

Review of Tachinids and Other Dipteran Parasitoids and Predators as Biological Control Agents in Colombia, Ecuador, and Peru

Revisión de los taquínidos y otros parasitoides y depredadores dípteros como agentes de control biológico en Colombia, Ecuador y Perú

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Abstract: The use of dipterans in the biological control of insect pests in Colombia, Ecuador, and Peru has mainly involved various species of tachinid flies (Diptera: Tachinidae) to control sugarcane stem borers of the genus *Diatraea* Guiling (Lepidoptera: Crambidae) via augmentative releases. Tachinid parasitoids also play an important role in the natural control of the solanaceous fruit borer *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae) in Colombia and Ecuador and have the potential to control the American palm weevil, *Rhynchophorus palmarum* L., and other species of *Rhynchophorus* Herbst (Coleoptera: Dryophthoridae) in Colombia and other countries where they are considered pests. There are no reviews on the usage of dipterans in biological control in the above countries. Besides those studies on sugarcane, the information on dipteran parasitoids in the scientific literature is scarce and composed mainly of occasional observations, checklists of natural enemies of certain cultivated crops, and biological notes in taxonomic studies. The main objective of this study is to provide a review of the species of Tachinidae used in biological control programs in Colombia, Ecuador, and Peru. Moreover, information on other dipterans families, e.g., Cecidomyiidae, Chamaemyiidae, Phoridae, and Syrphidae, which have been reported as natural enemies of insect pests, are also briefly discussed.

Keywords: Cecidomyiidae, *Diatraea* spp., Diptera, Phoridae, *Rhynchophorus palmarum*, Syrphidae, Tachinidae.

Resumen: el uso de dípteros en el control biológico de insectos plaga en Colombia, Ecuador y Perú se ha llevado a cabo principalmente con diversas especies de moscas taquínidas (Diptera: Tachinidae) para el control de los barrenadores del tallo de la caña de azúcar del género *Diatraea* Guiling (Lepidoptera: Crambidae) mediante liberaciones aumentativas. Los parasitoides taquínidos también juegan un papel importante en el control natural del perforador del fruto de las solanáceas, *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae) en Colombia y Ecuador y tienen potencial para controlar el picudo americano de las palmeras, *Rhynchophorus palmarum* L. y otras especies del género *Rhynchophorus* Herbst (Coleoptera: Dryophthoridae) en Colombia y demás países donde se consideran plagas. Además de los estudios sobre la caña de azúcar, la información sobre parasitoides dípteros en la literatura científica es escasa y se compone principalmente de observaciones ocasionales, listas de enemigos naturales de ciertos cultivos y notas biológicas en estudios taxonómicos. El objetivo principal de este estudio es proporcionar una revisión de las especies de Tachinidae utilizadas en programas de control biológico en Colombia, Ecuador y Perú. Además, también se analiza brevemente otras familias de dípteros, p.ej., Cecidomyiidae, Chamaemyiidae, Phoridae y Syrphidae, que han sido reportadas como enemigos naturales de insectos plaga.

Palabras clave: Cecidomyiidae, *Diatraea* spp., Diptera, Phoridae, *Rhynchophorus palmarum*, Syrphidae, Tachinidae.



Introduction

Of the 8,592 species of Tachinidae described worldwide, the Neotropical Region has the highest diversity compared to other regions, with 3088 described species (O'Hara et al., 2020). In terms of diversity and ecological significance, they are second only to parasitic Hymenoptera (e.g., Chalcidoidea, Ichneumonoidea) as insect parasitoids (Stireman et al., 2006). Tachinids often play a significant role in the regulation of herbivore populations and the structuring of natural and managed ecological communities because of their predominance as parasitoids of the larval stage of Lepidoptera and other groups of insect herbivores, e.g., Chrysomelidae, Hemiptera (Heteroptera), Scarabaeidae, and Hymenoptera (Symphyta) (Stireman et al., 2006). According to Grenier (1988), approximately 100 tachinid species have been involved worldwide in biological control programs for crops and forest pests, most with partial or complete success. In the Neotropical region, the use of Tachinidae as biocontrol agents has been carried out mainly to control sugarcane stem borers of the genus *Diatraea* Guelding (Lepidoptera: Crambidae), with different levels of success (Grenier, 1988). Despite being such an important group, the information on using Tachinidae as biological control agents in Colombia, Ecuador, and Peru is scarce and scattered. The recent book on the history of biological control in Latin America and the Caribbean by van Lenteren et al. (2019) compiles a great deal of information on the use of natural enemies in the region; however, the tachinids are only treated briefly. The objective of this study was to conduct a literature review to provide detailed information on the use of Tachinidae and other dipteran families (e.g., Cecidomyiidae, Chamaemyiidae, Phoridae) related to biological control for the above three countries.

