



A re-examination of *Tuta absoluta* parasitoids in South America for optimized biological control

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Abstract

We conducted a review of published information on *Tuta absoluta* parasitoids for the Neotropical region to (1) corroborate species records, (2) analyze associations including the *T. absoluta*, other insect and plant hosts and (3) identify research directions for enhancing their use as biological control agents. The literature review shows more than 50 species or morphospecies of Hymenoptera associated with *T. absoluta*, but less than a half (23) could be confirmed as parasitizing *T. absoluta*. Erroneous reports or invalid names of species, two new species records were found. Over a 100 pests and non-economically important insect and cultivated and non-cultivated plants directly or indirectly interact with *T. absoluta* in the region. Four *T. absoluta* parasitoid species include in their host range predatory insects or act as hyperparasitoids, a negative feature considered for a biological control agent. Five larval parasitoids have a narrow host range and could be considered for classical biological control programs in the areas of new invasion. Six Trichogrammatidae species are commercially used in various countries; of those, *T. minutum* and *T. pretiosum* are considered to be moderately generalist, being able to exploit several insect hosts. Apart from *Apanteles gelechiidivoris* and *Pseudapanteles dignus*, other native species have been the subject of field studies as biological control agents. The review presented here provides useful insights for identifying species that deserve further evaluation as *T. absoluta* biological control agents through augmentative or conservation strategies in South America, as well as for potential classical biological control programs in other continents.

Keywords Taxonomy · Parasitoid ecology · South American tomato pinworm · Host range · Food webs

Key message

- We provide a review of published records on *Tuta absoluta* parasitoids of the Neotropics.
- From more than 50 parasitoid species or morphospecies reported, only 23 hymenopteran species were confirmed as *T. absoluta* natural enemies.
- Other insect hosts, their host plants and the current knowledge on their potential as biological control agents were tracked.
- The low number of available parasitoids and those that have not yet been identified suggest that much work remains for optimizing the existing biological control services provided by *T. absoluta* parasitoids.

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Introduction

Parasitoids, as biological control agents, often exert strong host density reduction leading to suppression of pest densities and their economic damage (Debach and Rosen 1991; Hawikins and Cornell 2000). When compared to other biological control agents (i.e., predators and entomopathogenic organisms), insect parasitoids commonly show greater host search efficiency and host specificity, traits that are considered important in preventing nontarget host attacks. A number of parasitic insects have been imported from their native distribution regions and released in classical biological control programs against introduced invasive pests worldwide (e.g., Daane et al. 2016; Hardwick et al. 2016; Kenis et al. 2017; Tena et al. 2017; Cascone et al. 2018; Thancharoen et al. 2018). Approximately half of the commercially available biological control species belong to this entomophagous group (> 120 species), being mass-reared and released to control pests in horticultural crops (Zappalà et al. 2012; van Lenteren 2012; van Lenteren et al. 2018; Rossi Stacconi et al. 2018).

The Neotropical region is rich in native Hymenoptera species (Hanson and Gauld 1995); however, the magnitude of this diversity, as well as its history, biology and systematics, is poorly described (Fernández and Sharkey 2006). Yet, knowledge has been gained on several aspects of Neotropical parasitoids, and this provides the basis to develop effective biological control programs (several catalogues by De Santis; Parra et al. 2002; Parra and Zucchi 2004).

The South American tomato leaf miner *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is a key pest of tomato, native to this continent (Luna et al. 2015). During the last 12 years, *T. absoluta* was accidentally introduced to the Mediterranean Basin and dispersed throughout African and Eurasian continents (Desneux et al. 2011; Sankarganesh et al. 2017; Sylla et al. 2017; Mansour et al. 2018; Santana et al. 2019). Currently, this pest is threatening the tomato worldwide in many of its invaded regions (Campos et al. 2017; Biondi et al. 2018) and is considered to be a quarantine pest for the Australian (Plant Health Australia 2015) and North American (Bloem and Spaltenstein 2011) continents and for China, where approximately the 30% of the world's tomato production occurs (Xian et al. 2017; Han et al. 2018). The crop damage is caused when the larvae that mine leaves and fruits, reducing tomato production and commercial value. This microlepidopteran species can inflict up to 90% of crop losses when pest control measures fail (Desneux et al. 2011).

In South America, farmers have dealt with this pest for since the 1960s and chemical control is still the most widely employed tool (Guedes and Picanço 2012; Biondi et al. 2018). This can cause negative side effects, such as

pest resistance, environmental contamination and the disruption of natural biological control (Siqueira et al. 2000; Lietti et al. 2005; Desneux et al. 2007; Biondi et al. 2012, 2013a; Passos et al. 2018; Roditakis et al. 2018). Consequently, biological control and other non-chemical pest management techniques have recently gained importance. Attempts to control *T. absoluta* in its native region include the use of selective insecticides, pheromone traps, insect sterile technique and biological control by means of pathogenic and entomophagous species (Bueno et al. 2013; Cagnotti et al. 2012; Consoli et al. 1998; Luna et al. 2015; Silva et al. 2015, 2016; van Lenteren et al. 2016; Soares et al. 2019). In this context, *T. absoluta* biological control using insect parasitoids was considered to be a potential control tool, resulting in scientific and technological research mostly in some South American countries, such as Argentina, Brazil, Chile, Colombia and Peru. Existing literature shows records of species used in classical biological control programs involving importation, mass rearing and releasing of Trichogrammatidae wasps in tomato fields among South American countries (Han et al. 2019). In practice, few native parasitoid species have been targeted for detailed studies, to determine their effectiveness as biological control agents in this region (Desneux et al. 2010; Biondi et al. 2018).

Thus, this review is intended to summarize the existing information on *T. absoluta* parasitoid complex in South America in literature and databases, with the following goals: (1) to corroborate parasitoid species records from original papers and their taxonomic status; (2) to analyze their ecological interactions with *T. absoluta*, other insect hosts and plant hosts; and (3) to identify research directions for promoting their use as biological control agents by means of augmentative, conservative or classical biological control approaches.

