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REVIEW

Dipteran parasitoids as biocontrol agents

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Abstract Numerous studies conducted on a variety of temporal and spatial scales around the world show that dipteran parasitoids can exert effective control over some insect pests. This paper provides an overview of major examples of successful classical and augmentative biological control initiatives, organized by major dipteran families which include parasitoid species (i.e., Tachinidae, Phoridae, Sarcophagidae, Cryptochetidae, Bombyliidae, Syrphidae) and according to different global regions. In addition, examples of unsuccessful attempts at biological control using dipteran parasitoids are discussed, along with potential reasons for these failures. A notable drawback found during our literature review is that many parasitoids and host species are not correctly identified, and information on laboratory and field studies is rather scarce. Reproductive strategies of dipteran parasitoids and host-parasitoid associations need to be better investigated. Expanding the knowledge of these parasitoids is crucial for improving biocontrol strategies, especially against pests for which dipterans are key natural enemies.

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Introduction

Parasitoid flies (Diptera) are often overlooked or considered secondary to parasitoid wasps (Hymenoptera) in biological control programs (Feener and Brown 1997). For example, van Driesche et al. (2018) reported 163 parasitoid wasp species *vs*. only 13 parasitoid fly species (seven Tachinidae and six Phoridae) introduced for classical biological control in Canada, Mexico, the USA, and US overseas territories from 1985 to 2018. Globally, Greathead and Greathead (1992) reported 3210 parasitoid wasp introductions (384 successful) and 437 dipteran introductions, dominated by tachinids (37 successful). The gap is even more pronounced with regard to parasitoids used in augmentative biological control. According to van Lenteren (2012), 120 parasitoid wasp species were commercially available worldwide, compared to just three parasitoid flies (all tachinids). This disparity is partly due to the relatively lower number of dipteran parasitoids, as they represent about 20% of all parasitoids, the majority of which are hymenopterans (Feener and Brown 1997). Nevertheless, numerous studies across various spatial and temporal scales have shown that fly parasitoids play an important role in regulating populations of herbivorous insects. For example, the mortality rate of defoliating caterpillars caused by tachinid flies can be higher than that caused by parasitoid wasps (Stireman et al. 2006). This highlights the urgent need for increased research and funding to explore the potential of fly parasitoids in biological control programs. The biological, physiological, and behavioral traits of these entomophagous insects enable them to target hosts in a wide variety of habitats, including those concealed in plants or soil (Stireman et al. 2006). Moreover, climate change may disrupt host-parasitoid interactions in ecosystems where natural control by parasitoid flies is crucial for stability (Di Marco et al. 2023).

This work is not aimed at providing a fully comprehensive overview of the use of dipteran parasitoids in biological control worldwide. However, it outlines several examples of successful attempts involving the use of these insects in classical and augmentative strategies. Additionally, examples of failures are provided, and possible reasons are discussed. The potential of dipteran parasitoids in biocontrol is explored, with the goal of stimulating future research and development in this field. Information is organized according to the main families of dipteran parasitoids for which examples of biological control applications were found, i.e., Tachinidae, Phoridae, Sarcophagidae, Cryptochetidae, Bombyliidae, and Syrphidae. Within each family, the data are arranged by global region. To the best of our knowledge, the distribution of the attempts mentioned aligns with the actual distribution reported in the literature. Most attempts have been conducted in the Nearctic region, in contrast to the relatively few carried out in other regions. Regarding tachinids, the distribution mirrors the findings of Grenier (1988) regarding their use in biological control. This indicates that, over the past four decades, there has been limited progress in expanding the

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geographical coverage of attempts, especially concerning tachinids, which are the most important dipteran parasitoids.

Tachinidae

All Tachinidae with a known life history are endoparasitoids and their hosts are almost exclusively insects (Stireman et al. 2006). This large family exhibits high diversity, with approximately 8600 described species (O'Hara et al. 2020). Among these species, there are promising candidates for use as biological control agents. We give here examples of attempts across different geographic areas.

So far, tachinids have been poorly exploited in Europe. However, in a classical biological control program, the larval parasitoid *Myiopharus doryphorae* (Riley) was introduced from North America to Poland in 1967 to control the Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). It became established, but its impact on the target host species is unknown (Grenier 1988). In the following years, two more species, *Ceromasia auricaudata* Townsend and *Smidtia fumiferanae* Tothill, were introduced from North America to Poland for the control of *Choristoneura murinana* (Hübner) (Lepidoptera: Tortricidae) and also became established. However, their efficacy as biocontrol agents remains unknown (Gerber and Schaffner 2016). The tachinid *Istocheta aldrichi* (Mesnil), native to the eastern Palearctic Region, is one of the most important parasitoids of adults of the Japanese beetle, *Popillia japonica* (Newman) (Coleoptera: Scarabaeidae). Introduced to Terceira (Azores, Portugal) in 1993, it failed to become established, likely due to unsuitable overwintering conditions (Simões and Grenier 1999). However, *I. aldrichi* is currently being evaluated for introduction against the Japanese beetle in Europe (Brodeur et al. 2024). Moreover, laboratory experiments in the Azores showed promising results for the development of *Exorista larvarum* (L.) in three common noctuid pests of pastures and horticultural crops (Simões et al. 2004). In Italy, laboratory studies have been carried out to investigate the possibility of using *E. larvarum* for the control of targeted exotic lepidopteran pests. Despite encouraging results, field studies have not yet been performed (Martini et al. 2019).

In North America, most biocontrol programs using tachinids have been carried out against lepidopteran and leaf-chewing sawfly larvae (Dindo and Grenier 2022). A successful application was the importation of the specialist larval-pupal parasitoid *Cyzenis albicans* (Fallén) from Europe to different forest areas of Canada to control the winter moth *Operophtera brumata* (L.) (Lepidoptera: Geometridae). The fly became established and helped to control the populations of the target insect pest (Hulme and Green 1984). More recently, *C. albicans* was imported yearly (for 14 years) from British Columbia to the northeastern USA. By 2020, the parasitoid was established at most release sites, resulting in a considerable decline in winter moth populations (Elkinton et al. 2021). In the early 1900s, several parasitoids, including 16 tachinid species, were introduced from Europe to New England to control the spongy moth, *Lymantria dispar* (L.), and the brown tail moth, *Euproctis chrysorrhoea* (L.) (Lepidoptera: Erebidae) (Howard and Fiske 1911; Grenier 1988). *Blepharipa pratensis* (Meigen) and *Compsilura concinnata* (Meigen) became established in many US states and were also used in augmentative releases against the spongy moth (Grenier 1988). *Exorista larvarum* and *Parasetigena silvestris* (Robineau-Desvoidy) also became established after inoculative releases in the northern USA (Sabrosky and Reardon 1976), while *Blondelia nifriceps* Fallén failed to become established (Hoy 1976). While tachinids have likely contributed to the control of spongy moth populations in introduced areas, their actual impact is debated (Gray et al. 2008). On the other hand, *C. concinnata* likely explains the disappearance of the invasive browntail moth from most of its former introduction areas, but this generalist parasitoid is also suspected of impacting native lepidopterans (Oberhauser et al. 2017).

Tachinids have been used in classical and augmentative biocontrol of *Diatraea* sugarcane borers (Crambidae), especially *D. saccharalis* (F.), in the southern USA. From 1915 to 1971, *Lixophaga diatraeae* (Townsend), from Cuba, was widely introduced into sugarcane-producing states like Louisiana and Florida, USA (Grenier 1988). Despite the high mobility of the flies, augmentative releases of *L. diatraeae* were successful in various southern US locations (King et al. 1981). In Texas, repeated introductions of the parasitoid *Lydella jalisco* Woodley from its native range yielded limited success in a classical biocontrol

program against the Mexican rice borer, *Eoreuma loftini* (Dyar) (Lepidoptera: Crambidae) (Lauzière et al. 2001). Another species of *Lydella* Robineau-Desvoidy, *Lydella thompsoni* Herting (as *Lydella stabulans grisescens* Robineau-Desvoidy), a larval parasitoid of the European corn borer *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), was introduced in the USA from 1920 to 1938 and even spread to maize growing areas where it was not released (Romig et al. 1985). Following its decline in North America, in the mid-1970s, *L. thompsoni* was reintroduced to reinforce the populations and was well established in the east central USA (Mason et al. 1994). During the 1980s and 1990s, augmentative field release experiments were successfully carried out in the southern USA by using a native larval-pupal parasitoid of noctuids, *Archytas marmoratus* (Townsend), to control the fall armyworm *Spodoptera frugiperda* (J.E. Smith) and the corn earworm *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) in whorl-stage corn (Proshold et al. 1998). The releases were integrated with inherited sterility (substerilizing irradiation of corn earworm, reducing reproduction rates for several generations) (Mannion et al. 1995). *Lixadmontia franki* Wood and Cave, a parasitoid of the bromeliad-eating weevil, *Metamasius quadrilineatus* Champion (Coleoptera: Dryophthoridae) in Honduras, was imported from its native area into Florida, USA for the control of another weevil infesting bromeliads, *Metamasius callizona* (Chevrolat) (Coleoptera: Dryophthoridae), native of Mexico and Guatemala, with very limited results (Cooper et al. 2011). In another classical biological control program, the parasitoid *Ormia depleta* (Wiedemann), imported from Brazil, successfully controlled the mole cricket, *Scapteriscus* sp. (Orthoptera: Gryllotalpidae), introduced from South America, at several sites in southern Florida, USA (Frank and Parkman 1999). Moreover, *I. aldrichi* was introduced with success into the USA in the 1920s for the control of *P. japonica* (Bartlett et al. 1978). While considered a promising biocontrol agent, with relocation programs carried out in infested US areas, its effectiveness may be limited by poor host synchrony. For example, a strain collected from northern Japan has become established in the northeastern USA but may emerge too early relative to the emergence of Japanese beetles (Holloway 1960). Simões and Grenier (1999) confirmed that the diapause of *I. aldrichi* is an important biological characteristic that should be considered. Nevertheless, this tachinid became established throughout the eastern US states and Canada (Ontario and Québec) (Gagnon et al. 2023). A biological control program targeting *P. japonica* is currently underway in British Columbia, Canada, focusing on the introduction of *I. aldrichi* from the greater Montreal and Ottawa regions. The program also includes laboratory studies on the biology and rearing of this parasitoid, which are crucial for the success of biological control (Makovetski and Abram 2024).

With 3088 described species, the Neotropical Region has the highest tachinid diversity (O'Hara et al. 2020). Several species of Neotropical tachinids have been used in biological control programs in different countries (Stireman et al. 2006). In the 1930s, populations of *L. diatraeae* were transferred from one Caribbean island to another to control *Diatraea* spp. and became effectively established in Antigua, Dominica, Guadaloupe, and Saint Kitts (Grenier 1988). To control the same pests, the Amazonian fly [*Lydella* (*Metagonistylum*) *minense* (Townsend)], was introduced from Brazil, first to British Guiana in 1933 (Myers 1935), and then to the West Indies, with records of high parasitism rates in Guadaloupe, Martinique, and Santa Lucia (Cleare 1939). Establishment failed in Barbados and Antigua, possibly due to climatic or ecological differences between islands (Boulet 1986). Other tachinid flies antagonists of sugarcane borers were introduced to the Caribbean islands from Mexico [e.g., *Billaea* (*Paratheresia*) *claripalpis* (Wulp)] and Colombia [*Genea jaynesi* (Aldrich)], with varying degrees of success (Jiménez et al. 2018). Classical biological control with flies originating from outside the Neotropics was first performed by importing an unspecified tachinid from Massachusetts to Barbados in 1931-1932 to control lepidopteran pests of cotton, cover crops, sweet potatoes, and maize, but did not become established (van Lenteren et al. 2020).

In Bolivia an integrated pest management program of sugarcane borers was performed from 1969 to 2000 with augmentative releases of *Palpozenillia diatraeae* Townsend, previously collected from parasitized borer larvae in dead buds, and *B. claripalpis* imported from Peru (Pruett 1996). Also, in Bolivia, mole crickets have been kept at a low level by releasing a complex of natural enemies including the tachinid *O. depleta* (Franco et al. 2020). In Brazil,

an augmentative biocontrol program against *D. saccharalis* was started in the 1960s by using *Lydella minense* and *B.* (=*Paratheresia*) *claripalpis* (Parra 2014). In 1970, *B. claripalpis* and *L. minense* were imported from Peru and Brazil respectively, for the control of *Diatraea indigenella* Dyar (Lepidoptera: Crambidae) and *D. saccharalis*, where both species became established (Bueno and van Lenteren 2002). *Billaea claripalpis* was already reported in Colombia, but the native strain was not efficient in controlling *Diatraea* spp. For this reason, a Peruvian strain was imported to Colombia, resulting in an increase in parasitism efficiency (Gaviria 1998), which, however, has declined in recent years (Vargas et al. 2018). Currently, in Colombia, both *B. claripalpis* and *L. minense* are commercialized for the control of the *Diatraea* complex and produced in private insectaries and some sugar mills in the Department of the Cauca River Valley (CRV; Kondo et al. 2020). In CRV there is also a natural parasitism (10–70%) of *Diatraea* spp. by *G. jaynesi*. Maintaining nectar plants (for adult tachinid food) and broad-leaf weeds (as plant refuges) around sugarcane plantations could complement augmentative releases in an integrated pest management program (Jiménez et al. 2018). Unfortunately, mass rearing techniques for *G. jaynesi* have not yet been developed (Vargas et al. 2018). Furthermore, in Colombian plantations of *Solanum quitoense* Lamarck (Solanales: Solanaceae) attacked by the tomato fruit borer *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae), a natural parasitism rate of about 48% by *Lixophaga puscolulo* Carrejo and Woodley was recorded when farmers reduced insecticide applications (Díaz Montilla and Kondo 2024). Following this observation, the authors proposed conservation biological control strategies to increase natural populations of the parasitoid, including the collection of infested fruits to recover parasitoids for later release, the conservation of nectar plants and the use of insecticides only active by ingestion in the late afternoon (when tachinids are not active).

In Cuba, augmentative releases of the native parasitoid *L. diatraeae* in 1914 led to the cessation of chemical control against the sugarcane borer (Márquez et al. 2019). Scaramuzza (1930) described the fly's biology under laboratory conditions, which led to the development of mass rearing methods for the parasitoid. Moreover, in 1945, *L. minense* was successfully introduced to Cuba and reduced the sugarcane borers' infestation by more than 70% (Scaramuzza 1945). Between 1960 and 1973, the effects of several factors on the development of *L. diatraeae* were studied, including the repercussions of the burning of cane stubble on populations of the parasitoid and *D. saccharalis* (Ponce de León 1973). In 1980, the National Program for the Biological Control of *D. saccharalis* was created in Cuba, with a network of 43 laboratories for the mass rearing of *L. diatraeae*. Barba (1984) carried out studies on the economic efficiency of the Centers for the Reproduction of Entomophages and Entomopathogens (CREE) of the Ministry of Sugar (MINAZ), and developed a methodology for the mass application of these beneficial organisms. Castellanos (1995) highlighted innovations in *L. diatraeae* production and release, including optimal larval density for inoculation and the effects of post-inoculatory host feeding. In 1965, *B. claripalpis* was introduced from Peru to Ecuador to control *D. saccharalis* at the San Carlos Sugar Mill in Guayaquil, with great success, which was attributed to the hybridization of the Peruvian and Ecuadorian strains (Risco-Briceño 1996). Currently, in Ecuador, sugarcane growers maintain laboratories to mass produce and release *B. claripalpis* together with the hymenopteran parasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae), resulting in effective control of the sugarcane borer (Mendoza 2018). As in Colombia and Ecuador, augmentative biological control with tachinids in Peru has been focused on the control of *Diatraea* spp. through successful mass releases of *B. claripalpis* in an area of about 44,000 ha (Mujica and Whu 2020).

Biological control with tachinids in Venezuela has been successful, especially the introduction of *L. minense* against *Diatraea* spp. (Ferrer 2012). Starting in the 1950s, sugar mills and other institutions established laboratories for the mass production of parasitoids using artificial diets for their hosts, enabling large-scale, continuous releases. In 1975, the Integrated Control Service Laboratory (SERCOIN) started producing this Amazonian fly for the state sugar mills (CENAZUCA) (Ferrer and Guédez 1990). In the Caribbean Islands, *Phasia chilensis* (Macquart) (as "*Hyalomyia chilensis*") and *Acaulona peruviana* Townsend were released against the cotton stainers, *Dysdercus* spp. (Hemiptera: Pyrrhocoridae), to supplement the native *Acaulona erythropyga*

Sabrosky, but did not become established (van Lenteren and Bueno 2020). In addition, *Eucelatoria* sp. was introduced from the Cotton Insects Biological Control Laboratory, USDA (Tucson, USA) against *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), without success (Yaseen 1975). In Argentina, *Trichopoda pennipes* (Fabricius) [a senior synonym of *T. giacomellii* (Blanchard), see Dios and Nihei (2020)] was recorded as parasitizing the green stink bug *Nezara viridula* (L.) (Hemiptera: Pentatomidae) (Liljesthröm and Coviella 1999), reducing host densities when acting together with the hymenopterous egg parasitoid *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) (Liljesthröm and Rabinovich 2023). Hyperparasitism of tachinids, which may negatively impact biological control, has been documented in various geographical regions including the Neotropic (Grenier 1988). For example, in Brazil, the hymenopteran *Brachymeria koehleri* Blanchard (Chalcididae) was found to hyperparasitize the pupae of *Chetogena scutellaris* (Wulp), a parasitoid of the nymphalid *Opsiphanes invirae* Hübner (Tinôco et al. 2012).

The use of tachinids in biological control has been reported, to a limited extent, for Asia and Oceania. For example, *L. diatraeae* was imported to Guangxi, China to control *Chilo infuscatellus* Snellen (Lepidoptera: Crambidae) and other lepidopterous sugarcane pests, and acted as an effective biocontrol agent of stemborers in field trials (Deng et al. 2010). In Coimbatore (southern India), augmentative releases of *Sturmiopsis inferens* Townsend against *C. infuscatellus* reduced borer incidence in some trials but not others (Srikanth et al. 2009). The same tachinid species was also released in Ludhiana (northern India) to control the pink stem borer, *Sesamia inferens* (Walker) (Lepidoptera: Noctuidae) in Basmati rice. The lowest incidence of *S. inferens* was observed when a higher dose of 150 mated tachinid females per hectare was released (Singh and Sharma 2023). Difficulties in rearing, however, limited the potential of this species for widespread mass releases (Srikanth et al 2009). *Nemorilla maculosa* Meigen, introduced from Taiwan to Benin, showed promising results for controlling the cowpea pest *Maruca vitrata* (F.) (Lepidoptera: Crambidae) (Agbessenou et al. 2018). Moreover, *T. pennipes* (as "*T. giacomellii*") was successfully introduced to Queensland, Australia from Argentina and contributed to the control of *N. viridula* populations (Coombs and Sands 2000).

In Sub-Saharan Africa, tachinids are mainly used as natural enemies of lepidopteran stem borers of cereals and sugarcane (e.g., *Chilo* Zincken, *Eldana* Walker, *Busseola* Thurau, *Sesamia* Guenée) (Ndemah et al. 2007). Important parasitoids of these moths include *Descampsina sesamiae* Mesnil, *Schembria eldana* Barraclough, *Sturmiopsis parasitica* (Curran) and various *Linnaemya* Robineau-Desvoidy and *Actia* Robineau-Desvoidy species (Crosskey 1984). *Sturmiopsis parasitica* is effective against lepidopterous stemborers in maize and sugarcane (such as *Eldana saccharina* Walker), though its success varies regionally (CABI BIOCAT 2025). Studies suggest that there are at least two geographical strains of *S. parasitica* with different host preferences and efficacy (Dittrich et al. 2006). Tachinid parasitoids also play an important role as biocontrol agents in maize and sorghum. Many of the same species reported as parasitoids of stem borers in sugarcane are involved, with *S. parasitica* being the most common parasitoid (Chinwada et al. 2014), but also several species of *Drino* Robineau-Desvoidy, *Lydella*, *Paradrino* Mesnil, and *Siphona* Meigen. While few biological control introductions have been attempted in Sub-Saharan Africa, there have been some efforts to import tachinids from other regions to control lepidopteran and hemipteran pests. Most attempts have failed due to climatic problems, but there are exceptions, notably on islands (Grenier 1988). For a review of the use of tachinids as biocontrol agents in tropical Africa, see Cerretti et al. (2025).

These examples of tachinids utilized in classical or augmentative biological control field programs described above are summarized in Supplementary Table S1. Species used only in laboratory studies or experimental programs are not included.

Phoridae

With around 4500 described species across 280 genera, Phoridae is one of the most diverse yet understudied families of Diptera. Indeed, *Megaselia* Rondani is one of the largest insect genera, with around 1700 described species and potentially thousands more undescribed (Brown 2022). Many phorid species have parasitoid and predatory larval strategies, while others have saprotrophic, fungivorous or phytophagous larvae. It is hypothesized that parasitoid

and predatory strategies evolved multiple times, as their hosts include Coleoptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Orthoptera and Trichoptera, with a few species reared from arachnid, gastropod and annelid hosts (Disney 2012). Three of the five major subfamilies of phorids include species with parasitoid life strategies, namely Aenigmatiinae, Hypocerinae and Metopininae. Metopinine species that parasitize ants have been the focus of many ecological, systematic and behavioral studies (Feener and Brown 1997). Here, we explore these relationships with a focus on the genus *Pseudacteon* Coquillett and its application to the biological control of *Solenopsis* (Westwood) fire ants. Other phorid parasitoids belonging to several genera have been considered for the biological control of the leafcutter ants *Atta* spp. F. and *Acromyrmex* spp. Mayr (Myrmicinae: Attini) (Elizalde and Folgarait 2011).

Early observations by Pergande (1901) documented oviposition attempts by adult *Apocephalus* sp. Coquillett on *Camponotus* sp. Mayr ants, while Coquillett (1907) described *Pseudacteon crawfordi* from specimens collected in a nest of *Solenopsis geminata* (F.) (Hymenoptera: Formicidae). These two phorid genera have received considerable attention as potential biocontrol agents. Currently, *Apocephalus* includes more than 340 species and *Pseudacteon* comprises around 85 species. However, both contain multiple undescribed species. *Apocephalus* uses multiple taxa of ants (Formicidae) as hosts, including *Pheidole* Westwood (Myrmicinae), *Camponotus* Mayr (Formicinae), and several attine and ponerine (*s.l.*) species, while the subgenus *Mesophora* has a broader host range including bees, beetles, and paper wasps (Brown et al. 2018). In comparison, *Pseudacteon* species are associated with ant hosts, including *Solenopsis*, *Linepithema* Mayr, *Nylanderia* Emery, *Dorymyrmex* Mayr, *Formica* L., *Lasius* F., *Myrmica* Latreille, *Tapinoma* Förster, *Azteca* Forel, *Crematogaster* Lund, *Liometopum* Wheeler and others. Given that the genera *Solenopsis*, *Linepithema* and *Nylanderia* contain serious invasive species, while attines such as *Atta* and *Acromyrmex* are important agricultural pests, efforts have been made to identify classical and augmentative biological agents among their phorid parasitoids.

Some groups of ants host multiple species of parasitoid phorids, such as the 26 *Pseudacteon* species that parasitize *Solenopsis saevissima*-complex ants in South America and the 20 *Pseudacteon* species that parasitize the *S. geminata*-complex across South, Central and North America (Plowes et al. 2009). In the field, up to 14 species of *Pseudacteon* have been encountered at a single site (Folgarait et al. 2007), indicating an unusual degree of niche partitioning. Niche axes include worker size, host activity (nest defense *vs*. foraging trail), and diel and abiotic factors (Folgarait et al. 2007).

The intensive niche specialization by *Pseudacteon* may underly their high degree of host specificity and serve to make them prospective biological control candidates, but it begs the question of which species or combinations of species are needed for ecologically effective control. An early suggestion to consider these flies for potential biological control was made by Feener and Brown (1992), who showed a substantial reduction in foraging efficiency by *S. geminata* when disrupted by *Pseudacteon* flies. Similar results were found for the red imported fire ant *Solenopsis invicta* Buren (Orr et al. 1995; Porter et al. 1995), and a program ensued to evaluate *Pseudacteon* species from Argentina and Brazil as prospective biological control agents of this ant.

The principal argument for using *Pseudacteon* for biological control was their indirect impact (i.e., decreased colony protein consumption) and the reduction in interspecific competitive ability of the fire ants (Feener and Brown 1992). Parasitism rates of $<3\%$ have been reported based on the number of adult parasitoids recovered from nest samples (Calcaterra et al. 2008). This way of estimating parasitism rates substantially underestimates direct mortality since it is based on a biased population sample and does not account for the mortality of parasitized workers that die but fail to support viable emerging flies (50% survivorship, Plowes, unpublished). A further consideration on the impact of phorid flies on fire ants is the possibility that they may be pathogen vectors, although this has not been demonstrated in the field (Oi et al. 2009). Several pathogens are known to infect fire ants, including viruses and microsporidia, although the interactive effects of parasitoids and pathogens on fire ants have yet to be fully studied.

By 2004, ten species of *Pseudacteon* had been evaluated using sequential no-choice tests (Porter and Gilbert 2004), and by 2023, six species had been introduced and established at various sites. These species can be roughly characterized by the target worker

size (small, large), and host location site (nest, trail), although there is some degree of overlap. Since a key premise for introduction of phorids was their potential impact on foraging trails that are largely attended by small workers, the ideal biological control species would be ones that frequent foraging trails and attack small workers. It has also been an aim to introduce a functionally complete set of *Pseudacteon* species that exert pressure across a range of *Solenopsis* activities. Work continues to introduce small, foraging trail specialists such as *Pseudacteon obtusitus* Plowes, Folgarait and Gilbert or *P. nudicornis* Borgmeier. Some reviews have questioned the overall prospect for control of fire ants by parasitoid phorids alone (Oi et al. 2015). However, several measures of success have already been shown. While fire ant densities have declined across study sites in Texas, USA (Plowes and LeBrun, unpublished), some of those changes may be related to mortality factors other than parasitism by *Pseudacteon*, such as the presence of several pathogens, changes in social form, habitat modification, and native ant community dynamics. Another aspect that may contribute to population level effects is the existence of enormous seasonal peaks in *Pseudacteon* abundances, which coincide with high foraging activity by fire ants. During peak seasons, over 2000 female *Pseudacteon curvatus* Borgmeier have been collected in 24 h traps at individual ant nests, indicating a seasonally high parasitoid pressure (Plowes and LeBrun, unpublished).

Similar to other biological control efforts, key steps in the development of *Pseudacteon* for fire ant control have been host specificity testing, impact studies, rearing, and release and post-release monitoring. One of the most challenging steps has been the refining of methods for rearing of multiple species, some being particularly recalcitrant. Given that the host ants are eusocial insects, care was needed to maintain pseudocolonial nest conditions with queens and larval brood, to ensure that ant worker stress behaviors did not impact rearing success. Porter et al. (1997) and Vogt et al. (2003) described rearing methods for *Pseudacteon tricuspis* Borgmeier and *P. curvatus*, respectively, while additional insights and modifications were noted for *P. obtusitus* (Folgarait et al. 2020) and *Pseudacteon nocens* (Plowes et al. 2012). Biological control of social insects using parasitoids had not previously been attempted, and these recent efforts against fire ants have been challenging but have seen the successful establishment of sustained populations of multiple species of *Pseudacteon* and shown several indications of impacts on the fire ant targets. Effective biological control of fire ants in North America is likely to include not only the introduced parasitoids but also a broad range of other natural enemies.

Sarcophagidae

Flesh flies (Sarcophagidae) comprise some 3000 species (Pape et al. 2011), all of which incubate eggs in a bilobed pouch from the common oviduct, and the larva bursts open the chorion during or shortly after deposition (Pape 1996). A single species in the subfamily Miltogramminae, *Macronychia* sp. Rondani, has been suggested as a possible biocontrol agent for tabanids in the southwestern USA (Thompson and Love 1979). Maggots were recovered from adult tabanids, especially from the thoracic musculature, and the rate of parasitized tabanids fluctuated between 4 and 20% over the season (Thompson and Love 1979). Voucher specimens have not been recovered and the identity of the species needs verification (Pape, unpublished).

In the subfamily Sarcophaginae, the genus *Blaesoxipha* Loew contains parasitoids of darkling beetles and grasshoppers (Pape 1994). Caeliferan grasshoppers are parasitized as last instar nymphs or adults, with the incidence of parasitization of grasshopper populations varying from 0 to 50% (Middlekauff 1959). Suitable hosts are targeted by gravid females larvipositing directly on the body of flying or jumping grasshoppers, or by stalking grasshoppers on the ground and inserting a larva into the mouth or between the genital appendages, or by injecting a larva through a leg or an intersegmental membrane (Middlekauff 1959; Pape 1994). Several attempts have been made to use species of *Blaesoxipha* in the control of local grasshopper pests. The first attempt was made in the early days of biological control, with the import of *Blaesoxipha rufipes* (Macquart) from Australia to California, USA. The first shipment was completed in 1893 and others followed in 1900 (Bartlett et al. 1978), but the species did not become established (Pape 1996). Canada and Argentina engaged in a major exchange of *Blaesoxipha* spp., with small numbers of Canadian species shipped to Argentina during 1937-1939 and species from Argentina and