Materials and Methods

A literature review of scientific articles related to flies (Diptera) in biological control in Colombia, Ecuador, and Peru was conducted with particular emphasis on those flies of the Tachinidae family. The literature search was carried out in four databases, i.e., Google Scholar, Scielo, Scopus, and Web of Science, with the following terms: biocontrol, biological control, Cecidomyiidae, Diptera, Colombia, Ecuador, Peru, Phoridae, and Tachinidae. A search was also conducted by checking the Tachinid bibliography from 1980 to the present provided on the Tachinidae resources webpage (O'Hara, 2022). The search included journal papers, undergraduate theses, conference papers, book chapters, and other peer-reviewed literature available in English and Spanish. For the tachinids reported in Ecuador, the percentage of genera was calculated for each arthropod host per plant in the investigated regions. The frequency of reports was then plotted for both the parasitoid genera and their arthropod hosts, along with the genus-host associations.

Results and Discussion

Tachinids in the Biological Control of the Sugarcane Stem Borer *Diatraea* spp. (Lepidoptera: Crambidae) in Colombia

From the 1930s up to the 1950s, intense scientific research was conducted in Cuba, St. Kitts, Antigua, Guadeloupe, Barbados, Venezuela, Peru, Mexico, and later in Ecuador, Colombia, Brazil, and Costa Rica on the control of sugarcane borers using the tachinid fly parasitoids *Lixophaga diatraeae* (Townsend) and *Lydella minense* (Townsend) (Risco-Briceño, 1996). In Colombia, augmentative biological control strategies against *Diatraea* spp. in sugarcane plantations are implemented through the release of hymenopteran egg parasitoids, as well as dipteran and hymenopteran larval parasitoids (Vargas et al., 2015). Egg parasitoids include *Trichogramma exiguum* Pinto & Platner (Hymenoptera: Trichogrammatidae) and larval parasitoids include *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) and two species of tachinid flies, namely *Billaea claripalpis* (van der Wulp), and *L. minense* (Diptera: Tachinidae) (Löhr et al., 2018). *Billaea claripalpis* was imported from Peru in 1970 for the control of *Diatraea indigenella* Dyar & Heinrich (Altieri & Nicholls, 1999) and *Diatraea saccharalis* (Fabricius) (Bueno & van Lenteren, 2002).

Additionally, in 1970, *L. minense* was imported from Brazil to control the same two *Diatraea* species (Bueno & van Lenteren, 2002). *Billaea claripalpis* and *L. minense* successfully settled under the conditions of the Cauca River Valley (CRV). This region comprises areas in the Departments of Cauca, Quindío, Risaralda, and Valle del Cauca in southwestern Colombia. Around the same time, the tachinid fly *L. diatraeae* was imported from Cuba to control *D. saccharalis* (Bennett & Street, 1984) and released in the same region. However, the latter failed to establish (Bennett, 1971; Vargas et al., 2015). In the case of *L. minense*, this tachinid was known to be associated with *Diatraea* spp. in Brazil and Venezuela (Bennett, 1971) but not in Colombia. Its introduction to Colombia was a success, and today, *L. minense* is probably the most commercialized parasitoid in this South American country, where additional efforts have been made to standardize quality control parameters for its production (Obando et al., 2007).

As for *B. claripalpis*, although a population of this species had already been reported in the country at the time, the Colombian population was inefficient in controlling *Diatraea* spp. (Gaviria, 1998). For this reason, a Peruvian population of *B. claripalpis* was imported to Colombia, which increased its parasitoidism efficiency (Gaviria, 1998). However, according to field observations, the parasitoidism rate efficiency of the Peruvian population has declined in recent years (Vargas et al., 2018). Currently, in Colombia, *B. claripalpis* and *L. minense* are sold commercially for the control of the *Diatraea* complex (rice, sugarcane, maize) by small unregistered and registered laboratories and private laboratories in sugar mills in the CRV (Kondo et al., 2020). Besides the commercially available imported tachinid parasitoids, there is also a natural control of *Diatraea* spp. on sugarcane in the CRV provided by the tachinid fly *Genea jaynesi* (Aldrich). This tachinid fly maintains control levels between 10 and 70 % and, combined with the two introduced tachinid parasitoid species, results in parasitoidism rates that range from 20 to 90 % (Smith & Bellotti, 1996). Unfortunately, mass-rearing techniques for *G. jaynesi* have not been developed yet (Vargas et al., 2018).

