J Pest Sci
DOI 10.1007/s10340-013-0531-9

RAPID COMMUNICATION

Natural enemies of the South American moth, *Tuta absoluta*, in Europe, North Africa and Middle East, and their potential use in pest control strategies

Lucia Zappalà · Antonio Biondi · Alberto Alma · Ibrahim J. Al-Jboory · Judit Arnò · Ahmet Bayram · Anaïs Chailleux · Ashraf El-Arnaouty · Dan Gerling · Yamina Guenaoui · Liora Shaltiel-Harpaz · Gaetano Siscaro · Menelaos Stavrinides · Luciana Tavella · Rosa Vercher Aznar · Alberto Urbaneja · Nicolas Desneux

Received: 16 June 2013 / Accepted: 23 September 2013

Abstract The South American tomato leafminer, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), is an invasive Neotropical pest. After its first detection in Europe, it rapidly invaded more than 30 Western Palaearctic countries becoming a serious agricultural threat to tomato production in both protected and open-field crops. Among the pest control tactics against exotic pests, biological control using indigenous natural enemies is one of the most promising. Here, available data on the Afro-Eurasian natural enemies of *T. absoluta* are compiled. Then, their potential for inclusion in sustainable pest control packages is discussed providing relevant examples. Collections were conducted in 12 countries, both in open-field and protected susceptible crops, as well as in wild flora and/or using infested sentinel plants. More than 70 arthropod species, 20 % predators and 80 % parasitoids, were recorded attacking the new pest so far. Among the recovered indigenous natural enemies, only few parasitoid species, namely, some eulophid and braconid wasps, and especially mirid predators, have promising potential to be included in effective and environmentally friendly management strategies for the pest in the newly invaded areas. Finally, a brief outlook of the future research and applications of indigenous *T. absoluta* biological control agents are provided.

Keywords Biological control · Generalist predators · Integrated pest management · Invasive species · Parasitoid community · Western Palaearctic

Communicated by M. Traugott.

L. Zappalà · A. Biondi · G. Siscaro
Department of Agri-food and Environmental Systems Management, University of Catania, via Santa Sofia 100, 95123 Catania, Italy

A. Biondi · A. Chailleux · N. Desneux (✉)
French National Institute for Agricultural Research (INRA), 400 Route des Chappes, 06903 Sophia-Antipolis, France
e-mail: nicolas.desneux@sophia.inra.fr

A. Alma · L. Tavella
Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), University of Torino, via L. da Vinci 44, 10095 Grugliasco, TO, Italy

I. J. Al-Jboory
Department of Plant Protections, University of Baghdad, Abu Ghraib, Iraq

J. Arnò
Department of Entomology, IRTA, Ctra. Cabrils km.2, 08348 Cabrils, Barcelona, Spain

A. Bayram
Plant Protection Department, Agriculture Faculty, Dicle University, 21280 Diyarbakir, Turkey

A. El-Arnaouty
Department of Economic Entomology and Pesticides, Cairo University, Giza, Egypt

D. Gerling
Department of Zoology, Tel Aviv University, 69978 Tel Aviv, Israel

Y. Guenaoui
Department of Agronomy, University Ibn Badis of Mostaganem, 27000 Mostaganem, Algeria

L. Shaltiel-Harpaz
Northern R&D, Migal–Galilee Research Institute, P.O.B. 831, 11016 Kiryat Shmona, Israel

Published online: 23 October 2013

Introduction

The composition of worldwide biotic communities has greatly changed in recent years due to the collapse of natural barriers to wild species movements mainly in relation to human activities (Liebhold and Tobin 2008). Among the newly introduced insect species, some can become invasive, with subsequent significant economic impacts. The success or failure of a biological invasion may depend on the species' life history parameters, on its response to climatic conditions, on the competition with native species and on the impact of natural enemies (Grabenweger et al. 2010). This last factor may be crucial in the invasion mechanism and the success of an invader, in terms of distribution and abundance, and could be related to the absence or low efficacy of natural control in the new territories, as stated by the so-called *Enemy release hypothesis* (Keane and Crawley 2002). Indeed, it is assumed that natural enemies in the newly invaded areas need time to get adapted to and control the exotic species effectively. This may be due to the fact that native antagonists need to adjust their behaviour and/or physiology to be able to successfully develop on the exotic prey/host. For these reasons, natural enemy complexes on invaders may perform initially low percentage predation/parasitism (Cornell and Hawkins 1993). However, several examples of successful biological control using natural enemies that have not coevolved with the pest, the so-called *New species association*, are also known (Hokkanen and Pimentel 1984; O'Connell et al. 2012).

In this framework, gaining knowledge on indigenous natural enemies that get adapted to the new hosts and understanding their role in limiting the alien species are essential for establishing the basis of suitable and sustainable control strategies of exotic pests. This also applies to one of the latest invasive species that arrived in the Western Palaearctic region: the South American tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). This moth is a Neotropical species and is considered a key pest of the tomato in South America (Guedes and Picanço 2012; Luna et al. 2012), where it remained confined until its first record in Western Palaearctic, in Spain in 2006 (Desneux et al. 2010; Tropea Garzia et al. 2012). Afterwards, it rapidly spread throughout the Mediterranean basin, in Europe, North Africa and the Middle East (Desneux et al. 2011). *Tuta absoluta* is considered a typical invasive species because of its capacity to develop very quickly on tomato cultivations and to spread rapidly in new areas causing economically relevant damage (Desneux et al. 2010; Caparros Megido et al. 2012).

