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Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/1694158 since 2019-06-27T11:21:42Z

Published version:

DOI:10.1080/09583157.2019.1572711

Chiara Ferracini, Vanda H. P. Bueno, Maria Luisa Dindo, Barbara L. Ingegno, María G. Luna, Nadia G. Salas Gervassio, Norma E. Sánchez, Gaetano Siscaro, Joop C. van Lenteren, Lucia Zappalà & Luciana Tavella (2019): Natural enemies of Tuta⍰absoluta in the Mediterranean basin, Europe and South America, Biocontrol Science and Technology, pp. 1-31, doi 10.1080/09583157.2019.1572711]

Natural enemies of *Tuta absoluta* in the Mediterranean basin, Europe and South America

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Abstract

The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) represents a global threat to commercial tomato (*Solanum lycopersicum* L.) production, both in open field and greenhouse. Native to South America, it spread over the Mediterranean Basin, Europe, Africa and part of Asia in only 12 years, and currently it is reported in over 80 countries. Biological control is one of the options for its control and a large number of natural enemies has been reported in association with the pest, both in the areas of origin and of introduction. The egg parasitoid *T. pretiosum*, in South America, and the mirid predators *M. pygmaeus* and *N. tenuis*, in Europe and the Mediterranean basin, are used as commercial biocontrol agents. Even if several natural enemies might be promising candidates for biocontrol, their potential role in quantitative pest reduction has been seldom established under practical tomato production conditions.

Since climatic suitability indices predict a high probability for continued invasion by *T. absoluta*, mainly China and the USA, there is an urgent need for new control options. In order to minimize the use of broad spectrum insecticides, biocontrol techniques should be considered. As tomato is produced seasonally, augmentative biocontrol seems to be the most effective control option, but pest reduction might be optimized by adding conservation biocontrol, and by combining biocontrol within IPM programs.

Here, an overview of predators and parasitoids of *T. absoluta* in South American and Euro-Mediterranean regions, and their biological control efficacy under laboratory, semi-field and field conditions is provided.

Keywords: tomato leafminer, augmentative biological control, conservation biological control, natural enemy, invasive pest

1. *Tuta absoluta*: biology and control measures

The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) was originally described as *Phthorimaea absoluta* by Meyrick (1917) from a male specimen collected in the Andean region of Perú (http://www.cabi.org/isc/datasheet/49260, August 11, 2018). During the 1960s it spread over South America and is now a major pest of tomato, *Solanum lycopersicum* L., on this continent (Bahamondes & Mallea, 1969; Silva, Bueno, Caldeira Lins, & van Lenteren, 2015). In Europe, *T. absoluta* was first detected in eastern Spain in 2006 (Urbaneja, Vercher, Navarro, Garcıa Marí, & Porcuna, 2007), and is now quickly spreading all over the world, as it was recently summarized (Biondi, Guedes, Wan, & Desneux, 2018). An overview of the biology of this pest can be found in Tropea Garzia, Siscaro, Biondi, & Zappalà (2012). Damage is caused by larval feeding on tomato fruits, leaves, stems, buds and flowers (Gabarra et al., 2014). Since young larvae bore into plant parts (either leaves, stems or fruits), chemical control is complicated and frequent applications are needed. Without appropriate control measures crop losses up to 100% may occur (Biondi et al., 2018).

Besides tomato, the pest is able to develop on a number of other cultivated and wild Solanaceae plants (Caparrós Megido, Brostaux, Haubruge, & Verheggen, 2013a; Salas Gervassio, Pérez-Hedo, Luna, & Urbaneja, 2016a), and plants belonging to various other families (Amaranthaceae, Asteraceae, Poaceae and Fabaceae) (Bayram et al., 2015; Ingegno, Candian, Psomadelis, Bodino, & Tavella, 2017a), favouring its persistence year-round in agroecosystems and bordering natural vegetation.

Several control options are available to reduce *T. absoluta* numbers, which can be used as a stand-alone method or within Integrated Pest Management (IPM) programs (Biondi et al., 2018). However, in many countries, frequent chemical control is still widely used. Up to five sprays per week and 36 sprays per tomato production cycle (Guedes & Picanço, 2012) may still result in economic damage. Indeed, these frequent applications result in quick development of resistance to pesticides and negative effects on the environment and human health. Therefore, it is important to identify effective non-chemical, environmentally safer strategies to control the tomato leafminer, and biological control may offer such a solution. To date, data on current use of biological control of *T. absoluta* are mostly scattered and have not been comparatively discussed within the different invaded areas. This motivated us to review the literature on arthropod natural enemies and their biological control efficacy in South American and Euro-Mediterranean regions. Herein, we provide an overview of the best biocontrol options currently available, as well as future research needs to identify and apply new natural enemies.

2. Biological control agents of *Tuta absoluta*

Summaries of the current South American and Euro-Mediterranean knowledge about arthropod natural enemies of *T. absoluta* are reported alphabetically by order and family for predators (Table 1) and for parasitoids (Table 2). For predators, numerous publications report clear evidence of predation, but many others only mention the presence of natural enemies sharing the same environment as the pest, without specific data about their prey activity. Therefore we report only on those species that have been recorded in association with *T. absoluta*, or they have been tested in laboratory, semi-field, and/or field assays with *T. absoluta* as prey.

2.1. South America

2.1.1. Predators

More than 50 species of predators have been mentioned in association with *T. absoluta* in South America (e.g. Miranda, Picanço, Zanuncio, Bacci, & Marques da Silva, 2005, Biondi et al., 2018; Table 1). Some of these predators may cause high pest mortality (Miranda, Picanço, Leite, Zanuncio, & De Clercq, 1998), but their role in pest reduction has not been studied quantitatively. Many papers state the potential for use of these predators based on laboratory studies or experimental field studies, but they were seldomly followed by applied research (van Lenteren & Bueno, 2003).

Most of the predators mentioned by Bergmann et al. (1984), Bergmann, Imenes, Campos, Hojo, & Takematsu (1988), Miranda et al. (2005), and Probst, Pülschen, Sauerborn, & Zebitz (1999) are polyphagous and might attack *T. absoluta*. Some of these species are commercially used for augmentative control of other pests (van Lenteren, 2012; van Lenteren, Bolckmans, Kohl, Ravensberg, Urbaneja, 2018a). However, the large number of potential natural enemies listed for *T. absoluta* control in South America creates a problem for researchers: where to start and how to efficiently select better or the best species?

General evaluation criteria, such as climate adaptation, specificity, killing capacity, non-target impacts, ability to establish a population in the target crop, and feasibility of mass rearing, can be used to rapidly decide, in the evaluation process, which species of native predators seem inefficient for control of the pest (van Lenteren, 1980). However, information to evaluate most of the predators listed in Table 1 is still lacking. By using the above mentioned evaluation criteria, it is possible to conclude that several groups of predators – e.g. Araneae, Dermaptera, Formicidae, Sphecidae, and Vespidae – cannot be used in augmentative biological control programs, as their mass production is too difficult.

Other species show negative impacts, such as the acarid *Pyemotes* sp., which can kill high numbers of *T. absoluta*, but can also cause serious negative effects to humans (allergies, dermatitis). Also, species which are zoophytophagous (e.g. Miridae family) might cause much plant and fruit damage making their use in biological control programs either complicated or impossible (Arnó, Castañé, Riudavets, & Gabarra, 2010; Bueno & van Lenteren, 2012).

In the specific case of *T. absoluta* control, some additional criteria may help speeding up the evaluation process and identifying effective predators. Answers to questions like (1) can the predator easily walk on the tomato plant, or is it trapped in the glandular hairs, (2) can it reproduce and maintain a population on tomato, (3) does it also prey on the other pests occurring on tomato, and (4) does it cause damage to the tomato plants or fruits, all of which can assist in descarding non-relevant predators quickly. Several of the South American predator species mentioned in Table

1 are unable to walk on tomato because they get trapped in the glandular hairs, as the *Orius* species (Bueno et al., 2013), thus making them unsuitable for *T. absoluta* control. Other Anthocoridae species have been observed preying on *T. absoluta* (Table 1), but it seems relevant to first determine if they can survive and establish populations on tomato plants before embarking on further studies. Information about the pest kill capacity of South American predators is often qualitative. Data about lifetime predation by nymphal and adult stages of predators or, alternatively, about prey population reduction in greenhouse/field experiments are only available for a few species (van Lenteren et al. 2017; van Lenteren, Bueno, Calvo, Calixto, & Montes, 2018b).