According to Bennett (1969), females of *L. minense* are guided by the scent of the larvae of the stem borers and apparently show no preference amongst the various *Diatraea* species. Females will usually larviposit on any part of the plant that emits odors from the larvae of *Diatraea* spp. and are particularly attracted to the frass left by the stem borers at the entrances of the tunnels. To the best of the authors' knowledge, no information is available on the methods of host location for *B. claripalpis* and *G. jaynesi*. Bennett (1969) also indicated that although the development times of *L. minense*, *B. claripalpis*, and *G. jaynesi* may vary, they generally have similar life histories. The females of *L. minense* and *B. claripalpis* larviposit in the entrances of the perforations made by the sugarcane stem borers, through which the fly larvae enter the tunnels and move guided by negative phototaxis, eventually locating their host through the random exploration of the tunnels; later, with their sharp cephalopharyngeal skeleton, the tachinid larvae open the cuticle of their insect host larvae and penetrate them (Bennett, 1969). Given the similarities in host types and environmental conditions within the sugarcane agroecosystem, similar behavioral traits should occur in *G. jaynesi*. However, precise information about the behavior of this species is lacking, and further research is necessary to validate this assumption.

In the case of *L. minense* and *B. claripalpis*, the parasitoid larvae attach to the tracheae of their host or one of their tracheal tubes. In contrast, the larvae of *G. jaynesi* will remain attached to the site of penetration on the epidermis of the stem borer host. There, it produces a funnel structure and remains until its development is completed (Bennett, 1969). In most studied tachinid species under tropical conditions, the larval period usually takes 7 to 10 days, exiting the host's cuticle and pupating outside it (Bennett, 1969). In *L. minense*, the larval period lasts approximately 10 days, and the pupal stage lasts 10 to 15 days, while *B. claripalpis* has a larval period of around 11 days, and the pupal stage lasts 10 to 25 days (Aya et al., 2019). Unfortunately, no information on developmental time is available regarding *G. jaynesi*.

Generally, adult tachinids are highly active flying insects, making it challenging to track their movements in the field (Bennett, 1969). As a result, limited information is available about their dispersion and behavior in both natural environments and sugarcane agroecosystems. Still, Bennett (1969) noted that while adults of *B. claripalpis* are rarely observed in sugarcane fields, the presence of parasitized stem borer larvae indicates that they do visit these crops to search for larvae for parasitization. Adult *B. claripalpis* are mainly located in trees surrounding the sugarcane fields, where most detected individuals are females (Bennett, 1969). The few tachinid females collected in the trees surrounding the plantations were unfertilized or only recently fertilized. In contrast, those gathered on the crop were constantly fertilized, although not always ready to larviposit (Bennett, 1969). This suggests that after the emergence of the adult tachinids, they congregate in the trees surrounding the cultivated plot, where they feed on floral nectaries, copulate, and only females return to the crop to larviposit (Bennett, 1969). In this regard, Vargas et al. (2006) pointed out that *G. jaynesi* frequently feeds on the nectar of plants that grow in alleys, hedgerows, and edges of sugarcane crops.

In a study that monitored the populations of stem borers and their parasitoids during a crop cycle in three areas of the CRV (southern, central, and northern), Leyton-Flor et al. (2018) found that the appearance of parasitized larvae by these three tachinids was more evident from the seventh month of age of the sugarcane crop, which would indicate that tachinid populations are associated with the increase in the populations of their sugarcane stem borer hosts which built up with the age of the crop. Furthermore, the same authors found that in two of these three

areas (central and southern), the highest levels of parasitoidism were caused by *G. jaynesi* and *L. minense*. In contrast, in the northern area, most larvae were parasitized by the parasitoid wasp *C. flavipes*.

In Colombia, in areas where sugarcane is planted to produce ‘panela’ (unrefined whole cane sugar), Sarmiento-Naizaque et al. (2021) collected larvae of different sugarcane borers in the area known as the Suarez River Basin in the Departments of Santander and Boyacá between 2015 and 2017, from which they recovered different tachinid parasitoids species, namely *B. claripalpis*, *G. jaynesi*, and a few unidentified specimens of *Leskia* Robineau-Desvoidy, and *Phytomyptera* Rondani. The discovery of *Leskia* sp. constituted a new parasitoid record for sugarcane stem borers. Other *Leskiini* parasitoids have already been reported attacking *Diatraea* in South America, including *G. jaynesi*, *Leskiomina australis* Townsend, *Leskia arturi* (Guimarães, 1975), *Miobiopsis* (Wiedemann), and *Parthenoleskia parkeri* