DPG

REVIEW

Eiphosoma laphygmae, a classical solution for the biocontrol of the fall armyworm, *Spodoptera frugiperda*?

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Abstract

The fall armyworm, *Spodoptera frugiperda*, an American Lepidoptera, is invasive in Africa and Asia and currently one of the most damaging cereal pests in the tropics. The ichneumonid parasitoid, *Eiphosoma laphygmae*, is a potential classical biological control agent. We assessed existing knowledge on biology, identified natural distributions, collated reported parasitism rates from field studies and determined which other parasitoids co-occurred. We discussed the suitability of *E. laphygmae* for classical biological control as well as identified limitations and knowledge gaps. We conducted a systematic literature review and had 185 hits, retaining 52 papers. Reports on the natural distribution of *E. laphygmae* were restricted to the American tropics, ranging from North-East Mexico to Sao Paulo State, Brazil. There were only two single and unconfirmed records of it on other hosts, suggesting that the parasitoid may be specific to *S. frugiperda*, but this needs confirmation. In fields where *E. laphygmae* occurred naturally, it was the second most important contributor to fall armyworm mortality, after the braconid *Chelonus insularis*. On average, *E. laphygmae* parasitized 4.5% of fall armyworm in field studies. The highest parasitism rates were from Costa Rica (13%) and Minas Gerais, Brazil (14.5%). However, these parasitism rates are probably largely underestimated because of likely biases in sampling and parasitism rate calculations. *Eiphosoma laphygmae* appeared to establish better in more diverse, weedy systems. As African farming systems often have high diversity, this may favour the establishment and parasitism of *E. laphygmae* if eventually introduced as a classical biological control agent.

Keywords Biological control · *Eiphosoma laphygmae* · *Eiphosoma vitticolle* · Fall armyworm · Larval parasitism · Maize · *Spodoptera frugiperda*

Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E.Smith) (Lepidoptera: Noctuidae), is one of the most damaging pests of cereals in tropical and subtropical America (Cruz et al. 1996; Rwomushana et al. 2018). In 2016, the caterpillar was first observed in West Africa (Goergen et al. 2016) and then rapidly invaded sub-Saharan Africa, Asia and Australia (CABI 2021). It is reducing food security for millions of smallholders (Day et al. 2017). In Africa, many farmers have responded to the invasive species by using synthetic insecticides, some of which are classified as highly hazardous (FAO 2018a; Tambo et al. 2019).

Biological control is an environmentally and economically safer alternative to chemical insecticides (Rebek et al. 2012; Van Driesche and Bellows 1996) and classical biological through the introduction of exotic natural enemies is particularly suitable for invasive alien species (Van Driesche and Reardon 2004; Kenis et al. 2017). Consequently, the release of native enemies in Africa and Asia should be considered (Feldmann et al. 2019; Goergen et al. 2016). An egg parasitoid of FAW, *Telenomus remus* (Nixon) (Hymenoptera, Scelionidae), was first envisaged for introduction, but it was found to be already present in many African countries (Kenis et al. 2019). It is now recommended to increase the *T. remus* population through regular releases in augmentative biological control programmes (Kenis et al. 2019).

In the Americas, most parasitoids of FAW develop in larvae. *Eiphosoma laphygmae* (Costa Lima) (Hymenoptera: Ichneumonidae), often misidentified in literature as

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Eiphosoma vitticolle (Cresson) (frequently misspelled as *E. vitticole* or *E. viticolle*) (Gauld 2000), is such a larval parasitoid (Fernandez-Triana and Ravelo 2007). However, before releasing an exotic species, the basic biology, host range and interaction with the host must be understood (van Driesche and Bellows 1996).

Our objectives were: to synthesize knowledge on the distribution, habitat, taxonomy and biology of *E. laphygmae*; to quantify impact on FAW mortality in the field; to detail pest management impacts; to determine the most important parasitoids co-occurring with *E. laphygmae,* estimating to total parasitism in the field; to describe previous attempts at rearing and releasing *E. laphygmae;* and, based on this information, to discuss the potential of *E. laphygmae* as classical biological control agent.

Methods

Data inclusion and exclusion criteria

We conducted a literature search on 11 November 2019 on the search engine 'Web of Science'. The search was in 'all languages' and 'all documents types' for 'all years (1900–2019)' in the Web of Science Core Collection with the key word '*Eiphosoma*' and had 17 hits. We simultaneously searched in Agricola, CAB-Abstracts and Food Science and Technology Abstracts. We used the keyword '*Eiphosoma*' and searched in 'all fields' with no limitations, which led to 36 initial hits. We expanded the search strategy on 12 November 2019 to Google Scholar and searched with the term '*Eiphosoma vitticolle*' OR '*Eiphosoma laphygmae*'; this resulted in 121 initial hits. We obtained 10 additional sources through using snowballing of a review by Molina-Ochoa et al. (2003) and through Cockerell (1913). We repeated the same search strategy on all search engines on 05 March 2021 and had two additional hits; however, both were not relevant for this study. On the same date, we additionally searched for '*Eiphosoma viticolle*' OR '*Eiphosoma laphygmae*' on Google Scholar resulting in 54 initial hits. After removing double hits and a first screening for relevance, 73 sources remained. We excluded 21 sources that were not about the topic or were inaccessible after exhaustive attempts to procure them. Therefore, 52 papers were included in the analysis (Fig. 1).

Data extraction and synthesis

Papers written in Spanish or Portuguese were translated to English using DeepL Translator (available at: https://www.deepl.com/translator). We followed the suggestion of Gauld (2000) and considered all species reared from *Spodoptera*

larvae as *E. laphygmae* and not *E. vitticolle*. Many of the reviewed sources were published during 1966–2000 when the two species were considered synonyms and *E. vitticolle* considered the correct name (Gauld 2000; Townes and Townes 1966).

Data on parasitism were subject to a specific analysis. The parameters related to field parasitism, reported by different authors from the field, varied. Some described the percentage *E. laphygmae* contributed to all parasitized host larvae (total parasitism), while others mentioned the percentage of parasitism by *E. laphygmae* to all, parasitized and unparasitized host-larvae (parasitism rate). Where possible, we calculated missing information on total parasitism or parasitism rates for the analysis. Articles using artificial infestation (Figueiredo et al. 2006a, b, 2009) were excluded from the analysis on parasitism but included for assessing population dynamics. Where information on the month of data collection was given, we classified this according to the season of data collection into the first and second cropping season (Table 1).

Results

We obtained 52 hits. Thirty-five of these contained field records and contributed to assessing the species' natural distribution. In addition, information from five articles, to which we did not have access to, but were cited in Molina-Ochoa et al. (2003), contributed to assessing the species natural range. From the 52 papers, six publications were categorized as containing taxonomic records on *Eiphosoma.* Five papers contained information on the habitat of the genus. The biology and behaviour of *E. laphygmae* and its impact on the host were described in 11 references. Three sources contained information on the hosts of *E. laphygmae*, and eight references recorded information of the effect of pest management on the parasitoid. Attempts of rearing and release of the species are described in six publications. Fifteen papers provided quantitative information on the species parasitism rate in the field and co-occurring parasitoid species (Table 2).