In conclusion, (a) studies on predators of *T. absoluta* in South America are far from being complete, (b) one group of potential predators of *T. absoluta*, i.e. the South American Coleoptera (Table 1), appears to be understudied and deserves more attention, (c) many studies are restricted to the laboratory, (d) only a few of the complex of South American predators might kill enough prey and be suitable candidates for augmentative biocontrol programs, (e) based on current knowledge, Miridae seems to be the most promising family of natural enemies to be tested for control of *T. absoluta*, and (f) there is hardly any regional cooperation, while the pest problem is very serious and would merit better coordinated research.

2.1.2. Parasitoids

Parasitoid ecology predicts that host exposure plays a key role in the species richness of its parasitoids (Hawkins, 1994). Accordingly, exposed *T. absoluta* larval stages and eggs are attacked by a large number of parasitoid species, both in its region of origin and in newly invaded areas (Table 2). Parasitoid species attacking other *T. absoluta* developmental stages are less common but, in sum, they represent seven parasitoid guilds, as defined by Mills (1992): egg parasitoids, early larval endoparasitoids, late larval endoparasitoids, larval ectoparasitoids, egg-larval parasitoids, larval-pupal parasitoid, and pupal parasitoids.

A number of reviews exhaustively summarizes the main natural enemy species of *T. absoluta* in South America (Biondi et al., 2018; Luna et al., 2012, 2015). Research aimed at the biological control of *T. absoluta* was initiated about 25 years ago, mostly in Argentina, Brazil, Chile, Colombia and Perú, and over 50 species of primary parasitoids, native or introduced, were identified (Bacci et al., 2008; Colomo, Berta, & Chocobar, 2002; Colomo & Berta, 2006; De Santis, 1983; Faria, Torres, & Farias, 2000; García Roa, 1989; Garrido et al., 2017; Lange & Bronson, 1981; Luna et al., 2012; Marchiori, Silva, & Lobo, 2004; Miranda et al., 1998; Oatman & Platner, 1989; Puch, 2011; Uchoa-Fernandes & Campos, 1993; Vargas, 1970).

Despite the interest in *T. absoluta* biocontrol, to date, few parasitoid species have been selected in South America for more detailed studies to determine their effectiveness. These are egg parasitoids, early larval endoparasitoids and mid-larval ecto parasitoids, and results of these studies are reported in chapter 3.2.2.

2.2. Europe and Mediterranean basin

Biological control of *T. absoluta* in these regions has been mainly focused on resident natural enemies, due to the regulatory restrictions for import and release of exotic natural enemies applied (Bale, 2011). Furthermore, the Nagoya protocol born out to guarantee the fair and equitable sharing of benefits arising from the utilisation of genetic resources (including all biological control agents or BCAs) may hamper the achievement of best practice solutions greatly needed to protect against economic and habitat harm caused by invasive species (Pickett & Bugg, 1998, Smith, Hinz, Mulema, Weyl & Ryan 2018, van Lenteren, 2019).

Several reviews have been published to highlight the impact of native natural enemies in Europe and in the Mediterranean area on *T. absoluta* (Desneux et al., 2010; Gabarra et al., 2014; Ghoneim 2014a, 2014b; Giorgini, Guerrieri, Cascone, & Gontijo, 2018; Urbaneja et al., 2012; Zappalà et al., 2013). However, further surveys have been conducted since then in Europe, North Africa and the Middle East (Abbes, Biondi, Zappalà, & Chermiti, 2014; Biondi et al., 2013a; Sohrabi, Lotfalizadeh, & Salehipour, 2014).

More than 70 species of resident generalist natural enemies have been reported for *T. absoluta* in the Western Palaearctic region so far (Tables 1-2). Some of them spontaneously provide biological control services, some others have been successfully used within IPM programs (Ferracini et al., 2012a; Urbaneja et al., 2012; Zappalà et al., 2013). Their abundance is related to the presence of wild flora and can be enhanced through habitat management strategies and conservation biological control (Balzan & Moonen, 2014; Balzan, 2017; Ingegno, Candian, & Tavella, 2017b; Parolin, Bresch, Poncet, & Desneux, 2014).

2.2.1. Predators

Ten arthropod species, mainly hemipterans (belonging to Miridae, Anthocoridae and Nabidae families) have been reported preying on *T. absoluta* in newly invaded European countries since the first record of the pest (Zappalà et al., 2013). These predators include zoophytophagous bugs, which spontaneously colonize organic and IPM crops, where they can also build up populations before pest arrival by exploiting other prey species, such as whiteflies and aphids (Hemiptera), thrips (Thysanoptera), leafminers (Lepidoptera, Diptera), spider mites (Tetranychidae), other lepidopterans, using host plants as alternative food sources as well (Ingegno et al., 2017a). Some of these mirids are mass reared and released in greenhouses as biocontrol agents of various pests, including *T. absoluta* (Perdikis, Fantinou, & Lykouressis, 2011; Urbaneja et al., 2012). Furthermore, several laboratory, semi-field and field studies have confirmed their high predation potential (De Backer, Megido, Haubruge, & Verheggen, 2014; Jaworski, Bompard, Genies, Amiens-Desneux, & Desneux, 2013; Nannini et al., 2014; Shaltiel-Harpaz et al., 2016; Urbaneja, Montón, & Mollá, 2009), either alone or in combination with parasitic wasps sharing the same host/prey species (Cabello et al., 2012; Calvo, Lorente, Stansly, & Belda, 2012; Calvo, Soriano, Stansly, & Belda, 2016; Chailleux, Biondi, Han, Tabone, & Desneux, 2013a; Chailleux, Desneux, Arnó, & Gabarra, 2014) or with selective pesticides (Mollá, González-Cabrera, & Urbaneja, 2011; Zappalà, Biondi, Tropea Garzia, & Siscaro, 2012a).

Also, pre-plant applications by releasing zoophytophagous predators onto seedling nurseries and adding alternative foods to facilitate their settlement have shown interesting results (Calvo et al., 2012; Nannini, Atzori, Musio, Pisci, & Porcu, 2017; Urbaneja-Bernat, Alonso, Tena, Bolckmans, & Urbaneja 2013; Urbaneja-Bernat et al., 2015). Although their zoophytophagous behavior has recently been found to have positive effects, such as activating plant defenses against major insect pests (Naselli et al., 2016; Pérez-Hedo, Rambla, Granell, & Urbaneja, 2018), these predators are known to cause injury to plants and fruits under particular environmental conditions and with prey scarcity. Economic losses have been observed in tomato crops due to necrotic brown rings around stems and shoots, as well as damage on flowers and fruits caused by their feeding. From this perspective, the potential role of some crop and non-crop plants, for the correct management of *T. absoluta* and of its predators, is presently being investigated in order to achieve more efficient biological control (Biondi et al., 2016; Ingegno et al., 2017a, 2017b; Naselli et al. 2017a).

2.2.2. Parasitoids

Almost 50 species of Hymenoptera parasitoids of *T. absoluta* have been recorded in Europe. They belong to the families Eulophidae, Braconidae, Ichneumonidae, Trichogrammatidae, Pteromalidae and Chalcididae in decreasing order of species abundance (Zappalà et al., 2013). Some of these have been tested for their potential as biocontrol agents, namely the larval parasitoids *Bracon nigricans* Szépligeti (Hymenoptera: Braconidae) (Biondi, Desneux, Amiens-Desneux, Siscaro, & Zappalà, 2013b), *Necremnus tutae* Ribes & Bernardo [previously referred to as *Necremnus* sp. nr. *artynes* (Walker)] (Bodino, Ferracini, & Tavella, 2016; Calvo, Soriano, Bolckmans, & Belda, 2013; Ferracini et al., 2012b; Gebiola, Bernardo, Ribes, & Gibson, 2015) and *Stenomesius* sp. nr. *japonicus* (Ashmead) (Chailleux et al., 2014) (Hymenoptera: Eulophidae), as well as the egg parasitoid *Trichogramma achaeae* Nagaraja & Nagarkatti (Hymenoptera: Trichogrammatidae) (Cabello et al., 2009a; Cascone et al., 2015).

