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

2 **Chiara Ferracini¹, Vanda H. P. Bueno², Maria Luisa Dindo³, Barbara L. Ingegno¹, María G.**

3 **Luna^{4,7}, Nadia G. Salas Gervasio^{4,7}, Norma E. Sánchez⁴, Gaetano Siscaro⁵, Joop C. van**

4 **Lenteren^{2,6}, Lucia Zappalà⁵, Luciana Tavella¹**

5

6 ¹University of Torino, Dipartimento di Scienze Agrarie, Forestali e Alimentari, Largo P. Braccini 2,
7 10095 Grugliasco (TO), Italy,

8 ²Laboratory of Biological Control, Department of Entomology, Federal University of Lavras,
9 Lavras/MG, Brazil

10 ³Dipartimento di Scienze e Tecnologie Agro-Alimentari, Alma Mater Studiorum Università di
11 Bologna, Viale Fanin 42, 40127 Bologna, Italy

12 ⁴CEPAVE (CCT La Plata-CONICET y UNLP), Boulevard 120 entre 60 y 64, (1900) La Plata,
13 Argentina

14 ⁵Dipartimento di Agricoltura, Alimentazione e Ambiente (Di3A) – Sezione Entomologia applicata,
15 Università degli Studi di Catania, Via Santa Sofia 100, 95123 Catania, Italy

16 ⁶Laboratory of Entomology, Wageningen University, Wageningen, The Netherlands

17 ⁷Departamento de Ciencias Exactas y Naturales, Universidad Nacional de San Antonio de Areco .
18 UNSAdA, San Antonio de Areco, Argentina.

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22 Corresponding author: Chiara Ferracini, +390116708700, chiara.ferracini@unito.it

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26

27 **Abstract**

28 The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) represents a global threat
29 to commercial tomato (*Solanum lycopersicum* L.) production, both in open field and greenhouse.

30 Native to South America, it spread over the Mediterranean Basin, Europe, Africa and part of Asia in
31 only 12 years, and currently it is reported in over 80 countries. Biological control is one of the
32 options for its control and a large number of natural enemies has been reported in association with
33 the pest, both in the areas of origin and of introduction. The egg parasitoid *T. pretiosum*, in South
34 America, and the mirid predators *M. pygmaeus* and *N. tenuis*, in Europe and the Mediterranean
35 basin, are used as commercial biocontrol agents. Even if several natural enemies might be
36 promising candidates for biocontrol, their potential role in quantitative pest reduction has been
37 seldom established under practical tomato production conditions.

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

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

47

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

50

51

52 **1. *Tuta absoluta*: biology and control measures**

53 The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) was originally described
54 as *Phthorimaea absoluta* by Meyrick (1917) from a male specimen collected in the Andean region
55 of Perú (<http://www.cabi.org/isc/datasheet/49260>, August 11, 2018). During the 1960s it spread
56 over South America and is now a major pest of tomato, *Solanum lycopersicum* L., on this continent
57 (Bahamondes & Mallea, 1969; Silva, Bueno, Caldeira Lins, & van Lenteren, 2015). In Europe, *T.*
58 *absoluta* was first detected in eastern Spain in 2006 (Urbaneja, Vercher, Navarro, Garcia Marí, &
59 Porcuna, 2007), and is now quickly spreading all over the world, as it was recently summarized
60 (Biondi, Guedes, Wan, & Desneux, 2018). An overview of the biology of this pest can be found in
61 Tropea Garzia, Siscaro, Biondi, & Zappalà (2012). Damage is caused by larval feeding on tomato
62 fruits, leaves, stems, buds and flowers (Gabarra et al., 2014). Since young larvae bore into plant
63 parts (either leaves, stems or fruits), chemical control is complicated and frequent applications are
64 needed. Without appropriate control measures crop losses up to 100% may occur (Biondi et al.,
65 2018).

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

72 Several control options are available to reduce *T. absoluta* numbers, which can be used as a stand-
73 alone method or within Integrated Pest Management (IPM) programs (Biondi et al., 2018).

74 However, in many countries, frequent chemical control is still widely used. Up to five sprays per
75 week and 36 sprays per tomato production cycle (Guedes & Picanço, 2012) may still result in
76 economic damage. Indeed, these frequent applications result in quick development of resistance to
77 pesticides and negative effects on the environment and human health. Therefore, it is important to

78 identify effective non-chemical, environmentally safer strategies to control the tomato leafminer,
79 and biological control may offer such a solution. To date, data on current use of biological control
80 of *T. absoluta* are mostly scattered and have not been comparatively discussed within the different
81 invaded areas. This motivated us to review the literature on arthropod natural enemies and their
82 biological control efficacy in South American and Euro-Mediterranean regions. Herein, we provide
83 an overview of the best biocontrol options currently available, as well as future research needs to
84 identify and apply new natural enemies.