Taxonomy

Eiphosoma is a new world genus of Cremastinae (Ichneumonidae) with approximately 55 described, neotropical species, subdivided into 9 groups (Costa Lima 1953; Gauld 2000; Fernandez-Triana and Ravelo 2007; Onody et al. 2009). However, the genus is likely to have many more undescribed species (Gauld 2000). There have been four taxonomic reviews on *Eiphosoma*: Cockerell (1913), Costa Lima (1953), Gauld (2000), and Fernandez-Triana
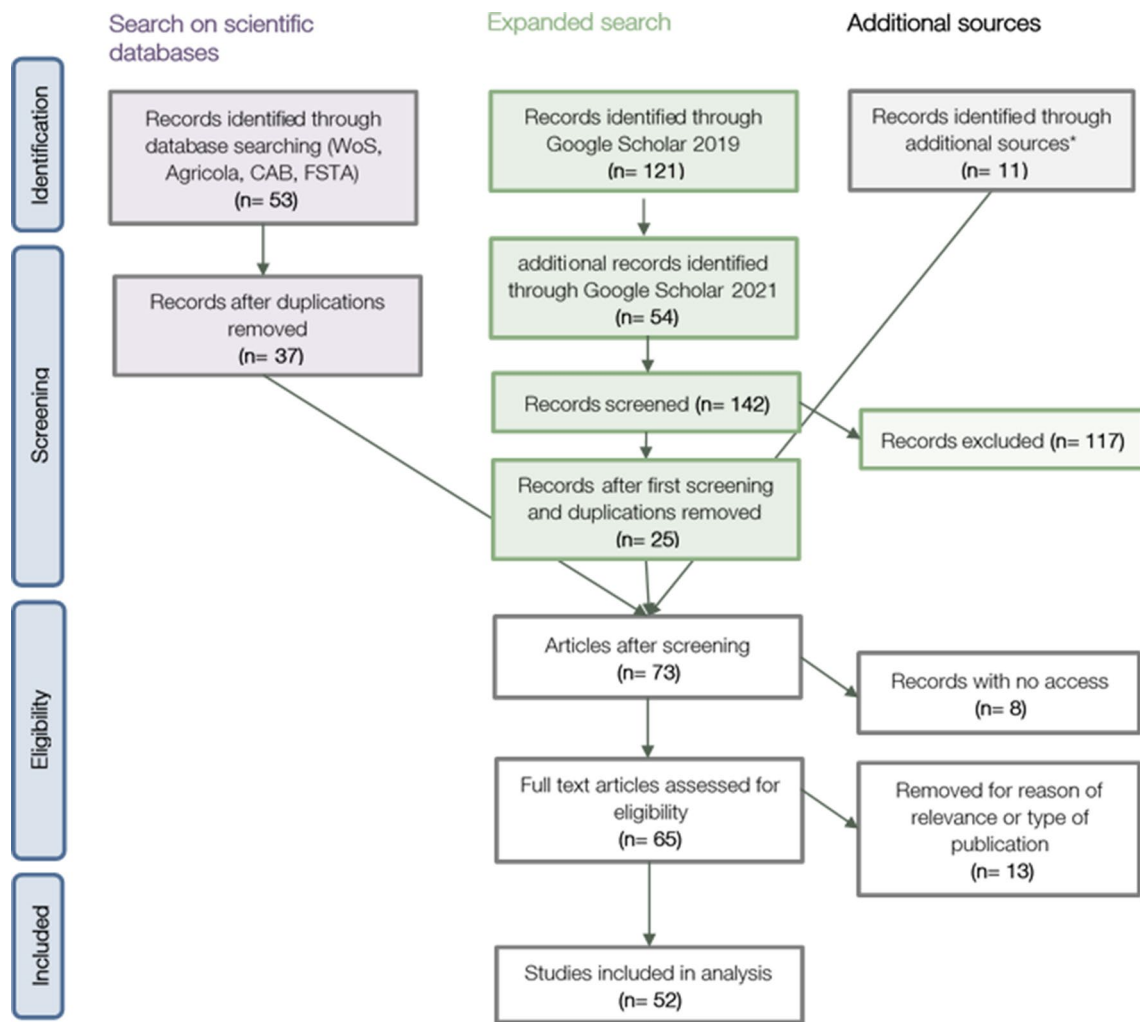
Fig. 1 PRISMA flow chart of the procedure of literature search (after Moher et al. 2009)

Table 1 Main cropping season and classification of duration of the first and second maize cropping season according to different countries and states

Country[a]	State	W/S[b]	First season	W/S[b]	Second season	Source[c]
BR	Minas Gerais	S	October–May	W	February–September[e]	Allen and Valdez (2016)
BR	Sao Paulo	S	October–May	W	January–September[e]	Allen and Valdez (2016)
BR	Maranhão	T	November–May[e]			Allen and Valdez (2016), FAO (2019)
CR		T	April–September[e]	T	August–January	FAO (2019)
HN		T	May–October[e]	T	August–February[d]	FAO (2019)
MX		S	April–February[e]	W	November–July	FAO (2019), USDA-FAS (2017)

[a]*BR* Brazil, *CR* Costa Rica, *HN* Honduras, *MX* Mexico

[b]Season of production: *S* summer, *W* winter, *T* tropical with no distinction between summer and winter

[c]Source for determining the seasons

[d]Honduras has a third maize cropping season from December–April

[e]Main cropping season in terms of production

Table 2 Summary of reviewed sources and their classification for the results

Classification	Topic	References
Distribution	Field records of *E. laphygmae*	Armenta et al. (2003), Ashley (1979), Bastidas et al. (2013), Canas and O'Neil (1998), Castro et al. (2009), Cave (1993), Cruz et al. (1997, 2009, 2010), Fernandes et al. (2020), Fernandez and Clavijo (1984), Figueiredo et al. (2006a, b, 2009), Gauld (2000), González-Moreno and Bordera (2012), Huis (1981), Jourdie et al. (2008), Lopez et al. (2002), Marenco and Saunders (1993), Medina et al. (1988)[a], Melo and Penteado-Dias (2009), von Mérey et al. (2011, 2012), Molina-Ochoa et al. (2004), Onody et al. (2012), Pair et al. (1986), Patel and Habib (1986), Patel and Habib (1982, 1984)[a], Raven (1996) cited in Rodriguez-Berrio et al. (2009), Ruìz-Cancino et al. (2010), Salas-Marina et al. (2018), Shimbori et al. (2017), Silva et al. (2008, 2012), Silveira et al. (1987)[a], Valicente (1989)[a], Wheeler et al. (1989), Yaseen et al. (1981)
Habitat	Habitat of genus *Eiphosoma*	Cortez and Trujillo (1994), Cortez-Madrigal (1998), Melo and Penteado-Dias (2009), Onody et al. (2012), Porter (1983)
Taxonomy	Taxonomic reviews	Cockerell (1913), Costa Lima (1953), Fernandez-Triana and Ravelo (2007), Gauld (2000)
	New *Eiphosoma* species	Melo et al. (2012), Onody et al. (2009)
Biology and behaviour	Behaviour during feeding and mating	Giraldo-Vanegas and Garcia (1994a)
	Behaviour during oviposition and attacked instars	Ashley et al. (1982), Ashley (1983), Giraldo-Vanegas and Garcia (1994a, 1995), Lopez et al. (2002), Penagos et al. (2005)
	Effect of parasitism on *S. frugiperda* and instar of *E. laphygmae* emergence	Ashley (1983), Marenco and Saunders (1993), Penagos et al. (2005), Pérez-Kepp (2007), Wheeler et al. (1989)
	Immature stages of *E. laphygmae*	Giraldo-Vanegas and Garcia (1992, 1994b)
Parasitism rates and population dynamics	Parasitism rates of *E. laphygmae* in the field and population dynamics which co-occurring parasitoids	Armenta et al. (2003), Cruz et al. (1997, 2009, 2010), Figueiredo et al. (2006a, b, 2009), Jourdie et al. (2008), Marenco and Saunders (1993), von Mérey et al. (2011, 2012), Molina-Ochoa et al. (2004), Patel and Habib (1986), Silva et al. (2008), Wheeler et al. (1989)
Specificity	Host species of *E. laphygmae*	Cave (1993), Gauld (2000), Ruìz-Cancino et al. (2010)
Pest management impacts	Effect of growth regulators	von Mérey et al. (2012)
	Effect of green leaf volatiles	von Mérey et al. (2011)
	Effect of Bt-maize	Castro et al. (2009)
	Effect of insecticides	Fernandez and Clavijo (1984), Figueiredo et al. (2006b), Penagos et al. (2005)
	Effect of polyhedrosis virus	Cruz et al. (1997), Figueiredo et al. (2009)
Rearing and release of *E. laphygmae*	Records of rearing and attempted release of *E. laphygmae*	Ashley (1983), Giraldo-Vanegas and Garcia (1992, 1994b, 1995), Lopez et al. (2002), Yaseen et al. (1981)

