solanaceous plants, looking for evidence of attack by leafminers. Because only foliar attack was observed, we collected 200 leaves with damage per plant species on each sampling date for further study in the laboratory. Plant specimens were also gathered to prepare a reference herbarium, and species identifications were made based on studies by Marzocca (1976) and Zuloaga and Morrone (1999), as well as electronic databases (Flora de Argentina: http://www.floraargentina.edu.ar; Tropicos: http://www.tropicos.org; amongst others).

Leaves were examined under a stereoscopic microscope (SMZ 645; Nikon, Japan) to check for the presence of leafminers and larval ectoparasitoids. To determine presence of larval endoparasitoids, living mining insects were individually reared in plastic Petri dishes (diameter 10 cm, height 2 cm) lined with moistened filter paper and provided with their corresponding plant species as food. Dishes were labelled with information on date, sampling site and host plant species, and subsequently maintained in a walk-in chamber (LD 14 : 10 h at 25 ± 2 °C and 70% relative humidity) until the formation of gelechiid or parasitoid pupae and subsequent adult emergence. Host larvae that died during rearing were dissected to search for immature parasitoids under a stereoscopic microscope. Parasitoid pupae were preserved in labelled vials until adult emergence for further identification.

Insect species identification

Taxonomic determinations of gelechiid species were made by using the superficial characters (e.g. wing pattern, labial palpi) and male genital characters after dissection (Lee *et al.*, 2009). Voucher specimens were deposited in Hasbrouck Insect

Table 1 Crop and wild solanaceous plants, relative abundance of gelechiid and parasitoid species, and parasitoid guilds registered at La Plata Horticultural Belt (34°56′S, 57°59′W), Buenos Aires province, Argentina, 2013–2015

Host plant	Gelechiid species (relative abundance)	Parasitoid (relative abundance)	Guild of parasitoid
Cropped			
Capsicum annuum			
Solanum melongena	*Tuta absoluta* (100%)	**Braconidae**	
		Pseudapanteles dignus (97%)	L-endo
		Eulophidae	
		Dineulophus phthorimaeae (1.5%)	L-ecto
		Ichneumonidae	
		Ichneumonidae 1 (<1%)	L-endo
		Campopleginae1 (<1%)	L-endo
Noncropped			
Brugmansia arborea			
Datura ferox			
Nicotiana glauca	Gelechiid 1 (1%)		
	Tuta absoluta (99%)	**Braconidae**	
		Agathidinae 1 (58.9%)	L-endo
		Agathidinae 3 (2.2%)	L-endo
		Bracon sp (1.5%)	L-endo
		Hormiinae 1 (1.5%)	L-ecto
		Hormiinae 2 (2.2%)	L-ecto
		Microgastrinae 3 (2.2%)	L- endo
		Orgilus sp (1.5%)	L-endo
		Pseudapanteles dignus (30%)	L-endo
Nicotiana longiflora			
Salpichroa origanifolia	*Tuta absoluta* (100%)	**Braconidae**	
		Microgastrinae 2 (100%)	L-endo
Solanum americanum	*Tuta absoluta* (100%)	**Braconidae**	
		Agathidinae 2 (10%)	
		Microgastrinae 1 (3.5%)	L-endo
		Pseudapanteles dignus (62.5%)	L-endo
		Encyrtidae	
		Copidosoma sp (10%)	E-L
		Eulophidae	
		Chrysocharis sp (3.5%)	L-endo
		Eulophidae 1 (3.5%)	L-ecto
		Ichneumonidae	
		Ichneumonidae 1 (7%)	L-endo
Solanum chenopodioides			
Solanum pygmaeum			
Solanum sarrachoides			
Solanum sisymbriifolium	*Phthorimaea operculella* (25%)		
	Gelechiid 2 (2.5%)		
	Tuta sp. (3.33%)		
	Tuta absoluta (69.17%)	**Braconidae**	
		Microgastrinae 4 (25%)	L-endo
		Pseudapanteles dignus (75%)	L-endo
S	5	18	
N	3548[a]	438[b]	

[a]N number of gelechidae larvae.
[b]N number of parasitoid wasps.
S, species richness.