Although chemical control has been the first strategy adopted in the newly invaded areas, alternative control measures are being investigated (Cagnotti et al. 2012; Cocco et al. 2013) in compliance with the EU Directive on sustainable use of pesticides (Directive 2009/128/EC). In the case of *T. absoluta*, the need for alternative control methods is strengthened by the development of resistance to insecticides by the pest (Haddi et al. 2012; Gontijo et al. 2013) as well as the side effects of pesticides on beneficial arthropods (Arnó and Gabarra 2011; Biondi et al. 2012, 2013a; and see Desneux et al. 2007 for a thorough review).

On the other hand, various predators and parasitoids spontaneously attack *T. absoluta* in tomato crops in Europe and in North Africa. Some of these, mainly native Miridae, have been already employed in integrated pest management (IPM) strategies (Castañé et al. 2011; Mollá et al. 2011; Cabello et al. 2012; Zappalà et al. 2012b; Chailleux et al. 2013a). However, several screenings for effective natural enemy species in the invaded area are still ongoing (Chailleux et al. 2012; Gabarra et al. 2013). More than 70 species of generalist natural enemies have been reported for *T. absoluta* in the Western Palaearctic region so far. These have been sampled both on open-field and protected susceptible crops as well as on wild flora and/or using infested sentinel plants. Here, we take into account all the available data, aiming to give a comprehensive picture of the composition of the species that spontaneously provide biological control services and their current role in *T. absoluta* control programmes.

Predators

Fifteen arthropod species were recorded preying on the South American tomato leafminer in the last few years in newly invaded Western Palaearctic countries (Table 1). They mainly belong to the order Hemiptera (ten species) and in particular to the families Miridae, Anthocoridae and Nabidae in descending order of species numbers. These predators include zoophytophagous bugs that usually colonize and establish in organic and IPM crops where they are also able to build up their populations before pest arrival, exploiting alternative preys, such as whiteflies, thrips, aphids, spider mites, leafminers and other Lepidoptera, and host plants [e.g. *Dittrichia viscosa* (L.) and

M. Stavrinides
Department of Agricultural Sciences, Biotechnology and Food Science, Cyprus University of Technology, Arch. Kyprianos 30, 3036 Limassol, Cyprus

R. Vercher Aznar
Instituto Agroforestal del Mediterráneo (IAM), Universitat Politècnica de València, Camino de Vera s/n, 40622 Valencia, Spain

A. Urbaneja
Departamento de Entomología, Centro de Protección Vegetal, Instituto Valenciano de Investigaciones Agrarias (IVIA), Moncada, Valencia, Spain

Table 1 Predators observed feeding on *Tuta absoluta* in Western Palaearctic countries

Order: Family	Species	Known distribution[a]	*T. absoluta* instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Mesostigmata: Phytoseiidae	*Amblyseius swirskii* Athias-Henriot	Western Palaearctic	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. (2010)
	Amblyseius cucumeris (Oudemans)	Cosmopolitan	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. (2010)
Hemiptera: Miridae	*Dicyphus* sp.		Eggs and young larvae	France, Italy	Open-field and protected crop sampling	Summer	Biondi et al. (2013b), Zappalà et al. unpublished data
	Dicyphus errans (Wolff)	Western Palaearctic	Eggs and L1	Algeria, Italy	Open-field and protected crop sampling	Spring–autumn in the open field; all year round in greenhouses	Boualem et al. (2012), Ferracini et al. (2012b), Ingegno et al. (2013)
	Dicyphus maroccanus Wagner	Mediterranean basin	Eggs and young larvae	Spain	Open-field and protected crop sampling	Summer	Mollá et al. (2010)
	Dicyphus tamaninii Wagner	Western Palaearctic	Eggs and young larvae	Algeria	Not specified	Not specified	Guenaoui et al. (2011a)
	Macrolophus pygmaeus (Rambur)	Western Palaearctic	Eggs and young larvae	Algeria, France, Italy, Spain	Open-field and protected crop sampling	Spring, summer, autumn	Arnó et al. (2009), Mollá et al. (2010), Guenaoui et al. (2011a), Boualem et al. (2012), Biondi et al. (2013b), Ingegno et al. (2013)
	Nesidiocoris tenuis (= *Cyrtopeltis tenuis*) (Reuter)	Cosmopolitan	Eggs and young larvae	Algeria, Cyprus, Egypt, France, Jordan, Iran, Israel, Italy, Morocco, Spain, Turkey	Open-field and protected crop sampling	All year round	Arnó et al. (2009), Guenaoui et al. (2011a), Karabuyuk (2011), Rizzo et al. (2011), Al-Jboory et al. (2012), Boualem et al. (2012), El-Arnaouty and Kortam (2012), Biondi et al. (2013b), R. Bouharroud pers. comm., T. Kiliç pers. comm., Martinou and Stavrinides unpublished data, Shaltiel-Harpaz and Gerling unpublished data
Hemiptera: Anthocoridae	*Orius* sp.		Not specified	Jordan	Open-field and protected crop sampling	Winter–spring	Al-Jboory et al. (2012)
	Orius albidipennis (Reuter)	South Europe, North Africa and Asia	Not specified	Jordan	Open-field and protected crop sampling	Winter–spring	Al-Jboory et al. (2012)
Hemiptera: Nabidae	*Nabis* sp.		Eggs and young larvae	Iran	Open-field crop sampling	Summer	H. Madadi pers. comm.
	Nabis pseudoferus ibericus	Western Palaearctic	Not specified	Spain	Not specified	Not specified	Mollá et al. (2010)
Neuroptera: Chrysopidae	*Chrysoperla carnea* species group		Not specified	Egypt	Open-field crop sampling	Not specified	El-Arnauty unpublished data
Hymenoptera: Sphecidae	Undetermined species		Larvae	Spain	Not specified	Not specified	Mollá et al. (2008)

Table 1 continued

Order: Family	Species	Known distribution[a]	*T. absoluta* instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Hymenoptera: Formicidae	*Tapinoma nigerrimum* (Nylander)	Western Palaearctic	Larvae	Algeria	Open-field and protected crop sampling	Summer	Guenaoui et al. (2011b)

[a] Kerzhner and Josifov (1999)

Solanum nigrum (L.)] as alternative food sources (Perdikis et al. 2007; Desneux and O'Neil 2008; Ingegno et al. 2008).

The most widely spread species are mirids belonging to the tribe Dicyphini, with *Nesidiocoris tenuis* (Reuter) spontaneously recovered in eleven countries almost all year round both in protected and open-field tomato crops and *Macrolophus pygmaeus* (Rambur) observed preying on *T. absoluta* eggs and young instar larvae in three countries. Guenaoui et al. (2011a) reported *M. caliginosus* Wagner as a predator of *T. absoluta* on tomatoes in Algeria. However, considering the great number of misconceptions comprised in the classification history of this species [=*M. melanotoma* (Costa)] and in agreement with the most recent taxonomical reconsiderations (Martinez-Cascales et al. 2006; Castañé et al. 2013), this record is likely to refer to *M. pygmaeus*; therefore, it was included accordingly in Table 1. Four other Dicyphini species [*Dicyphus* sp., *D. errans* (Wolff), *D. maroccanus* Wagner and *D. tamaninii* Wagner] were sampled from infested tomato plants in Algeria, France, Italy and Spain (Table 1). Anthocorids belonging to the *Orius* genus were found in open-field and protected tomato crops infested by *T. absoluta* in Jordan. Species of the *Nabis* genus were occasionally found in Iran and Spain. In addition, lacewings belonging to the *Chrysoperla carnea* species group were found feeding on *T. absoluta* in open-field tomato plants and two species of predatory mites [*Amblyseius swirskii* Athias-Henriot and *A. cucumeris* (Oudemans)] were also reported from the moth eggs and first instar larvae in Spain. The ant *Tapinoma nigerrimum* (Nylander) (Hymenoptera: Formicidae) was found in Algeria preying on *T. absoluta* larvae. One unidentified species of Hymenoptera Sphecidae was recovered in Spain feeding on larval instars of the moth (Table 1).

Parasitoids

A large number of parasitoid species (more than 50) were recorded developing on all the young instars and eggs of the moth in the newly invaded areas (Table 2). Overall, the most abundant parasitoid family was the Eulophidae one with 28 recovered species. *Neochrysocharis formosa* (Westwood) [=*Closterocerus formosus* (Westwood)] was one of the most widely spread, being found in four countries (Algeria, France, Italy and Spain). So far, this is the only species recorded on *T. absoluta* both in Europe and in South America, where it was mentioned as a potential biocontrol agent based on its wide host range (Noyes 2013) and the presence in other crops, with parasitism rates on *T. absoluta* ranging between 1.5 and 11.2 % (Luna et al. 2011). *Closterocerus clarus* (Szelenyi) was recovered on *T. absoluta* young larvae in Turkey. Six species belonging to the genus *Necremnus* were found developing on *T. absoluta* in Algeria, Egypt, France, Italy, Spain and Tunisia, including two entities that were identified as *N.* sp. near *artynes* and *N.* sp. near *tidius*. *Necremnus artynes* was the most abundant species in Northwestern Algeria (Guenaoui et al. 2011b). Urbaneja et al. (2012) found *N. metalarus* (Walker) developing on *T. absoluta*-infested tomato plants in Spain. However, the taxonomy of this genus is currently under revision; therefore, most of these records may need to be verified (Ferracini et al. 2012a; Zappalà et al. 2012a). Besides, other aspects of their biology and ecology should also be further investigated. The ectoparasitoids *Pnigalio incompletus* (Bouček) and *P. cristatus* (Ratzeburg), which are often associated due to their shared hosts (i.e. Diptera, Lepidoptera and Coleoptera leafminer larvae) (Noyes 2013), emerged from *T. absoluta* larvae both in Italy and in Turkey. Wasps identified as *P. soemius* or belonging to *P. soemius* species complex were recovered in Italy and in Spain (Table 2). This is a Palaearctic complex of generalist parasitoids, with intense predatory behaviour both as larvae and adults (Bernardo et al. 2006). *Stenomesius* near *japonicus* was recovered in France and in the North East of Spain on *T. absoluta* second and third instar larvae and an unidentified species belonging to the same genus was found in Algeria. Two species belonging to the genus *Elasmus* were recorded on *T. absoluta*; one, which was not identified at the species level, was found in Italy, while *Elasmus phthorimaeae* Ferrière was recorded in Eastern Spain (Table 2). Specimens of *Sympiesis* sp. near *flavopicta* and of *Hemiptarsenus ornatus* (Nees) emerged from larvae collected in open-field tomato crops in Israel. Another *Hemiptarsenus* species, *H. zilahisebessi* Erdös, and *Diglyphus isaea* (Walker) were found in association with *T. absoluta* in Algeria. The larval parasitoid *Diglyphus*

Table 2 Parasitoids recovered on *Tuta absoluta* in Western Palaearctic countries

Order: Family	Species	Known distribution[a]	*T. absoluta* instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Hymenoptera: Ichneumonidae	*Diadegma* sp.		Mature larvae–pupae	Italy	Open-field crop sampling	Autumn	Zappalà et al. (2012a)
	Diadegma ledicola Horstmann	Western Palaearctic	Mature larvae–pupae	Italy	Open-field crop sampling	Summer, autumn	Ferracini et al. (2012a)
	Diadegma pulchripes (Kokujev)	Palaearctic	Mature larvae–pupae	Italy	Open-field (potato) crop sampling, sentinel infested plant	Summer, autumn	Zappalà et al. (2012a)
	Hyposoter didymator (Thunberg)	Australasian, Western Palaearctic	Not specified	Algeria	Protected crop sampling	Spring	Boualem et al. (2012)
	Temelucha anatolica (Sedivy)	Palaearctic	Not specified	Spain	Open-field crop sampling	Not specified	Gabarra et al. (2013)
	Zoophthorus macrops Bordera & Horstmann	Spain	Not specified	Spain	Open-field crop sampling	Not specified	Gabarra et al. (2013)
Hymenoptera: Braconidae	*Agathis* sp.		Larvae not specified	Italy	Open-field crop sampling	Summer	Ferracini et al. (2012a)
	Agathis fuscipennis Zetterstedt	Western Palaearctic	Larvae not specified	Italy	Open-field sampling of infested *Solanum nigrum*	Autumn	Loni et al. (2011)
	Apanteles sp.		Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. (2013)
	Bracon sp.		Mature larvae	Tunisia	Sentinel infested plants	Spring, summer	Abbes et al. (2013)
	Bracon (=*Habrobracon*) *didemie* Beyarslan	Turkey	Mature larvae	Turkey	Open-field and protected crop sampling	Spring	Doganlar and Yigit (2011)
	Bracon (=*Habrobracon*) *hebetor* Say	Cosmopolitan	Mature larvae	Algeria, Israel, Italy, Turkey	Open-field and protected crop sampling	Spring, summer	Doganlar and Yigit (2011), Ferracini et al. (2012a), Guenaoui and Dahliz unpublished data, Shaltiel-Harpaz and Gerling unpublished data
	Bracon (=*Habrobracon*) *nigricans* (=*concolorans, concolor, mongolicus*) Szépligeti	Palaearctic	Mature larvae	Egypt, France, Italy, Jordan, Spain	Open-field and protected crop sampling, sentinel infested plants	Spring, summer	Al-Jboory et al. (2012), Urbaneja et al. (2012), Zappalà et al. (2012b), Biondi et al. (2013b), El-Arnaouty unpublished data
	Bracon (=*Habrobracon*) sp. near *nigricans*		Mature larvae	Israel, Spain	Open-field crop sampling, sentinel infested plants	Spring, summer	Gabarra and Arnó (2010), Gabarra et al. (2013), Shaltiel-Harpaz and Gerling unpublished data
	Bracon (=*Habrobracon*) *osculator* (Nees)	Palaearctic	Mature larvae	Italy	Open-field and protected crop sampling, sentinel infested plants	Summer, autumn	Ferracini et al. (2012a), Zappalà et al. (2012a)
	Chelonus sp.		Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. (2013)
	Choeras semele (Nixon)	Western Palaearctic	Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. (2013)
	Cotesia sp.		Not specified	Spain	Open-field crop sampling	Not specified	Gabarra et al. (2013)
	Diolcogaster sp.		Not specified	Spain	*Solanum nigrum*	Not specified	Gabarra et al. (2013)