Data collection

We generated a list of *T. absoluta* parasitoids searching in Google Scholar using the keywords “*Tuta absoluta*” and its synonyms; all parasitoid specific names reported for *T. absoluta* and their synonyms; and common names in Portuguese and Spanish for *T. absoluta* (e.g., “traça do tomateiro,” “polilla del tomate,” “cogollero del tomate,” etc.). We selected information published in primary literature sources, non-peer reviewed papers (technical reports, etc.), as well as review papers that summarized the *T. absoluta* natural enemies complex in the Neotropical region (e.g., Desneux et al. 2010; Biondi et al. 2018). The online Taxapad (Yu et al. 2012) and Universal Chalcidoidea Database (Noyes 2018) databases as well as specific papers and catalogs were accessed to confirm the species-level status and to search for

other relevant taxonomic and ecological information. Only records at the specific level were considered. Morphospecies defined at family or genus levels were excluded because of the difficulty of tracking their hosts (insects or plants), as well as other biological or ecological traits of importance for pest control. Both native and introduced parasitoid species to South America were taken into account. In few cases, we discarded from the analysis those uncertain species records that lacked solid supporting bibliography confirming their association with *T. absoluta*. Species-specific categories on their insect and plant host specificity levels as well as their potential economic importance were generated.

Results

Twenty-three of ≈ 50 hymenopteran species or morphospecies cited in the literature were confirmed as attacking *T. absoluta* (Table 1). Another 24 morphospecies recorded only at the genus level were excluded; these were: *Archytas* sp., *Elfia* sp. and a not specified fly (Diptera Tachinidae); *Conura* sp. and *Invreia* sp. (Hymenoptera: Chalcididae); *Arrhenophagus* sp. and *Copidosoma* sp. (Hymenoptera: Encyrtidae); *Chrysonotomyia* sp., *Horimenus* sp., *Elasmus* sp., *Sympiesis* sp., *Tetrastichus* sp. and *Zagrammosoma* sp. (Hymenoptera: Eulophidae); *Anastatus* sp. (Hymenoptera: Eupelmidae); *Trichogramma* sp. (Hymenoptera: Trichogrammatidae); *Agathis* sp., *Apanteles* sp., *Bracon* sp., *Chelonus* sp., *Earinus* sp. and *Orgilus* sp. (Hymenoptera: Braconidae); and *Diadegma* sp., *Pristomerus* sp. and *Temelucha* sp. (Hymenoptera: Ichneumonidae).

We found multiple citations for *Pseudapanteles dignus* (Muesebeck) and *Apanteles dignus* (Muesebeck), *Dineulophus phthorimaeae* De Santis and *Retisympiesis phthorimaeae* (Blanchard) and *Neochrysocharis formosus* (Westwood), *Neochrysocharis formosa* (Westwood) and *Closterocerus formosus* (Westwood). Such species were synonymized being firstly mentioned the current valid names. In the case of *Apanteles gelechiidivoris* Marsh and *Dolichogenidea gelechiidivoris* (Marsh), although both names are commonly used as synonyms, in a worldwide checklist on Microgasterinae (Hymenoptera: Braconidae) that is about to be published, the valid name will be defined (Fernández-Triana pers. comm.). Associations of *T. absoluta* with *Copidosoma desantisi* Annecke and Mynhardt (Hymenoptera: Encyrtidae) in Chile, and *Trichogramma dendrolimi* Matsumura in Chile and *T. lopezandinense* Sarmiento (Hymenoptera: Trichogrammatidae) in Colombia could not be found neither in the databases nor in the original papers where they were mentioned. *Trichogramma dendrolimi* was introduced in Brazil to control other insect pests than *T. absoluta* (Querino and Zucchi 2003). A similar situation occurred with *Trichogramma telengai* Sorokina that is cited

for Chile; the species is a junior synonym of *T. bezdenkovii* Bezdenko, and it is associated with *Rhyacionia buoliana* (Denis and Schiffmüller) in that country (Noyes 2018). The confirmed *T. absoluta* parasitoid species belong to the guilds of egg endoparasitoid, egg prepupal endoparasitoid, early larval endoparasitoid, larval ectoparasitoid, larval–prepupal endoparasitoid, prepupal–pupal ectoparasitoid and pupal endoparasitoid (Mills 1994). We also found two new records not listed previously (Desneux et al. 2010; Biondi et al. 2018): the pupal endoparasitoid *Conura bruchi* (Blanchard) (Hymenoptera: Chalcididae) (De Santis and Monetti 2008) and the egg endoparasitoid *Trichogrammatoidea brasiliensis* (Ashmead) (Hymenoptera: Trichogrammatidae) (De Santis 1989).

Tuta absoluta parasitoid diversity displayed a wide range of taxa among representing three superfamilies and nine families. Other insect and plant hosts comprise a complex of hundreds of species. Some species are generalists, for example, *N. formosus* with over 100 species of hosts in four different orders (Diptera, Coleoptera, Hymenoptera and Lepidoptera), whereas other species behave as more selective or specialists, being confined to insect hosts belonging to Gelechiidae (< 5 insect host species) and related to solanaceous plants. Examples of such species are: *Copidosoma gelechiae* Haward, *D. phthorimaeae*, *Goniozus nigrifemur* Ashmead, *A. gelechiidivoris*, *Bracon lucileae* Marsh and *P. dignus* (Table 1).