Some references contribute to multiple topics/classifications

[a] Access to these sources was not available; they are all cited in Molina-Ochoa et al. (2003)

and Ravelo (2007). After the publications of these reviews, Onody et al. (2009) and Melo et al. (2012) both described a new species from Brazil.

Although the genus *Eiphosoma* is easy to identify, it is difficult to distinguish species from each other (Gauld 2000). Townes and Townes (1966) synonymized *E.*

laphygmae with *E. vitticolle.* Nevertheless, Gauld (2000) resurrected *E. laphygmae* from this synonymity, mainly because of different rearing records but also because of minor morphological and colour differences. Within their group, the completely yellow mesopleuron mainly distinguishes *E. vitticolle* from *E. laphygmae,* which has black marks on the mesopleuron (Gauld 2000). Gauld (2000) stated that all specimens, which have been reared from *Spodoptera* larvae, are *E. laphygmae,* not *E. vitticolle*. The host of *E. vitticolle* is unknown (Gauld 2000). However, many of the works cited in this paper were written during the period when the two species were synonymized.

Distribution and habitat

Eiphosoma laphygmae is widely distributed in the American neotropics, from Sao Paulo in southern Brazil (Melo et al. 2012; Onody et al. 2012; Patel and Habib 1986) to Tamaulipas, northern Mexico (Ruíz-Cancino et al. 2010; Gauld 2000; Pair et al. 1986) (Figs. 2, 3). It is also present in the Caribbean, from Cuba to Trinidad (Gauld 2000; Fernandez-Triana and Ravelo 2007).

Eiphosoma spp. are known to live in lowlands (below 1500 m), open and degraded habitats (Fernandez-Triana and Ravelo 2007). They tend to prefer open forests, fields

Fig. 2 Countries from which *E. laphygmae* has been reported with sources (*n* = 40)
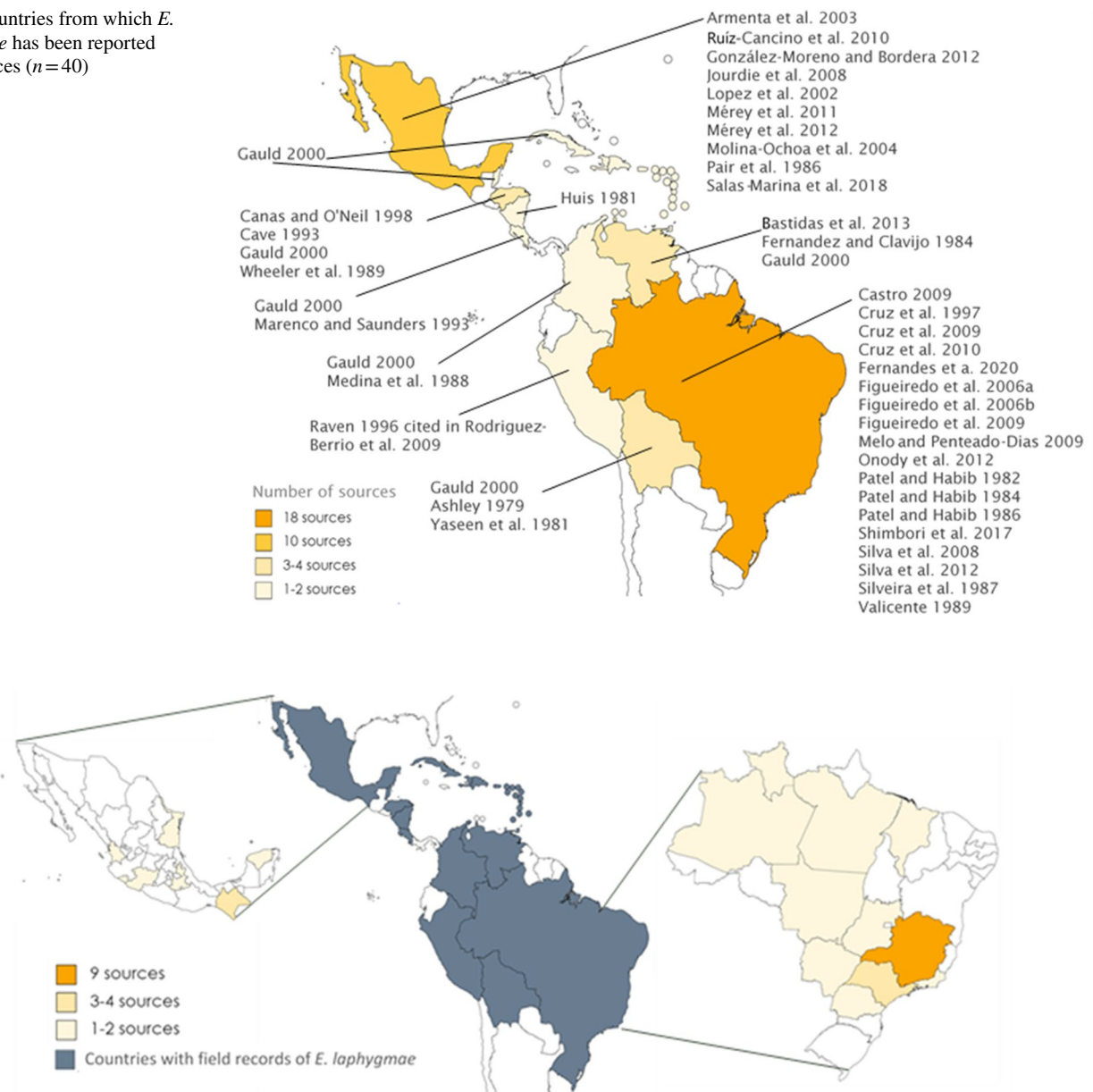

Fig. 3 Field observations of *E. laphygmae* at the state level in Mexico (*n* = 10) and Brazil (*n* = 18). See Fig. 2 for references

and sunny habitats (Porter 1983). *Eiphosoma* spp. are most diverse in the semi-deciduous mesophilic forest, followed by the Amazonian forest and the Cerrado (Melo and Penteado-Dias 2009). Onody et al. (2012) observed populations of *Eiphosoma* spp. in different organic gardens and stated that the management had a greater influence on them than climatic variables. Cortez and Trujillo (1994) tested the effect of three different agroecosystems on the natural enemies of FAW. The occurrence of control agents was higher in more diversified systems; this result is also supported by other authors (Cortez and Trujillo 1994; Molina-Ochoa et al. 2004; Onody et al. 2012). Cortez-Madrigal (1998) found that *E. laphygmae* was the predominant species in maize fields with weeds, while *Chelonus. insularis* (Cresson, 1865) (Hymenoptera: Braconidae) dominated in maize without weeds.

Biology and behaviour

Upon emergence, adults search for food by continuously moving their antennae perpendicularly, in a type of 'drumming' movement, rapidly opening their antennae to search for food (Giraldo-Vanegas and Garcia 1994a). In the laboratory, adults can be fed with honey and maize pollen (Giraldo-Vanegas and Garcia 1995). Upon finding food, *E. laphygmae* positions its body horizontally and straightens the antennae in a 45° angle from the body (Giraldo-Vanegas and Garcia 1994a). *Eiphosoma laphygmae* does not feed on the body fluids of the host as many other parasitoids do (Giraldo-Vanegas and Garcia 1994a). Adults can mate immediately after emergence, and females have even been observed to allow multiple copulations on the day of emergence so there is no pre-mating period (Giraldo-Vanegas and Garcia 1994a). This creates a competitive advantage as females become fertile quickly (Giraldo-Vanegas and Garcia 1994a).

López et al. (2002) reported that reproduction begins 6–8 days after emergence at 24.5 °C, while Giraldo-Vanegas and Garcia (1995) observed, at the same temperature, a pre-oviposition period of 1.6–3.5 days, depending on the available food (Table 3). To locate the host, a female follows the 'track' left behind by FAW-larvae by 'drumming' with her antennae. From the authors' description, it is unclear what is creating this 'track' for *E. laphygmae* (e.g. host-silk, host-salvia, host-frass). When the female has strong stimuli, she bends forward to oviposit. However, if she senses that there is no larva, but rather frass, she straightens up and continues to search (Giraldo-Vanegas and Garcia 1994a). Once a larva is detected, she continues the 'drumming' movement and inserts the ovipositor with preference to the central part of the larvae at the level of the pleura. No paralysis of the host has been observed (Giraldo-Vanegas and Garcia 1994a). In Chiapas, Mexico, in field cage trials, *E. laphygmae* was most active in the morning between 08:00 and 11:00 h and in early evening from 16:00 to 18:00 h (López et al. 2002). Ashley (1983) let the species oviposit by exposing *S. frugiperda* larvae on a disk of artificial diet. He reported that *E. laphygmae* preferred to search for FAW-larvae by piercing into depressions, which were cut into the diet beforehand, with their ovipositor.

López et al. (2002) stated that the parasitoid attacked the second, third and fourth FAW instars, while Penagos et al. (2005) reported that it attacked only second and third instars. However, other authors observed that *E. laphygmae* primarily oviposit on first and second instars (Ashley et al. 1982; Ashley 1983). Data from López et al. (2002) indicated that parasitism rates by *E. laphygmae* are higher on young maize plants, up to an age of 18 days after emergence, than on older plants. However, the same trial data also revealed that first- and second-instar larvae were more abundant on plants 11–18 days post-emergence, while third- and fourth-instar larvae dominated 25- to 39-day-old maize. Larval density can affect parasitism rates (López et al. 2002). In a field trial, higher larval density increased total parasitism of *S. frugiperda.* However, the higher parasitism levels were mainly due to an increase in the proportion of larvae parasitized by *Ch. insularis* (López et al. 2002). Due to its behaviour, *E. laphygmae* may receive kairomonal stimulation, and it may have chemoreceptors in the antennae, as they are important in searching for food, mating and oviposition (Giraldo-Vanegas and Garcia 1994a).

Table 3 Mean preoviposition period, oviposition period and daily oviposition rate of *E. laphygmae* fed with three different sources of food under laboratory conditions. *Source*: adapted from Giraldo-Vanegas and Garcia (1995)

Food source	Preoviposition[c] (days)	Oviposition period[d] (days)	Daily oviposition rate[e]
Water	$3.5^a \pm 1.3$	$9.8^b \pm 1.5$	$0.23^a \pm 0.03$
Water + honey	$3.2^{a,b} \pm 1.3$	$14.4^{a,b} \pm 3.5$	$0.57^b \pm 0.18$
Water + honey + pollen	$1.6^b \pm 0.6$	$17.2^a \pm 4.0$	$0.83^b \pm 0.19$

[*]The means within each column with the same letter (i.e. a, b) do not differ significantly ($p < 0.05$)

[c]Period before oviposition of the first egg

[d]Period between oviposition of the first egg until the last egg

[e]Number of eggs per larvae and day

Giraldo-Vanegas and Garcia (1995) studied the influence of food on *E. laphygmae* reproduction. Water, water and honey, and a mixture of water, honey and maize pollen were compared. Daily oviposition rate, preoviposition and oviposition period were significantly different for treatments with honey compared to the treatment with only water (Table 3). Since the egg production depends on the nutrition of the adults, it is assumed that *E. laphygmae* is synovigenic (Flanders 1950; Giraldo-Vanegas and Garcia 1995). Synovigenic females require a source of protein for continuous egg production throughout their adult life (Hagen 1950, 1953).

Spodoptera frugiperda larvae can prevent the development of *E. laphygmae* through melanization and hemocytic encapsulation of the parasitoid egg (Pérez-Kepp 2007). In choice tests, where some hosts were infected by an invertebrate iridescent virus, oviposition by *E. laphygmae* was significantly higher on infected larvae (33%) than on uninfected ones (17%) (López et al. 2002). Infected larvae were unresponsive to the attacking female. On the contrary, when uninfected larvae were touched by the parasitoid, they waved the upper half of their body actively back and forth at a rate of 1.2 s^{-1} (López et al. 2002). Infected larvae often died prematurely and so the endoparasitoid did not develop. So *E. laphygmae* parasitized these infected larvae, although they were unsuitable hosts. This implies a time-limited than an egg-limited reproduction (López et al. 2002). According to the optimal foraging theory (Godfray 1994), egg-limited parasitoids have very high fitness costs when they oviposit on an unsuitable host, but these costs are insignificant for time-limited wasps (Godfray 1994; López et al. 2002). In Lopéz et al.'s experiment, all females that stung an infected host transmitted the virus to subsequently attacked larvae (López et al. 2002). Yet females emerging from infected hosts did not transmit the virus (López et al. 2002).

Ashley (1983) studied growth pattern alterations in FAW after oviposition by different species and found a significantly prolonged duration of the second instar when parasitized by *E. laphygmae*. Maximum larval weight was reduced by 62% compared with non-parasitized sixth-instar larvae, and by 17% for non-parasitized fourth-instar larvae (Ashley 1983). The development of immature *E. laphygmae* has been studied by Giraldo-Vanegas and Garcia (1992, 1994b). In brief, the life cycle from oviposition to adult emergence lasted, on average, 27.8 ± 1.5 days at 24.5 °C and 70% ± 10% relative humidity (Giraldo-Vanegas and Garcia 1994b). *Eiphosoma laphygmae* has four larval instars and a prepupal stage in the cocoon (Giraldo-Vanegas and Garcia 1992) (Table 4).

The female deposits her egg in the haemocele of the host; there it floats freely until it stops at the posterior of the host's body (Giraldo-Vanegas and Garcia 1994b). Two days after oviposition, the first larva hatches, developing slowly during the first nine days and feeding on the

Table 4 Number of observations (*N*) and duration (mean ± s.e.) of instars of *Eiphosoma laphygmae*. *Source*: Adapted from Giraldo-Vanegas and Garcia (1994b)

Instar[a]	Days[b]	*N*	Duration (days)[c]
Egg	0–4	n.a	2.06 ± 1.08
I	2–10	84	4.49 ± 2.51
II	8–12	43	2.84 ± 1.40
III	11–15	37	2.89 ± 1.33
IV	13–16	39	2.64 ± 1.11
V Prepupa	n.a	23	1.12 ± 0.33
Pupa	n.a	36	11.81 ± 0.88

[a]Under laboratory conditions (24 °C and 70% ± 10% relative humidity)

[b]Days since oviposition during which the instars were observed

[c]Mean duration of the instar under laboratory conditions with standard deviation

haemolymph by cuticular absorption (Giraldo-Vanegas and Garcia 1994b). Since the larva initially does not consume any vital organs, the host develops normally in the early instars (Giraldo-Vanegas and Garcia 1994b). The larva moves within the haemocele of its host to its caudal appendage up to the level of the Malpighian tubules (Giraldo-Vanegas and Garcia 1994b). The loss of the cephalic capsule differentiates the second instar from the first; here, the larvae possibly begin to feed on sources other than the haemolymph (Giraldo-Vanegas and Garcia 1994b). Growth rate increases noticeably from the 10th to 13th day after parasitism, hampering host development, and the larvae feeds on adipose tissue and, then, later all organs of the host except for the integument. One to two days before emergence the host drills into the soil or any other substrate and goes into a prepupal stage, in which it also prepares its pupal cell. Before emerging, the larva is in reverse position in the host, with its head capsule pointing towards the posterior end of the host (Giraldo-Vanegas and Garcia 1994b). The FAW is in its fifth instar when *E. laphygmae* emerges (Ashley 1983; Marenco and Saunders 1993; Penagos et al. 2005; Wheeler et al. 1989). Once emerged, the larva immediately begins to weave a silk cocoon (Giraldo-Vanegas and Garcia 1994b). At 24.5 °C, the fourth instar was observed for 13–16 days after parasitism (Giraldo-Vanegas and Garcia 1994b). López et al. (2002) observed that *E. laphygmae* emerged from the host 12 days after parasitism at 26 °C, so development rate increased with higher temperature. Once in the cocoon, the prepupal stage lasts one day (Giraldo-Vanegas and Garcia 1994b). At 26 °C, the pupal stage lasts 12 days for males and 13 days for females (López et al. 2002). The emerging adult breaks the cocoon with its jaws then rests, hardens the cuticula, spreads its wings, cleans its body and searches for food (Giraldo-Vanegas and Garcia 1994b).

Specificity of *E. laphygmae*

Based on the reviewed literature, *E. laphygmae* seems to be highly specific to *S. frugiperda* in the Americas. However, Gauld (2000) mentioned one specimen of *E. laphygmae* as a parasitoid of *Alabama argillacea* (Hübner), the cotton leafworm, in Venezuela. The specimen was found at the United States National Museum of Natural History and had been collected by Clavijo and Ribot in 1970. Ruíz-Cancino et al. (2010) also mention *Alabama argillacea* as a host of the parasitoid. However, the authors cited Gauld (2000), and it is unclear whether they refer to the same specimen as Gauld (2000) or another one. The cotton leafworm, once the most important cotton pest, which was native to the Americas, apparently became extinct by the end of the twentieth century (Wagner 2009). Additionally, *Anticarsia gemmatalis* was reported as a host of *E. laphygmae* in Honduras (Cave 1993). It is unclear how many parasitized specimens were found, and on which crop they were collected. *Eiphosoma laphygmae* has never been reported as a parasitoid of *A. argillacea* and *A. gemmatalis* in field studies, although *A. gemmatalis* is an important pest of soybean (Knaak and Fiuza 2005). It is possible that the host species were misidentified or mixed up during rearing.

Eiphosoma laphygmae parasitism rates and population dynamics

On average, *E. laphygmae* parasitized 4.5% (*n* = 19) of the FAW in the fields in the Americas, the median being lower (3.1%) (*n* = 19) (Table 5). Parasitism rates by *E. laphygmae* in the field were highly variable between different sites (Fig. 4), ranging from 0.7% of all collected FAW larvae in Sao Paulo, Brazil (Patel and Habib 1986), to 14.5% in Minas Gerais (Brazil) (Cruz et al. 2010). Sampling technique was similar for 14 locations, whereby larvae were collected from the plants and reared under controlled conditions. Only in Honduras were plants cut and dissected for larvae (Wheeler et al. 1989). However, the season of data collection can influence parasitism rates. von Mérey et al. (2012) reported much higher parasitism rates by *E. laphygmae* in the second cropping season than in the first one in Mexico but does not quantify it. Only three out of the 15 reviewed studies collected data in a second cropping season (Cruz et al. 2010; Marenco and Saunders 1993; von Mérey et al. 2011), yet these reported highest parasitism rates of all reviewed locations (14.5%,13.0% and 6.7% respectively). In Brazil, in the state Minas Gerais the mean parasitism rate of *E. laphygmae* in the first cropping season was 2.7% (*n* = 6), while Cruz et al. (2010) found 14.5% in the second cropping season. In Honduras, *E. laphygmae* was most abundant from July to September on maize (first cropping season) but was most abundant on sorghum in the second cropping

season (unpublished data, Cave 1993). The contribution of the species to total parasitism varies also greatly between sites. In the same year *E. laphygmae's* contribution to total parasitism was 100% in Tejabán (Mexico) and 3.3% in Los Mezcales (Mexico) (Molina-Ochoa et al. 2004). *Chelonus insularis* was the dominant parasitoid in 15 of 25 sites where *E. laphygmae* was observed (Fig. 5) and was responsible for 48% of total parasitism of the three most dominant species. *Ch. insularis* was followed by *E. laphygmae,* the most dominant parasitoid in 4 out of 25 locations and contributing 27% to total parasitism of the three most dominant species (Fig. 6). Other parasitoids contributing significantly to total parasitism were *Campoletis flavincincta* (Ashmead) and *Pristomerus spinator* (Fabricius). Marenco and Saunders (1993) observed that high parasitism by *E. laphygmae* coincided with low levels of *Pristomerus spinator*, implying that the two parasitoids are in competition. Other natural enemies were: *Meteorus sp.*, *Archytas marmoratus* (Townsend), *Archytas incertus* (Macquart), *Lespesia sp.*, *Lespesia lanei* (Guimaraes), *Ophion flavidus* (Brullé), *Hexamermis sp.*, *Exasticolus fusciornis* (Cameron) and *Chelonus cautus* (Cresson).

Pest management impacts

von Mérey et al. (2012) assessed the impact of plant growth regulators on *E. laphygmae*; however, no impact was found (von Mérey et al. 2012). von Mérey et al. (2011) assessed the effect of green leaf volatiles on parasitism rates of *S. frugiperda;* no effect was found for *E. laphygmae* (von Mérey et al. 2011). Castro et al. (2009) compared the impact of conventional versus genetically modified *Bacillus thuringiensis* maize (Bt-maize) on natural enemies of *S. frugiperda*. There were fewer FAW-larvae on Bt-maize, but only in the first 15 days after plant emergence, which seemed to be related to a higher number of natural enemies, including *E. laphygmae,* in conventional fields, but it is unclear whether this difference was significant (Castro et al. 2009).

There have been few studies on the effect of insecticides on *E. laphygmae*. In a field trial testing the effect of the organophosphate pesticide chlorpyrifos on natural enemies of the FAW, *E. laphygmae* accounted for 12.3% of larval mortality before spraying. After spraying, the insecticide was responsible for 97.54% larval mortality, whereas *E. laphygmae* was accounted for 0.25% larval mortality (Figueiredo et al. 2006b). Fernandez and Clavijo (1984) observed that the natural enemy population, including *E. laphygmae*, were significantly lower using diazinon, a non-systemic organophosphate insecticide, than when using Thuricide, containing *B. thuringiensis* var. *kurstaki*. Figueiredo et al. (2009) assessed natural enemy population before and after spraying *Baculovirus spodoptera*, a nuclear polyhedrosis virus. The contribution of *E. laphygmae* to larval mortality

Table 5 Total parasitism of *Spodoptera frugiperda* (J. E. Smith) larvae in maize and sorghum fields at different locations in the Americas

Country[a]	State[b]	Location	Year[c]	E.sp.[d]	Crop[e]	Sampling[f]	Pr. sp.[g]	N	p. rate E.sp.(%)[h]	t. p. (%)[i]	E.sp. cont. t. p. (%)[j]	Source
BR	MG	Sete Lagoas	n.a.	sp.	M	l, ncut	C.f.	n.a.	n.a.	16.4	15.6	Cruz et al. (1997)
BR	MG	Sete Lagoas	n.a.	1	M	l, ai, cut	C.i.	n.a.	n.a.	55.3	18.5	Figueiredo et al. (2009)
BR	MG	Sete Lagoas	2001–2002	1	M	l, ai, cut	C.i.	2198	12.9	52.5	24.6	Figueiredo et al. (2006b)
BR	MG	Sete Lagoas	2002–2003	1	M,S	l, ai, cut	C.i.	n.a.	n.a.	40.7	13.0	Figueiredo et al. (2006c)
BR	MG	Sete Lagoas	2008	1	M	l, ncut	C.i.	109	14.5	36.4	39.9	Cruz et al. (2010)
BR	MG	21 Municipalities	2007–2008	1	M	l, ncut	C.i.	4107	4.7	23.1	20.2	Cruz et al. (2009)
BR	MG	15 Municipalities	2008–2009	1	M	l, ncut	C.f.	4609	3.1	19.4	15.7	Cruz et al. (2009)
BR	MG	15 Muncipalities	2009–2010	1	M	l, ncut	A.m.	3937	3.5	18.4	19.3	Cruz et al. (2009)
BR	MN	3 locations	2003–2004	1	M	l, ncut	C.i.	698	1.6	21.5	7.3	Silva et al. (2008)
BR	SP	location 1	1976–1980	v	M	n.a.	C.t.	855	2.6	27.8	9.3	Patel and Habib (1986)
BR	SP	location 2	1976–1980	v	M	n.a.	C.f.	678	0.7	24.9	3.0	Patel and Habib (1986)
MX	CH	Jaritas	2005	v	M,S	l, ncut	E.sp.	150	2.7	4.0	67.5	Jourdie et al. (2008)
MX	CH	Jaritas	2005	v	M,S	l, ncut	C.i.	150	4.7	16.0	29.4	Jourdie et al. (2008)
MX	CH	Jaritas	2005	v	M,S	l, ncut	C.i.	56	8.9	58.9	15.1	Jourdie et al. (2008)
MX	CH	Frontera Hidalgo	1998	v	M	l, cut	C.i.	463	n.a.	n.a.	2.4	Armenta et al. (2003)
MX	COL	Pueblo Juárez	2000	v	M	l, ncut	E.sp.	90	2.2	4.4	50.0	Molina-Ochoa et al. (2004)
MX	COL	Los mezcales	2000	v	M	l, ncut	C.i.	90	1.1	33.3	3.3	Molina-Ochoa et al. (2004)
MX	MI	Tejabán	2000	v	M	l, ncut	E.sp.	90	3.3	3.3	100.0	Molina-Ochoa et al. (2004)
MX	MI	Las yeguas Parácuaro	2000	v	S	l, ncut	E.sp.	90	2.2	3.1	71.0	Molina-Ochoa et al. (2004)
MX	MI	El Ciríán	2000	v	M	l, ncut	P.s	90	5.6	42.2	13.3	Molina-Ochoa et al. (2004)
MX	NY	El Pichón	2000	v	M	l, ncut	M.sp.	95	1.1	4.2	26.2	Molina-Ochoa et al. (2004)
MX	PS	Agua Fria	2009	v	M	n.a.	C.i.	n.a.	6.8	37.6	18.0	von Mérey et al. (2011)
MX	PS	Agua Fria	2008, 2009	v	M	l, cut	C.i.	n.a.	n.a.	n.a.	16.4	von Mérey et al. (2012)
CR	CG	Turrialba	1984, 1985	v	M	n.a.	C.i.	1528	13.0	65.0	20.0	Marenco and Saunders (1993)
HN	OL,EP	5 locations	1984	v	M	l, cut	C.i.	1456	2.3	45.0	5.1	Wheeler et al. (1989)

Predominant parasitoid species, parasitism rate of *Eiphosoma vitticole* (Cresson) or *Eiphosoma laphygmae* (Costa Lima) and contribution of *E. sp* to total parasitism

Additionally, field data on the year, season and sampling method of data collection are provided

[a] *BO* Bolivia, *BR* Brazil, *CR* Costa Rica, *HN* Honduras, *MX* Mexico

[b] *CH* Chiapas, *COL* Colima, *CG* Cartago, *MG* Minas Gerais, *MI* Michoacan, *MN* Maranhão, *NY* Nayarit, *PS* Puebla State, *SP* Sao Paulo

[c] Year of data collection: If the year of data collection is separated by ',' data were collected in two consecutive years

[d] Species identified by authors: l = *E.laphygmae* (Costa Lima), v = *E. vitticole* (Cresson), sp. = *E.sp* not identified but the species parasitized *S. frugiperda* larvae

[e] Crop from which data were collected: *M* maize, *S* sorghum

[f] l = larvae (collected and reared individually on diet until death or parasitoid emergence), ai = artificial infestation with *S. frugiperda* egg masses, cut = plants were cut in the field and dissected for larvae, ncut = larvae were collected from standing plants without cutting and dissecting the plants

[g] Most dominant parasitoid at location: *A.m.* = *Archytas marmoratus* (Townsend), *C.f.* = *Campoletis flavicincta* (Ashmead), *C.i.* = *Chelous insularis* (Cresson), *C.t.* = *Chelonus texanus* (Cresson), *E.sp.* = *Eiphosoma laphygmae* (Costa Lima) or *Eiphosoma vitticolle* (Costa Lima), *M.sp.* = *Meteorus sp.*, *P.s.* = *Pristomerus spinator* (Fabricius)

[h] Parasitism rate of *E.sp* (percentage of all collected *S.frugiperda*-larvae parasitized by *E.sp*)

[i] Total parasitism = percentage of parasitized *S. frugiperda*-larvae of all collected host-larvae

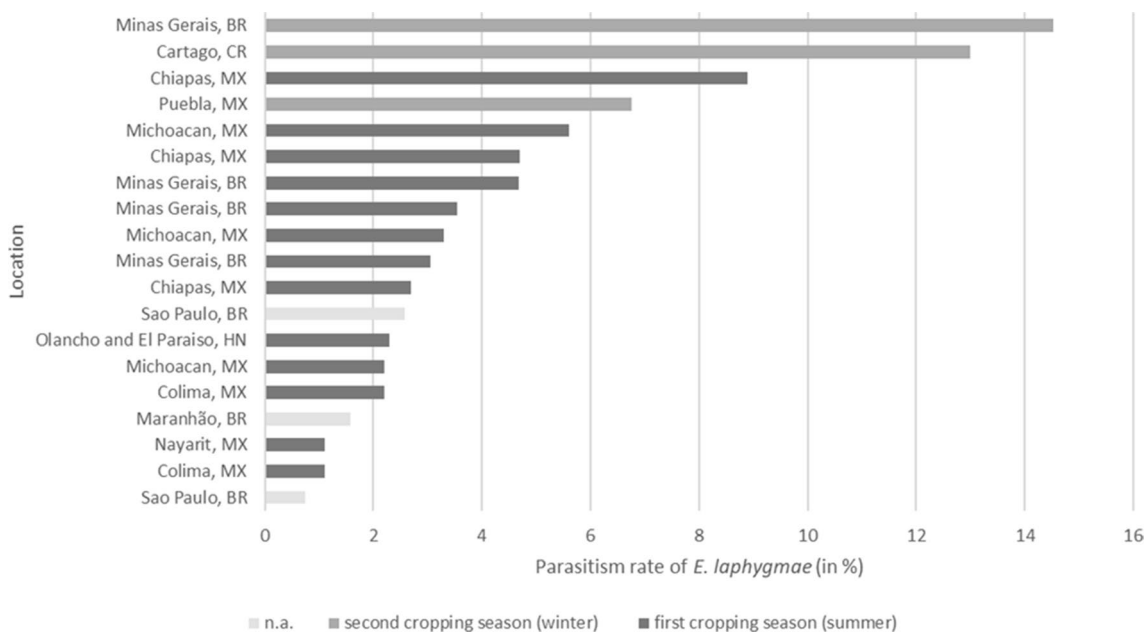[j] Percentage of larvae parasitized by *E.sp.* of all parasitized larvae

Fig. 4 Total parasitism of *S. frugiperda* and parasitism rate of *E. laphygmae* at different locations in the Americas. *BR* Brazil, *CR* Costa Rica, *HN* Honduras, *MX* Mexico. References: Cruz et al. (2009, 2010), Marenco and Saunders (1993), Jourdie et al. (2008), von Méréy et al. 2011, Molina-Ochoa et al. (2004), Patel and Habib (1986), Wheeler et al. (1989), Silva et al. (2008)
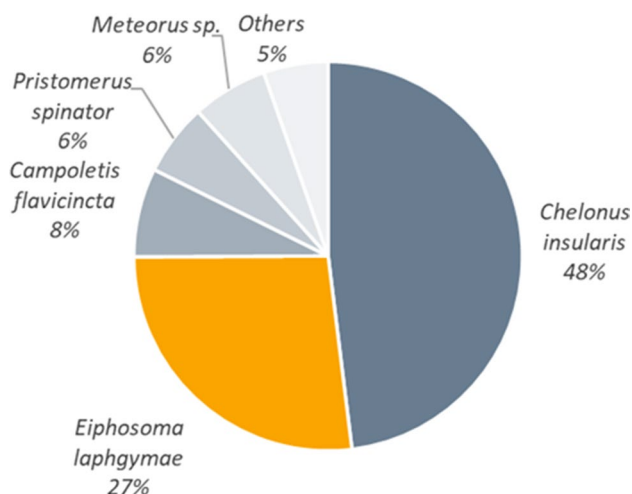

Fig. 5 Mean contribution of different parasitoids of *Spodoptera frugiperda* (J.E. Smith) to total parasitism of the three most dominant species in fields where *Eiphosoma laphygmae* (Costa Lima) or *Eiphosoma vitticole* (Cresson) have been observed (*n* = 25 different locations throughout the Americas). References: Armenta et al. (2003), Cruz et al. (1997, 2009, 2010), Figueiredo et al. (2006b, c, 2009), Jourdie et al. (2008), Marenco and Saunders (1993), Meréy et al. (2011, 2012), Molina-Ochoa et al. (2004), Patel and Habib (1986), Silva et al. (2008), Wheeler et al. (1989)

before spraying was 18.5% and after spraying 8.5%, while the virus was responsible for 50% of the mortality at the highest dosage of application (1000 larval equivalents of

virus/ha). Cruz et al. (1997) also showed that the mortality caused by parasitoids was lower with increasing dosage of nuclear polyhedrosis virus. In a laboratory experiment *E. laphygmae* also parasitized larvae, which were treated externally with 200 ppm Spinosad, even though the endoparasitoid could not develop, since all host-larvae died as a result of the applied insecticide (Penagos et al. 2005).

Previous attempts at rearing and releasing *E. laphygmae*

Little information is available on rearing *E. laphygmae* in the laboratory. Ashley (1983) let *E. laphygmae* oviposit on disks of diet with 0.5-cm-deep depressions. The disks were supported by a piece of hardware cloth and put in the centre of a plexiglass cylinder. The authors let around 100 newly hatched larvae enter into the depressions, before the parasitoids were put in the cage for 48 h, temperature was at 28 °C. López et al. (2002) exposed third-instar larvae for choice tests, and Giraldo-Vanegas and Garcia (1992, 1994b, 1995) exposed around 150 six-day-old larvae to oviposition; both authors worked at 24.5 °C. Lòpez et al. (2002) report that adding some FAW frass facilitated oviposition.

One thousand pairs of *E. laphygmae* originating from Bolivia were released in Florida as classical biological control agents since the parasitoid does not occur naturally in USA (Ashley et al. 1982). However, it was unsuccessful (Ashley et al. 1982; Meagher et al. 2016), possibly because

Fig. 6 Frequency of the predominant parasitoid of *Spodoptera frugiperda* (J.E. Smith) and second and third most abundant species in field observations where *Eiphosoma laphygmae* (Costa Lima) or *Eiphosoma vitticole* (Cresson) occurred
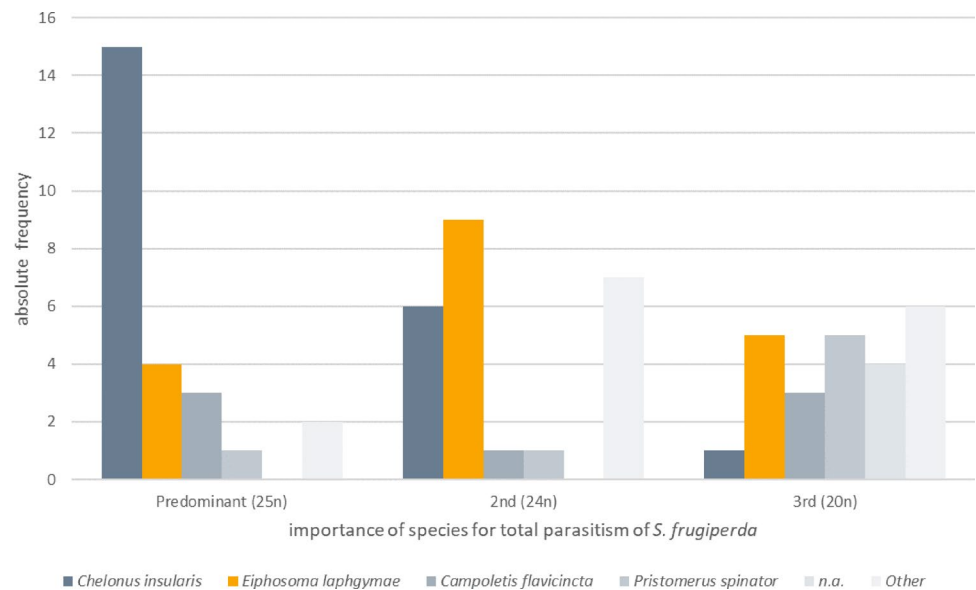
Discussion

Based on this review, *E. laphygmae* can be considered as a promising biological control agent against FAW in Africa and Asia because of its importance in the parasitoid complex of FAW in its native range, its apparent specificity and the lack of congeneric species in Africa and Asia.

Much information on the biology of *E. laphygmae* is already available. However, many knowledge gaps remain. In particular, its specificity needs to be better assessed and efficient laboratory rearing methods need to be developed before *E. laphygmae* can be introduced as classical biocontrol agent. Currently, classical biological control must include a proper assessment of the potential risk posed by the introduction of the agent, in particular on non-target hosts or prey (Hajek et al. 2016). Various protocols for specificity tests are available (e.g. Van Driesche and Reardon 2004), and analyses of previous introductions of classical biocontrol agents show that such natural enemies rarely become problematic when proper testing is done (Barratt 2011; Hokkanen et al. 2003; Myers and Cory 2017; van Driesche et al. 2010; van Driesche and Hoddle 2016). Concerns have been raised about potential non-target effects of classical biocontrol agents (e.g. Howarth 1991). However, Lynch and Thomas (2000) analysed 5000 cases of parasitoid or predator introductions and concluded that non-target effects have been recorded in only 1.7% of cases and the majority of

these only caused minor effects. Van Driesche et al. (2010) showed that of 21 reviewed insect biocontrol programmes, 84% of introductions had positive effects on biodiversity, 5% had positive effects on ecosystems services, and 48% increased product harvesting from natural systems.

However, any candidate needs to fulfil the "Guidelines for the export, shipment, import and release of biological control agents and other beneficial organisms" before a release in Africa (FAO and IPPC 2016) and country-specific requirements. Specificity tests for *E. laphygmae* should include closely related African and Asian Noctuids, such as other *Spodoptera* species. Also, studies should focus on laboratory rearing methods to ensure that sufficient adults are available for releases at the continental scale. First trials showed that laboratory cultures are hampered by low parasitism rates and strongly male-biased sex ratio (T. Allen and M. Kenis, unpublished data). Factors affecting parasitism success and sex ratio in laboratory rearing should be better investigated.

In its native range, *E. laphygmae* is confined to the tropical areas and has been rarely reported in the subtropics. *Eiphosoma laphygmae* is apparently absent from USA and Argentina (e.g. Pair et al. 1986; Murúa et al. 2009; Hay-Roe et al. 2016; Meagher et al. 2016). In Mexico, there are several studies either without any record of the species (e.g. Vírgen et al. 2013; Hoballah et al. 2004; Ordóñez-García et al. 2015) or where *E. laphygmae* was observed only in few sampled locations (Jourdie et al. 2008; Molina-Ochoa et al. 2004), possibly because these were situated in cooler, mountainous regions. This implies that while *E. laphygmae* might be effective as a biocontrol agent within tropical zones of the invasive range of FAW, it might be less suitable in subtropical zones of China, most of South Africa and invaded mountain areas such as in East Africa and the Himalayas. If *E.*

the native parasitoids preferred to attack the same instars as *E. laphygmae* (Ashley et al. 1982). Yaseen et al. (1981) introduced *E. laphygmae* from Bolivia in Trinidad, but also reported the presence of the species prior to the introduction at the same location.

laphygmae is deemed a suitable biological control agent for FAW, it would be recommended to use strains from locations climate-matched to the target area (Hoelmer and Kirk 2005).

In South America north of Argentina, *E. laphygmae* has been found in nearly all studies on the parasitoid complex of FAW and it is usually considered as being one of the three main species of the complex, as shown in our review. In fields where *E. laphygmae* occurred, based on the three most frequent species, *Ch. insularis* contributed 47% to total parasitism and *E. laphygmae* to 27%. *Chelonus insularis* has the largest natural distribution of all FAW parasitoids in the Americas, and it is, at the continental scale, the most important parasitoid of FAW in its native region (Molina-Ochoa et al. 2003). However, it is considered less specific than *E. laphygmae*, being recorded from several other Lepidoptera (Yu et al. 2005), and several other *Chelonus* spp. are among the main parasitoids of FAW in Africa and Asia (Agboyi et al. 2020; Gupta et al. 2020; Durocher-Granger et al. 2021). Thus, compared to *E. laphygmae*, the introduction of *Ch. insularis* in Africa or Asia would involve a higher risk of undesirable effects on non-target hosts and of competition with native parasitoids.

In general, larval parasitism rates mentioned in the literature are low from Latin America. We found mean parasitism by *E. laphygmae* to be 4.3% with up to 15% reported, and only *Ch. insularis* sometimes showed higher parasitism. However, the parasitism rates found in the literature are most likely largely underestimated. As with most hymenopteran larval parasitoids of FAW, *E. laphygmae* parasitizes the smaller, early FAW instars (Ashley et al. 1982; Ashley 1983; López et al. 2002; Penagos et al. 2005) and kills it in its fifth instar (Ashley 1983; Marenco and Saunders 1993; Penagos et al. 2005; Wheeler et al. 1989). Thus, sampling including larger larvae would underestimate the mean parasitism across larval stages. Small *S. frugiperda* larvae are often hidden in the plant whorl (FAO 2018b), so these parasitized larvae are less likely to be sampled. Furthermore, parasitized larvae grow and eat much less (Ashley 1983), causing much less damage than healthy larvae, the latter being much more obvious in the field. In addition, studies usually calculate parasitism by dividing the number of parasitoids divided by the number of larvae collected. However, parasitized larvae, especially those parasitized by *E. laphygmae,* are much more likely to die in the laboratory before maturation than healthy larvae, which, again, leads to an underestimation of parasitism rates (Jourdie et al. 2008; von Mérey et al. 2011).

Agricultural management practices, such as spraying insecticides and herbicides, can impact parasitism rates by *E. laphygmae* and other parasitoids substantially (Cortez-Madrigal 1998; Figueiredo et al. 2006b). In the Americas, most maize fields are either sprayed with chemical insecticides or planted with GM maize. The latter also affects parasitoid populations because FAW parasitoids are strongly host-density-dependent (Durocher-Granger et al. 2021). Area-wide control of FAW and other crop pests has a strong negative long term effect on parasitoids and, therefore, in such environments it is not surprising that field parasitism assessments, even when conducted on unsprayed, non-GM maize varieties, will provide low parasitism rates.

More generally, biological control needs to be adapted to the regional level, since dominance of parasitoid species varies greatly between different locations even within the same state (Silva et al. 2008; Cruz et al. 2009). Differences in agroecosystems can explain such variation in nearby localities (Silva et al. 2008). Onody et al. (2012) have shown that the differences in prevalence of *Eiphosoma* spp. depend more on crop management than on climatic variation within a region. We observed a tendency that *E. laphygmae* established better in more diverse systems. The species has only been found in two of 12 locations in Sao Paulo by Patel and Habib (1986) but in all three organic gardens in Sao Paulo (Onody et al. 2012). Also, Cortez-Madrigal (1998) observed that *E. laphygmae* predominated in weedy maize fields, while *Ch. insularis* predominated in weeded ones. *E. laphygmae* is assumed to be synovigenic (Giraldo-Vanegas and Garcia 1995), producing eggs throughout the adult stage by relying on continuing nutrition, so weed flowers serve as an important source of food (Syme 1975) and vegetation rich in nectar and pollen can facilitate establishment (Leius 1963). In tropical Africa, agroecosystems tend to be more diverse than in the Americas, as much more mixed cropping is practiced (Kenis et al. 2019). Before the arrival of FAW, insecticide use by smallholder farmers in Africa was relatively low (Sheahan and Barrett 2017). This situation potentially favours *E. laphygmae* establishment as a classical biological control agent.

Declarations

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