Collection at Arizona State University and the División de Entomología, Museo de La Plata, Argentina.

Systematic identification of parasitoids, with an emphasis on *P. dignus*, was made using taxonomic keys (Wharton *et al.*, 1997; Colomo *et al.*, 2002; Luna *et al.*, 2010) and a comparison with reference material.

Statistical analysis

The relative abundance of gelechiid leafminers and parasitoids during the 2-year study period was estimated for each plant species and for total collected larvae. Parasitoid guilds were determined according to Mills (1994).

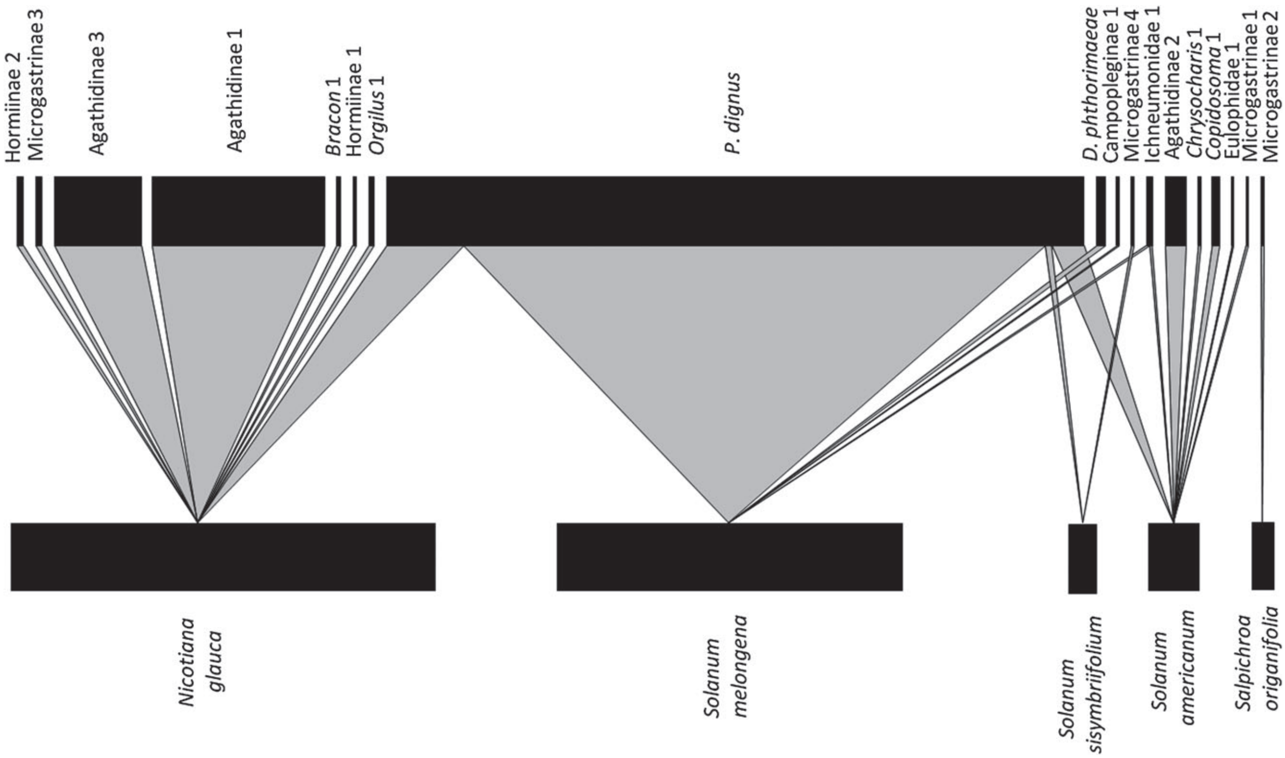

Figure 1 Parasitoid food web based on *Tuta absoluta* at La Plata Horticultural Belt (34°56′S, 57°59′W), Buenos Aires province, Argentina, 2013–2015. Each species at the upper trophic level is represented by a rectangle, the size of which is proportional to the species abundance, whereas bars in the bottom level indicate the relative proportion of *T. absoluta* larvae reared on each host plant. The width of the lines linking species indicates the strength of interactions (number of parasitoids obtained on each host plant).

A quantitative food web depicting all trophic interactions recorded at the field was constructed using the Bipartite package in the R environment for statistical computing (R Development Core Team, 2014). Because *T. absoluta* was the only leafminer species associated with parasitoids, the trophic web was represented as a bipartite one, in which bar widths are proportional to the relative abundance of *T. absoluta* in each plant host.

Seasonality of *T. absoluta* and *P. dignus* in solanaceous host plants was analyzed by plotting phenological profiles of the presence of both species.

Mean ± SEM numbers of *T. absoluta* larvae per leaf and the percentage of parasitism by *P. dignus* in each host plant for each sampling date were calculated.

Results

Twelve solanaceous species were recorded in the study sites: the crops *Solanum melongena* L. (eggplant) and *Capsicum annuum* L. (sweet pepper), and the weeds *Datura ferox* L. (fierce thorn – apple), *Nicotiana longiflora Cav*. (longflower tobacco), *Nicotiana glauca* Graham (tree tobacco), *Salpichroa origanifolia* (Lam.) Baill. (lily of the valley vine), *Solanum americanum* Mill. (American black nightshade), *Solanum sisymbriifolium* Lam. (sticky nightshade), *Brugmansia arborea* L. (angel's trumpets), *Solanum chenopodioides* Lam. (goosefoot nightshade), *Solanum sarrachoides* Sendtner (hoe nightshade) and *Solanum pygmaeum* Cav. Eggplant and sweet pepper were grown under greenhouse and wild plants were found in the vicinity of crops.

Five out of 12 solanaceous species yielded a total of five gelechiid leafminer species (Table 1). The highest gelechiid richness (four species) was recorded on *S. sisymbriifolium*, whereas sweet pepper, *B. arborea*, *D. ferox*, *N. longiflora*, *S. chenopodioides*, *S. pygmaeum* and *S. sarrachoides* did not host gelechiid species.

During the present study, we reared 3548 gelechiid larvae in the laboratory and 2706 of these reached the adult stage. The relative abundance of *T. absoluta* was 98.6% of total collected larvae. *Tuta absoluta* was recorded from one crop and four noncrop plants (Table 1). Regarding the other gelechiids, only the potato tubermoth *Phthorimaea operculella* Zeller was present in *S. sisymbriifolium.*

Tuta absoluta was parasitized by different species complexes when feeding on the distinct host plants. From the total mining larvae reared in the laboratory, 438 individuals of *T. absoluta* were parasitized by 18 Hymenoptera species and morphospecies: 13 in the Braconidae, one in Encyrtidae, three in Eulophidae and one in Ichneumonidae. Most parasitoid species belonged to the koinobiont endoparasitoid guild, and all species were solitary with the exception of *Copidosoma* sp., which was polyembrionic (egg-larval parasitoid guild). Larvae of other gelechiid species were not parasitized (Table 1). *Pseudapanteles dignus* relative abundance ranged from 30% to 97% (Table 1).

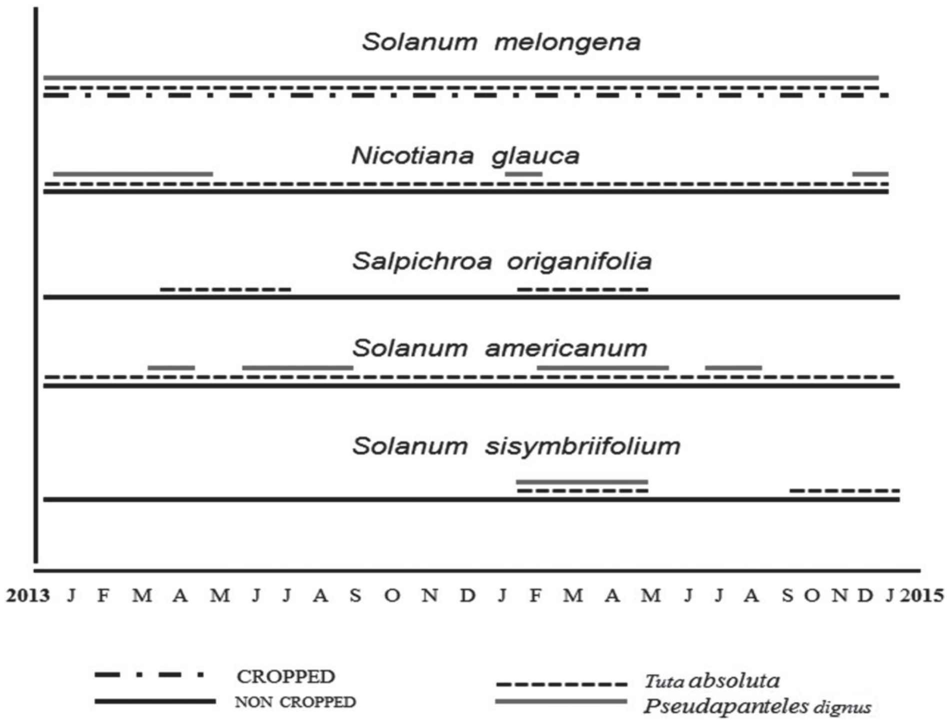

Figure 2 Phenological profiles showing the seasonality of *Tuta absoluta* and *Pseudapanteles dignus* within five different solanaceous species at La Plata Horticultural Belt (34°56′S, 57°59′W), Buenos Aires province, Argentina, 2013–2015.

As shown in the depicted quantitative food web (Fig. 1), the relative abundance of *T. absoluta* was highest in eggplant, followed by the wild plants *N. glauca*, *S. americanum*, *S. sisymbriifolium* and *S. origanifolia*. Greater parasitoid species richness associated with *T. absoluta* was found in *N. glauca* ($S = 8$) and *S. americanum* ($S = 7$). In general, *P. dignus* was the dominant parasitoid species and its parasitism was related to the abundance of *T. absoluta* in each host plant, being highest when the pest fed on eggplant.

Tuta absoluta and *P. dignus* showed different seasonality in the various solanaceous host plants. They co-occurred year-round in eggplant, whereas their presence was sporadic during periods ranging from 2 to 5 months in the wild solanaceous plants *S. americanum*, *S. sisymbriifolium* and *N. glauca.* In *S. origanifolia*, despite the presence of *T. absoluta*, *P. dignus* was not observed (Fig. 2).

Tuta absoluta density and *P. dignus* parasitism exhibited a pattern of coupled oscillations in eggplant and *S. americanum*, although they showed cycles of increase and collapse in *N. glauca* and *S. sisymbriifolium.* Density values of *T. absoluta* were higher in eggplant and *N. glauca* (approximately 0.5 larvae per leaf) than in *S. americanum* and *S. sisymbriifolium* (<0.1 larvae per leaf). Parasitism rates reached up to 33%, 31%, 29% and 17% in eggplant, *S. americanum*, *S. sisymbriifolium* and *N. glauca*, respectively (Fig. 3).

Discussion

The present study describes, for the first time, the *T. absoluta*–*P. dignus* interaction in solanaceous plants other than tomato, sweet pepper and potato (Cardona & Oatman, 1971; Oatman & Platner, 1989; Bennett, 1995). This information enlarges the natural host plant range of *T. absoluta*, and confirms the narrow *P. dignus* host range in this region. In a study of the parasitoid assemblages reared on Geometridae larvae in Alpine forests, Kenis *et al.* (2005) found that many parasitoid species showed more specificity to species of insect host than to host plant. Coincidentally, in the present study, *P. dignus* exhibited a higher host specificity, parasitizing *T. absoluta* irrespective of the host plant. This suggests that low-density levels of *T. absoluta* populations should be safeguarded to preserve *P. dignus* in the agroecosystem.

The results of the present study support our hypothesis that the *T. absoluta*–*P. dignus* interaction is part of a complex food web consisting of crop and wild solanaceous plants growing in the vicinity of crops, many of which are attacked by *T. absoluta* and other gelechiids, which in turn are hosts of *P. dignus* and other larval parasitoids.

The food web based on *T. absoluta* revealed interesting points worthy of consideration in future biological control and integrated pest management programmes. The occurrence of low densities of this leafminer on various wild plants, common in horticultural fields, enables the existence of a rich parasitic complex. It is possible that these plants benefit parasitoids, providing host and nonhost resources (e.g. floral and extrafloral nectar) and shelters when the crop is not present (Fiedler *et al.*, 2008). Also of interest is the finding that only *P. dignus* appears to establish a persistent interaction with *T. absoluta* in eggplant and *S. americanum*, even though the parasitoid complex present in these horticultural farms had a richness of 18 parasitoid species.

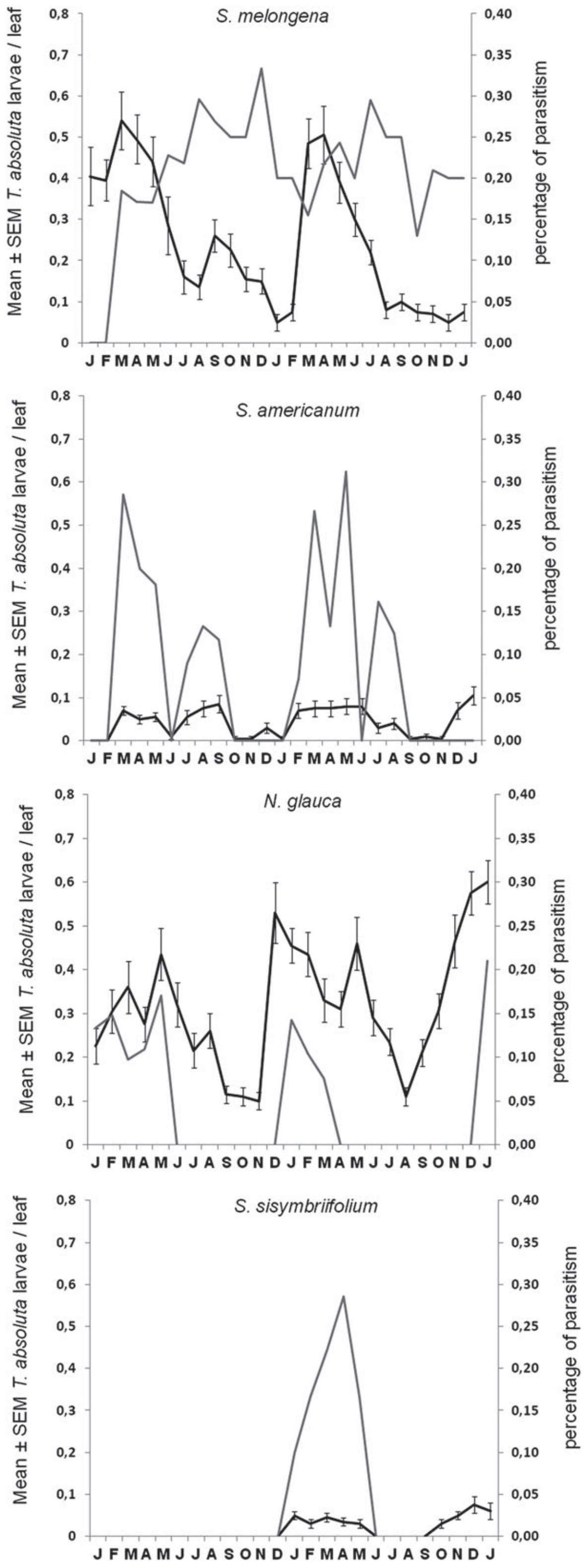

Figure 3 Mean ± SEM number of *Tuta absoluta* larvae per leaf and percentage of parasitism of *Pseudapanteles dignus* in four different solanaceous species at La Plata Horticultural Belt (34°56′S, 57°59′W), Buenos Aires province, Argentina, 2013–2015. Black line: density of *T. absoluta*; grey line: percentage of parasitism for *P. dignus*.

The interaction found in these two solanaceous plants was similar to that found in tomato by Nieves *et al.* (2015) throughout the crop cycle, exhibiting typical host–parasitoid oscillations. Eggplant and tomato represent concentrated resources, which are easy to find for the pest, allowing its fast population increase and the subsequent colonization of the parasitoid. Unlike crops, in *S. americanum*, *N. glauca* and *S. sisymbriifolium*, the *T. absoluta*–*P. dignus* interaction displayed cycles of increase and extinction; however, at the agroecosystem scale, this interaction occurred throughout the year. At this scale, the interaction appears to persist within a metapopulation structure (Levins, 1969; Hanski, 1998). Different habitat patches would support *P. dignus* subpopulations that exhibit relatively independent, dynamic cycles of different duration, although these are unable to persist without re-colonization processes. Metapopulation dynamics would ensure the long-term persistence of *P. dignus*, preventing local populations from ecological extinction (Letourneau, 1998).

Even though *T. absoluta* abundance in *N. glauca* was relatively high and similar to *S. melongena*, *P. dignus* parasitism was sporadic and low. In *N. glauca*, one Agathidinae species at a higher abundance than *P. dignus* could outcompete this parasitoid.

In annual crop systems, the intensive use of broad-spectrum pesticides and cyclical patterns of cultivation, harvesting and lying fallow contribute to the loss of natural enemies (Barbosa, 1998). Noncrop plants can provide habitat and resources to natural enemies, and several studies support the role of wild plants in enhancing arthropod-mediated ecosystem services in agricultural landscapes and avoiding the ecological extinction of natural enemies (Fiedler *et al.*, 2008; Isaacs *et al.*, 2009; Gurr *et al.*, 2012; Blaauw & Isaacs, 2015).

The results of the present study indicate that wild *N. glauca*, *S. americanum* and *S. sisymbriifolium* would help to maintain the *T. absoluta*–*P. dignus* interaction in solanaceous crops. Furthermore, predators commonly inhabit tomato crops and increasing attention is being paid to the potential of predators for controlling this pest in America (de Medeiros *et al.*, 2009; Bueno *et al.*, 2013; Pereira *et al.*, 2014; Speranza *et al.*, 2014) and the Mediterranean basin (Urbaneja *et al.*, 2012; Chailleux *et al.*, 2013; Ingegno *et al.*, 2013; Zappalà *et al.*, 2013; Abbas *et al.*, 2014). Recent studies demonstrate the positive impact of plant diversification on populations of beneficial insects against *T. absoluta* in agricultural systems (Zappalà *et al.*, 2013; Bawin *et al.*, 2015).

Promoting diversity in agroecosystems may protect other pests or benefit the fourth trophic level (e.g. hyperparasitoids) (Messelink *et al.*, 2014). In the present study, after a thorough direct inspection of plants, neither other herbivores of horticultural importance, such as whiteflies or aphids (with the exception of *P. operculella*), nor hyperparasitoids were found.

Regarding the possibility of implementing a conservation biological control of *T. absoluta* in Argentina by preserving insect–plant food webs, current practices of pesticide use should be modified. This would entail reducing the number of applications and/or the use of selective pesticides. In addition, other plant protection techniques under investigation should be encouraged to provide growers with tools for implementing an integrated pest management programme, aiming to minimize pesticide use in horticultural farms.

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