Uruguay sent to Canada during 1938-1939, with releases in various sites across Canada (Lloyd 1951; McLeod 1951). None of these introduced species are known to have been established (Bartlett et al. 1978; Pape 1996). In the early 1970s, grasshopper parasitoids were reared in Pakistan and flown as diapausing pupae to the USA for testing on local caeliferan grasshoppers (Rees 1985). The flies were identified as *Blaesoxipha* sp. near *cinereogrisea* Rohdendorf, *Blaesoxipha rufipes* (Macquart) and *Sarcophaga ruficornis* (F.), but only a few specimens of the latter species reproduced in the laboratory after arrival, and only once. However, *S. ruficornis* is known to breed in vertebrate carrion (Nandi 2002), and the specimens were probably misidentified. A more recent attempt at introducing *Blaesoxipha lapidosa* Pape to Sand Island, Honolulu, Hawaii, USA was also unsuccessful (Hardy 1981). Using species of *Blaesoxipha* for pest grasshopper control is still being proposed (e.g., by Elsayed and Sayed 2014), but it has never emerged as a practical alternative to other biological control measures because of difficulties and high costs associated with rearing large numbers of flies and releasing them across large areas often involved in grasshopper outbreaks (Dakhel et al. 2020).

Some flesh flies have a larval development reminiscent of parasitoids, but they are better classified as predators, due to the less specialized interaction with their prey. For example, the larvae of *Agria* spp. Robineau-Desvoidy prey on mature larvae or newly-formed pupae of moths (Kuhlmann 1995), those of *Sarcophaga* Meigen subgenus *Heteronychia* Brauer and Bergenstamm prey on snails (Baker 2002), and those of *Sarcophaga aldrichi* Parker prey on weakened or parasitized moth pupae (Hahn et al. 2000).

Cryptochetidae, Bombyliidae, Syrphidae

Two cryptochetid species of Australian origin [i.e., *Cryptochetum iceryae* (Williston) and *C. monophlebi* Skuse] were successfully introduced into California, USA and Mauritius against the cottony cushion scale, *Icerya purchasi* Maskell and the Seychelles scale *I. seychellarum* (Westwood) (Hemiptera: Monophlebidae), but they were later neglected due to the higher efficacy and ease of handling of another important natural enemy of these scales, the predator *Novius cardinalis* (Mulsant) (Coleoptera: Coccinellidae) (Greathead 1986). In the 1990s, *C. iceryae* was introduced from California, USA to Israel to control *I. purchasi*, being able to suppress the target insect in two years at some release sites (Mendel and Blumberg 1991). *Cryptochetum jorgepastori* Cadalha, introduced to Israel from Spain, contributed to control the pine scale, *Palaeococcus fuscipennis* (Burmeister) (Hemiptera: Monophlebidae) (Mendel et al. 1998).

Limited biocontrol attempts have been conducted with bombyliids, which are hard to maintain in captivity. For example, *Villa cana* (Meigen) appeared to regulate some populations of *Thaumetopoea pityocampa* (Denis and Schiffermüller) (Biliotti et al. 1965). Moreover, *Exhyalanthrax* spp. Becker showed potential as biocontrol agents of tse-tse flies (Greathead 1980). Finally, the hoverfly *Volucella inanis* (L.), an ectoparasitoid of *Vespula* Thomson (Hymenoptera: Vespidae) species, is regarded as a promising candidate for classical biological control in New Zealand, where *Vespula germanica* (F.) and *V. vulgaris* (L.) have become invasive, but no applied programs have been implemented to date (Stratford et al. 2024).

Concluding remarks and perspectives

This review concludes that dipteran parasitoids offer great potential for biological control but further research is needed. Data accessibility was challenging due to the prevalence of incomplete records in difficult-to-obtain national and regional publications. However, after an exhaustive bibliographic review we gathered the information contained in a bibliography (see Supplementary Material S1), including those not cited in the text. A significant challenge, particularly with tachinids, was the frequent lack of clear species-level identification in the scientific literature (Kondo et al. 2020). Many records were only identified to genus level or simply listed as "tachinids," hindering accurate assessment. Furthermore, host identification was often poorly documented. In the Neotropical Region, classical biocontrol frequently involved introducing natural enemies from other countries within the same region (van Lenteren et al. 2020).

We also found that information on experimental studies is quite scarce. Most of them were conducted using flies that emerged in the laboratory from parasitized field-collected hosts, although rearing was not

established due to the difficulties involved, especially when dealing with parasitoids whose hosts were stink bugs or coleopterans (Vargas et al. 2018). The majority of these experimental studies involved quantifying the proportion of parasitized hosts, in some cases distinguishing between sexes and/or developmental stages of the attacked host, and assessing the effect of parasitism on the feeding behavior, longevity, fecundity and fertility of the host. Moreover, there are studies investigating the parasitism behavior and host-parasitoid relationship in tachinids, but they involved relatively few species.