Thirteen species of the parasitoid complex are native to the Neotropics or to the American continent. Five species, mainly Trichogrammatidae, were intentionally introduced from other continents or moved among countries in that region as biological control agents against *T. absoluta* or other lepidopteran hosts (Table 1). Information related to the importation of many of these biological control agents in Latin America is often lacking or published in non-peer-reviewed articles. There are reports that mention *Trichogramma fasciatum* (Perkins), originally from Mexico, that was released in South America to control the sugar cane borer *Diatraea saccharalis* (Fabricius) (Lepidoptera: Pyralidae) (Burrell and McCormick 1962); *T. minutum* Riley was imported from North America to Chile and Peru for *T. absoluta* and *Heliothis zea* (Boddie) biological control (Lepidoptera: Noctuidae) (Klein Koch 1977); *T. pinto* Voegelé, originally from the Holarctic region, that was imported to South America for controlling several lepidopteran pests (Iannaconne and Lamas 2003; Querino and Zucchi 2003) and *Trichogrammatoidea bactrae* Nagaraja introduced from Australia to Argentina and Chile to mainly control the pink bollworm, *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae) (Hutchison et al. 1989; Riquelme Virgala and Botto 2010). The egg prepupal parasitoid *C. gelechiae* was imported from Australia to Peru as a natural enemy of *Phthorimaea operculella* (Zeller) (De Santis 1979). For

Table 1 List of confirmed parasitoid species attacking *Tuta absoluta* (Lepidoptera: Gelechiidae) in South America

<i>Superfamily</i> /family	Species	Mode of parasitism ^a	Other insect hosts ^b	Plant hosts (including tomato) ^c	Countries	Native/imported	Economic significance ^d	References
<i>Chalcidoidea</i>								
Aphelinidae	<i>Encarsia porteri</i> (Mercet)	Egg endoparasitoid	3	3	Argentina, Brazil, Chile, Ecuador, Peru	N	2	Cáceres et al. (2011), Luft et al. (2015) and Noyes (2018)
Chalcididae	<i>Conura bruchi</i> (Blanchard)	Pupal endoparasitoid (also as hyperparasite)	3	No reports	Argentina, Brazil	N?	1	De Santis (1967), Herring and De Santis and Montetti (2008)
Encyrtidae	<i>Copidosoma gelechiae</i> Howard	Egg prepupal	1	3	Peru	I	4	Peck (1963), De Santis (1979), Gordh (1979) and Noyes (2018)
	<i>Copidosoma koehleri</i> Blanchard	Egg prepupal (also as hyperparasite)	3	3	Argentina, Bolivia, Brazil, Chile, Peru, Uruguay, Venezuela	N?	4	Doutt (1948), De Santis (1967, 1979), Herring (1975) and Noyes and Hayat (1994)
Eulophidae	<i>Dineulophus phthorimacae</i> De Santis	Larval ectoparasitoid	1	1	Argentina, Chile, Peru, Uruguay	N	1	Vargas (1970), De Santis (1983, 1989), Botto (1999) and Colomo et al. (2002)
	<i>Neochrysocharis formosus</i> (Westwood)	Larval–prepupal (also as hyperparasite)	3	3	Argentina	I?	4	Noyes (2018)
Pteromalidae	<i>Dibrachys microgastri</i> (Bouché)	Prepupal–pupal ectoparasitoid (also as hyperparasite)	3	3	Chile, Peru	I?	2	De Santis (1983) and Peters and Baur (2011)
Trichogrammatidae	<i>Trichogramma exiguum</i> Pinto & Platner	Egg endoparasitoid	2	2	Chile, Colombia, Peru, Uruguay	N	4	Desneux et al. (2010), Querino and Zucchi (2003) and IDMA—Instituto de Desarrollo y Medio Ambiente Perú (2018)
	<i>Trichogramma fasciatum</i> (Perkins)	Egg endoparasitoid	2	2	Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Peru, Venezuela	I	4	De Santis (1979) and Colomo et al. (2002)
	<i>Trichogramma minutum</i> Riley	Egg endoparasitoid (also as hyperparasite)	3	3	Argentina, Bolivia, Brazil, Chile, Colombia, Guyana, Peru, Uruguay, Venezuela	I	4	Desneux et al. (2010)

Table 1 (continued)

Superfamily/family	Species	Mode of parasitism ^a	Other insect hosts ^b	Plant hosts (including tomato) ^c	Countries	Native/imported	Economic significance ^d	References
<i>Trichogrammatidae</i>	<i>Trichogramma nerudai</i> Pintureau & Gerding	Egg endoparasitoid	2	2	Argentina, Chile	N	4	Cáceres et al. (2011) and Riquelme Virgala and Botto (2010)
	<i>Trichogramma pintoi</i> Voegelé	Egg endoparasitoid	2	3	Argentina, Brazil ^e , Peru	I	4	Desneux et al. (2010)
	<i>Trichogramma pretiosum</i> Riley	Egg endoparasitoid	3	3	Argentina, Brazil, Chile, Colombia, Ecuador, Peru, Uruguay, Venezuela	N	4	Vargas (1970), Miranda et al. (1998), Colomo et al. (2002), Parra and Zucchi (2004), Cáceres et al. (2011), Querino and Zucchi (2011) and Luft et al. (2015)
<i>Chrysoidea</i>	<i>Trichogramma rojasi</i> Nagaraja & Nagarkatti	Egg endoparasitoid	3	2	Argentina, Brazil, Chile, Peru	N	2	Colomo et al. (2002), Cáceres et al. (2011), Ghoneim (2014), Luft et al. (2015) and Botto (1999)
	<i>Trichogrammatoidea bactrae</i> Nagaraja	Egg endoparasitoid	3	2	Argentina	I	4	Riquelme Virgala and Botto (2010) and Cagnotti et al. (2018)
<i>Bethylidae</i>	<i>Trichogrammatoidea brasiliensis</i> (Ashmead)	Egg endoparasitoid	3	3	Brazil, Chile, Colombia, Peru	N	2	De Santis (1989) and Noyes (2018)
	<i>Goniozus nigrifemur</i> Ashmead	Larval ectoparasitoid	1	2	No reports	No reports	No reports	Vargas (1970), Uchoa-Fernandes and de Campos (1993), Miranda et al. (1998) and Ghoneim (2014)
<i>Ichneumonidae</i>	<i>Apanteles</i> (= <i>Dolichogenidea</i>) <i>gelethidivoris</i> Marsh	Larval–prepupal endoparasitoid	1	1	Colombia, Chile, Peru	N	3	Oatman and Platner (1989), Bajonero et al. (2008), Bajonero (2017), Morales et al. (2014) and Yu et al. (2012)

Table 1 (continued)