85

86 **2. Biological control agents of *Tuta absoluta***

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

94

95 **2.1. South America**

96 **2.1.1. Predators**

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

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

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

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

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

130 I are unable to walk on tomato because they get trapped in the glandular hairs, as the *Orius* species
131 (Bueno et al., 2013), thus making them unsuitable for *T. absoluta* control. Other Anthocoridae
132 species have been observed preying on *T. absoluta* (Table 1), but it seems relevant to first determine
133 if they can survive and establish populations on tomato plants before embarking on further studies.
134 Information about the pest kill capacity of South American predators is often qualitative. Data about
135 lifetime predation by nymphal and adult stages of predators or, alternatively, about prey population
136 reduction in greenhouse/field experiments are only available for a few species (van Lenteren et al.
137 2017; van Lenteren, Bueno, Calvo, Calixto, & Montes, 2018b).
138 In conclusion, (a) studies on predators of *T. absoluta* in South America are far from being complete,
139 (b) one group of potential predators of *T. absoluta*, i.e. the South American Coleoptera (Table 1),
140 appears to be understudied and deserves more attention, (c) many studies are restricted to the
141 laboratory, (d) only a few of the complex of South American predators might kill enough prey and
142 be suitable candidates for augmentative biocontrol programs, (e) based on current knowledge,
143 Miridae seems to be the most promising family of natural enemies to be tested for control of *T.*
144 *absoluta*, and (f) there is hardly any regional cooperation, while the pest problem is very serious and
145 would merit better coordinated research.

146 **2.1.2. Parasitoids**

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

154 A number of reviews exhaustively summarizes the main natural enemy species of *T. absoluta* in
155 South America (Biondi et al., 2018; Luna et al., 2012, 2015). Research aimed at the biological

156 control of *T. absoluta* was initiated about 25 years ago, mostly in Argentina, Brazil, Chile,
157 Colombia and Perú, and over 50 species of primary parasitoids, native or introduced, were
158 identified (Bacci et al., 2008; Colomo, Berta, & Chocobar, 2002; Colomo & Berta, 2006; De Santis,
159 1983; Faria, Torres, & Farias, 2000; García Roa, 1989; Garrido et al., 2017; Lange & Bronson,
160 1981; Luna et al., 2012; Marchiori, Silva, & Lobo, 2004; Miranda et al., 1998; Oatman & Platner,
161 1989; Puch, 2011; Uchoa-Fernandes & Campos, 1993; Vargas, 1970).

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

166

167 **2.2. Europe and Mediterranean basin**

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

175 Several reviews have been published to highlight the impact of native natural enemies in Europe
176 and in the Mediterranean area on *T. absoluta* (Desneux et al., 2010; Gabarra et al., 2014; Ghoneim
177 2014a, 2014b; Giorgini, Guerrieri, Cascone, & Gontijo, 2018; Urbaneja et al., 2012; Zappalà et al.,
178 2013). However, further surveys have been conducted since then in Europe, North Africa and the
179 Middle East (Abbes, Biondi, Zappalà, & Chermiti, 2014; Biondi et al., 2013a; Sohrabi,
180 Lotfalizadeh, & Salehipour, 2014).

181 More than 70 species of resident generalist natural enemies have been reported for *T. absoluta* in
182 the Western Palaearctic region so far (Tables 1-2). Some of them spontaneously provide biological
183 control services, some others have been successfully used within IPM programs (Ferracini et al.,
184 2012a; Urbaneja et al., 2012; Zappalà et al., 2013). Their abundance is related to the presence of
185 wild flora and can be enhanced through habitat management strategies and conservation biological
186 control (Balzan & Moonen, 2014; Balzan, 2017; Ingegno, Candian, & Tavella, 2017b; Parolin,
187 Bresch, Poncet, & Desneux, 2014).

188 **2.2.1. Predators**

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

206 Also, pre-plant applications by releasing zoophytophagous predators onto seedling nurseries and
207 adding alternative foods to facilitate their settlement have shown interesting results (Calvo et al.,
208 2012; Nannini, Atzori, Musio, Pesci, & Porcu, 2017; Urbaneja-Bernat, Alonso, Tena, Bolckmans, &
209 Urbaneja 2013; Urbaneja-Bernat et al., 2015). Although their zoophytophagous behavior has
210 recently been found to have positive effects, such as activating plant defenses against major insect
211 pests (Naselli et al., 2016; Pérez-Hedo, Rambla, Granell, & Urbaneja, 2018), these predators are
212 known to cause injury to plants and fruits under particular environmental conditions and with prey
213 scarcity. Economic losses have been observed in tomato crops due to necrotic brown rings around
214 stems and shoots, as well as damage on flowers and fruits caused by their feeding. From this
215 perspective, the potential role of some crop and non-crop plants, for the correct management of *T.*
216 *absoluta* and of its predators, is presently being investigated in order to achieve more efficient
217 biological control (Biondi et al., 2016; Ingegno et al., 2017a, 2017b; Naselli et al. 2017a).