Table 2 continued

Order: Family	Species	Known distribution[a]	*T. absoluta* instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
	Dolichogenidea litae (Nixon)	Western Palaearctic, Afrotropical	Not specified	Spain	Open-field crop sampling, sentinel infested plants	Not specified	Gabarra et al. (2013)
Hymenoptera: Chalcididae	*Brachymeria secundaria* (Ruschka)	Turkey	Larvae not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit (2011)
	Hockeria unicolor (Walker)	Turkey	Larvae not specified	Turkey, Spain	Protected crop sampling, sentinel infested plants	Spring	Doganlar and Yigit (2011), Gabarra et al. (2013)
Hymenoptera: Eulophidae	*Baryscapus bruchophagi* (Gahan)	Turkey	Not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit (2011)
	Chrysocharis sp.		Larvae not specified		Protected crop sampling, sentinel infested plants	Spring, summer, autumn	Zappalà et al. (2012a)
	Cirrospilus sp.		Larvae not specified	Algeria	Protected crop sampling	Spring	Guenaoui unpublished data
	Closterocerus clarus (Szelenyi)	Turkey	L1	Turkey	Protected crop sampling	Spring	Doganlar and Yigit (2011)
	Diglyphus sp.		L2	Algeria	Protected crop sampling	Spring	Guenaoui unpublished data
	Diglyphus crassinervis Erdös	Palaearctic	Not specified	Spain	Open-field crop sampling	Not specified	Gabarra et al. (2013)
	Diglyphus isaea (Walker)	Australasian, Nearctic, Palaearctic, Oriental	Larvae not specified	Algeria, Spain	Protected crop sampling, uncultivated tomato, sentinel infested plants	Not specified	Boualem et al. (2012), Gabarra et al. (2013)
	Elachertus sp.		Larvae not specified	Italy	Sentinel infested plants	Autumn	Zappalà et al. (2012a)
	Elachertus inunctus species group		Larvae not specified	Italy	Sentinel infested plants	Spring	Zappalà et al. (2012a)
	Elasmus sp.		Larvae not specified	Italy	Open-field crop sampling, sentinel infested plants	Summer	Zappalà et al. (2012a)
	Elasmus phthorimaeae Ferriere	Western Palaearctic	Not specified	Spain	Uncultivated tomato, *Solanum nigrum*	Not specified	Gabarra et al. (2013)
	Hemiptarsenus ornatus (Nees)	Palaearctic, Oriental	Larvae not specified	Israel	Open-field crop sampling	Not specified	Shaltiel-Harpaz and Gerling unpublished data
	Hemiptarsenus zilahisebessi Erdös	Palaearctic	L2	Algeria	Protected crop sampling	Not specified	Guenaoui et al. (2011b)
	Necremnus sp.		Larvae not specified	Italy, Spain	Open-field crop sampling, sentinel infested plants	Spring	Zappalà et al. (2012a), Gabarra et al. (2013)
	Necremnus artynes (Walker)	Palaearctic and nearctic	L2–L3	Algeria, Egypt, Spain, France	Open-field and protected crop (tomato, eggplant) sampling, *Solanum nigrum*, sentinel infested plants	Spring, summer	Gabarra and Arnó (2010), Mollá et al. (2010), Delvare et al. (2011), Guenaoui et al. (2011b), Kolai et al. (2011), Rizzo et al. (2011), Boualem et al. (2012), El-Arnauty unpublished data

Table 2 continued

Order: Family	Species	Known distribution[a]	*T. absoluta* instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
(Hymenoptera: Eulophidae)	*Necremnus* near *artynes*		L1–L2–L3	Italy, France, Tunisia, Spain	Open-field and protected crop (tomato, eggplant) sampling, sentinel infested plants, uncultivated tomato, *Solanum nigrum*	Spring, summer	Ferracini et al. (2012a), Zappalà et al. (2012a), Abbes et al. (2013), Biondi et al. (2013b), Gabarra et al. (2013)
	Necremnus metalarus Walker	Western Palaearctic and Nearctic	L2-L3	Spain	Open-field and protected crop sampling	Not specified	Urbaneja et al. (2012)
	Necremnus tidius (Walker)	Palaearctic and Nearctic	Not specified	Italy	Not specified	Not specified	Riciputi (2011)
	Necremnus near *tidius*		L1–L2	Italy	Open-field and protected crop sampling	Spring, summer	Ferracini et al. (2012a), Zappalà et al. (2012a)
	Neochrysocharis sp.			Algeria	Protected crop sampling	Spring	Boualem et al. (2012)
	Neochrysocharis formosa (Westwood) (=*Closterocerus formosus*)	Cosmopolitan	L1-L2-L3	Algeria, France, Italy, Spain	Open-field and protected crop sampling, sentinel infected plants, *Solanum nigrum*	Spring, summer	Lara et al. (2010), Guenaoui et al. (2011b), Ferracini et al. (2012a), Zappalà et al. (2012a), Biondi et al. (2013b), Gabarra et al. (2013)
	Pnigalio (=*Ratzeburgiola*) *cristatus* (Ratzeburg)	Palaearctic	L1–L2	Italy, Spain, Turkey	Open-field and protected crop sampling, sentinel infested plants	Spring, summer, autumn	Doganlar and Yigit (2011), Ferracini et al. (2012a), Zappalà et al. (2012a), Gabarra et al. (2013)
	Pnigalio sp. *soemius* complex		L1–L2	Italy	Open-field and protected crop sampling	Summer, autumn	Ferracini et al. (2012a), Zappalà et al. (2012a)
	Pnigalio soemius (Walker)	Palaearctic, oriental	Not specified	Spain	Open-field crop sampling	Not specified	Gabarra et al. (2013)
	Pnigalio incompletus (Boucek) (= *Ratzeburgiola incompleta*)	Western Palaearctic	Not specified	Italy, Turkey	Protected crop sampling	Spring	Doganlar and Yigit (2011), Zappalà et al. (2012a)
	Stenomesius sp.		L2–L3	Algeria	Protected crop sampling	Spring	Guenaoui et al. (2011b)
	Stenomesius sp. near *japonicus*		L2–L3	France, Spain	Open-field and protected crop (tomato, eggplant) sampling, sentinel infested plants, *Solanum nigrum*	Spring, summer	Gabarra and Arnó (2010), Biondi et al. (2013b), Gabarra et al. (2013)
	Sympiesis sp.		Not specified	Algeria, Italy	Protected crop sampling, sentinel infested plants	Spring	Boualem et al. (2012), Zappalà et al. (2012a)
	Sympiesis sp. near *flavopicta*		Not specified	Israel	Open-field crop sampling	Not specified	Shaltiel-Harpaz and Gerling unpublished data