Superfamily/family	Species	Mode of parasitism ^a	Other insect hosts ^b	Plant hosts (including tomato) ^c	Countries	Native/imported	Economic significance ^d	References
	<i>Bracon lucileae</i> Marsh	Early larval endoparasitoid	1	1	Argentina, Brazil, Colombia	N	1	Oatman and Platner (1989), Uchoa-Fernandes and Campos (1993), Berta and Colomo (2000), Colomo et al. (2002), Cáceres et al. (2011) and Yu et al. (2012)
	<i>Bracon lulensis</i> Berta & Colomo	Early larval endoparasitoid	1	1	Argentina	N	1	Berta and Colomo (2000) and Yu et al. (2012)
	<i>Bracon tutus</i> Berta & Colomo	Early larval endoparasitoid	1	1	Argentina	N	1	Berta and Colomo (2000) and Yu et al. (2012)
	<i>Pseudapanteles</i> (= <i>Apan- teles</i>) <i>dignus</i> (Muesebeck)	Larval–prepupal endoparasitoid	1	1	Argentina, Mexico, Cuba, Puerto Rico, USA (California, Florida) Hawaii	N	3	Botto (1999), Colomo et al. (2002), Cáceres et al. (2011) and Salas Gervasio et al. (2016)
Ichneumonidae	<i>Campoplex haywardi</i> Blanchard	Larval–pupal endoparasitoid	2	2	Argentina, Brazil, Brazil–Uruguay	N	2	Colomo et al. (2002) and Desneux et al. (2010)

Bold is a visual aid to indicate higher level for a given insect host range/plant host range/economic significance category

^aAs defined by Mills (1994)

^bOther insect hosts: 1—<5 spp., all Gelechiidae; 2—Lepidoptera in general; 3—more than one insect orders

^cPlant hosts: 1—one family; 2—> one family, cultivated; 3—several families, cultivated and non-cultivated

^dEconomic significance: 1—only recorded; 2—laboratory studies; 3—field assessment; 4—classical or augmentative biological control agent

^eNot confirmed in Brazil (Zucchi and Querino 2004)

other five species, information on their origin and geographic distribution is confusing or not reliable (Table 1).

Among the reviewed species, ten can be considered of economic importance because they have been used or are currently commercialized as biological control agents of *T. absoluta* and other insect pests (Table 1): *C. gelechia*, *Copidosoma koehleri* Blanchard, *N. formosus*, *Trichogramma exiguum* (Girault), *T. fasciatum*, *T. minutum*, *T. nerudai* Pintureau and Gerding, *T. pintoi*, *T. pretiosum* Riley, *T. bactrae*. Two species, *A. gelechiidivoris* and *P. dignus*, are under field evaluation in South American countries with promising results (Morales et al. 2013; Bajonero 2017; Salas Gervassio 2017; Salas Gervassio et al. in prep.).

A brief review on the current knowledge of the main insect and plant host associations per each of the 23 species registered as *T. absoluta* parasitoids for the Neotropical region is provided below.

Superfamily Chalcidoidea

Family Aphelinidae

Encarsia porteri (Mercet). It is the only *Encarsia* species for which the development of males in lepidopterous eggs has been reported. Among hosts species of *E. porteri*, there are whiteflies (Hemiptera: Aleyrodidae) of the genus *Aleurocanthus*, *Aleurothrixus*, *Trialeurodes vaporariorum* (Westwood). It was reported attacking *T. absoluta* eggs in Argentina (Luft et al. 2015). It also parasitizes other lepidopterans of economic importance such as *Sitotroga cerealella* (Olivier) (Gelechiidae); *Anticarsia gemmatilis* Hubner, *Helicoverpa gelotopoeon* (Dyar), *H. zea*, *Rachiplusia nu* (Guenée) (Noctuidae); *Colias lesbia* Fabricius (Pieridae), *D. saccharalis*, *Ephestia kuehniella* Zeller, *Galleria mellonella* (Linneus) (Pylalidae); *Cydia pomonella* L., *Epinotia aporema* Walsingham (Tortricidae); and *Plutella xylostella* (L.) (Yponomeutidae). Diverse plant hosts associates include important South American cultivated species: *Chamaesyce hirta* L. (Euphorbiaceae), *Glycine max* L., *Medicago sativa* L., *Phaseolus lunatus* L., *Phaseolus vulgaris* L. (Fabaceae), *Gossypium* sp. and *Hibiscus rosa-sinensis* L. (Malvaceae), *Zea mays* L. (Poaceae), and *Solanum lycopersicum* L. and *S. tuberosum* L. (Solanaceae) (Noyes 2018; Yu et al. 2012).

Family Chalcididae

Conura bruchi (Blanchard). It was recorded as a primary endoparasitoid of pupae of three lepidopteran species, *Coleophora haywardi* Pastrana (Coleophoridae), *Psilopygida crispula* (Dognin) (Saturniidae) (De Santis 1967; Herting 1976), *T. absoluta* (Gelechiidae) and also from *Nematus desantisi* Smith (Hymenoptera: Tenthredinidae) (De Santis and Monetti 2008). It has been also recorded as

a hyperparasitoid of *Apanteles crispulae* Blanchard (Hymenoptera: Braconidae) (De Santis 1967). Information on the biology, distribution and other associated species is lacking (Blanchard 1943).

Family Encyrtidae

Copidosoma gelechia Howard. This species was imported from Australia to Peru in 1949 as a biological control agent against *Phthorimaea operculella* (Zeller), but releases were not continued. There exists only one record for South America as an endoparasitoid of *T. absoluta* in Peru (De Santis 1979). Other lepidopteran host species are the gelechiids *Gnorimoschema gallaeasteriella* (Kellicott), *G. gallaesolidaginis* (Riley) and *G. salinaris* Busck and the tortricid *Epi-blema scudderiana* (Clemens) (Gordh 1979; Peck 1963). As plant associates, *C. gelechia* was found, apart from solanaceous species, in *Solidago canadensis* L. (Asteraceae) (Rothman and Darling 1990).