Among all the groups of dipteran parasitoids, most information on studies and applied use involves tachinids. Successes were relatively rare, but some of them were remarkable, e.g., the use of *L. diatraeae*, *L. minense* and *B. claripalpis* for the control of sugarcane borers in different Neotropical countries (Grenier 1988; Parra 2014; Kondo et al. 2020; Gaviria Vega et al. 2024). Interestingly, in addition to scientific research on tachinids as natural enemies of pests, some private agricultural firms have started rearing these biocontrol agents for internal use. For example, several sugar mills in Latin America mass-produce tachinids, releasing them into the field to control sugarcane borers and thus producing their own bioinput. Moreover, several augmentative biological control initiatives in the Neotropical Region were undertaken alongside the implementation of conservation biological control strategies. Therefore, the establishment of spontaneous plants which provide adult tachinids with food and refuge near crop fields is part of integrated pest management programs in the region. However, many efforts at biological control using tachinids, particularly in classical biological control, have either been unsuccessful or yielded only partial success. The reasons for failures can be numerous. In the past, before the advent of efficient means of transport, such as air sending, the duration of carriages posed a significant challenge, a problem which has now been overcome (Grenier 1988). The low number of parasitoids released, often linked to challenges in rearing, can also contribute to failures (Dindo and Grenier 2022). The host transfer imposed on tachinid parasitoids was often unfavorable. For example, *M. callizona* was very poorly parasitized by *L. franki*, a regular parasitoid of *M. quadrilineatus*, although both weevils infest bromeliads and live in wet environments (Cooper et al. 2011). The absence of alternative hosts, which parasitoids can use when the regular hosts are unavailable in certain seasons, may also explain the differences in control efficacy observed in different countries using the same host-parasitoid system. For example, *Blondelia nigriceps*, introduced in North America against the spongy moth, failed to establish for multiple reasons including the absence of alternative hosts, besides the low number of insects released and the inadequate conditions for the parasitoid to overwinter in the area of introduction (Hoy 1976). Differences among parasitoid strains may also explain some of the variations in the success achieved, as observed in Barbados, where populations of *L. diatraeae* obtained from Antigua, Cuba, Dominican Republic and Jamaica and released on several occasions between 1930 and 1960 failed to control the target insect pest *D. saccharalis* (van Lenteren and Colmenarez 2020). Thus, in *L. diatraeae*, genetic variability during laboratory rearing could be affected by genetic drift caused by a population bottleneck, resulting in unfavourable loss of variability or possibly advantageous selection (Pintureau et al. 1995).

Concerning other dipteran parasitoids, phorids play a crucial role as biocontrol agents of ants. Some groups of ants host a large number of parasitoid phorid species, showing niche partitioning among hosts based on factors such as worker size, ant activity, and abiotic factors. Given this, coupled with the social habit of host ants, utilizing phorids in biological control programs poses a particularly challenging task. However, successful establishment of multiple species of parasitoids has been documented, with demonstrated impacts on host populations (Feener and Brown 1992; Orr et al. 1995; Porter et al. 1995). Regarding sarcophagids, we highlight that the use of some species in the control of grasshopper pests represents one of the earlier attempts of classical biocontrol initiatives, with the first shipment of parasitoids made by the end of the nineteenth century. With respect to cryptochetids and bombyliids, very little information can be found, and limited biocontrol attempts have been made with these natural enemies. However, one cryptochetid was involved in the first successful classical biological control program carried out in California, USA against the cottony cushion scale in 1888, although its role was soon overlooked (Greathead 1986). About syrphids, which are mostly

predators, one ectoparasitoid species has shown the potential to be used in classical biological control against *V. germanica* and *V. vulgaris* (Stratford et al. 2024).

The highly diverse morphology of dipteran parasitoids, with many striking features and convergent characteristics between groups, makes determination very difficult (Toma 2012). There are also many questions that still need to be investigated regarding reproductive strategies of dipteran parasitoids and the structure of host-parasitoid assemblages, which may improve the design and implementation of biological control programs against important pests. Although several studies have demonstrated that parasitism by tachinids is often highly dependent on habitat, knowledge of the ecology of most tachinid species is at best poorly understood, mostly because of the difficulty in rearing most species in the laboratory (Stireman et al. 2006). These issues, including the key aspects of dipteran biology relevant to rearing, were discussed by Dindo and Grenier (2022). Overall, challenges associated with the production of dipteran parasitoids have limited their exploitation as biocontrol agents in classical and augmentative strategies, and undermined their potential as regulators of economically important invertebrate pests (Dindo and Grenier 2022). Therefore, efforts should focus on enhancing knowledge not only of dipteran parasitoid biology, but also of their rearing, as the success of biocontrol programmes (especially augmentative) largely relies on the development of efficient rearing procedures for culturing the entomophagous insect involved (Greathead 1986).

In conclusion, while dipteran parasitoids are promising biological control agents, their application faces several challenges. These include fragmented research, difficulties in the mass rearing of certain species, the existence of different strains (and possibly cryptic species) with different parasitization capabilities, and also regulatory barriers to their international movement (Gaviria Vega et al. 2024). Future efforts should focus on advancing comprehensive research to deepen our understanding of dipteran parasitoids, and also predators (Burgio et al. 2025), develop effective mass rearing techniques, advocate for regulatory changes, and implement biological control strategies that effectively include the use of these beneficial insects.

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