218 **2.2.2. Parasitoids**

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

230

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

233 **3.1 South America**

234 **3.1.1. Predators**

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

241 Among the predators listed in Table 1, less than 10 species might be suitable for use in
242 augmentative biological control after application of the evaluation criteria mentioned in section
243 2.1.1 (one coccinellid, one chrysopid, one thrips and several hemipterans of the following genera:
244 *Annona*, *Campyloneuropsis*, *Engytatus*, *Macrolophus*, *Tupiocoris*). These predators could also play
245 a role in conservation biological control, together with spiders, dermapterans, carabids, formicids,
246 sphecids and vespids. If none of the native South American predators and parasitoids alone or in
247 combination will provide sufficient control, import and release of exotic natural enemies might be
248 considered. However, the currently best effective natural enemies in Europe, predatory mirids,
249 might not be good candidates for importation to new areas because of their wide prey range and
250 zoophytophagous behavior. Environmental risk assessments of these European mirids are in fact
251 expected to present unacceptable risk. Besides, even if safe and effective natural enemies are found
252 outside South America, operating procedures related to the Nagoya protocol (Cock et al., 2010; van
253 Lenteren, 2019) will have to be followed before their importation and release.

254 Heteropteran predators comprise about 8% of all arthropod natural enemy species used in pest
255 management worldwide today (van Lenteren, 2012). These generalist predators, and particularly
256 mirids, are currently popular in biocontrol programs as they can be used for simultaneous control of

257 several pests in the same crop. Nowadays, mirid predators are used on a large scale for control of *T.*
258 *absoluta* in Europe (Calvo et al., 2012, and see section 3.2.1), but the most popular species,
259 *Nesidiocoris tenuis* (Reuter), may cause serious damage to tomato plants and fruits under certain
260 conditions (Arnó et al., 2010; Castañé, Arnó, Gabarra, & Alomar, 2011; Calvo, Bolckmans, Stansly,
261 & Urbaneja, 2009; Calvo et al., 2012; Moerkens et al., 2016). Salas Gervassio et al. (2016a) have
262 also reported that under certain climatic conditions, as higher temperatures, *N. tenuis* has a greater
263 ability to outcompete other mirid species. Hence, this potential negative impact needs to be taken
264 into account for the South American Miridae as well. In particular, the following species have
265 recently obtained much attention: *C. infumatus*, *Engytatus varians* (Distant), and *M. basicornis*
266 (Bueno et al., 2013; van Lenteren, Hemerik, Lins, & Bueno, 2016; van Lenteren et al., 2017; van
267 Lenteren, et al. 2018b). These three species appear well adapted to the climatic situations in Brazil
268 (Bueno, Calixto, Montes, & van Lenteren, 2018), establishing populations on tomato (Silva, Bueno,
269 Montes, & van Lenteren, 2016a), without being caught into the glandular hairs of tomato (Bueno et
270 al., 2013). They attack not only *T. absoluta* but also a number of other lepidopteran pests and
271 *Bemisia tabaci* (Gennadius), which can occur on tomato (Bueno et al., 2018). They have pest kill
272 capacities similar or higher than those of the successful European mirid species (van Lenteren et al.,
273 2017, van Lenteren, Bueno, Montes, Hemerik, & de Jong, 2018c). Besides, they are easy to mass
274 rear by using the same technology as applied for European Miridae, and, furthermore, they show
275 little plant and fruit injury and no economic yield loss due to zoophytophagy (Silva, Bueno, Calvo,
276 & van Lenteren, 2016b; van Lenteren et al., 2018b). Furthermore, they are attracted to herbivore
277 induced volatiles produced by tomato after attack by either *T. absoluta* or *B. tabaci* (Silva, Bueno,
278 Peñaflor, Bento, & van Lenteren, 2018). Under semi-practical greenhouse conditions two out of the
279 three mirid species were able to significantly reduce *T. absoluta* populations (van Lenteren et al.,
280 2018b), but further testing in commercial tomato greenhouses and fields is necessary to determine
281 release rates and frequencies.

282 **3.1.2. Parasitoids**

283 Egg parasitoids

284 Mass rearing and parasitism capacity of the egg parasitoids *Trichogramma nerudai* Pintureau &
285 Gerding and *Trichogrammatoidea bactrae* Nagaraja were investigated in laboratory and field
286 conditions in Argentina (Cáceres, Aguirre, Miño, & Almonacid, 2011; Riquelme Virgala & Botto,
287 2010; Tezze & Botto, 2004). Experimental releases with *T. nerudai* were carried out in northeastern
288 Argentina, and the species could be recovered in later seasons; however, this biocontrol program
289 was not continued (Cáceres et al., 2011). *Trichogrammatoidea bactrae* resulted in 90% of immature
290 survival when reared on *T. absoluta* eggs in the laboratory. Moreover, the third *Trichogramma*
291 species evaluated, *T. pretiosum* Riley, was extensively studied in Brazil (Parra & Zucchi, 2004).
292 Parasitoid lineages originating from Colombia and Brazil were released in small- to large-scale in
293 experimental and commercial fields by Haji et al. (1995), who found that a release rate of 450,000
294 wasps per hectare resulted in 20 to 68% parasitized eggs of the tomato leafminer. Studies on the
295 functional response of *T. pretiosum* have been carried out (Faria et al., 2000). Faria, Torres,
296 Fernandes, & Farias (2008) found that *T. absoluta* parasitism by *T. pretiosum* can reach up to 28%
297 in cages with tomato plants, and that parasitism occurs mainly in the upper part of the tomato plant.
298 Pratisoli & Parra (2000) found that development and reproduction of *T. pretiosum* reared on *T.*
299 *absoluta* eggs at different temperatures was poor and similar when reared on eggs of another
300 gelechiid host, *Phthorimaea operculella* (Zeller). The combined use of *Bacillus thuringiensis*
301 Berliner and different release rates of *T. pretiosum* in stalked tomato crops has been evaluated,
302 showing good tomato yield under greenhouse conditions (Medeiros, Boas, Vilela, & Carrijo, 2009;
303 Parra & Zucchi, 2004). In Chile, González (2003) assessed the effect of insecticide use on *T.*
304 *nerudai* and *T. pretiosum* and concluded that chemical control should be avoided at least five to six
305 days after the parasitoid inundative release. They recommended selecting low toxicity products
306 (thiacloprid, mineral oil and detergent) with six to seven days residual effects as maximum.
307 However, it is important to mention that natural parasitism of *T. absoluta* eggs is quite rare. Eggs
308 suffer more by predation or other mortality causes (dislodging, dissection, etc.). According to