Copidosoma koehleri Blanchard. Its distribution covers Argentina (Blanchard 1940), Bolivia (Noyes and Hayat 1994), Brasil (Herting 1975), Chile (Herting 1975; Douth 1948), Venezuela (Ferrer 2001; Noyes 2018), Peru and Uruguay (De Santis 1979; Herting 1975). The species was found parasitizing different species of Gelechiidae (Lepidoptera), such as *T. absoluta* (De Santis 1979), *P. operculella* (De Santis 1979; Ferrer 2001) and *Symmetrischema tangolias* (Gyen); and the Tortricidae *Grapholita molesta* (Busck) (De Santis 1967; Guerrieri and Noyes 2005). Laboratory studies of interspecific competition with the two parasitoids *Apanteles subandinus* Blanchard and *Chelonus blackburni* Cameron (Hymenoptera: Braconidae) showed inconclusive results on *C. koehleri* ability to outcompete other *P. operculella* biological control agents (Whiteside 1981; Ballal et al. 1989). Moreover, it was proved that it is a hyperparasitoid of *Diglyphus isaea* Walker (Hymenoptera: Eulophidae) (Ozawa et al. 2002). As plant hosts, *C. koehleri* can be found in: *Schinus molle* L. (Anacardiaceae), *Borago officinalis* L. (Boraginaceae), *Azadirachta indica* A. Juss. (Meliaceae), *Fagopyrum esculentum* Moench. (Polygonaceae), *Capsicum annuum* L., *S. lycopersicum*, *Nicotiana* sp., *Solanum chacoense* Bitter., *Solanum pinnatisectum* Dunal., *Solanum polytrichon* Rydb., *S. tuberosum* (Solanaceae), *Lantana camara* L. (Verbenaceae). *Copidosoma koehleri* was introduced and released in California in 1964 to control *P. operculella* but apparently, it failed to establish (Noyes 1988).

Family Eulophidae

Dineulophus phthorimaeae De Santis. It was De Santis 1983) and Peru (De Santis and Fidalgo 1994) as an ectoparasitoid of *Gnorimoschema operculella* and *T. absoluta* (Lepidoptera: Gelechiidae) (De Santis 1983, 1989; De Santis and

Monetti 2008) infesting *S. lycopersicum* and *S. tuberosum* (Berta de Fernandez and Colomo de Correa 1991; De Santis 1983). The species description was carried out by De Santis in 1983, using material labeled by Blanchard as *Rhetisymphisis phthorimaeae*, collected by Lopez Mansilla in 1939. *R. phthorimaeae* is not considered a valid name because Blanchard never described the species beyond having named it. Laboratory and field research done on this ectoparasitoid species by Savino et al. (2012, 2016) showed that it has an extremely sinovigenic reproductive strategy and it practices non-reproductive host feeding, a parasitoid mechanism that causes a significant host mortality. When competing with the larval endoparasitoid *P. dignus*, younger *D. phthorimaeae* females avoided multiparasitism, but older females did not discriminate heterospecific parasitized larvae. This eulophid is a potentially effective biological control agent for *T. absoluta*, and it could be used through augmentative as well as conservative biological control strategies in IPM programs. Furthermore, when acting together with *P. dignus* in tomato crops, they can exert an important control of this pest (up to 80% of host larvae mortality).

Neochrysocharis formosus (Westwood). Formerly named as *Closterocerus formosus* and often wrongly cited as *N. formosa*, it was reported for Argentina and Mexico (Luna et al. 2011; Hansson 1997). It is a polyphagous species known to attack a wide variety of leaf miners and gall-forming insects. As stated above, it has been recorded as a primary parasitoid from over 100 species of hosts in five different orders of insects, and also as a hyperparasitoid of *D. isaea*. It is present in cultivated and non-cultivated plant species, and in total, it has been recorded from more than 60 different plant species in 26 families: Apiaceae, Aquifoliaceae, Asclepiadaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Cucurbitaceae, Cupressaceae, Euphorbiaceae, Fabaceae, Fagaceae, Liliaceae, Oleaceae, Pinaceae, Poaceae, Portulacaceae, Ranunculaceae, Resedaceae, Rosaceae, Rubiaceae, Rutaceae, Salicaceae, Solanaceae, Tamaricaceae, Urticaceae (Thompson 1955; Noyes 2018; Luna et al. 2011). Recently, it was found parasitizing *T. absoluta* in Europe (Zappalà et al. 2012; Biondi et al. 2013b).

Family Pteromalidae

Dibrachys microgastri (Bouché). It is a cosmopolitan species (De Santis 1983; Peters and Baur 2011) listed for 57 countries (Noyes 2018). As a primary parasite or hyperparasite, this species is associated mainly with insects belonging to eight insect orders: Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera (including hyperparasites), Lepidoptera, Neuroptera and Stepsiptera, and also with spiders (Peters and Baur 2011; Dzhankmen 2017). It was recorded as parasitizing the prepupal and pupal stages of *T. absoluta* in Chile and Peru (De Santis 1983). In Argentina, it was

found hyperparasitizing *Mastrus ridens* Horstmann (Braconidae) and *Ascogaster quadridentata* Wesmæel (Ichneumonidae) (D'Hervé and Aquino 2016).

Family Trichogrammatidae

Trichogramma exiguum Pinto and Platner. It is a Neotropical species, mass-reared and released in Colombia and Peru (Noyes 2018; Desneux et al. 2010; IDMA—Instituto de Desarrollo y Medio Ambiente Perú 2018). Its primary hosts are eggs of the following lepidopteran species: *Erinnyis ello* (L.) (Sphingidae), *Alabama argillacea* (Meyrick), *H. zea*, *Heliothis virescens* (Fabricius) and *Sacadodes pyralis* Dyar (Noctuidae), *Dione junio junio* (Cramer) (Nymphalidae), *D. saccharalis*, *Neoleucinodes elegantalis* (Guenée) and *Palpita persimilis* Walker (Crambidae), *Dichomeris* sp. and *S. cerealella*, *T. absoluta* (Gelechiidae), *Pococera atramentalis* Lederer (Pyralidae), *Argyrotaenia sphaleropa* (Meyrick) and *Bonagota cranaodes* (Meyrick) (Tortricidae). Host plants are important crops for South America: cassava, several *Citrus* sp., cotton, sugarcane, corn, sorghum, passion fruit and olive orchards (Querino and Zucchi 2003).

Trichogramma fasciatum (Perkins). Although it was introduced for biological control of insect pest species on crops other than tomatoes, it was found naturally parasitizing *T. absoluta* eggs. Other insect hosts comprise the lepidopteran species *E. ello*, *Oxydia trychiata* Guenée (Geometridae), *Acleris gloveranus* (Walsingham), *Corcyra cephalonica* (Stainton), *C. pomonella*, several *Diatraea* sp., *Maruca vitrata* (Fabricius), *Mescinia peruella* Schaus, *Procerata sacchariphaga* (Bojer), *Sitotroga* sp., and the noctuids *A. argillacea*, *Euproctis chrysorrhoea* (L.) (Noctuidae), several species of *Helicoverpa* and *Heliothis*, *Lymantria monacha* (L.), *Mamestra brassicae* (L.), *S. pyralis* and *Spodoptera frugiperda* (Smith) (De Santis 1979; Colomo et al. 2002; Noyes 2018). Associated plant hosts are cultivated species, as *Brassica oleracea* L., *Cedrela odorata* L. and *C. tonduzii* C.DC, cotton, sugarcane and corn (Yu et al. 2012).

Trichogramma minutum Riley. It is an extremely generalist species. It is widely commercialized as a biological control agent and introduced in South America. Insect host range includes pest species belonging to Hemiptera, as *Aleyrodes* sp., seven species of Coleoptera Chrysomeloidea and several Tenebrionoidea. Over 50 host species of Macrolepidoptera and more than 70 species of Microlepidoptera are reported. Dipteran hosts include Brachycera and Cyclorhapha species, Hymenoptera Symphyta and parasitic wasps, as other Trichogrammatidae and Braconidae. It is important to mention that *T. minutum* wasps can attack eggs of other beneficial entomophagous species, such as predatory species of orders Neuroptera and Coleoptera, the coccinellid ladybird *Coleomegilla maculata* (DeGeer), as well as parasitic wasps of Hymenoptera Braconidae and *Trichogramma japonicum*

Ashmead. Plant host associates are diverse, crop and non-crop species. The list comprises *Abies* sp., *Picea* sp. and *Pinus* sp., oak, birch and poplar trees; horticultural crops as beet, lettuce, cabbage, pumpkin, peas and beans; passion fruit, citrus, plum and apple orchards; extensive crops as soybean, cassava, cotton, rice, sugarcane, sorghum, trefoil, corn; and uncultivated species, as *Asclepias* sp., *Cyperus* sp., *Datura* sp., several Malvaceae and *Nicotiana* sp. (De Santis 1979; Noyes 2018; Yu et al. 2012).

Trichogramma nerudai Pintureau and Gerding. Native to Chile, it was introduced and released to Argentina (Querino and Zucchi 2003; Riquelme Virgala and Botto 2010) and associated with two species of Lepidoptera: *S. cerealella*, *T. absoluta* (Gelechiidae), *H. zea* (Noctuidae), *E. kuehniella* (Pyralidae), *C. pomonella*, *R. buoliana* (Tortricidae), *P. xylostella* (Yponomeutidae). Plants associated: *Pinus radiata* D. Don, *P. contorta* Douglas, *P. ponderosa* Douglas, *P. taeda* L. (Pinaceae); *Z. mays* (Poaceae), *Malus domestica* Borkh (Rosaceae), *S. lycopersicum* (Solanaceae), *Brassica oleracea* L. (Brassicaceae) (Pintureau et al. 1999; Querino and Zucchi 2003; Noyes 2018).

Trichogramma pinto Voegelé. It was introduced and massively reared as a biological control agent in Argentina and Peru for controlling *H. zea*, and the tortricids *Cydia leguminis* (Heinrich) and *C. pomonella* (Pinto 1999). Its spontaneous occurrence in Brazil could not be confirmed, and Querino and Zucchi (2004) speculate that it is probably a new species in this country. It has a wide host range among lepidopterans, comprising the species *Antheraea pernyi* Guerin-Meneville and *Samia cynthia* (Drury) (Saturniidae), *C. cephalonica* (Pyralidae), *Cydia nigricana* (Fabricius) (Tortricidae), *E. kuehniella*, *Lycaeides melissa* (Edwards) and *Plebejus acmon* (Westwood and Hewitson), (Lycaenidae), *Ostrinia nubilalis* (Hubner) (Crambidae), *Platyptilia carduidactyla* (Riley) (Pterophoridae), *P. xylostella*, *S. cerealella* and *Vanessa* sp. (Nymphalidae). Among noctuid hosts, there are *Agrotis segetum* (Denis and Schiffermuller), *H. armigera*, *Leucoma salicis* (L.), *M. brassicae* and *Ochropleura fennica* (Tauscher). As host plants, *T. pinto* can be found in cultivated as cotton and *Salix* trees, and in uncultivated species or weeds, like *Baccharis*, *Chrysothamnus*, the black thistle, the wild buckwheat, the American licorice and *Malva* sp. (Noyes 2018).

Trichogramma pretiosum Riley. Mass-reared and released in Brazil, Chile, Colombia, Ecuador and Peru. It is a Neotropical species associated principally with: Curculionidae (Coleoptera); Anthocoridae and Lygaeidae (Hemiptera); Arctiidae, Blastobasidae, Danaidae, Gelechiidae, Geometridae, Hesperidae, Lycaenidae, Lymantriidae, Noctuidae, Notodontidae, Nymphalidae, Oecophoridae, Papilionidae, Pieridae, Pyralidae, Sphingidae, Syntomidae, Tortricidae, Yponomeutidae (Lepidoptera); and Chrysopidae (Neuroptera) (Noyes 2018; Querino and Zucchi 2011).

Trichogramma rojasi Nagaraja and Nagarkatti. It is distributed in Argentina, Brazil, Chile, Cuba and Peru (Noyes 2018). Host species include Lepidoptera, Gelechiidae: *Anarsia gemmatalis*, *T. absoluta*; Hesperidae: *Prenes ares* Felder; Noctuidae: *A. gemmatalis*, *Mocis latipes* Guenée, *Pseudaletia sequax* Franclemont, *R. nu*, *S. frugiperda*; Pieridae: *C. lesbia*, *Tatochila* sp.; and Pyralidae: *C. cephalonica*. Host plants are all cultivated and belong to the following families: Fabaceae: *G. max*, *M. sativa*, *P. vulgaris*, *Trifolium* sp and Poaceae: *Panicum maximum* Jacq, *Z. mays* (Nagaraja and Nagarkatti 1973; Zucchi and Monteiro 1997; Querino and Zucchi 2003; Noyes 2018).

Trichogrammatoidea bactrae Nagaraja. It is an exotic parasitoid introduced in Argentina in the 1990s, to be evaluated as biological control agent of *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae) in cotton and later of *T. absoluta* in tomato. Preliminary laboratory studies showed that this parasitoid is more efficient than *T. pretiosum* and *T. rojasi*, two local species, in parasitizing *T. absoluta* eggs (Botto 1999; Riquelme Virgala and Botto 2010). Inundative releasing experiments were done by Cagnotti et al. (2018). They evaluated dispersion and persistence of the wasp in tomato greenhouses with the aim of adjusting *T. bactrae* releasing points and pest control. It is associated with Anthomyiidae, Sciomyzidae (Diptera); Blastobasidae, Gelechiidae, Hesperidae, Oecophoridae, Pieridae, Pyralidae, Sphingidae, Tortricidae and Yponomeutidae (Lepidoptera). Host plants registered are members of the Araceae, Brassicaceae, Cyperaceae, Fabaceae, Malvaceae, Poaceae, Proteaceae and Solanaceae families (Noyes 2018).

Trichogrammatoidea brasiliensis (Ashmead). It is distributed in Brazil, Chile, Colombia and Peru (De Santis 1989; Noyes 2018). Among the insect host species, there are *T. absoluta*, *P. operculella*, *R. nu*, *E. aporema*, *S. cerealella*, *H. zea* (Lepidoptera) and *Kerria lacca* Kerr (Hemiptera). Diverse plant hosts associates include families Asteraceae, Fabaceae, Malvaceae, Meliaceae, Poaceae and Solanaceae (Noyes 2018).

Superfamily Chrysoidea

Family Bethyloidea

Goniozus nigrifemur Ashmead. Besides *T. absoluta*, other host species include the pink bollworm *P. gossypiella*. However, further information on its biology, distribution and other associated species is still lacking. Few quantitative data are available on the biology and behavior of this species. It is a gregarious arrhenotokous ectoparasitoid, it prefers the third and fourth host larval stage and the pupa is protected by a silken cocoon (Vargas 1970; Luft 1993, 1996; Uchoa-Fernandes and de Campos 1993; Miranda et al. 1998). Brewer and Varas (1971) evaluated a massive-rearing

protocol and releases of this parasitoid in Córdoba (Argentina) to control *P. gossypiella* and *R. buoliana*.

Superfamily Ichneumonoidea

Family Braconidae

Apanteles gelechiidivoris Marsh. Native to South America, namely Chile, Colombia and Peru, this species was introduced in California (Yu et al. 2012). As primary hosts, there are mentioned three gelechiid species: *T. absoluta* (Bajonero et al. 2008), *P. operculella* (Morales et al. 2014) and *Keiferia lycopersicella* (Walsingham) (Yu et al. 2012) infesting *S. lycopersicum* or *S. tuberosum* (Solanaceae) (Oatman and Platner 1989). It is considered the most important parasitoid for natural and augmentative biological control in Colombian tomato crops (García Roa 1989; Bajonero 2017).

Bracon lucilae Marsh. It is a Neotropical species. Insect primary hosts are larvae of the following lepidopteran species (Gelechiidae): *T. absoluta* (Uchoa-Fernandes and de Campos 1993; Colomo et al. 2002), *P. operculella* (Yu et al. 2012) and *Scrobipalpula isochlora* Meyrick (Oatman and Platner 1989). Associated plant hosts are solanaceous cultivated and non-cultivated species, such as *S. lycopersicum*, *S. tuberosum* and *S. saponaceum* Dunal (Oatman and Platner 1989).

Bracon lulensis Berta and Colomo and *Bracon tutus* Berta and Colomo. Both species were described as larval parasitoids of *T. absoluta* in northern Argentinian tomato crops (Berta and Colomo 2000). However, further information on the biology, distribution and other associated species is lacking.

Pseudapanteles dignus (Muesebeck). It is distributed in the New World, originally described by Muesebeck in 1938 as *Apanteles dignus*, and revised by Mason in 1981 (Yu et al. 2012; Fernández-Triana et al. 2014). It was imported to Hawaii for the biological control of *K. lycopersicella*, from 1975 to 1982, but no further information is available about its establishment (Nakao and Funasaki 1979; Nakao et al. 1981; Lai and Funasaki 1985). Other host records include the gelechiids *P. operculella*, *Tildenia gudmannella* Walsingham and *Symmetrischema capsica* (Bradley and Povolný) (Cardona and Oatman 1971; Fernández-Triana et al. 2014). The associated plants include members of the Solanaceae family, such as *S. lycopersicum*, *S. tuberosum*, *Capsicum annum* L., *Solanum sisymbriifolium* Lam., *S. americanum* Mill., *Nicotiana glauca* Graham (Cáceres et al. 2011; Salas Gervassio et al. 2016). Currently, experimental releases of this parasitoid to evaluating its efficiency as a biological control of *T. absoluta* in tomato greenhouse in Argentina are being carried out (Salas Gervassio 2017, Salas Gervassio et al. ms in prep.).

Family Ichneumonidae

Campoplex haywardi Blanchard. It is a Neotropical species. Other insect hosts known apart from *T. absoluta* are *P. operculella* (Gelechiidae) in *S. tuberosum* (potato) (Yu et al. 2012) and *Ithome* sp. (Lepidoptera: Walshiidae) in legume trees (Colomo et al. 2002). It has been imported in California to control *P. operculella* but apparently, it did not establish (Nechols et al. 1995).

Discussion

Regarding our first objective to corroborate the parasitoid species records from original papers and their taxonomic status, it is clear from this review that more than a half of the complex of *T. absoluta* parasitoids reported for South America, including Tachinids, needs further examination to confirm their species-level identifications, insect and plant resources used and more importantly, their impact on *T. absoluta* population. For instance, 24 of the records fell into the category of morphospecies, at genus level, from which little biological information can be collected. We also report two duplicated records, one erroneous record and four junior synonyms.

In relation to their ecological interactions with *T. absoluta*, other insect hosts and plant hosts, ca. eight species of the *T. absoluta* parasitoid complex showed to have a quite narrow insect or plant host ranges reported. However, the lack of records on other insect hosts may be due to a poor knowledge of their distribution or biological features rather than its absence (Luna et al. 2011). Nevertheless, the diversity and the abundance of guilds of native parasitoids species associated with *T. absoluta* show that many of them are able to coexist thanks to a complex food web that also include alternative insect hosts, as well as the vegetation supporting those herbivores (Mills 1994).

When comparing the South American parasitoid complex of *T. absoluta* in its native and invaded ranges of distribution, a strong pattern of adaptation to the new host can be observed, with 53 species forming new associations in about 12 years from the invasion start (Desneux et al. 2010; Zapalà et al. 2013; Biondi et al. 2018). It is interesting that only one cosmopolitan parasitoid species, *N. formosus*, was found in association with *T. absoluta* in both native and recently invaded areas. Since many of them have been registered at genus level, probably a similar study should be done to confirm the interactions among the species records with *T. absoluta* in invaded areas.

The interest for developing *T. absoluta* biological control programs in South American countries led to the indiscriminate introduction of several generalist parasitoid species that did not coevolved with *T. absoluta*. Classical and

neoclassical biological control agents can have undesirable effects on nontarget hosts, being either other phytophagous or beneficial arthropods (Simberloff and Stiling 1996; Louda et al. 2003). This, for example, was the case for the generalist egg parasitoid *T. minutum*, imported from North America into Argentina, Bolivia, Brazil, Chile, Colombia, Guyana, Peru, Uruguay and Venezuela (Querino and Zucchi 2003; IDMA—Instituto de Desarrollo y Medio Ambiente Perú 2018). The species parasitizes eggs of predatory species of chrysopids and coccinelids, and it can act as a hyperparasitoid of braconids and other trichogrammatids (Yu et al. 2012). The introduction of this natural enemy in South America is a clear example of the need to conduct rigorous pre-importation studies when a classical biological control program is implemented. Multi-host field samplings in the native area (Daane et al. 2016), host range laboratory testing (Desneux et al. 2012; Girod et al. 2018), a careful analysis of the published literature data (van Lenteren and Manzaroli 1999; Charles 2012), as well as the correct taxonomic identification (Desneux et al. 2009; Beltrà et al. 2015; Guerrieri et al. 2016), are recommended in order to better assess the specificity of natural enemies as candidates for classical biological control programs of any invasive insect pest, in a perspective of specific risk–benefit analysis (Heimpel and Cock 2018). In particular, here we identified one eulophid (*D. phthorimaea*) and five braconid species (*A. gelechidiivoris*, *B. lucilae*, *B. lulensis*, *B. tutus* and *P. dignus*) with higher specificity (double category 1 in Table 1) that deserve greater attention for potential classical biological control programs of *T. absoluta* in the recently invaded areas, where the pest is causing considerable economic and environmental damage (Campos et al. 2017; Biondi et al. 2018). The species *C. bruchi*, *C. koehleri*, *D. microgastri* and *N. formosus* should be dismissed as biological control agents since they can act as hyperparasitoids (Yu et al. 2012; Noyes 2018).

Augmentative biological control for *T. absoluta* is commercially available in South America through the sale of the parasitoids *T. pretiosum* (in Brazil, Chile, Colombia, Ecuador and Peru), *T. nerudai* in Chile and *T. bactrae* in Chile and Peru. Besides, two other *Trichogramma* species, *T. exiguum* and *T. pintoi*, are mass-reared and commercialized by local companies in South America for controlling other lepidopteran pests). Finally, three further *Trichogramma* species (*T. galloi* Zucchi in Brazil, *T. cacoeciae* Marchal and *T. fuentesi* Torre in Peru) are marketed, but there are no records on their associations with *T. absoluta* (Noyes 2018; Yu et al. 2012). Therefore, a careful host and host-plant suitability assessment (Chailleux et al. 2012; 2013; Cascone et al. 2015; Thiery and Desneux 2018) is needed before potential inclusion of these *Trichogramma* species in biological or integrated *T. absoluta* control programmes.

Conservation biological control, often described as the field of biological control with the greatest potential for use in developing world agriculture (Wyckhuys et al. 2013), has received practically no attention in South America. As demonstrated in Salas Gervassio et al. (2016), *T. absoluta* trophic web, including interactions with dozens of parasitoid species, along with an unknown number of other entomophagous arthropods, inhabiting cultivated and wild solanaceous plants should be protected to help maintaining *T. absoluta* populations at low levels in horticultural farms. Much more efforts are thus needed in order to understand how functional biodiversity, at the landscape and farm levels, and to contribute increasing the ecological services provided by *T. absoluta* parasitoids (Holzschuh et al. 2010; Zappalà et al. 2012). This is particularly important for *T. absoluta* Neotropical parasitoids because we found over a hundred of alternative host insects, infesting cultivated and non-cultivated plants, that indirectly (via apparent competition) interact with *T. absoluta* in the region.

The results of this paper are intended to identify research directions for promoting the use of native biological control agents by means of augmentative or conservation tactics in the region. Overall, we conclude that the bibliography contains many unreliable *T. absoluta* parasitoid records. However, we identified several native parasitoid species, with a quite narrow insect host range (categories 1 or 2 in Table 1) from the complex of *T. absoluta* in South America, deserve more attention to be used in (1) conservative and augmentative biological control strategies in South America, and some of them (2) for being considered potential classical biological control programs in the newly invaded areas.

Author contribution statement

All authors conceived the research and performed the bibliographic research. NGSG, DA and MGL wrote the first manuscript draft. All authors interpreted the data and revised the first manuscript draft.

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Compliance with ethical standards

Conflict of interest The authors have declared that no conflict of interest exists.

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