Journal of Economic Entomology, 116(2), 2023, 331–341
https://doi.org/10.1093/jee/toad029
Advance Access Publication Date: 9 March 2023
Review

ENTOMOLOGICAL SOCIETY OF AMERICA
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Review

Prospects for classical biological control of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in invaded areas using parasitoids from the Americas

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Subject Editor: Michael Brewer

Received on 20 December 2022; revised on 17 January 2023; accepted on 6 February 2023

Fall *armyworm*, *Spodoptera frugiperda* (J.E. Smith) is a polyphagous agricultural pest threatening food security worldwide. This American species recently invaded most of Africa, many Asian countries, and Oceania, where it mainly damages maize. Classical biological control (CBC) through the introduction of natural enemies from its area of origin is considered as a potential management approach. The paper reviews the prospects and constraints of a CBC programme against *S. frugiperda* using larval parasitoids, which are considered the most suitable natural enemies for introduction against this pest. The most important larval parasitoids in its native range are presented and discussed for their suitability as CBC agents, based the following criteria: their frequency of occurrence and parasitism levels, specificity, climatic suitability and absence of closely related species parasitizing *S. frugiperda* in the area of introduction. The ichneumonid *Eiphosoma laphygmae* Costa-Lima (Hymenoptera: Icheumonidae) is considered as a potential candidate for introduction because of its specificity and its importance as a parasitoid of the pest in most of its native range. The most frequent and important parasitoid of *S. frugiperda* in the Americas, the braconid *Chelonus insularis* Cresson (Hymenoptera: Braconidae), would most probably contribute to the control of *S. frugiperda* if released in invaded areas. However, it is oligophagous and would most certainly parasitize nontarget species. Before introducing *C. insularis*, or any other parasitoid species, the potential nontarget effects will have to be assessed and the risks will have to be weighed against the benefits of improving the natural control of this important pest.

Key words: biological control, biological invasion, parasitoid, parasitism, specificity

Introduction

Fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a highly destructive pest of Poaceae, in particular maize, rice and sorghum, but many other crops from different families are also attacked (Montezano et al. 2018). It is native to the tropical and subtropical regions of North, Central, and South America (Kenis et al. 2023). First detected on the African continent in January 2016 in Nigeria (Goergen et al. 2016), *S. frugiperda* has now already been reported in almost all sub-Saharan Africa, Egypt, Canary Islands, and most tropical and subtropical Asian countries, as well as Australia, New Zealand and some Pacific islands (CABI 2023). The invasion of *S. frugiperda* threatens food security of more than 200 million people in Africa, whose main staple food is maize, which is by far the most susceptible crop in all invaded areas (Rwomushana et al. 2018). Eschen et al. (2021) estimated that *S. frugiperda* causes annual yield losses of USD 9.4 Bn in Africa alone.

While, in several countries in its native range, the pest is mostly controlled by deploying GM crops, in the invaded regions, the main response has been a massive use of broad-spectrum chemical insecticides, often utilized without the necessary safety precautions, which causes serious concerns for the environment and human health (Tambo et al. 2020a). There is an urgent need to develop sustainable management methods that are adapted to the maize production systems in Africa and Asia, such as biological control and integrated pest management approaches (Kenis et al. 2023). Classical biological control (CBC), i.e., the introduction of natural enemies from the area of origin of the target pest, is a particularly suitable strategy for controlling invasive insects that spread over wide areas and invade different habitats. CBC's aim is to permanently establish new biological control agents to increase natural mortality (Van Driesche and Bellows 1996, Kenis et al. 2017). It should not be confounded with augmentative, or inundative biological control, which involves regular releases of mass cultured natural enemies to achieve temporary control (Van Driesche and Bellows 1996). CBC has been successfully used against a whole range of invasive insects in the past (Clausen 1978, Cock et al. 2015, 2016). One of the most spectacular examples of CBC against a tropical crop pest is the control of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), in Africa (Neuenschwander 2001). In the 1970s, this previously unknown mealybug suddenly appeared in Central Africa where it quickly became a devastating pest of cassava. From there it rapidly spread to most cassava production regions of sub-Saharan Africa, threatening the livelihood of tens of millions of smallholder farmers and their families. A large international program was set up and found the origin of this species in Paraguay, where a parasitoid, *Anagyrus lopezi* De Santis (Hymenoptera: Encyrtidae), was collected. The parasitoid was reared and released in all regions affected by the mealybug. It quickly brought *P. manihoti* under control, with cost:benefit ratio calculations varying from 1:199 to 1:738 (Cock et al. 2015). *Phenacoccus manihoti* was also introduced more recently into Southeast Asia where the release of the same parasitoid species resulted in a similar success (Wyckhuys et al. 2018).

Considering the similarities between the invasions of *P. manihoti* and *S. frugiperda*, including their origin and the fact that they both threaten key staple food crops in tropical Africa and Asia, it is tempting to consider that the same approach should be used to control *S. frugiperda*. However, there are many differences between the two cases. The paper reviews the prospects and constraints of a classical biological control program against *S. frugiperda* in the regions of invasion. It presents the most important natural enemies of *S. frugiperda* in the native range of the pest and discusses their role in controlling *S. frugiperda* populations. The main species are assessed for their suitability as CBC agents in Africa, Asia, Oceania, and Europe.

Prospects for the CBC of *S. frugiperda*

History

So far, there is no published information on the introduction of CBC agents against *S. frugiperda* in its invasion range. However, in the past, several CBC projects have been conducted to control the insect in its native range, either by moving parasitoids from one region to another where they were absent, or by introducing parasitoids of other *Spodoptera* spp. from other continents. For example, *Archytas incertus* Giglio-Tos (Diptera: Tachinidae) was moved from Argentina to the USA, *Eiphosoma vitticolle* Cresson (Hymenoptera: Ichneumonidae) from Bolivia to the USA and *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) from the USA to the Caribbean (Cock 1985, Rosen et al. 1994). Cock (1985) and Rosen et al. (1994) also list at least ten parasitoids from other *Spodoptera* spp. collected in other continents and released in various countries in the Americas in the first half of the 20th century. However, only one species, the egg parasitoid *Telenomus remus* (Nixon) (Hymenoptera: Scelionidae), introduced from India, became established and spread to the whole distribution range of *S. frugiperda* in the Americas, where it never became a significant natural enemy but has been frequently used as augmentative biological control agent (Wengrat et al. 2021, Colmenarez et al. 2022).

Arguments Against CBC of *S. frugiperda*

A first analysis suggests that the CBC biological control of *S. frugiperda* is not very promising compared to that of *P. manihoti*, for the following reasons:

(a) *Spodoptera frugiperda* is a pest in its area of origin, in contrast to *P. manihoti*. Intuitively, it is unlikely that the introduction of natural enemies that are not able to control the insect in its native range will do so in the invaded range.

(b) Many publications from the Americas suggest that parasitoids, which should be considered as the most promising CBC agents of *S. frugiperda* (see below), do not cause significant mortality in *S. frugiperda* populations. Egg parasitism is usually negligible and observed larval parasitism rates are often lower than 30% (e.g., Pair et al. 1986, Molina-Ochoa et al. 2004, Wyckhuys and O'Neil 2006, Ruíz-Nájera et al. 2007, Murúa et al. 2009, Vírgen et al. 2013, Ordóñez-García et al. 2015). There is no defined minimum parasitism rate below which a parasitoid cannot be considered as an efficient CBC agent. However, Hawkins and Cornell (1994) found that the probability of successful control significantly increases with the maximum parasitism rate within the host's native range and that no CBC was achieved for any pest suffering less than 32% maximum parasitism in its native range.

(c) In contrast, parasitism rates of *S. frugiperda* in Africa and Asia is unusually high for a recent invasive species. Over 60 parasitoid species have already adopted the new species in its new range (Kenis et al. 2023 and references therein). Egg parasitism by *T. remus* is much higher in Africa and Asia than in the Americas. For example, it reached over 50% is some samples in East Africa (Sisay et al. 2019), up to 26% in Ghana and 14 % in Benin (Agboyi et al. 2020), and about 30% in China (Huo et al. 2019, Tang et al. 2020). *Trichogramma chilonis* Ischi (Hymenoptera: Trichogrammatidae), another egg parasitoid, reaches 16–24% egg mass parasitism in India (Navik et al. 2021) and is also rather abundant in China (Tang et al. (2020) and Africa (Sisay et al. 2019). In Ghana, larval parasitism rates varied between 5% and 38% (Agboyi et al. 2020) and between 13% and 53% in East Africa, depending on countries and years (Sisay et al. 2019). In addition, some of the main parasitoids of *S. frugiperda* in the invaded range belong to the same genera as potential candidates for introduction (e.g., *Chelonus* spp., *Cotesia* spp., see below), which suggests potentially important competitive interactions between native and introduced species.

(d) In the history, CBC has been, on average, significantly less successful against lepidopteran pests than against other insects such as Sternorrhyncha (mealybugs, scales, aphids, and whiteflies) but also Coleoptera and Hymenoptera (Kenis et al. 2017).

Arguments in Favor of CBC of *S. frugiperda*

Despite the low potential for full control of the pest in the invaded regions and the issues that may be encountered in the selection of a suitable agent, CBC against *S. frugiperda* is worth trying, for the following reasons:

(1) *Spodoptera frugiperda* is a severe and widespread pest. Decreases in yields and massive increases in insecticide use have a serious impact on food security and livelihood, and probably even more on human health and the environment (De Groote et al. 2020, Abro et al. 2021, Tambo et al. 2021). Thus, even a small average decrease of population levels and damage at continental scale, through a parasitoid introduction, has the potential to have a huge economic, social, and environmental impact because of the huge number of smallholder households impacted.

(2) With *S. frugiperda*, it is not necessary to reach full control of the pest to prevent yield losses. Moderate foliar damage does not necessarily cause yield losses because maize plants are able

to compensate for defoliation, especially at an early stage of the plant growth (Hruska 2019). Damage by *S. frugiperda* to the reproductive tissues late in the crop season has a more direct consequence on yields. However, an introduced parasitoid may help reduce populations down to a level at which the effect on yields becomes minimal.

(3) Some studies observed high average rates of parasitism in the native range, such as 75% in Nicaragua (Gladstone 1991) or 65% in Costa Rica (Marenco and Saunders 1993) and 42% in Honduras (Wheeler et al. 1989) The low apparent parasitism rates observed in many studies in the Americas may be due to two factors. Firstly, the extensive use of GM crops and broad-spectrum pesticides probably directly affects parasitoids, and the resulting low density of *S. frugiperda* indirectly induces low parasitism rates because, in general, parasitoids are density dependant (Ramirez-Romero et al. 2007, Desneux et al. 2010, Han et al. 2016). In Florida, Meagher et al. (2016) studied parasitism of *S. frugiperda* in sweet corn and found that larval parasitism rates were much higher in unsprayed fields (average 44%, up to 91% in some fields) than in fields sprayed with insecticides (15%). The low rates of parasitism mentioned in the literature may also result from underestimations due to sampling and calculation methods (Vickery 1929, Allen et al. 2021). Most studies on field parasitism of *S. frugiperda* do not separate between larval instars. Most larval parasitoids of *S. frugiperda* kill their host before maturity whereas some mostly attack late-instar larvae. Thus, sampling mature or young larvae will inevitably underestimate total parasitism. In Honduras, Wheeler et al. (1989) separated their sampled into small, medium, and large larvae and found 80.5% parasitism, mostly by the Braconidae *Chelonus insularis* Cresson, in samples containing medium larvae. In Southern Texas, the parasitism rate of 1st to 4th instar larvae was 43.5%, by a cohort of hymenopteran parasitoids dominated by *C. insularis*, and the parasitism of older larvae was 17.4%, mostly by the Tachinidae *Archytas marmoratus* (Townsend) (Vickery 1929). Furthermore, parasitized larvae grow slower and eat much less (Hoballah et al. 2004, Agboyi et al. 2019) and cause much less damage than healthy larvae. Consequently, during field sampling, fat healthy larvae on damaged plants are much more likely to be found and sampled than small, parasitized larvae hidden in apparently healthy plants. Finally, the method used by many authors to calculate parasitism rates, i.e., dividing the number of parasitoids obtained by the number of larvae collected, also leads to underestimations because parasitized larvae are more likely to die in the laboratory before maturation than healthy larvae (M. Kenis, unpublished data).

(4) When natural enemies are introduced from one continent to another as part of a CBC program, it is not uncommon that parasitism or predation rates are higher in the region of introduction than in the region of origin, on the same host. Occasionally, damage by the introduced pest is becoming lower than in the region of origin, as for the introduction of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae), a European species causing cyclic outbreaks in Europe and which was fully controlled by two introduced parasitoids in eastern Canada (Embree 1991).

(5) The case of *O. brumata* shows that, although CBC has been, on average, less successful on lepidopteran pests than on some other insect orders (Kenis et al. 2017), moths can also be successfully controlled by CBC. This includes several noctuid pests of cereals, e.g., *Mythimna separata* Walker, controlled in New Zealand by the Braconidae *Cotesia ruficrus* (Haliday) introduced from Pakistan (Cameron et al. 1989), or *Sesamia nonagrioides* (Lefebvre) in Cape Verde controlled by the eulophid *Pediobius furvus* (Gahan) introduced from Kenya (van Harten et al. 1990). Of particular interest is the CBC success obtained in the first half of the 20th century against the African armyworm *Spodoptera exempta* (Walker) in Hawaii, through the introduction of a cohort of *S. frugiperda* parasitoids from the USA and Mexico (Clausen 1978, Lai and Funasaki 1983).

(6) Personal observations suggest that population levels and damage by *S. frugiperda* are lower in the Americas than in Africa (M. Kenis, unpublished data), where farmers commonly spray insecticides several times during the crop cycle (Tambo et al. 2020b, 2021), whereas, in the Americas, most farmers typically spray only once per season. However, this may be due to a better knowledge of the pest and its management in the native range. It would be interesting to compare population levels more precisely across continents and countries.

Selection of Natural Enemies for Introduction

In the Americas, over 150 species of natural enemies (parasitoids, predators, and pathogens) of *S. frugiperda* have been reported (see lists in Luginbill 1928; Gardner and Fuxa 1980; Molina-Ochoa et al. 2003a, 2003b; Bahena and Cortez 2015). Selecting the most efficient and safest natural enemy species among them is a challenge. Kenis and Seehausen (2023) list several criteria used to select parasitoids and predators for introduction against an invasive arthropod pest. Nowadays, the two main criteria are the ability to control the target pest in the area of origin, or in other areas of introduction, and the specificity for their host or prey to prevent nontarget effects. Other important criteria include climate suitability, the composition of the natural enemy complex in the region of introduction, and the occurrence of sibling species or biotypes with specific attributes. Based on these criteria, it appears that the only plausible candidates are larval parasitoids (including egg-larval and larval-pupal parasitoids). *Telenomus remus* and *Trichogramma* spp. are commonly reported as egg parasitoids of *S. frugiperda* in the Americas (Molina-Ochoa et al. 2003a). However, none of them reach high rates of parasitism outside the context of augmentative biological control (Varella et al. 2015, Jaraleño-Teniente et al. 2020, Wengrat et al. 2021), *T. remus* is already present in Africa and Asia (Kenis et al. 2019, Colmenarez et al. 2022) and *Trichogramma* spp. are usually highly polyphagous (Zucchi et al. 2009). Pupal parasitoids of *S. frugiperda* are poorly known (Molina-Ochoa et al. 2003a). All known predators of *S. frugiperda* are polyphagous (Luginbill 1928, Bahena and Cortez 2015). Pathogens are rarely used as classical biological control agents of arthropod pest and the main species occurring in the Americas (Gardner and Fuxa 1980, Molina-Ochoa et al. 2003b, Bahena and Cortez 2015) either also occur in the invaded continents (e.g., *Metarhizium rileyi; S. frugiperda* nuclear polyhedrosis virus [SfNPV]) or are poorly known (Kenis et al. 2023).

Larval parasitoids of *S. frugiperda* have been extensively sampled in North, Central and South America. Molina-Ochoa et al. (2003a) provided a detailed list of parasitoid species with countries and references. Since then, new field surveys were conducted in various countries (e.g., Murúa et al. 2009, Barreto-Barriga et al. 2017, Hernández-García et al. 2017, Contreras-Cornejo et al. 2018, González-Maldonado et al. 2020), but no new important parasitoid species was found. A selection of larval parasitoids is presented below. They are presented per genus because, in several cases, there have been confusions in the identification of the parasitoids at species level. To comply with the main criterion that a parasitoid selected for

CBC should be an important natural enemy in its region of origin, only larval parasitoid genera that fulfil the following conditions are discussed: (i) they have been reported on *S. frugiperda* in at least 5 countries, (ii) they are mentioned as the most abundant parasitoids in at least two studies, (iii) they reach 20% parasitism in at least one study. The main species of these genera are being assessed against the selection criteria. Table 1 summarizes the assessments and details are given in the text below. The genera are presented in alphabetical order.

Aleiodes (Hymenoptera: Braconidae)

Most records of *Aleiodes* spp. on *S. frugiperda* refer to *Aleiodes laphygmae* (Viereck). In addition, *Aleiodes vaughani* Muesebeck is mentioned in Honduras by Wheeler et al. (1989) with 0.1% parasitism, in Mexico by Ruiz-Najera et al. (2007), who reported 1.4% parasitism and in Nicaragua (van Huis et al. 1981). *Aleiodes terminalis* (Cresson) is a species from temperate regions in North America, which is mentioned in several publications as parasitoid of *S. frugiperda* but only one original record could be found in Luginbill (1928), who mentioned one single specimen reared from *S. frugiperda*. This assessment will be based only on *A. laphygmae*.

Aleiodes spp. are larval parasitoids that parasitize young larvae and mummify their host in the fourth instar to develop in, and emerge from the mummy. Details of its biology have been studied in Texas by Vickery (1929). *Aleiodes laphygmae* has a broad distribution from Southern USA to Chile (Molina-Ochoa et al. 2003a, Yu et al. 2016) but it is most abundant on *S. frugiperda* in Central America (van Huis et al. 1981, Wyckhuys and O'Neil 2006)

Abundance/frequency.

Despite its widespread occurrence on *S. frugiperda*, *A. laphygmae* has been only occasionally described as a main parasitoid of *S. frugiperda*. However, Wyckhuys and O'Neil (2006) state that it was the dominant parasitoid species in their experimental fields in Nicaragua. Also in Nicaragua, van Huis (1981) considered *A. laphygmae* as one of the two most abundant hymenopteran parasitoids in the study sites. Interestingly, in an experiment to assess parasitism of *S. frugiperda* in turf grass in Georgia, *A. laphygmae* was the only significant parasitoid with a parasitism rate of 18.1% in small larvae (Braman et al. 2004). It was also one of the main parasitoids of *S. frugiperda* in a maize field and a pasture field in Florida (Hay-Roe et al. 2016) and in maize and sorghum fields in US states where *S. frugiperda* does not overwinter (Pair et al. 1986). It is possible that parasitism by *A. laphygmae* has been largely underestimated or even unnoticed by unexperienced researchers because it kills 4th-instar larvae (of the size of third instars, see Vickery 1929) before the pest is able to cause much leaf injury, and parasitized larvae look rather similar to small dead larvae. van Huis (1981) mentioned that, in the first year of his study, when mostly mature larvae were collected, he did not find *A. laphygmae* whereas, in the following year, when samples included small larvae, up to 28% parasitism by this parasitoid was observed.

Specificity.

The vast majority of host records for *A. laphygmae* are *S. frugiperda* (Yu et al. (2016). Yu et al (2016) and Cave (1993) also record four other species as hosts. They do not provide primary publications for *Spodoptera ornithogalli* (Guenée) (Lepidoptera: Noctuidae) and *Spodoptera exempta*. Ruberson et al. (1994) reared *A. laphygmae* from *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) in Georgia, but only at one site where it caused 0.8% parasitism. It was also reared in very low numbers from *Mythimna unipuncta* (Haworth) (Lepidoptera: Noctuidae) by (Burrell 1967). Considering the high number of studies on parasitoids of *S. exigua* and *M. unipuncta*, it is possible that these records are either erroneous or accidental. However, since *A. laphygmae* is present in high numbers on transient populations in USA (Pair et al. 1986), it may attack other hosts in these regions.

Climatic suitability.

Little is known about the climatic requirements of *A. laphygmae*. Considering its wide distribution ranging from South Carolina to Chili (Yu et al. 2016), most areas invaded by *S. frugiperda* should be suitable. However, the fact it is most abundant in Central America and much less in other areas could be considered in the choice of potential release areas.

Similar species in the regions of introduction.

There is no record of an *Aleiodes* sp. in Africa, nor of any species of the subfamily Rogadinae, sharing a similar biology. However, it could compete with all the other parasitoids using young *S. frugiperda* larvae as a resource. In India, only one study found an *Aleoides* sp. on *S. frugiperda* without giving information on its abundance (Keerthi et al. 2022).

Archytas (Diptera: Tachinidae)

Many tachinid flies parasitize *S. frugiperda* larvae in the Americas. The most frequently mentioned species are *Archytas* spp. These are large tachinid flies laying hatching larvae on the host plant beside host larvae, which the larvae penetrate soon after hatching. They kill and emerge from their host at the pupal stage (Vickery 1929, Hughes 1975, Reitz 1995). The species most commonly associated with *S. frugiperda* in the most recent literature is *A. marmoratus*, which is reported in most American countries, from USA to Argentina (Molina-Ochoa et al. 2003a). In the old North American literature (e.g., Luginbill 1928, Vickery 1929), is was mentioned as *Archytas*

Table 1. Main American parasitoids of *Spodoptera frugiperda* with assessment of the criteria used for selecting classical biological control agents for introduction in invasion areas. xxxx: very positive assessment for this criterion; xxx: positive; xx negative; x: very negative. Assessments are made with high uncertainty for *Campoletis* spp. because of the confusion related to species identifications

Parasitoid species	Parasitism rates	Frequency of occurrence	Specificity	Climatic range	Similar spp. in invaded areas
Aleiodes laphygmae	xx	xx	xxx	xxx	xxx
Archytas marmoratus	xxx	xxx	xx	xxxx	xxx
Campoletis spp.	xxx	xxx	xx?	xxxx?	xx
Chelonus insularis	xxxx	xxxx	xx	xxx	x
Cotesia marginiventris	xxx	xx	x	xxxx	x
Eiphosoma laphygmae	xxx	xxx	xxxx	xx	xxx

piliventris van der Wulp, a synonym of *A. marmoratus* (O'Hara et al. 2021). Molina-Ochoa et al. (2003a) also mention *Archytas incertus* (Macquart) as common parasitoid of *S. frugiperda* in many American countries, but this is likely *A. marmoratus* because *A. incertus* is known only from Argentina, Brazil, Uruguay, and Paraguay (O'Hara et al. 2021). *Archytas analis* (F.) (=*A. plangens* Curran) is also sometimes recorded from *S. frugiperda* in various countries (Cave 1993, Molina-Ochoa et al. 2003a), but it seems less abundant on this host than *A. marmoratus*.

Abundance/frequency.

Archytas marmoratus is frequently found throughout the range of *S. frugiperda* in the Americas, albeit not often as a major parasitoid. In South Texas and Northern Mexico, it was the most common parasitoid reared from medium and large larvae (Vickery 1929, Pair et al. 1986). It is commonly observed in Central and Southern Mexico and Central America, but usually in low numbers (e.g., Cave 1993, Marenco and Saunders 1993, Delfín-González et al. 2007, Ruíz-Nájera et al. 2007, Rios-Velasco et al. 2011, Vírgen et al. 2013). In a large survey in Mina Gerais state, Brazil, *A. marmoratus* was the main tachinid reared from *S. frugiperda* and the most abundant parasitoid reared from mature larvae. *Archytas incertus* was also one of the three main parasitoids in Maranhao state, Brazil (Silva et al. 2008). Similarly, in a study in Northern Argentina, *Archytas* sp. was one of the main three parasitoids of *S. frugiperda* (Murúa et al. 2009).

Specificity.

Archytas marmoratus is oligophagous. In North America, it is reported from a dozen species of Noctuidae (Arnaud 1978, Cave 1993). Besides *S. frugiperda*, it is an important parasitoid of other pests such as *Heliothis virescens* F. and *Helicoverpa zea* (Boddie) (Hughes 1975) (Lepidoptera: Noctuidae).

Climatic suitability.

Considering that *A. marmoratus* is distributed from USA to Argentina, its climatic suitability should cover the whole invasion range.

Similar species in the regions of introduction.

No *Archytas* sp. has been recorded from *S. frugiperda* in Africa and Asia, but other tachinids parasitizing late instar larvae have adopted the invasive moth, such as *Drino* spp. in Africa and *Exorista* spp. in Asia (Kenis et al. 2023). *Drino quadrizonula* (Thomson) is particularly abundant in Zambia, where it is the dominant parasitoid of late instar larvae (Durocher-Granger et al. 2020).

Campoletis (Hymenoptera: Ichneumonidae)

Campoletis spp. are endoparasitoids that parasitize young larvae and kill their host before maturity. Two species are frequently mentioned as parasitoids of *S. frugiperda*, *C. sonorensis* (Cameron), and *C. flavicincta* (Ashmead) in tropical regions (Molina-Ochoa et al. 2003a). These two species are hardly distinguishable by means of morphological characters, and it is likely that they have been often mistaken in the literature (Camargo et al. 2015). Camargo et al. (2015) even suggest, after both morphological and molecular studies, that they should be synonymized and that all specimens collected in Brazil should be named *C. sonorensis,* but they also encourage further studies on the taxonomy of *Campoletis* species attacking *S. frugiperda*. Another species, *C. grioti* (Blanchard) has been recorded from *S. frugiperda* in its southern range in Argentina, Uruguay, and Brazil (Virla et al. 1999). It has been studied in quarantine in USA as a potential biological control agent but has apparently not been released (Ashley 1983, Frank and McCoy 1993). Other *Campoletis* spp. reported from *S. frugiperda* include *C. curvicauda* (Blanchard) in Peru and *C. oxylus* (Cresson) in USA, whereas many studies refer simply to *Campoletis* sp. (Molina-Ochoa et al. 2003a).

Abundance/frequency.

Most studies on parasitism of *S. frugiperda* in the Americas report a *Campoletis* species as one of the main parasitoids of the pest, from USA to Argentina. In the Southern USA, Pair et al. (1986) mention *C. sonorensis* as a frequent parasitoid of *S. frugiperda*. In Durango, Mexico, *C. sonorensis* was the dominant parasitoid at high elevations (+1,600 m a.s.l.) (González-Maldonado et al. 2014), with an average of 23% parasitism. Also at high elevations in Durango, García-Gutiérrez et al. (2013) found parasitism rates up to 44.5% by *C. sonorensis*. *Campoletis* spp. are usually less abundant on *S. frugiperda* in Central America and Southern Mexico even though *Campoletis sonorensis* was the second most abundant parasitoid in Nicaragua in a study by Wyckhuys and O'Neil (2006). In contrast, *Campoletis* spp. seem more important parasitoids of *S. frugiperda* in South America. In Brazil, *C. sonorensis* and *C. flavicincta* are very common on this host (Cruz et al. 2009, 2010; Camargo et al. 2015). In large surveys in Mina Gerais, *C. flavicincta* was one of the main three parasitoids (Cruz et al. 2009). It was also the main parasitoid in Rio Grande do Sul State (Dequech et al. 2004). *Campoletis grioti* is the most important parasitoid of *S. frugiperda* in Argentina, where the pest is transient (Virla et al. 1999, Murúa et al. 2009). The average parasitism by *C. grioti* observed by Murúa et al. (2009) in 3 provinces was 12%. Berta et al. (2000) reported 5% and 50% parasitism by *C. grioti* in maize fields with and without insecticide application, respectively. Murúa et al. (2006) also reported parasitism rates of 39% and 5% parasitism in two regions. In Southern Brazil, Luchini and Almeida (1980) reported that *C. grioti* is the most important parasitoid of *S. frugiperda*, causing 95% parasitism. However, all *Campoletis* collected from *S. frugiperda* in Southern Brazil by Camargo et al. (2015) were identified as *C. sonorensis*, suggesting possible misidentifications or synonyms.

Specificity.

Twenty-one host species are reported for *C. sonorensis*, 27 for *C. flavincinta* and 7 for *C. grioti*. (Yu et al. 2016). However, considering the uncertainty regarding the taxonomy of the genus and potential misidentifications in the literature, it is possible that the species attacking *S. frugiperda* is/are more specific than thought. Populations reared from *S. frugiperda* in the Americas should be tested for their specificity in laboratory assays. Specificity could also be tested by collecting other potential hosts in the field, and taxonomic identifications supported by molecular studies.

Climatic suitability.

Campoletis spp. have been collected in all climatic zones where *S. frugiperda* occurs in the Americas. However, the number, identity, and respective distribution of *Campoletis* species attacking *S. frugiperda* remain unclear and, therefore it is not possible to provide definite assessments of their climatic suitability. They are often abundant at high elevations, e.g., in Mexico (García-Gutiérrez et al. 2013, González-Maldonado et al. 2014). Cam*poletis grioti* is the main parasitoid of *S. frugiperda* in subtropical Argentina, where pest populations are transient and, thus, may be suitable for climatically similar regions in other continents.

Similar species in the regions of introduction.
There is no record of a *Campoletis* species attacking *S. frugiperda* in Africa. *Campoletis chlorideae* Uchida has been reported as a common parasitoid of the pest in India (Shylesha et al. 2018, Sharanabasappa et al. 2019, Keerthi et al. 2022) and it has also been mentioned from China (Niu et al. 2021).

Chelonus (Hymenoptera Braconidae)

Molina-Ochoa et al. (2003a) cite three *Chelonus* species as parasitoids of *S. frugiperda*: *C. antillarum* (Marshall), *C. cautus* Cresson, and *C. insularis* Cresson (Syn. *C. texanus* Cresson). However, only the latter is frequent and widespread on this host and will be treated here. *Chelonus insularis* occurs on *S. frugiperda* throughout its host's distribution range, from USA to Chile (Molina-Ochoa et al. 2003a, Yu et al. 2016). It is an egg-larval parasitoid, killing its host in its 4th and 5th larval instars. Details on its biology can be found in Luginbill (1928), Vickery (1929), Medina et al. (1988), and Rezende et al. (1995). *Chelonus insularis* has been introduced in 1942 as classical biological control agent and became established in Hawaii to control *Spodoptera exempta* (Lepidoptera: Noctuidae). It was also introduced in South Africa (against *Loxostege frustralis* Zeller (Lepidoptera: Crambidae)) and Egypt (against *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae)), apparently without success (Clausen 1978).

Abundance/frequency.
Chelonus insularis is mentioned as the main parasitoid of *S. frugiperda* in most studies in North, Central, and South America. It is the only parasitoid of this pest frequently reported to reach parasitism rates higher than 20%. Only some examples are mentioned here. Before the GM crop era, Vickery (1929) stated that it was the most important parasitoid of *S. frugiperda* in the Gulf Coast States. On maize in Southern Texas, he measured an average of 33% parasitism in small instars, and parasitism rates climbed to 65% in July–August. More recently, in sweet corn in Florida, Meagher et al. (2016) found parasitism rates of 37.2% by *C. insularis* in unsprayed fields. However, in fields sprayed with insecticides, parasitism rates were low (0.9%–2.3%) and *C. insularis* was dominated by *Cotesia marginiventris*. In large surveys in different Mexican States, Molina-Ochoa et al. (2004) and Jourdie et al. (2008) both mentioned *C. insularis* as the most frequently collected parasitoid, even though total parasitism was lower than 20% in the two studies. In Nicaragua, Gladstone (1991) observed a parasitism rate by *C. insularis* of 47.2% and 42.1% in small and medium instar larvae, respectively. In Costa Rica, *C. insularis* also dominated all other parasitoids with an average parasitism rate of 43% (Marenco and Saunders 1993). *Chelonus insularis* is also the most frequent and abundant parasitoid of *S. frugiperda* in South America, e.g., in Brazil (Cruz et al. 2009, 2010). Allen et al. (2021) calculated that, in all South and Central America literature records of *S. frugiperda* parasitism, in which the parasitoid *Eiphosoma laphygmae* Costa-Lima was present, *C. insularis* dominated at 15 out of 25 sites, representing 45% of total parasitism. It is also present in Northern Argentina, where *S. frugiperda* is considered as transient, but not as a dominant parasitoid (Murúa et al. 2009).

Specificity.
Chelonus insularis is an oligophagous species. Yu et al. (2016) list 20 other hosts, including six other *Spodoptera* spp. Most reported hosts are Noctuidae, but also two Crambidae [*Achyra rantalis* (Guenée) and *Loxostege sticticalis* (L.)], two Pyralidae [*Elasmopalpus lignosellus* (Zeller) and *Ephestia elutella* (Hübner)], and one Erebidae [*Anomis flava* (F.)]. Host records in the literature are overwhelmingly *S. frugiperda*, but data on *S. exigua* and *Helicoverpa zea* as hosts are also numerous (see Yu et al. 2016 for references).

Climatic suitability.
Chelonus insularis is the most abundant parasitoid of *S. frugiperda* throughout its native range. Thus, it is likely that it would be able to establish in most invaded regions where the moth is permanently established. However, the maximum entropy model presented by Tepa-Yotto et al. (2021) predicts that it may not be able to establish in the Sahel region. In large surveys for parasitism of *S. frugiperda* in the USA and Northern Mexico, Pair et al. (1986) showed that, while it was the most abundant parasitoid in areas where its host overwinters (Southern Florida and Mexico), it gradually disappeared further North in areas where the moth is transient. They suggested that *C. insularis* may not be able to overwinter in Georgia and further North.

Similar species in the regions of introduction.
In both Africa and Asia, *Chelonus* species have been among the most abundant parasitoids of *S. frugiperda* since its introduction. In West Africa, *C. bifoveolatus* Szépligeti is a dominant parasitoid, e.g., reaching an average of 19% parasitism in Ghana (Agboyi et al. 2020). It is also common on *S. frugiperda* in Uganda (Otim et al. 2021) and in Zambia (Durocher-Granger et al. 2020). Another species, *C. curvimaculatus* Cameron, is rather abundant in Zambia (Durocher-Granger et al. 2020) and Kenya (Sisay et al. 2019). In Egypt, *Chelonus intermedius* (Thomson) has been recorded, reaching 31% parasitism at one site (Youssef 2021). In India, *Chelonus formosanus* Sonan has been reported as one of the most abundant parasitoids of *S. frugiperda* (Firake and Behere 2020, Gupta et al. 2020). *Chelonus formosanus* and *C. munakatae* Munakata are also present on the same host in China (Li et al. 2019, Tang et al. 2020).

Cotesia (Hymenoptera: Braconidae)

Cotesia spp. are endoparasitoids, usually attacking young instar larvae and killing mid-instar larvae when they are solitary. Some species are gregarious, in which case mature instars can be killed. At least four *Cotesia* (previously *Apanteles*) species have been recorded from *S. frugiperda* in the Americas: *Cotesia congregata* (Say), *Cotesia glomeratus* (L.) *Cotesia marginiventris* and *Cotesia ruficrus* (Molina-Ochoa et al. 2003a). However, misidentifications may have occurred, and only *C. marginiventris* has been well studied and is known to reach high parasitism rates. Thus, only this species will be treated here. *Cotesia marginiventris* is a solitary larval parasitoid, parasitizing first instar larvae and emerging from fourth instars. More details of its biology can be found in Vickery et al. (1929). It has been introduced in many parts of the world as biological control agent against other pests. For example, it was introduced and successfully established against *Spodoptera exempta* and *Spodoptera mauritia* (Boisduval) (Lepidoptera: Noctuidae) in Hawaii, where it provided substantial control (Clausen 1978; Lai and Funasaki 1983). It was also established in Fiji against *Mythimna separata* (Waterhouse and Norris 1987) in Australia against *Helicoverpa armigera* (Waterhouse and Sands 2001) and in Cape Verde against *Trichoplusia ni* (Hübner) (van Harten et al. 1990) (Lepidoptera: Noctuidae), without controlling the target pests. It would be interesting to check whether populations established in Australia and Cape Verde parasitize the newly arrived *S. frugiperda*.

Abundance/frequency.

Cotesia marginiventris is particularly abundant in USA and Northern Mexico (Vickery 1929, Meagher et al. 2016). For example, it accounted for 47.3% parasitism of *S. frugiperda* larvae on sweet corn in South Florida, with parasitism rates varying between 9 and 17% (Meagher et al. 2016). However, in Central and South Mexico, it is a less important component of the parasitoid complex of *S. frugiperda* (Molina-Ochoa et al. 2004). Similarly, it is frequent but not very abundant in Central America, with only 1% parasitism in small and medium instars in Nicaragua (Gladstone 1991) and 0.7% in Costa Rica (Marenco and Saunders 1993). In South America, *C. ruficrus* has been more frequently cited than *C. marginiventris* (Molina-Ochoa et al. 2003a) but, in general, both species are only minor parasitoids of *S. frugiperda* (e.g., Figueiredo et al. 2006, Cruz et al. 2009).

Specificity.

Cotesia marginiventris is, according to the literature, a highly polyphagous species. Yu et al. (2016) mention 79 hosts, mostly Noctuidae, but also Pyralidae, Pieridae, Plutellidae, Geometridae, and Ethmiidea. Besides *S. frugiperda* and other *Spodoptera* spp., other frequently recorded hosts include the Noctuidae *Helicoverpa zea*, *Heliothis virescens*, and *Hypena scabra* (F.) (Yu et al. 2016 and references therein).

Climatic suitability.

Cotesia marginiventris occurs in tropical, semi-tropical, and temperate climates. It is distributed from Argentina to Northern US states such as Wisconsin, Ohio, and Maryland (Yu et al. 2016). Based on its present distribution, Tepa-Yotto et al. (2021) built a maximum entropy model showing that *C. marginiventris* would be able to establish in nearly all countries invaded by *S. frugiperda*. However, geographic and host biotypes may occur, and populations attacking *S. frugiperda* in tropical climates may have a more restricted climatic range. It also remains to be seen why *C. marginiventris* is rather uncommon on *S. frugiperda* in many parts of South and Central America.

Similar species in the regions of introduction.

Several *Cotesia* spp. parasitize *S. frugiperda* in Africa and Asia (Kenis et al. 2023). In Africa, *Cotesia icipe* Fernandez-Triana and Fiaboe is one of the main parasitoids of *S. frugiperda*. It is particularly abundant in Eastern Africa (Sisay et al. 2019) but also common in Southern Africa (Durocher-Granger et al. 2020) and West Africa (Agboyi et al. 2020). In Asia, *Cotesia glomerata* (L.) and *C. ruficrus* have been recorded on *S. frugiperda* in China and India, respectively (Kenis et al. 2023)

Eiphosoma (Hymenoptera: Ichneumonidae)

Eiphosoma laphygmae is most likely the only species of the genus attacking regularly *S. frugiperda*. Most old records refer to another species, *E. vitticolle* (sometimes misspelled as *E. viticolle* or *E. vitticole* in the literature), but in the most recent revision of the American species, Gauld (2000) stated that all the New World specimens of *Eiphosoma* spp. that he has seen from *S. frugiperda* belong to *E. laphygmae*. Thus, we consider here that all records of *Eiphosoma* spp. on *S. frugiperda* refer to *E. laphygmae*.

Eiphosoma laphygmae is a larval endoparasitoid that parasitizes first and second instar larvae of *S. frugiperda* and kills them when they are in their fifth instar. A review of its biology is provided by Allen et al. (2021). It occurs from Southern Mexico to Brazil and in the Caribbean from Cuba to Trinidad (Gauld 2000). It does not occur at the northern (USA, Northern Mexico) and southern edges (Argentina) of the distribution range of *S. frugiperda*. It was introduced as a classical biological control agent from Bolivia to the USA but did not become established (Ashley et al. 1982, Meagher et al. 2016).

Abundance/frequency.

Eiphosoma laphygmae is one of the most frequently encountered parasitoid of *S. frugiperda* (see review in Allen et al. 2021). It is particularly frequent in Brazil where it is usually mentioned as one of the main two or three parasitoids, reaching average parasitism rates of 14.5% and up to 30% parasitism in some samples (e.g., Figueiredo et al. 2006; Cruz et al. 2009, 2010). In Central America, significant parasitism rates were also observed, e.g., average of 13% in Costa Rica (Marenco and Saunders 1993).

Specificity.

Yu et al. (2016) only cite one other host for *E. laphygmae*, *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae), from a single museum specimen collected on cotton in Venezuela (Gauld 2000). In a publication on *S. frugiperda* parasitoids in Central America, Cave (1993) also mentions *Anticarsia gemmatalis* (Hübner) (Lepidoptera: Erebidae) as parasitoid of *E. laphygmae* (under *E. vitticolle*) but without mentioning any other detail. Both *A. gemmatalis* and *A. argillacea* are common species with well-known parasitoid complexes (Yu et al. 2016). This suggests that these two records may result from misidentifications of the host or the parasitoid, or that parasitism by *E. laphygmae* is accidental and very rare on these two species.

Climatic suitability.

In the Americas, *E. laphygmae* clearly has a more limited distribution than several other parasitoids because it is absent from the most Northern and Southern ranges of the distribution of *S. frugiperda* (e.g., USA and Argentina). Consequently, the maximum entropy (Maxent) models of Tepa-Yotto et al. (2021), which are mostly based on climatic data of its present distribution, predict a relatively narrow climatic niche for *E. laphygmae* compared to *C. insularis* and *C. marginiventris* in the invaded continents, in particular, in Africa where it is potentially limited to equatorial regions. However, it is not clear whether this somewhat more limited range is due to a restricted climatic suitability or to its higher specificity for *S. frugiperda*, which does not allow the parasitoid to survive on other hosts when *S. frugiperda* is not available.

Similar species in the regions of introduction.

There is no *Eiphosoma* sp. recorded from *S. frugiperda* in Africa and Asia. The most closely related species are *Pristomerus* spp. which belong to the same sub-family (Cremastinae), and are occasionally collected from *S. frugiperda* in Africa (Agboyi et al. 2020, Durocher-Granger et al. 2020). However, several taxonomically unrelated species also attack young host larvae and kill them before maturity, e.g., *Coccygidium* spp., *Cotesia* spp. *Microplitis* spp., *Charops* spp., and *Campoletis* spp. (Kenis et al. 2023).

Other Parasitoids

Several other parasitoid species are occasionally found to be abundant on *S. frugiperda* in the Americas but are less systematically reported and are usually highly polyphagous. The Ichneumonidae

Pristomerus spinator (F.) and the Braconidae *Meteorus laphygmae* (Viereck), occasionally reached parasitism rates over 20% at some sites in surveys in Mexico by Molina-Ochoa et al. (2004). *Meteorus laphygmae* was also, next to *C. insularis*, the most important parasitoid of small instar larvae of *S. frugiperda* in Southern Texas (Vickery 1929). These two parasitoids are polyphagous, with over 30 hosts reported by Yu et al. (2016). *Ophion* spp. (Hymenoptera: Ichneumonidae) are also frequently cited parasitoids of *S. frugiperda* in various regions, but often under different species names (Vickery et al. 1929, Cave et al. 1993, Molina-Ochoa et al. 2003a). *Ophion flavidus* Brulle was the most abundant parasitoid in a study in Chiapas, with 5.8% parasitism (Ruíz-Nájera et al. 2007). The gregarious Eulophidae, *Euplectrus plathypenae* Howard, is also occasionally found in abundance on *S. frugiperda*, e.g., in Yucatan (Delfín-González et al. 2007).

Besides *Archytas marmoratus*, other important Tachinidae parasitoids of *S. frugiperda* include *Lespesia archippivora* (Riley) and *Winthemia* spp. (Molina-Ochoa et al. 2003a). *Lespesia archippivora* is mentioned by Cave (1993) as probably the most common parasitoid of *S. frugiperda* in Central America. Although this is not the case for many studies in Central America, it was the most abundant parasitoid in surveys in Yucatan (Delfín-González et al. 2007) and reached 55.1% parasitism in mature instars in Nicaragua (Gladstone 1991). It is a highly polyphagous species with over 70 host species known in North America alone (Arnaud 1978).

Parasitic nematodes of the genus *Hexamermis* (Nematoda: Mermithidae) are also regularly cited attacking FAW larvae, in particular in Central America (Gardner and Fuxa 1980, van Huis 1981, Castro et al. 1989, Wyckhuys and O'Neil 2006, Ruiz-Nájera et al. 2013), sometimes reaching high rates of parasitism, e.g., up to 71% parasitism in Honduras (Castro et al. 1989).

Conclusions

The two main characteristics of a suitable classical biological control agent against *S. fruigiperda* in its invasion range should be a high efficacy, to be able to affect pest populations, and a high host specificity, to avoid nontarget effects. Based on these criteria, the most appropriate parasitoid for introduction is *E. laphygmae*. This parasitoid is, among the main parasitoids of *S. frugiperda,* the one that appears to have the narrowest host range. However, this specificity for *S. frugiperda* still needs to be confirmed experimentally. Compared to other parasitoids of the moth, it seems to have a narrower climatic range, being absent from the most northern and southern ranges of its host distribution, but it is not clear whether this absence from sub-tropical areas is due to climatic factors or to the fact that, in these regions, *S. frugiperda* is mostly transient and *E. laphygmae* is not able to maintain populations on other hosts. *Aleiodes laphygmae* is another apparently rather specific parasitoid, albeit less common than *E. laphygmae,* in particular in South America. Nevertheless, it could also be considered for introduction into Africa, Asia or Oceania. Other American parasitoids of interest are *Campoletis* spp. There is some confusion in the identity of the species attacking *S. frugiperda* and, therefore, their host range cannot yet be estimated based on the literature. Populations collected from various regions in the Americas should be tested for their specificity and compared, including using molecular methods. However, the fact that they are often cited as the most abundant parasitoid species at higher elevations or higher latitudes suggests that they could be suitable for introduction in climatically similar regions in Africa, Asia, and Oceania.

Chelonus insularis is definitely the most abundant and widespread parasitoid of *S. frugiperda* in its native range. It is likely that the introduction of *C. insularis* in the invasion range would result in some impacts on *S. frugiperda* populations and, thus, in damage levels. However, *C. insularis* would undoubtedly also attack some other Noctuidae and nontarget effects cannot be ruled out, either on populations of rare species or on the regulation of other pest species, including other *Spodoptera* spp. Furthermore, other *Chelonus* species are among the most abundant parasitoids of *S. frugiperda* in Africa and Asia, suggesting important competitive interactions between congeneric species. Before introducing *C. insularis,* or any other parasitoid species into areas invaded by *S. frugiperda,* the potential nontarget effects will have to be clearly assessed and the risks will have to be weighed against the socio-economic benefits of improving the natural control of such an important pest.

Acknowledgments

CABI is an international intergovernmental organization and we gratefully acknowledge the core financial support from our member countries and lead agencies. See https://www.cabi.org/aboutcabi/who-we-work-with/key-donors/ for details.

Funding

This study was financially supported by the Foreign, Commonwealth and Development Office (FCDO), UK, the Directorate-General for International Cooperation (DGIS), Netherlands, the European Commission Directorate-General for International Cooperation and Development (DEVCO), and the Swiss Agency for Development and Cooperation (SDC) through the CABI Plantwise Plus Programme.

Author Contributions

MK: Conceptualization-Lead, Investigation-Lead, Methodology-Lead, Project administration-Lead, Writing – original draft-Lead.

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