3. BIOLOGICAL CONTROL WITH ENTOMOPHAGOUS INSECTS, AND THEIR EFFECTIVENESS UNDER LABORATORY, SEMI-FIELD AND FIELD CONDITIONS

3.1 South America

3.1.1. Predators

Although several publications recommend use of predators in biological control programs of *T. absoluta*, we were unable to find any documentation in the scientific or technical literature showing their practical application in South America. To our best knowledge, only one assay has been carried out with *Campyloneuropsis infumatus* (Carvalho) and *Macrolophus basicornis* (Stål) in greenhouse, showing how these two Neotropical mirids were able to significantly reduce *T. absoluta* populations (van Lenteren et al., 2018b).

Among the predators listed in Table 1, less than 10 species might be suitable for use in augmentative biological control after application of the evaluation criteria mentioned in section 2.1.1 (one coccinellid, one chrysopid, one thrips and several hemipterans of the following genera: *Annona*, *Campyloneuropsis*, *Engytatus*, *Macrolophus*, *Tupiocoris*). These predators could also play a role in conservation biological control, together with spiders, dermapterans, carabids, formicids, sphecids and vespids. If none of the native South American predators and parasitoids alone or in combination will provide sufficient control, import and release of exotic natural enemies might be considered. However, the currently best effective natural enemies in Europe, predatory mirids, might not be good candidates for importation to new areas because of their wide prey range and zoophytophagous behavior. Environmental risk assessments of these European mirids are in fact expected to present unacceptable risk. Besides, even if safe and effective natural enemies are found outside South America, operating procedures related to the Nagoya protocol (Cock et al., 2010; van Lenteren, 2019) will have to be followed before their importation and release.

Heteropteran predators comprise about 8% of all arthropod natural enemy species used in pest management worldwide today (van Lenteren, 2012). These generalist predators, and particularly mirids, are currently popular in biocontrol programs as they can be used for simultaneous control of several pests in the same crop. Nowadays, mirid predators are used on a large scale for control of *T. absoluta* in Europe (Calvo et al., 2012, and see section 3.2.1), but the most popular species, *Nesidiocoris tenuis* (Reuter), may cause serious damage to tomato plants and fruits under certain conditions (Arnó et al., 2010; Castañé, Arnó, Gabarra, & Alomar, 2011; Calvo, Bolckmans, Stansly, & Urbaneja, 2009; Calvo et al., 2012; Moerkens et al., 2016). Salas Gervassio et al. (2016a) have also reported that under certain climatic conditions, as higher temperatures, *N. tenuis* has a greater ability to outcompete other mirid species. Hence, this potential negative impact needs to be taken into account for the South American Miridae as well. In particular, the following species have recently obtained much attention: *C. infumatus*, *Engytatus varians* (Distant), and *M. basicornis* (Bueno et al., 2013; van Lenteren, Hemerik, Lins, & Bueno, 2016; van Lenteren et al., 2017; van Lenteren, et al. 2018b). These three species appear well adapted to the climatic situations in Brazil (Bueno, Calixto, Montes, & van Lenteren, 2018), establishing populations on tomato (Silva, Bueno, Montes, & van Lenteren, 2016a), without being caught into the glandular hairs of tomato (Bueno et al., 2013). They attack not only *T. absoluta* but also a number of other lepidopteran pests and *Bemisia tabaci* (Gennadius), which can occur on tomato (Bueno et al., 2018). They have pest kill capacities similar or higher than those of the successful European mirid species (van Lenteren et al., 2017, van Lenteren, Bueno, Montes, Hemerik, & de Jong, 2018c). Besides, they are easy to mass rear by using the same technology as applied for European Miridae, and, furthermore, they show little plant and fruit injury and no economic yield loss due to zoophytophagy (Silva, Bueno, Calvo, & van Lenteren, 2016b; van Lenteren et al., 2018b). Furthermore, they are attracted to herbivore induced volatiles produced by tomato after attack by either *T. absoluta* or *B. tabaci* (Silva, Bueno, Peñaflor, Bento, & van Lenteren, 2018). Under semi-practical greenhouse conditions two out of the three mirid species were able to significantly reduce *T. absoluta* populations (van Lenteren et al., 2018b), but further testing in commercial tomato greenhouses and fields is necessary to determine release rates and frequencies.

3.1.2. Parasitoids

Egg parasitoids

Mass rearing and parasitism capacity of the egg parasitoids *Trichogramma nerudai* Pintureau & Gerding and *Trichogrammatoidea bactrae* Nagaraja were investigated in laboratory and field conditions in Argentina (Cáceres, Aguirre, Miño, & Almonacid, 2011; Riquelme Virgala & Botto, 2010; Tezze & Botto, 2004). Experimental releases with *T. nerudai* were carried out in northeastern Argentina, and the species could be recovered in later seasons; however, this biocontrol program was not continued (Cáceres et al., 2011). *Trichogrammatoidea bactrae* resulted in 90% of immature survival when reared on *T. absoluta* eggs in the laboratory. Moreover, the third *Trichogramma* species evaluated, *T. pretiosum* Riley, was extensively studied in Brazil (Parra & Zucchi, 2004). Parasitoid lineages originating from Colombia and Brazil were released in small- to large-scale in experimental and commercial fields by Haji et al. (1995), who found that a release rate of 450,000 wasps per hectare resulted in 20 to 68% parasitized eggs of the tomato leafminer. Studies on the functional response of *T. pretiosum* have been carried out (Faria et al., 2000). Faria, Torres, Fernandes, & Farias (2008) found that *T. absoluta* parasitism by *T. pretiosum* can reach up to 28% in cages with tomato plants, and that parasitism occurs mainly in the upper part of the tomato plant. Pratissoli & Parra (2000) found that development and reproduction of *T. pretiosum* reared on *T. absoluta* eggs at different temperatures was poor and similar when reared on eggs of another gelechiid host, *Phthorimaea operculella* (Zeller). The combined use of *Bacillus thuringiensis* Berliner and different release rates of *T. pretiosum* in stalked tomato crops has been evaluated, showing good tomato yield under greenhouse conditions (Medeiros, Boas, Vilela, & Carrijo, 2009; Parra & Zucchi, 2004). In Chile, González (2003) assessed the effect of insecticide use on *T. nerudai* and *T. pretiosum* and concluded that chemical control should be avoided at least five to six days after the parasitoid inundative release. They recommended selecting low toxicity products (thiacloprid, mineral oil and detergent) with six to seven days residual effects as maximum. However, it is important to mention that natural parasitism of *T. absoluta* eggs is quite rare. Eggs suffer more by predation or other mortality causes (dislodging, dissecation, etc.). According to

Hirose (1994), host egg size restricts the species composition and richness in egg parasitoid assemblages of Lepidoptera. For *T. absoluta* eggs, which barely reach 0.08 mm^3 of volume, expected richness is ≈ 2 species (Luft, Luna, Galise, Speranza, & Virla, 2015).

So far, the parasitoid species commercialized in South America, although not exclusively for *T. absoluta* biocontrol, belong to the egg parasitoid guild and are: *T. galloi* Zucchi and *T. pretiosum* in Brazil (Bug Agentes Biológicos and Koppert, Brazil); *T. bactrae*, *T. nerudai*, and *T. pretiosum* in Chile (Biobichos Ltda.); *T. pretiosum* in Colombia (BioAgro, Biodefensas Agrícolas Ltda., Ingenio Providencia, Scientia Colombia S.A.S.); *T. pretiosum* in Ecuador (small-scale production); and *T. bactrae*, *T. cacaeciae* Marchal, *T. exiguum* Pinto & Platiner, *T. fuentesi* Torre, *T. pintoi* Voegele, and *T. pretiosum* in Perú (Senasa; www.senasa.gov.pe). Costs of inundative release of *T. pretiosum* to control *T. absoluta* can reach ≈ 125 US$ per hectare in Chile, for example. In general, this biocontrol agent is used in combination with other pest control tactics, or IPM, including microbial insecticides based on *B. thuringiensis* against larvae, and pheromone traps to catch adults, among others (Luna, Sánchez, & Salas Gervassio, 2017).

Larval parasitoids

Larval parasitoids could have an important effect in reducing *T. absoluta* populations since they establish tight host-parasitoid interactions in tomato crops and kill pre-reproductive stages of *T. absoluta* (Luna et al., 2017). Among the known species (Table 2), the native *Pseudapanteles (Apanteles) dignus* (Muesebeck) and *Dineulophus phthorimaeae* De Santis have been thoroughly studied in Argentina and Chile, and parasitism rate is reported over 60%. The life history traits, functional response and population parameters of *P. dignus* were investigated in the laboratory, as well as spatial pattern and impact of parasitism in tomato crops under natural conditions (Luna, Sánchez, & Pereyra, 2007, 2015; Nieves et al., 2015; Sánchez, Pereyra, & Luna, 2009). Furthermore, its biological attributes and functional response were determined, as well as the competition with *D. phthorimaeae* (Luna et al., 2015; Savino, Coviella, & Luna, 2012; Savino, Luna, Salas Gervassio, & Coviella, 2016). In Chile, Larraín (1986) described field parasitism of *T. absoluta* larvae by *D. phtorimaeae* and provided guidelines for its conservation.

Although both parasitoids have valuable attributes as natural enemies, *P. dignus* seems to be a more promising candidate for conservation biological control and/or seasonal augmentative release. In fact, it parasitizes few gelechiid species, and it shows seasonal synchronization with host populations and aggregative response to host density, and an instantaneous attack rate greater than the intrinsic growth rate of the host as well (Luna et al., 2007; Nieves et al., 2015; Salas Gervassio, Luna, Lee, Salvo, & Sánchez, 2016b). Currently, the following studies are being conducted with *P. dignus* in Argentina, to: 1) optimize its mass rearing (MG Luna, unpublished data); 2) estimate parasitoid release rates through semi-field trials in greenhouses (N Salas Gervassio, unpublished data); 3) assess the role of plant diversity adjacent to crops in promoting parasitoid´s presence (Salas Gervassio et al., 2016b). Previous augmentative releases of *P. dignus* in northeastern Argentina did not result in successful control in protected tomato crops (Cáceres et al., 2011). Moreover, Luna, Wada, LaSalle, & Sánchez (2011) mentioned *Neochrysocharis (Closterocerus) formosa* (Westwood) as a potential biocontrol agent based on its wide host range and presence in other crops, with parasitism rates of *T. absoluta* ranging between 1.5 and 11.2%.

In Colombia, life cycle attributes under different temperature conditions and functional response of *Apanteles gelechiidivoris* Marsh were investigated (Bajonero, Córdoba, Cantor, Rodríguez, & Cure, 2008). Morales, Rodríguez, & Cantor (2013) designed preliminary protocols for an affordable, high quality mass rearing system, with optimal temperatures for rearing this braconid. Furthermore, a mass rearing protocol to produce and release *A. gelechiidivoris* in greenhouse tomato crops against *T. absoluta* was developed (Cantor Rincón, Rodríguez, & Cure Hakim, 2011).

In sum, the braconids *A. gelechiidivoris* and *P. dignus* show biological potential to be developed as commercial biocontrol agents of *T. absoluta*. However, economical analyses should be done to determine their cost/benefit ratio for tomato crops grown in South America.

3.2. Europe and Mediterranean basin

3.2.1. Predators

Several species of predators, such as *Dicyphus errans* (Wolff), *Macrolophus pygmaeus* (Rambur), *N. tenuis* and *Nabis pseudoferus* Remane, have been evaluated as natural enemies of *T. absoluta.* Moreover, their use in augmentative and conservation biological control has been recently discussed by Giorgini et al. (2018). Currently, augmentative release of the mirid *N. tenuis* is considered as a standard augmentative biocontrol method in protected crops in the Mediterranean area thanks to its wide predatory capacity on various pests apart from *T. absoluta,* such as whiteflies, thrips and mites (Calvo et al., 2016; Urbaneja et al., 2012). Sanchez, La-Spina, & Lacasa (2014) performed trials with *N. tenuis* under greenhouse in southern Spain, highlighting that in tomato crops *T. absoluta* density was lower where the predator had been released without any significant influence of the prey abundance. In addition, the crop yield was higher in the treatments with *N. tenuis* than in those without, even if the percentage of damaged fruit was similar.

The involvement of herbivore-induced plant volatiles in prey location by *D. errans*, *M. pygmaeus* and *N. tenuis* was investigated in olfactometer and wind tunnel, providing evidence that the mirids are able to discriminate between infested and healthy tomato plants using olfactory cues (De Backer et al., 2015; Ingegno, Ferracini, Gallinotti, Alma, & Tavella, 2013; Bouagga et al., 2018). In the laboratory, the predators *M. pygmaeus* and *N. tenuis* demonstrated similar predation characteristics in intraspecific interactions. However, *N. tenuis* has proven to be more effective in preying on *T. absoluta* than *M. pygmaeus* as it can consume more eggs at higher prey densities. Nevertheless, the combination of the two predator species may lead to better pest suppression at high *T. absoluta* population densities (Michaelides, Sfenthourakis, Pitsillou, & Seraphides, 2018). Finally, the evidence of plant defense induction through *N. tenuis* feeding punctures (Naselli et al., 2016; Bouagga et al., 2018) opens new insights into the role of predators in pest management.

3.2.2. Parasitoids

Egg parasitoids

The egg parasitoid *T. achaeae*, commercially available in Europe and North Africa, may achieve high parasitism rates (>90%) under greenhouse conditions, both alone and in combination with the mirid predator *N. tenuis* (Cabello et al., 2009a, 2015; Oliveira et al., 2017). A laboratory screening of 29 European strains/species of *Trichogramma* parasitoids was performed to assess their potential in controlling *T. absoluta*. Their performance was strongly influenced by the testing conditions. One strain of *T. euproctidis* (Girault) appeared promising compared to *T. achaeae*, because it showed a higher parasitism rate, higher fertility, higher proportion of females and the capacity of diapause during cold storage. However, it did not perform well under greenhouse conditions (Chailleux et al., 2012). In Tunisia, two native species of *Trichogramma* (*T. bourarachae* Pintureau & Babault and *T. cacaeciae*) were effective in reducing *T. absoluta* densities when released in open field or protected tomato crops. Indeed, in open field *T. cacaeciae* reached an average parasitisim rate of 54.7%, significantly reducing the number of *T. absoluta* eggs and larvae per leaf, while under greenhouse conditions the egg parasitization averaged 57.1% and reduced the number of mines per leaf by 78.9% (Cherif & Lebdi-Grissa, 2013). *Trichogramma bourarachae* under greenhouse conditions reached an average parasitisim rate of 63.9% with a reduction in leaf damage of 87.6% (Zouba, Chermiti, Chraiet, & Mahjoubi, 2013).

Larval parasitoids

Among larval parasitoids, *B. nigricans* was tested under laboratory conditions. The wasp showed a good behavioral plasticity in host exploitation. Therefore, despite the relatively low parasitism (around 30%), in laboratory the braconid proved to be potentially effective due to host feeding (Biondi et al., 2013b).

Particular attention has been given to eulophid parasitoids, especially to the genus *Necremnus*. Earlier records published as *N.* sp. nr *artynes*, and most of the records published as *N. artynes*, belong to *N. tutae.* Similarly, the records of *N. metalarus* (Walker) parasitizing *T. absoluta* probably also refer to dark forms of *N. tutae* (Gebiola et al., 2015). The effectiveness of this eulophid has been investigated by Calvo et al. (2013), in combination with *N. tenuis*, finding the predator preplant application sufficient for pest control (Calvo et al., 2016). In the laboratory, *N. tutae* caused high larval mortality of *T. absoluta* because of host feeding and parasitism (Ferracini et al., 2012b; Bodino, Ferracini, & Tavella, 2018). Greater intrinsic rate of increase was recorded at high temperatures (30°C), suggesting the high potential by *N. tutae* in reducing this pest in Mediterranean greenhouses as well (Calvo et al., 2013). Furthermore, this larval parasitoid was the only species recovered in sprayed greenhouses (Zappalà et al., 2012c). Recently, functional responses and lifetime foraging behaviors of *N. tutae* and *N. cosmopterix* Ribes & Bernardo were investigated, highlighting a higher maximum estimated host-killing rate by the latter species (Bodino et al., 2018).

In a comparative study, *S.* sp. nr. *japonicus* females lived longer than *N. tutae* and were consequently more efficient in terms of number of parasitized and killed hosts. The highest number of offspring were produced when the wasp developed on 3rd-instar larvae, resulting in larger adults and a higher proportion of females (Chailleux et al., 2014).

In an intraguild interaction study, the predator *N. tenuis* and the two larval parasitoids *N. tutae* and *B. nigricans* were also investigated, and the predator was shown to (1) scavenge on parasitized *T. absoluta* larvae, and (2) attack and feed upon larvae of both parasitoid species resulting in reduced emergence of both (Naselli et al., 2017b). These laboratory data, if confirmed also in field conditions, suggest that *N. tenuis* could have a detrimental impact on parasitoid population in case of multiple releases. Furthermore, the provision of different flowers may benefit survival and egg load for different parasitoid species (*B. nigricans*, *N. tutae*, *S.* sp. nr. *japonicus*), though without encouraging the pest (Arnó, Oveja, & Gabarra, 2018).

4. DISCUSSION, PERSPECTIVES AND CONCLUSIONS

After its invasion in Europe about 12 years ago, *Tuta absoluta* has gained quite a diverse parasitoid assemblage. Although about 70 species of predators and 100 species of parasitoids have been found in association with *T. absoluta*, solutions for effective and economically realistic biocontrol are not available in South America, and current options for biological control of this pest are not optimal in Europe and the Mediterranean basin. It is also important to mention that much more taxonomic work is needed to confirm the list of natural enemies. At least 20 predator and 34 parasitoid species are still under a morphospecies status (Tables 1 and 2) and they deserve further study. Besides, for many of the reported confirmed species, there are only systematic papers and biological or ecological studies are lacking. Interestingly, in both regions parasitoid species mainly represent host larval guilds. Hymenopteran ichneumonids, braconids, chalcidids, eulophids and trichogrammatids are well represented in both South America and Europe. Instead, dipteran tachinids and hymenopteran encyrtids, aphelinids and bethylids seem to be absent in Europe.

Regarding their use as commercial biocontrol agents, in Europe and the Mediterranean basin the mirid predators *M. pygmaeus* and *N. tenuis* are both mass produced on a large scale and were used for *T. absoluta* control on about 12,500 ha of tomatoes in 2017; *M. pygmaeus* is used mainly in northern Europe, and *N. tenuis* in the Mediterranean basin (J. Calvo, personal communication, August 25, 2018). In particular, *N. tenuis* is considered as the best predator species, but the increase of its use is hindered by the fact that it may cause serious plant and fruit damage when prey density is low. In South America, only the egg parasitoid *T. pretiosum* is used on less than 1,000 ha of tomato crops for control of *T. absoluta*. Although *T. pretiosum* can attack and reproduce on this pest, it needs to be released in large numbers and at regular intervals to achieve some degree of pest suppression, as reproduction and offspring quality are rather poor when developing on *T. absoluta* eggs. Thus, our conclusion is that the current availability of useful natural enemies is limited and biocontrol of *T. absoluta* is presently far from satisfactory.

Tomato is the second most consumed vegetable fruit worldwide, and the global production is over 160 million tons, produced on 4.7 million ha (http://faostat.fao.org/site/339/default.aspx). Knowing that tomato is produced on hundreds of thousands of hectares where *T. absoluta* is already present, biocontrol is currently playing a very modest role.

The need for environmentally safe, economically sustainable and effective control strategies is even stronger in developing countries. In Africa, where tomato is seen as a very promising crop for horticultural expansion, the agricultural sector across the continent, and particularly the many small scale farmers, is currently experiencing significant impacts from *T. absoluta*. The pest has been reported in 17 African countries (https://www.cabi.org/ISC/datasheet/49260, October 5, 2018), and losses of up to 80% of the total harvest have led to a three-fold increase in tomato prices in Tanzania in 2016 (Pratt et al., 2017). The situation in Asia is equally difficult when looking at the Middle East (e.g. Al-Jboory, Katbeh-Bader, & Shakir, 2012) and South West India (e.g. Kalleshwaraswamy et al., 2015). The fast spread over the entire Indian region (Sankarganesh et al., 2017), where tomato production is a significant economic activity, may also represent a high risk to large parts of China (Xian et al., 2017). Since climatic suitability indices predict a high probability for continued invasion with further spread expected to reach China and the USA within a decade by 2028 (Xian et al., 2017), it is clear that the search and evaluation of natural enemies of *T. absoluta* are far from being over. An early-warning assessment is necessary, and since invasion is irreversible, management of the pest requires finding reliable and feasible biological control solutions in invaded countries, as well as those at risk.

To make progress with biocontrol of *T. absoluta*, a critical (re-)evaluation of natural enemies known to be associated with the pest is needed. Based on current knowledge there are less than 10 species of predators and three parasitoids in South America, and in Europe and the Mediterranean basin less than five predators and three parasitoids might be considered promising candidates for augmentative biological control of this pest. Additional species that are difficult to rear, but may contribute considerably to pest mortality in (semi) natural agro-ecosystems should be considered, in conservation biocontrol programs. If (re-) evaluation of the known natural enemies does not result in cost-effective solutions, the next step might be to start prospecting for new natural enemies. Regulatory restrictions mentioned above (see chapter 2.2), make the importation of exotic natural enemies very laborious, so searching for new natural enemies should include not only the place of origin, but areas where the pest may soon invade. New natural enemies have to be investigated by using specific evaluation criteria making it possible to quickly prioritize species. In the case of areas not yet invaded by *T. absoluta*, the following approach might be considered. First, design an emergency IPM program based on methods already easily available, and check if any of the best performing natural enemies in the areas where *T. absoluta* occurs are also present in the non-invaded area.Then, if none of the currently used natural enemies for *T. absoluta* control is found in the non-invaded area, prospecting for natural enemies should be pursued, with a preference for species that attack closely related pest species. If such an approach does not result in promising candidates, importation of exotic species from the pest's area of origin might be considered, but can be a lengthy, expensive process due to national and international regulations.

A final consideration concerns cooperation among researchers. During past decades, research on natural enemies of *T. absoluta* has largely been done in isolation, resulting in testing the same species at various locations. We strongly believe that organizations such as the regional sections of the Food and Agricultural Organization of the United Nations (FAO.org) and/or the International Organization for Biological Control (IOBC-Global.org) may take the initiative to coordinate research on key invasive pests by implementing a regular exchange of results at regional levels. For developing countries, the research stations of the Consortium of International Agricultural Research Centers (CGIAR.org) might play a coordinating role, as well. Due to the seriousness of the pest in invaded areas and the threat for not yet invaded regions, coordinated efforts can strongly aid in optimizing biocontrol research and application.

Acknowledgements

The Authors would like to thank David Núñez Naranjo (Colegio Nacional E Salazar Gómez, Ecuador), Lorena Barra (INIA, Chile), Demian Kondo and Alba M. Cotes (Corpoica, Colombia), Maria Manzano (Universidad Nacional de Colombia, Palmira, Colombia), Norma Mujica (CGIAR, Perú) for providing useful information which improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Table 1 Predators associated with *Tuta absoluta* in South America (SA), Europe (E) and Mediterranean basin (M)

Order	Family	Species	Target stage	Area (SA/E/M)	References	Status[1]
Araneae	Lycosidae	unidentified species	larvae, pupae	SA	Desneux et al. (2010)	L
		Tanimlanmamis sp.		M	Öztemiz (2012)	R
	Oxiopidae	unidentified species		SA	Desneux et al. (2010)	R
	Gnaphosidae	unidentified species		SA	Desneux et al. (2010)	R
	Thomisidae	*Misumenops pallidus* Keyserling	larvae	SA	Medeiros (2007), Medeiros et al. (2011)	R
	Salticidae	not specified		SA	Desneux et al. (2010)	R
Acari	Pyemotidae	*Pyemotes* sp.	larvae, pupae, adults	SA	Oliveira et al. (2007)	R
	Phytoseiidae	*Amblyseius cucumeris* (Oudemans)	eggs, early larvae	E	Mollá et al. (2010)	R
		Amblyseius swirskii Athias-Henriot	eggs, early larvae	E	Medeiros et. al (2011), Mollá et al. (2010)	R
Dermaptera	Labiduridae	*Doru lineare* (Eschscholtz)	eggs	SA	Desneux et al. (2010)	R
		Labidura riparia (Pallas)	pupae		Desneux et al. (2010)	R
Thysanoptera	Aeolothripidae	*Franklinothrips vespiformis* Crawford	eggs	SA	Desneux et al. (2010)	R
	Phlaeothripidae	unidentified species	eggs	SA	Miranda et al. (1998)	R
	Thripidae	*Scolothrips sexmaculatus* Pergande	eggs	SA	Desneux et al. (2010)	R
Hemiptera	Anthocoridae	*Amphiareus constrictus* (Stål)		SA	Pereira et al. (2014), Queiroz et al. (2015)	L
		Blaptostethus pallescens Poppius		SA	Pereira et al. (2014), Queiroz et al. (2015)	L
		Lasiochilus sp.	early larvae, pupae	SA	Bacci et al. (2008)	L/SF
		Orius sp.	eggs, early larvae, pupae	SA/M	Al-Jboory et al. (2012), Bacci et al. (2008), Salehi et al. (2016), Sannino & Espinosa (2010)	R/SF
		Orius albidipennis (Reuter)	-	M	Al-Jboory et al. (2012)	R
		Orius insidiosus (Say)	eggs, larvae	SA	Desneux et al. (2010), Lins et al. (2011)	R/L
		Orius laevigatus (Fieber)	eggs, early larvae	E	Gabarra and Arnó (unpublished data), Urbaneja et al. (2012)	R
		Orius majusculus (Reuter)	eggs, early larvae	E	Gabarra and Arnó (unpublished data), Urbaneja et al. (2012)	R
		Orius tristicolor (White)		SA	Pereira et al. (2014), Queiroz et al. (2015)	L

	Xylocoris sp.	eggs, early larvae, pupae	SA	Bacci et al. (2008), Desneux et al. (2010)	R/SF
Nabidae	*Nabis pseudoferus ibericus* Remane	eggs, early larvae	E	Cabello et al.,(2009b), Mollá et al. (2010)	R/L/SF
	Nabis spp.	eggs, early larvae	SA/E/M	Desneux et al. (2010), Sannino & Espinosa (2010), Vargas et al. (1970), Zappalà et al. (2013)	R
Miridae	*Annona bimaculata* (Distant)	eggs, early larvae	SA	Bacci et al. (2008)	R/SF
	Campyloneuropsis infumatus (Carvalho)	eggs, larvae	SA	Bueno et al. (2013), van Lenteren et al. (2017, 2018b)	L/SF
	Dicyphus errans (Wolff)	eggs, early larvae	E/M	Boualem et al. (2012), Ferracini et al. (2012b), Ingegno et al. (2013, 2017a, b)	R/L/SF
	Dicyphus maroccanus Wagner*	eggs, early larvae	E	Colazza et al. (2014), Ingegno et al. (unpublished data)	R/L
	Dicyphus sp.	eggs, early larvae	E	Biondi et al. (2013b), Zappalà et al. (unpublished data)	R
	Dicyphus tamaninii Wagner	eggs, early larvae	M	Guenaoui et al. (2011a)	R
	Engytatus varians (Distant)	eggs, larvae	SA	Bueno et al. (2013), van Lenteren et al. (2017, 2018b)	L/SF
	Hyaliodocoris insignis(Stål)	eggs, early larvae	SA	Bacci et al. (2008)	R/SF
	Macrolophus basicornis Stål	eggs, larvae	SA	Bueno et al. (2013), van Lenteren et al. (2017, 2018b)	L/SF
	Macrolophus pygmaeus (Rambur)	eggs, early larvae	E/M	Arnó et al. (2009), Biondi et al. (2013b), Boualem et al. (2012), Guenaoui et al. (2011), Ingegno et al. (2013), Michaelides et al. (2018), Mollá et al. (2010),	R/L/SF/F
	Nesidiocoris tenuis (Reuter)	eggs, early larvae	E/M	Al-Jboory et al. (2012), Arnó et al. (2010), Biondi et al. (2013b),Bouagga et al. (2018), Boualem et al. (2012), El Arnaouty & Kortam (2012), Guenaoui et al. (2011a), Karabuyuk (2011), Michaelides et al. (2018), Naselli et al. (2016), Rizzo et al. (2011), Sanchez et al. (2014), Zappalà et al. (2013)	R/L/SF/F
	Tupiocoris cucurbitaceus (Spinola)	eggs	SA	Biondi et al. (2018), López et al. (2011)	R
Phymatidae	*Phymata* sp.	larvae	SA	Desneux et al. (2010)	R
Reduviidae	*Debilia* sp.	larvae	SA	Desneux et al. (2010)	R
	Zelus obscuridorsis (Stål)	larvae (out of mine), adults	SA	Luna et al. (2015), Speranza et al. (2014)	R/L
Berytidae	*Metacanthus tenellus* Stål	eggs, larvae	SA	Oliver & Bringas (2000)	R
Lygeidae	*Geocoris punctipes* (Say)	eggs, larvae	SA	Bueno et al. (2012, 2013, 2016a, b), Desneux et al. (2010),	L

	Pentatomidae	*Podisus nigrispinus* (Dallas)	larvae, adults	SA	Desneux et al. (2010), Medeiros (2007), Medeiros et al. (2011), Torres et al. 2002, Vivan (2002a, 2002b, 2003)	R/SF
Neuroptera	Chrysopidae	*Chrysoperla* sp.	larvae	SA	Desneux et al. (2010)	R
		Chrysoperla carnea species group	-	M	Zappalà et al. (2013)	R
		Chrysoperla externa (Hagen)		SA	Carneiro & Medeiros (1997)	?
		Chrysopa sp.	larvae	SA	Desneux et al. (2010)	R
Coleoptera	Carabidae	unidentified species	pupae	SA	Desneux et al. (2010)	R
		Calosoma granulatum Perty	larvae, pupae	SA	Desneux et al. (2010)	R
		Calosoma sp.	larvae, pupae	SA	Desneux et al. (2010)	R
		Lebia concina L.	larvae, pupae	SA	Desneux et al. (2010)	R
		Lebia sp.	larvae, pupae	SA	Desneux et al. (2010)	R
		Selenophorus sp.	larvae, pupae	SA	Desneux et al. (2010)	R
	Coccinellidae	*Chilocorus* sp.	larvae	SA	Vasicek (1983)	
		Coleomegilla maculata DeGeer	eggs, larvae	SA	Desneux et al. (2010)	R
		Cycloneda sanguínea Linnaeus	eggs	SA	Miranda et al. (2005)	R
		Eriopis connexa (Germar)	eggs	SA	Desneux et al. (2010)	R
	Anthicidae	*Anthicus* sp.		SA	Miranda et al. (2005)	R
Hymenoptera	Formicidae	*Pheidole* sp.	larvae, pupae	SA	Desneux et al. (2010)	R
		Solenopsis geminata (Fabricius)	larvae, pupae	SA	Desneux et al. (2010)	R
		Solenopsis saevissima (Smith)	larvae, pupae	SA	Desneux et al. (2010)	R
		Tapinoma nigerriumu (Nylander)	larvae	M	Guenaoui et al. (2011b)	
	Vespidae	*Brachygastra lecheguana* (Latreille)	larvae	SA	Bacci et al. (2008), Desneux et al. (2010), Medeiros (2007), Medeiros et al. (2011), Picanço et al. (2011)	R/SF
		Polistes sp.	larvae	SA	Desneux et al. (2010), Vargas et al. (1970)	R
		Polybia fastidiosuscula Lepeletier	larvae	SA	Biondi et al. (2018), Picanço et al. (2011)	R
		Polybia ignobilis (Haliday)	larvae	SA	Desneux et al. (2010), Picanço et al. (2011)	R
		Polybia scutellaris (White)	larvae	SA	Desneux et al. (2010), Picanço et al. (2011)	R
		Polybia sp.	larvae	SA	Desneux et al. (2010), Medeiros (2007), Medeiros et al. (2011)	R
		Protonectarina sylveirae (Saussure)	larvae	SA	Bacci et al. (2008), Desneux et al. (2010), Picanço et al. (2011)	R/SF
		Protopolybia exigua (Saussure)	larvae	SA	Desneux et al. (2010), Picanço et al. (2011)	R

	Synoeca cyanea Fabricius	larvae	SA	Desneux et al. (2010), Picanço et al. (2011)	R
Sphecidae	unidentified species	larvae	E	Mollá et al. (2008)	R

Table 2 Parasitoids associated with *Tuta absoluta* in South America (SA), Europe (E) and Mediterranean basin (M)

Order	**Family**	**Species**	**Target stage**	**Area (SA/E/M)**	**References**	**Status**[1]
Diptera	Tachinidae	unidentified species	larvae	SA	Colomo et al. (2006)	R
		Archytas sp. Jaennicke	larvae	SA	Desneux et al. (2010)	R
		Phytomyptera (*Elfia)* sp. Rondani	larvae	SA	Desneux et al. (2010)	R
Hymenoptera	Ichneumonidae	*Campoplex haywardi* Blanchard	larvae, pupae	SA	Colomo et al. (2002)	R
		Cryptinae gen. sp.	larvae	E	Zappalà et al. (2012a)	R
		Diadegma sp. Förster	larvae, pupae	SA/E	Colomo et al. (2002), Zappalà et al. (2012a)	R
		Diadegma ledicola Horstmann	late larvae, pupae	E	Ferracini et al. (2012a)	R
		Diadegma pulchripes (Kokujev)	late larvae, pupae	E	Zappalà et al. (2012a)	R
		Hyposoter didymator (Thunberg)	larvae	M	Boualem et al. (2012)	R
		Pristomerus sp. Curtis	larvae	SA	Desneux et al. (2010)	R
		Temelucha sp. Förster	early larvae	SA	Colomo et al. (2002)	R
		Temelucha anatolica (Sedivy)	larvae, pupae	E	Gabarra et al. (2014)	R
		Zoopthorus macrops Bordera &Horstmann	larvae, pupae	E	Gabarra et al. (2014)	R
	Braconidae	*Agathis* sp. Salisbury	early larvae	SA/E	Colomo et al. (2002), Ferracini et al. (2012a)	R
		Agathis fuscipennis Zetterstedt	larvae	E	Loni et al. (2011)	R
		Apanteles sp. Förster	larvae	SA/E	Bacci et al. (2008), Barbosa et al. (2011), Gabarra et al. (2014), Marchiori et al. (2004), Medeiros et al. (2009), Miranda et al. (1998), Uchoa-Fernandes & Campos (1993)	R
		Apanteles gelechiidivoris Marsh	larvae	SA	Bajonero et al. (2008), Cantón Rincon et al. (2011), Morales et al. (2013, 2014), Vargas (1970)	R/L/SF
		Bracon sp. Fabricius	larvae	SA/E/M	Abbes et al. (2014), Zappalà et al. (2011)	R/L
		Bracon didemie Beyarslan	late larvae	M	Doğanlar & Yigit (2011)	R
		Bracon hebetor Say	late larvae	E/M	Doğanlar & Yigit (2011), Ferracini et al. (2012a), Zappalà et al. (2013)	R
		Bracon lucileae Marsh	early larvae	SA	Berta & Colomo (2000), Cáceres et al. (2011)	R
		Bracon lulensis Berta & Colomo	early larvae	SA	Berta & Colomo (2000)	R
		Bracon nigricans Szépligeti	late larvae	E	Biondi et al. (2012c; 2013b), Zappalà et al. (2012b, 2013)	R/L

	Bracon sp. near *nigricans*	late larvae	E/M	Gabarra et al. (2014), Zappalà et al. (2012b; 2013)	R
	Bracon osculator Nees	late larvae	E	Ferracini et al. (2012a), Zappalà et al. (2012a)	R
	Bracon tutus Berta & Colomo	early larvae	SA	Berta & Colomo (2000)	R
	Chelonus sp. (Microchelonus)	eggs, larvae	SA/E	Colomo et al. (2002), Desneux et al. (2010), Gabarra et al. (2014)	R
	Choeras semele (Nixon)	larvae, pupae	E	Gabarra et al. (2014)	R
	Cotesia sp. Cameron	larvae, pupae	E	Gabarra et al. (2014)	R
	Diolcogaster sp. Ashmead	larvae, pupae	E	Gabarra et al. (2014)	R
	Dolichogenidea litae (Nixon)	larvae, pupae	E	Gabarra et al. (2014)	R
	Earinus sp. Wesmael	larvae	SA	Bacci et al. (2008), Barbosa et al. (2011), Colomo et al. (2002), Marchiori et al. (2004), Medeiros et al. (2009), Miranda et al. (1998), Uchoa-Fernandes & Campos (1993)	R
	Orgilus sp. Haliday	late larvae	SA	Colomo et al. (2002)	R
	Pseudapanteles (=Apanteles) dignus (Muesebeck)	larvae	SA	Berta & Pérez (2011), Cáceres et al. (2011), Colomo et al. (2002), Luna et al. (2007, 2010, 2015), Garrido et al. (2017), Nieves et al. (2015), Puch (2011), Salas Gervassio et al. (2016b), Sánchez et al. (2009)	R/L
Chalcididae	*Brachymeria secundaria* (Ruschka)	larvae	M	Doğanlar & Yigit (2011), Gabarra et al. (2014)	R
	Copidosoma sp. Ratzeburg	larvae	SA	Vasicek (1983)	R
	Hockeria unicolor Walker	larvae	E/M	Doğanlar & Yigit (2011), Gabarra et al. (2014)	R
	Psilochalcis (=*Invreia*) sp. Kieffer				
	Spilochalcis (=*Conura*) sp. Thomson	pupae	SA	Cáceres et al. (2011), Vargas (1970)	R
Pteromalidae	*Halticoptera aenea* (Walker)	larvae	E	Zappalà et al. (2012b)	R
	Pteromalus intermedius (Walker)	larvae	M	Doğanlar & Yigit (2011)	R
	Pteromalus semotus (Walker)	larvae, pupae	E	Gabarra et al. (2014)	R
Eupelmidae	*Anastatus* sp. Motschulsky	eggs	SA	Desneux et al. (2010)	R
Encyrtidae	*Arrhenophagous* sp. Aurivillius	eggs	SA	Desneux et al. (2010)	R
	Copidosoma sp. Ratzeburg	egg, larvae	SA	Colomo et al. (2002)	R
	Copidosoma desantisi Annecke & Mynhardt	egg, larvae	SA	Vargas (1970)	R
	Copidosoma koehleri Blanchard	eggs	SA	Desneux et al. (2010)	R
Eulophidae	unidentified species	larvae	SA	Bacci et al. (2008), Barbosa et al. (2011), Marchiori et al. (2004), Medeiros et al. (2009), Miranda et al. (1998), Uchoa-Fernandes & Campos (1993)	R
	Baryscapus bruchofagi (Gahan)	-	M	Doğanlar & Yigit (2011)	R

Chrysocharis sp.Ashmead	larvae	E	Zappalà et al. (2012b)	R
Chrysocharis pentheus (Walker)	larvae	E	Rizzo et al. (2011)	R
Chrysonotomyia sp. Ashmead	larvae	SA	Desneux et al. (2010)	R
Cirrospilus (Zagrammosoma) sp. Westwood	larvae, pupae	SA/M	Desneux et al. (2010), Vargas (1970), Zappalà et al. (2013)	
Closterocerus clarus (Szelenyi)	early larvae	M	Doğanlar & Yigit (2011)	R
Closterocerus formosus Westwood[2]	larvae	SA/E	Desneux et al. (2010), Zappalà et al. (2011)	R
Diglyphus sp. Förster	early larvae	M	Zappalà et al. (2013)	R
Diglyphus crassinervis Erdös	larvae, pupae	E	Gabarra et al. (2014), Rizzo et al. (2011)	R
Diglyphus isaea (Walker)	larvae	E/M	Boualem et al. (2012), Gabarra et al. (2014)	R
Dineulophus phthorimaeae de Santis	mid-larvae	SA	Colomo et al. (2002), de Santis (1983), Larraín (1986), Luna et al. (2010), Savino et al. (2012, 2016), Vargas (1970)	R/L/SF/F
Elachertus sp. Narendran	larvae	E	Zappalà et al. (2012b)	R
Elachertus inunctus Nees	larvae	E	Zappalà et al. (2012b)	R
Elasmus sp. Westwood	larvae, pupae	SA/E	Desneux et al. (2010), Zappalà et al. (2012b)	R
Elasmus phtorimaeae Ferriere	larvae, pupae	E	Gabarra et al. (2014)	R
Hemiptarsenus spp. Westwood	larvae	E	Sannino & Espinosa (2010)	R
Hemiptarsenus ornatus (Nees)	larvae	M	Zappalà et al. (2013)	
Hemiptarsenus zilahisebessi Erdös	larvae	M	Dehliz & Guenaoui (2015)	R
Horismenus sp. Blanchard	larvae, pupae	SA	Desneux et al. (2010)	
Necremnus sp. Thomson	larvae	E	Gabarra et al. (2014), Sannino & Espinosa (2010), Zappalà et al. (2012a)	R
Necremnus artynes (Walker)	larvae	E/M	Boualem et al. (2012), Delvare et al. (2011), Guenaoui et al. (2011b), Kolai et al. (2011), Mollá et al. (2010), Rizzo et al. (2011)	R/L
Necremnus cosmopterix Ribes & Bernardo	larvae	E	Biondi et al. (2018), Bodino et al. (2018)	R/L
Necremnus metalarus (Walker)	larvae	E	Urbaneja et al. (2012)	R
Necremnus near *artynes*[3]	larvae	E/M	Abbes et al. (2014), Biondi et al. (2013b), Calvo et al. (2013), Ferracini et al. (2012b), Gabarra et al. (2014), Zappalà et al. (2012b)	R/L
Necremnus near *tidius*[4]	early larvae	E	Ferracini et al. (2012a), Zappalà et al. (2012b)	R/L
Necremnus tidius (Walker)	larvae	E	Bodino et al. (2016), Ferracini et al. (2011), Riciputi (2011)	R

	Necremnus tutae Ribes & Bernardo	larvae	E	Bodino et al. (2016, 2018), Calvo et al. (2013), Ferracini et al. (2012b), Zappalà et al. (2012c)	R/L
	Neochrysocharis sp. Erdös	-	M	Boualem et al. (2012)	R
	Neochrysocharis formosa (Westwood)	early larvae	SA/E/M	Biondi et al. (2013b), Colomo et al. (2002), Dehliz & Guenaoui (2015), Desneux et al. (2010), Ferracini et al. (2012a), Gabarra et al. (2014), Lara et al. (2010), Luna et al. (2011), Zappalà et al. (2011, 2012b)	R
	Pnigalio christatus (Ratzeburg)	early larvae	E/M	Doğanlar & Yigit (2011), Ferracini et al. (2012a), Gabarra et al. (2014), Zappalà et al. (2012b)	R
	Pnigalio incompletus (Boucek)	-	E/M	Doğanlar & Yigit (2011), Zappalà et al. (2012b)	R
	Pnigalio soemius (Walker)	late larvae	E	Gabarra et al. (2014)	R
	Pnigalio sp. *soemius* complex	early larvae	E	Ferracini et al. (2012a), Zappalà et al. (2012b)	R
	Retisympiesis phthorimaea Blanchard	larvae	SA	Desneux et al. (2010)	R
	Stenomesius sp. Westwood	larvae	M	Dehliz & Guenaoui (2015)	R
	Stenomesius sp. near *japonicus*	larvae	E	Biondi et al. (2013b), Chailleux et al. (2014), Gabarra & Arnó (2010), Gabarra et al. (2014)	R/L
	Sympiesis sp. Graham	larvae	SA/E/M	Boualem et al. (2012), Desneux et al. (2010), Zappalà et al. (2012b)	R
	Sympiesis sp. near *flavopicta*	larvae	M	Zappalà et al. (2013)	R
	Tetrastichus sp. Förster	larvae	SA	Desneux et al. (2010)	R
Aphelinidae	*Encarsia porteri* (Mercet)	eggs	SA	Cáceres et al. (2011), Luft et al. (2015)	R
Trichogrammatidae	*Trichogramma* sp. Westwood	eggs	SA	Biondi et al. (2013b), Boualem et al. (2012), Desneux et al. (2010), Gabarra & Arnó (2010), Gabarra et al. (2014), Zappalà et al. (2012b), Zappalà et al. (2013),	R
	Trichogramma achaeae Nagaraja & Nagaratti	eggs	E/M	Biondi et al. (2013b), Cabello et al. (2009a, 2015), Cascone et al. (2015), Ghoneim (2014b), Oliveira et al. (2017)	R/L/SF
	Trichogramma bourarachae Pintureau & Babault	eggs	M	Zouba et al. (2013)	R/L/SF/F
	Trichogramma cacaeciae Marchal	eggs	M	Cherif & Lebdi-Grissa (2013), Zouba et al. (2013)	R/L/SF/F
	Trichogramma dendrolimi Matsumura	eggs	SA/E/M	Desneux et al. (2010)	R
	Trichogramma euproctidis (Girault)	eggs	SA	Chailleux et al. (2012)	R/L/SF
	Trichogramma evanescens Westwood	eggs	M	Öztemiz (2014)	SF
	Trichogramma exiguum (Girault)	eggs	SA/M	Desneux et al. (2010), Ghoneim (2014b)	R
	Trichogramma fasciatum (Perkins)	eggs	SA	Colomo et al. (2002)	R
	Trichogramma lopezandinensis Sarmiento	eggs	SA	Desneux et al. (2010)	R
	Trichogramma minutum Riley	eggs	SA	Desneux et al. (2010)	R

	Trichogramma nerudai Pintureau & Gerding	eggs	SA	Cáceres et al. (2011), Luft et al. (2015), Tezze & Botto (2004)	R/L/F
	Trichogramma pintoi Voegele	eggs	SA	Desneux et al. (2010)	R
	Trichogramma pretiosum Riley	eggs	SA	Bacci et al. (2008), Barbosa et al. (2011), Cáceres et al. (2011), Colomo et al. (2002), de Oliveira et al. (2017), Faria et al. (2000, 2008), Luft et al. (2015), Medeiros et al. (2009, 2011), Miranda et al. (1998), Parra & Zucchi (2004), Pratissoli & Parra (2000), Vargas (1970)	R/L
	Trichogramma rojasi Nagaraja & Nagarkatti	eggs	SA	Cáceres et al. (2011), Colomo et al. (2002), Ghoneim (2014b), Luft et al. (2015)	R
	Trichogramma telengai Sorokina	eggs	M	Ghoneim (2014b)	R
	Trichogrammatoidea bactrae Nagaraja	eggs	SA	Riquelme Virgala & Botto (2010), Cagnotti et al. 2018	R/SF
Bethylidae	*Goniozus nigrifemur* Ashmead	larvae	SA	Bacci et al. (2008), Barbosa et al. (2011), Marchiori et al. (2004), Medeiros et al. (2009), Miranda et al. (1998), Uchoa-Fernandes & Campos (1993), Vargas (1970)	R