309 Hirose (1994), host egg size restricts the species composition and richness in egg parasitoid
310 assemblages of Lepidoptera. For *T. absoluta* eggs, which barely reach 0.08 mm³ of volume,
311 expected richness is \approx 2 species (Luft, Luna, Galise, Speranza, & Virla, 2015).
312 So far, the parasitoid species commercialized in South America, although not exclusively for *T.*
313 *absoluta* biocontrol, belong to the egg parasitoid guild and are: *T. galloi* Zucchi and *T. pretiosum* in
314 Brazil (Bug Agentes Biológicos and Koppert, Brazil); *T. bactrae*, *T. nerudai*, and *T. pretiosum* in
315 Chile (Biobichos Ltda.); *T. pretiosum* in Colombia (BioAgro, Biodefensas Agrícolas Ltda., Ingenio
316 Providencia, Scientia Colombia S.A.S.); *T. pretiosum* in Ecuador (small-scale production); and *T.*
317 *bactrae*, *T. cacaeciae* Marchal, *T. exiguum* Pinto & Platiner, *T. fuentesi* Torre, *T. pinto* Voegelé,
318 and *T. pretiosum* in Perú (Senasa; www.senasa.gov.pe). Costs of inundative release of *T. pretiosum*
319 to control *T. absoluta* can reach \approx 125 US\$ per hectare in Chile, for example. In general, this
320 biocontrol agent is used in combination with other pest control tactics, or IPM, including microbial
321 insecticides based on *B. thuringiensis* against larvae, and pheromone traps to catch adults, among
322 others (Luna, Sánchez, & Salas Gervassio, 2017).

323 Larval parasitoids

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

334 Luna, Salas Gervasio, & Coviella, 2016). In Chile, Larraín (1986) described field parasitism of *T.*
335 *absoluta* larvae by *D. phtorimaeae* and provided guidelines for its conservation.

336 Although both parasitoids have valuable attributes as natural enemies, *P. dignus* seems to be a more
337 promising candidate for conservation biological control and/or seasonal augmentative release. In
338 fact, it parasitizes few gelechiid species, and it shows seasonal synchronization with host
339 populations and aggregative response to host density, and an instantaneous attack rate greater than
340 the intrinsic growth rate of the host as well (Luna et al., 2007; Nieves et al., 2015; Salas Gervasio,
341 Luna, Lee, Salvo, & Sánchez, 2016b). Currently, the following studies are being conducted with *P.*
342 *dignus* in Argentina, to: 1) optimize its mass rearing (MG Luna, unpublished data); 2) estimate
343 parasitoid release rates through semi-field trials in greenhouses (N Salas Gervasio, unpublished
344 data); 3) assess the role of plant diversity adjacent to crops in promoting parasitoid's presence
345 (Salas Gervasio et al., 2016b). Previous augmentative releases of *P. dignus* in northeastern
346 Argentina did not result in successful control in protected tomato crops (Cáceres et al., 2011).

347 Moreover, Luna, Wada, LaSalle, & Sánchez (2011) mentioned *Neochrysocharis (Closterocerus)*
348 *formosa* (Westwood) as a potential biocontrol agent based on its wide host range and presence in
349 other crops, with parasitism rates of *T. absoluta* ranging between 1.5 and 11.2%.

350 In Colombia, life cycle attributes under different temperature conditions and functional response of
351 *Apanteles gelechiidivoris* Marsh were investigated (Bajonero, Córdoba, Cantor, Rodríguez, & Cure,
352 2008). Morales, Rodríguez, & Cantor (2013) designed preliminary protocols for an affordable, high
353 quality mass rearing system, with optimal temperatures for rearing this braconid. Furthermore, a
354 mass rearing protocol to produce and release *A. gelechiidivoris* in greenhouse tomato crops against
355 *T. absoluta* was developed (Cantor Rincón, Rodríguez, & Cure Hakim, 2011).

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

360 **3.2. Europe and Mediterranean basin**

361 **3.2.1. Predators**

362 Several species of predators, such as *Dicyphus errans* (Wolff), *Macrolophus pygmaeus* (Rambur),
363 *N. tenuis* and *Nabis pseudoferus* Remane, have been evaluated as natural enemies of *T. absoluta*.
364 Moreover, their use in augmentative and conservation biological control has been recently
365 discussed by Giorgini et al. (2018). Currently, augmentative release of the mirid *N. tenuis* is
366 considered as a standard augmentative biocontrol method in protected crops in the Mediterranean
367 area thanks to its wide predatory capacity on various pests apart from *T. absoluta*, such as
368 whiteflies, thrips and mites (Calvo et al., 2016; Urbaneja et al., 2012). Sanchez, La-Spina, & Lacasa
369 (2014) performed trials with *N. tenuis* under greenhouse in southern Spain, highlighting that in
370 tomato crops *T. absoluta* density was lower where the predator had been released without any
371 significant influence of the prey abundance. In addition, the crop yield was higher in the treatments
372 with *N. tenuis* than in those without, even if the percentage of damaged fruit was similar.
373 The involvement of herbivore-induced plant volatiles in prey location by *D. errans*, *M. pygmaeus*
374 and *N. tenuis* was investigated in olfactometer and wind tunnel, providing evidence that the mirids
375 are able to discriminate between infested and healthy tomato plants using olfactory cues (De Backer
376 et al., 2015; Ingegno, Ferracini, Gallinotti, Alma, & Tavella, 2013; Bouagga et al., 2018). In the
377 laboratory, the predators *M. pygmaeus* and *N. tenuis* demonstrated similar predation characteristics
378 in intraspecific interactions. However, *N. tenuis* has proven to be more effective in preying on *T.*
379 *absoluta* than *M. pygmaeus* as it can consume more eggs at higher prey densities. Nevertheless, the
380 combination of the two predator species may lead to better pest suppression at high *T. absoluta*
381 population densities (Michaelides, Sfenthourakis, Pitsillou, & Seraphides, 2018). Finally, the
382 evidence of plant defense induction through *N. tenuis* feeding punctures (Naselli et al., 2016;
383 Bouagga et al., 2018) opens new insights into the role of predators in pest management.

384 **3.2.2. Parasitoids**

385 Egg parasitoids

386 The egg parasitoid *T. achaeae*, commercially available in Europe and North Africa, may achieve
387 high parasitism rates (>90%) under greenhouse conditions, both alone and in combination with the
388 mirid predator *N. tenuis* (Cabello et al., 2009a, 2015; Oliveira et al., 2017). A laboratory screening
389 of 29 European strains/species of *Trichogramma* parasitoids was performed to assess their potential
390 in controlling *T. absoluta*. Their performance was strongly influenced by the testing conditions. One
391 strain of *T. euproctidis* (Girault) appeared promising compared to *T. achaeae*, because it showed a
392 higher parasitism rate, higher fertility, higher proportion of females and the capacity of diapause
393 during cold storage. However, it did not perform well under greenhouse conditions (Chailleux et al.,
394 2012). In Tunisia, two native species of *Trichogramma* (*T. bourarachae* Pintureau & Babault and *T.*
395 *cacaeciae*) were effective in reducing *T. absoluta* densities when released in open field or protected
396 tomato crops. Indeed, in open field *T. cacaeciae* reached an average parasitism rate of 54.7%,
397 significantly reducing the number of *T. absoluta* eggs and larvae per leaf, while under greenhouse
398 conditions the egg parasitization averaged 57.1% and reduced the number of mines per leaf by
399 78.9% (Cherif & Lebdi-Grissa, 2013). *Trichogramma bourarachae* under greenhouse conditions
400 reached an average parasitism rate of 63.9% with a reduction in leaf damage of 87.6% (Zouba,
401 Chermiti, Chraiet, & Mahjoubi, 2013).

402 Larval parasitoids

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

407 Particular attention has been given to eulophid parasitoids, especially to the genus *Necremnus*.
408 Earlier records published as *N. sp. nr artynes*, and most of the records published as *N. artynes*,
409 belong to *N. tutae*. Similarly, the records of *N. metalarus* (Walker) parasitizing *T. absoluta* probably
410 also refer to dark forms of *N. tutae* (Gebiola et al., 2015). The effectiveness of this eulophid has
411 been investigated by Calvo et al. (2013), in combination with *N. tenuis*, finding the predator pre-

412 plant application sufficient for pest control (Calvo et al., 2016). In the laboratory, *N. tutae* caused
413 high larval mortality of *T. absoluta* because of host feeding and parasitism (Ferracini et al., 2012b;
414 Bodino, Ferracini, & Tavella, 2018). Greater intrinsic rate of increase was recorded at high
415 temperatures (30°C), suggesting the high potential by *N. tutae* in reducing this pest in
416 Mediterranean greenhouses as well (Calvo et al., 2013). Furthermore, this larval parasitoid was the
417 only species recovered in sprayed greenhouses (Zappalà et al., 2012c). Recently, functional
418 responses and lifetime foraging behaviors of *N. tutae* and *N. cosmopterix* Ribes & Bernardo were
419 investigated, highlighting a higher maximum estimated host-killing rate by the latter species
420 (Bodino et al., 2018).

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

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

433

434 **4. DISCUSSION, PERSPECTIVES AND CONCLUSIONS**

435 After its invasion in Europe about 12 years ago, *Tuta absoluta* has gained quite a diverse parasitoid
436 assemblage. Although about 70 species of predators and 100 species of parasitoids have been found
437 in association with *T. absoluta*, solutions for effective and economically realistic biocontrol are not

438 available in South America, and current options for biological control of this pest are not optimal in
439 Europe and the Mediterranean basin. It is also important to mention that much more taxonomic
440 work is needed to confirm the list of natural enemies. At least 20 predator and 34 parasitoid species
441 are still under a morphospecies status (Tables 1 and 2) and they deserve further study. Besides, for
442 many of the reported confirmed species, there are only systematic papers and biological or
443 ecological studies are lacking. Interestingly, in both regions parasitoid species mainly represent host
444 larval guilds. Hymenopteran ichneumonids, braconids, chalcidids, eulophids and trichogrammatids
445 are well represented in both South America and Europe. Instead, dipteran tachinids and
446 hymenopteran encyrtids, aphelinids and bethylids seem to be absent in Europe.

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

459 Tomato is the second most consumed vegetable fruit worldwide, and the global production is over
460 160 million tons, produced on 4.7 million ha (<http://faostat.fao.org/site/339/default.aspx>). Knowing
461 that tomato is produced on hundreds of thousands of hectares where *T. absoluta* is already present,
462 biocontrol is currently playing a very modest role.

463 The need for environmentally safe, economically sustainable and effective control strategies is even
464 stronger in developing countries. In Africa, where tomato is seen as a very promising crop for
465 horticultural expansion, the agricultural sector across the continent, and particularly the many small
466 scale farmers, is currently experiencing significant impacts from *T. absoluta*. The pest has been
467 reported in 17 African countries (<https://www.cabi.org/ISC/datasheet/49260>, October 5, 2018), and
468 losses of up to 80% of the total harvest have led to a three-fold increase in tomato prices in
469 Tanzania in 2016 (Pratt et al., 2017). The situation in Asia is equally difficult when looking at the
470 Middle East (e.g. Al-Jboory, Katbeh-Bader, & Shakir, 2012) and South West India (e.g.
471 Kalleshwaraswamy et al., 2015). The fast spread over the entire Indian region (Sankarganesh et al.,
472 2017), where tomato production is a significant economic activity, may also represent a high risk to
473 large parts of China (Xian et al., 2017). Since climatic suitability indices predict a high probability
474 for continued invasion with further spread expected to reach China and the USA within a decade by
475 2028 (Xian et al., 2017), it is clear that the search and evaluation of natural enemies of *T. absoluta*
476 are far from being over. An early-warning assessment is necessary, and since invasion is
477 irreversible, management of the pest requires finding reliable and feasible biological control
478 solutions in invaded countries, as well as those at risk.

479 To make progress with biocontrol of *T. absoluta*, a critical (re-)evaluation of natural enemies known
480 to be associated with the pest is needed. Based on current knowledge there are less than 10 species
481 of predators and three parasitoids in South America, and in Europe and the Mediterranean basin less
482 than five predators and three parasitoids might be considered promising candidates for
483 augmentative biological control of this pest. Additional species that are difficult to rear, but may
484 contribute considerably to pest mortality in (semi) natural agro-ecosystems should be considered, in
485 conservation biocontrol programs. If (re-) evaluation of the known natural enemies does not result
486 in cost-effective solutions, the next step might be to start prospecting for new natural enemies.

487 Regulatory restrictions mentioned above (see chapter 2.2), make the importation of exotic natural
488 enemies very laborious, so searching for new natural enemies should include not only the place of

489 origin, but areas where the pest may soon invade. New natural enemies have to be investigated by
490 using specific evaluation criteria making it possible to quickly prioritize species. In the case of areas
491 not yet invaded by *T. absoluta*, the following approach might be considered. First, design an
492 emergency IPM program based on methods already easily available, and check if any of the best
493 performing natural enemies in the areas where *T. absoluta* occurs are also present in the non-
494 invaded area. Then, if none of the currently used natural enemies for *T. absoluta* control is found in
495 the non-invaded area, prospecting for natural enemies should be pursued, with a preference for
496 species that attack closely related pest species. If such an approach does not result in promising
497 candidates, importation of exotic species from the pest's area of origin might be considered, but can
498 be a lengthy, expensive process due to national and international regulations.