Table 2 continued

Order: Family	Species	Known distribution[a]	*T. absoluta* instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Hymenoptera: Pteromalidae	*Halticoptera aenea* (Walker)	Nearctic, Palaearctic	Larvae not specified	Italy	Sentinel infested plants	Spring	Zappalà et al. (2012a)
	Pteromalus intermedius (Walker)	Turkey	Larvae not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit (2011)
	Pteromalus semotus (Walker)	Palaearctic, Nearctic, Oriental, Australasian	Not specified	Spain	Sentinel infested plants	Not specified	Gabarra et al. (2013)
Hymenoptera: Trichogrammatidae	*Trichogramma* spp.		Eggs	Algeria, Egypt, France, Iran, Italy, Spain	Protected crop sampling, sentinel infested plants	Spring, summer, autumn	Gabarra and Arnó (2010), Boualem et al. (2012), Zappalà et al. (2012a), Biondi et al. (2013b), Gabarra et al. (2013), El-Arnaouty unpublished data, H. Madadi pers. comm.
	Trichogramma achaeae Nagaraja & Nagarkatti	Nearctic, Neotropical, Oriental, Palaearctic	Eggs	France	Protected crop sampling	Summer	Biondi et al. (2013b)
	Trichogramma bourarachae Pintureau & Babault	Western Palaearctic	Eggs	Tunisia	Open-field crop sampling, sentinel infested plants	Spring	Zouba et al. (2013)

[a] Yu and Van Actherberg (2010), Noyes (2013)

crassinervis Erdös was recorded on *T. absoluta* only in Spain. Specimens classified as belonging to the *Elachertus inunctus* species group emerged from artificially infested sentinel plants in Italy; wasps identified as *Baryscapus bruchophagi* (Gahan) were found in Turkey. Finally, five other eulophid species, not identified at the species level (*Chrysocharis* sp., *Cirrospilus* sp., *Diglyphus* sp., *Elachertus* sp. and *Sympiesis* sp.), were also found spontaneously parasitizing the new host (see Table 2 for details).

Almost 30 % of the recovered species were Ichneumonoidea, more precisely six species belonged to the family Ichneumonidae and the remaining fourteen to the family Braconidae. Among the six ichneumonids, those belonging to the *Diadegma* genus [*Diadegma* sp., *D. ledicola* Horstmann and *D. pulchripes* (Kokujev)] were found parasitizing *T. absoluta* mature larvae and pupae in Italy. The other three ichneumonid wasps were recorded in Algeria [*Hyposoter didymator* (Thunberg)] and in Spain [*Temelucha anatolica* (Sedivy) and *Zoophthorus macrops* Bordera and Horstmann] on unspecified host instar stages. Among braconid wasps, some species were found on wild flora, (namely, *S. nigrum*), i.e. *Agathis fuscipennis* Zetterstedt, recovered in Italy, and *Apanteles* sp., *Chelonus* sp., *Choeras semele* (Nixon), *Dolichogenidea litae* (Nixon) and *Diolcogaster* sp., recorded in Spain (Table 2). *Bracon* species were already reported as *T. absoluta* parasitoids in the pest native areas (Desneux et al. 2010), and several species belonging to this genus were found developing on the exotic pest in the newly invaded areas. Some of these were found in various countries, such as *B. hebetor* Say, a worldwide distributed and very polyphagous species (Yu and Van Actherberg 2010), which was recovered on *T. absoluta* in Algeria, Israel, Italy and Turkey. The Palaearctic species *B. nigricans* (Szépligeti) was recorded parasitizing *T. absoluta* mature larvae in France, Israel (where it was reported as *B.* near *nigricans*), Italy, Jordan (where it was reported as *B. concolorans*) and Spain; whereas *B. osculator* (Nees) and *B. didemie* Beyarslan were found only in Italy and in Turkey, respectively. Two braconid wasps, not identified at the species level, *Agathis* sp. and *Bracon* sp., emerged from parasitized larvae collected in Italy and Tunisia. However, some of these records should be verified, evaluating the suitability of *T. absoluta* as host for the reported parasitoids. Indeed, many ichneumonid species are known to develop on noctuid tomato pests; therefore, if sampling was not carefully conducted, the record can be related to a co-infestation of the crop by *T. absoluta* and noctuids.

Three pteromalid species, *Halticoptera aenea* (Walker), *Pteromalus intermedius* (Walker) and *P. semotus* (Walker), were found developing on the moth larvae in Italy, Turkey and Spain respectively. Moreover, two species of chalcidid wasps, *Brachymeria secundaria* (Ruschka) and *Hockeria unicolor* Walker, were associated with *T. absoluta* in Turkey. *Tuta absoluta* eggs were parasitized spontaneously by *Trichogramma achaeae* Nagaraja & Nagarkatti in France, by *Trichogramma bourarachae* Pintureau & Babault in Tunisia and by various other unidentified *Trichogramma* species in Algeria, Egypt, France, Iran, Italy and Spain (Table 2). In South America, more than 12 species of Trichogrammatidae, four Encyrtidae and one Eupelmidae gen. sp. were reported as *T. absoluta* egg parasitoids (Desneux et al. 2010). This higher richness may be due to climatic factors as well as a more intensive monitoring of egg parasitism in the *T. absoluta* native region where many biological control programmes have been performed using egg parasitoids (Parra and Zucchi 2004; Guedes and Picanço 2012).

Potential for use of indigenous natural enemies

Studies have been carried out under laboratory conditions to assess the suitability of *T. absoluta* for various predator and parasitoid species. The seminal studies of Urbaneja et al. (2009) and Arnó et al. (2009) reported that *N. tenuis* and *M. pygmaeus* adults do actively feed on eggs (up to ~60 day^{-1}) and young larvae (~2 day^{-1}) of the moth. These results were confirmed in larger-scale (greenhouse) experiments (Mollá et al. 2011 and Bompard et al. 2013 for *N. tenuis* and *M. pygmaeus*, respectively). Similar results were obtained in the laboratory by Guenaoui et al. (2011a) with *N. tenuis* and *M. caliginosus*, by Cabello et al. (2009) studying *N. pseudoferus ibericus*, by Arnò et al. (unpublished data) for the bugs *D. tamaninii*, *O. majusculus* and *O. laevigatus*, and by Ferracini et al. (2012b) for *D. errans*.

Other studies were aimed to assess the development of mirid species when feeding on the new prey (Mollá et al. 2014) and the biology and behaviour of parasitoid species on *T. absoluta*. In the case of parasitoids, it clearly emerged that under laboratory conditions, *N.* sp. near *artynes*, *N.* sp. near *tidius* and *B. nigricans* were able to reduce significantly *T. absoluta* populations not only owing to the parasitism activity but also thanks to non-reproductive host-killing activity, namely, host-feeding and host-stinging behaviours (Ferracini et al. 2012a; Biondi et al. 2013c).

Besides the *environmental resistance* that all the recovered fortuitous natural enemies can spontaneously offer in realistic field conditions, there are several approaches that can be artificially implemented to enhance their role in regulating pest populations. Indeed, these indigenous natural enemies can be *inoculated, augmented* and *conserved* in the cultivated environment. Inoculation of mass reared *N. tenuis* has been successfully applied in tomato nurseries for the early installation of the predator population in the young crop (Calvo et al. 2012) or directly in greenhouses with the concomitant application of microbial pesticides (Desneux et al. 2010; Mollá et al. 2011). By contrast, although this generalist predator, as well as *M. pygmaeus*, has been largely employed in biological and integrated *T. absoluta* control programmes with contrasting results (Arnó et al. 2009; Abbes and Chermiti 2012; Nannini et al. 2012; Trottin-Caudal et al. 2012), it often prompts insecticide applications at high densities due to damages caused to plants and fruits (e.g. Calvo et al. 2009; Arnó et al. 2010; Castañé et al. 2011). On the other hand, *M. pygmaeus* has recently proved unable to build up its populations when feeding only on this prey (Mollá et al. 2014). Thus, higher levels of prey species diversity, such as the concomitant infestations of whiteflies (Bompard et al. 2013), are required for effective inoculative applications of this predator species.

Commercially available *T. acheae* individuals are now used against *T. absoluta* by periodic inundative releases (50 adults/m^2) in commercial greenhouses successfully (Cabello et al. 2012; Trottin-Caudal et al. 2012), whereas similar control levels can be achieved by combining the lower release rate of this egg parasitoid with mirid predators, i.e. *M. pygmaeus* and *N. tenuis* (Calvo et al. 2012; Chailleux et al. 2013a, b). Fairly good control was obtained in Southern Spain with multiple releases of *N. artynes*, although the reduction was not enough to limit fruit damage to the level reached by *N. tenuis* when released in the nursery (Calvo et al. 2012; Urbaneja et al. 2012).

Finally, the data so far obtained by laboratory bioassays, as well as through various research projects conducted in open-field and protected tomato crops in the Western Palaearctic area, suggest that the potentially effective indigenous antagonist species in *T. absoluta* control are the predators *M. pygmaeus* and *N. tenuis*, and the parasitoids *T. acheae*, *N.* sp. near *artynes*, *N. formosa*, *S.* cf. *japonicus* and *B. nigricans*. The applications of these indigenous organisms, individually and in association, should be further increased via conservation and augmentation strategies.

Future outlook

Several entomophagous species recovered on *T. absoluta*, such as *Dicyphus* spp., *Diadegma* spp., *Bracon* spp., *Necremnus* spp. and *N. formosa*, have been recorded in the past as widely spread on tomato crops also in those countries where they were not yet found in association with *T. absoluta* (Kerzhner and Josifov 1999; Yu and Van Achterberg 2010; Noyes 2013). Thus, these species most likely will be found associated to *T. absoluta* in other countries very soon, as expected in Iran (Baniameri and Cheraghian 2012). For this reason, further surveys in areas with still few records of *T. absoluta* natural enemies are encouraged. On the other hand, all the records of *T. absoluta* predator species obtained so far are derived from direct field observation and sampling, and from experimental laboratory bioassays, while no studies have been conducted using newly developed analytical techniques, such as the predator gut content molecular analysis (King et al. 2008; Juen et al. 2012). Indeed, these tools may be very useful to get an exhaustive assessment of the arthropod fauna which actually preys on new invasive pests (Harwood et al. 2007).

Moreover, applied aspects of the biology and ecology of the natural enemy species already identified as the potential key natural enemy species should be further investigated. These are, for example, their potential for mass rearing (Canale and Benelli 2012; Cicero et al. 2012), dispersal capacity (Tabone et al. 2012; Zappalà et al. 2012c), functional response to host densities (Madadi et al. 2011; Savino et al. 2012), foraging and host-searching behaviours (Gontijo et al. 2012; Ramirez-Romero et al. 2012). This is particularly needed for those species groups with an uncertain taxonomy (namely, *Necremnus*, *Bracon* and *Trichogramma* spp.), since different biological and ecological traits can be highlighted among different parasitoid cryptic species (Heimpel et al. 1997; Desneux et al. 2009b). Furthermore, in order to set up potential commercial mass rearing and/or to commercialize natural enemies throughout different countries, their taxonomy should be definitively clarified (Gordh and Bearsley 1999; Stouthamer 2008).

In order to reduce the cost of multiple egg parasitoid releases (Cabello et al. 2012) and/or plant damage of the released omnivorous predators (Castañé et al. 2011), further studies aimed at setting economically sound mass rearing protocols of other indigenous natural enemies are to be developed. This should be aimed at rearing entomophagous species having the least secondary effects on the plants (phytophagy) as well as the minimum potential for intraguild predation on other beneficials present in the crop.

The overall increase of knowledge on the indigenous natural enemy complex would help all habitat management strategies. These should be aimed at increasing the functional biodiversity within the crop and within the farm, such as rational weed management for increasing food and alternative preys/hosts for indigenous predators and parasitoids (Gardiner et al. 2009; Balzan and Wäckers 2013; Tena et al. 2013). The increase in the abundance and diversity of the natural enemy community could also be obtained through the use of the *banker plants* technique (Parolin et al. 2012a, b). Actually, the first banker plant system was developed in greenhouse tomatoes using tomato plants both as crop and banker plants (Stacey 1977). However, this made pest control harder and resulted in reduced application of the technique by the growers. Since then, this technique has been successfully tested in tomato crops using non-crop banker plants for various pest-natural enemy systems (Lambert et al. 2005; Xiao et al. 2011).

To fully exploit this strategy for *T. absoluta* control, increasing knowledge on the prey/host range of its generalist entomophagous species is crucial (Ingegno et al. 2011; Desneux et al. 2009a, 2012). Indeed, the potential applications to enhance the natural enemies' populations in the crop could be numerous. In our case, an example is the installation or conservation in the tomato crop of *Parietaria officinalis* L. plants infested by *Cosmopterix pulchrimella* Chambers (Lepidoptera: Cosmopterigidae), which is an alternative host of *N. artynes* (Ferracini et al. 2012a). Another source of *T. absoluta* antagonists could be represented by the proximity of potato plants infested by the potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), which is often attacked both by the endoparasitoid *D. pulchripes* and by the ectoparasitoid *B. nigricans* (Yu and Van Actherberg 2010). However, although increasing the "right diversity" (Landis et al. 2000) has been proved to reduce pest pressure effectively and to enhance natural enemy activity, *P. operculella* is a serious potato pest and this application should be carefully evaluated before being implemented. An important role may be also played by *D. viscosa* which is already reported as a refuge plant for several predatory bugs that do move to tomato crops providing important biological control services (Perdikis et al. 2007, 2011). However, as recently highlighted by Castañé et al. (2013) for *Macrolophus* spp., a clarification in the taxonomy of the species related to tomato is strongly needed for effective applications.

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