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

509

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515

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518

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1072 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 |
| | | <i>Tanimlanmamis</i> sp. | | M | Öztemiz (2012) | R |
| | Oxiopidae | unidentified species | | SA | Desneux et al. (2010) | R |
| | Gnaphosidae | unidentified species | | SA | Desneux et al. (2010) | R |
| | Thomisidae | <i>Misumenops pallidus</i> Keyserling | larvae | SA | Medeiros (2007), Medeiros et al. (2011) | R |
| Acari | Salticidae | not specified | | SA | Desneux et al. (2010) | R |
| | Pyemotidae | <i>Pyemotes</i> sp. | larvae, pupae, adults | SA | Oliveira et al. (2007) | R |
| | Phytoseiidae | <i>Amblyseius cucumeris</i> (Oudemans) | eggs, early larvae | E | Mollá et al. (2010) | R |
| | | <i>Amblyseius swirskii</i> Athias-Henriot | eggs, early larvae | E | Medeiros et. al (2011), Mollá et al. (2010) | R |
| | Dermaptera | Labiduridae | <i>Doru lineare</i> (Eschscholtz) | eggs | SA | Desneux et al. (2010) |
| <i>Labidura riparia</i> (Pallas) | | | pupae | | Desneux et al. (2010) | R |
| Thysanoptera | Aeolothripidae | <i>Franklinothrips vespiformis</i> Crawford | eggs | SA | Desneux et al. (2010) | R |
| | Phlaeothripidae | unidentified species | eggs | SA | Miranda et al. (1998) | R |
| | Thripidae | <i>Scolothrips sexmaculatus</i> Pergande | eggs | SA | Desneux et al. (2010) | R |
| Hemiptera | Anthocoridae | <i>Amphiareus constrictus</i> (Stål) | | SA | Pereira et al. (2014), Queiroz et al. (2015) | L |
| | | <i>Blaptostethus pallescens</i> Poppius | | SA | Pereira et al. (2014), Queiroz et al. (2015) | L |
| | | <i>Lasiochilus</i> sp. | early larvae, pupae | SA | Bacci et al. (2008) | L/SF |
| | | <i>Orius</i> 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 |
| | | <i>Orius albidipennis</i> (Reuter) | - | M | Al-Jboory et al. (2012) | R |
| | | <i>Orius insidiosus</i> (Say) | eggs, larvae | SA | Desneux et al. (2010), Lins et al. (2011) | R/L |
| | | <i>Orius laevigatus</i> (Fieber) | eggs, early larvae | E | Gabarra and Arnó (unpublished data), Urbaneja et al. (2012) | R |
| | | <i>Orius majusculus</i> (Reuter) | eggs, early larvae | E | Gabarra and Arnó (unpublished data), Urbaneja et al. (2012) | R |
| | <i>Orius tristicolor</i> (White) | | SA | Pereira et al. (2014), Queiroz et al. (2015) | L | |

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

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

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|-----------|---------------------------------|--------|----|--|---|
| Sphecidae | <i>Synoeca cyanea</i> Fabricius | larvae | SA | Desneux et al. (2010), Picanço et al. (2011) | R |
| | unidentified species | larvae | E | Mollá et al. (2008) | R |

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1089 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 | | |
| | | <i>Archytas</i> sp. Jaennicke | larvae | SA | Desneux et al. (2010) | R | | |
| | | <i>Phytomyptera (Elfia)</i> sp. Rondani | larvae | SA | Desneux et al. (2010) | R | | |
| Hymenoptera | Ichneumonidae | <i>Campoplex haywardi</i> Blanchard | larvae, pupae | SA | Colomo et al. (2002) | R | | |
| | | <i>Cryptinae</i> gen. sp. | larvae | E | Zappalà et al. (2012a) | R | | |
| | | <i>Diadegma</i> sp. Förster | larvae, pupae | SA/E | Colomo et al. (2002), Zappalà et al. (2012a) | R | | |
| | | <i>Diadegma ledicola</i> Horstmann | late larvae, pupae | E | Ferracini et al. (2012a) | R | | |
| | | <i>Diadegma pulchripes</i> (Kokujev) | late larvae, pupae | E | Zappalà et al. (2012a) | R | | |
| | | <i>Hyposoter didymator</i> (Thunberg) | larvae | M | Boualem et al. (2012) | R | | |
| | | <i>Pristomerus</i> sp. Curtis | larvae | SA | Desneux et al. (2010) | R | | |
| | | <i>Temelucha</i> sp. Förster | early larvae | SA | Colomo et al. (2002) | R | | |
| | | <i>Temelucha anatolica</i> (Sedivy) | larvae, pupae | E | Gabarra et al. (2014) | R | | |
| | | <i>Zoophthorus macrops</i> Bordera & Horstmann | larvae, pupae | E | Gabarra et al. (2014) | R | | |
| | | Braconidae | | <i>Agathis</i> sp. Salisbury | early larvae | SA/E | Colomo et al. (2002), Ferracini et al. (2012a) | R |
| | | | | <i>Agathis fuscipennis</i> Zetterstedt | larvae | E | Loni et al. (2011) | R |
| | | | | <i>Apanteles</i> 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 |
| | | | | <i>Apanteles gelechiidivoris</i> Marsh | larvae | SA | Bajonero et al. (2008), Cantón Rincon et al. (2011), Morales et al. (2013, 2014), Vargas (1970) | R/L/SF |
| | | | | <i>Bracon</i> sp. Fabricius | larvae | SA/E/M | Abbes et al. (2014), Zappalà et al. (2011) | R/L |
| | | | | <i>Bracon didemie</i> Beyarslan | late larvae | M | Doğanlar & Yigit (2011) | R |
| <i>Bracon hebetor</i> Say | late larvae | | | E/M | Doğanlar & Yigit (2011), Ferracini et al. (2012a), Zappalà et al. (2013) | R | | |
| <i>Bracon lucileae</i> Marsh | early larvae | | | SA | Berta & Colomo (2000), Cáceres et al. (2011) | R | | |
| <i>Bracon lulensis</i> Berta & Colomo | early larvae | | | SA | Berta & Colomo (2000) | R | | |
| <i>Bracon nigricans</i> Szépligeti | late larvae | | | E | Biondi et al. (2012c; 2013b), Zappalà et al. (2012b, 2013) | R/L | | |

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|--------------|---|---------------|------|--|-----|
| | <i>Bracon</i> sp. near <i>nigricans</i> | late larvae | E/M | Gabarra et al. (2014), Zappalà et al. (2012b; 2013) | R |
| | <i>Bracon osculator</i> Nees | late larvae | E | Ferracini et al. (2012a), Zappalà et al. (2012a) | R |
| | <i>Bracon tutus</i> Berta & Colomo | early larvae | SA | Berta & Colomo (2000) | R |
| | <i>Chelonus</i> sp. (<i>Microchelonus</i>) | eggs, larvae | SA/E | Colomo et al. (2002), Desneux et al. (2010), Gabarra et al. (2014) | R |
| | <i>Choeras semele</i> (Nixon) | larvae, pupae | E | Gabarra et al. (2014) | R |
| | <i>Cotesia</i> sp. Cameron | larvae, pupae | E | Gabarra et al. (2014) | R |
| | <i>Diolcogaster</i> sp. Ashmead | larvae, pupae | E | Gabarra et al. (2014) | R |
| | <i>Dolichogenidea litae</i> (Nixon) | larvae, pupae | E | Gabarra et al. (2014) | R |
| | <i>Earinus</i> 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 |
| | <i>Orgilus</i> sp. Haliday | late larvae | SA | Colomo et al. (2002) | R |
| | <i>Pseudapanteles</i> (= <i>Apanteles</i>) <i>dignus</i> (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 | <i>Brachymeria secundaria</i> (Ruschka) | larvae | M | Doğanlar & Yigit (2011), Gabarra et al. (2014) | R |
| | <i>Copidosoma</i> sp. Ratzeburg | larvae | SA | Vasicek (1983) | R |
| | <i>Hockeria unicolor</i> Walker | larvae | E/M | Doğanlar & Yigit (2011), Gabarra et al. (2014) | R |
| | <i>Psilochalcis</i> (= <i>Invreia</i>) sp. Kieffer | | | | |
| | <i>Spilochalcis</i> (= <i>Conura</i>) sp. Thomson | pupae | SA | Cáceres et al. (2011), Vargas (1970) | R |
| Pteromalidae | <i>Halticoptera aenea</i> (Walker) | larvae | E | Zappalà et al. (2012b) | R |
| | <i>Pteromalus intermedius</i> (Walker) | larvae | M | Doğanlar & Yigit (2011) | R |
| | <i>Pteromalus semotus</i> (Walker) | larvae, pupae | E | Gabarra et al. (2014) | R |
| Eupelmidae | <i>Anastatus</i> sp. Motschulsky | eggs | SA | Desneux et al. (2010) | R |
| Encyrtidae | <i>Arrhenophagous</i> sp. Aurivillius | eggs | SA | Desneux et al. (2010) | R |
| | <i>Copidosoma</i> sp. Ratzeburg | egg, larvae | SA | Colomo et al. (2002) | R |
| | <i>Copidosoma desantisi</i> Annecke & Mynhardt | egg, larvae | SA | Vargas (1970) | R |
| | <i>Copidosoma koehleri</i> 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 |
| | <i>Baryscapus bruchofagi</i> (Gahan) | - | M | Doğanlar & Yigit (2011) | R |

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

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

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|------------|--|--------|----|--|-------|
| | <i>Trichogramma nerudai</i> Pintureau & Gerding | eggs | SA | Cáceres et al. (2011), Luft et al. (2015), Tezze & Botto (2004) | R/L/F |
| | <i>Trichogramma pinto</i> Voegelé | eggs | SA | Desneux et al. (2010) | R |
| | <i>Trichogramma pretiosum</i> 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), Pratisoli & Parra (2000), Vargas (1970) | R/L |
| | <i>Trichogramma rojasi</i> Nagaraja & Nagarkatti | eggs | SA | Cáceres et al. (2011), Colomo et al. (2002), Ghoneim (2014b), Luft et al. (2015) | R |
| | <i>Trichogramma telengai</i> Sorokina | eggs | M | Ghoneim (2014b) | R |
| | <i>Trichogrammatoidea bactrae</i> Nagaraja | eggs | SA | Riquelme Virgala & Botto (2010), Cagnotti et al. 2018 | R/SF |
| Bethylidae | <i>Goniozus nigrifemur</i> 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 |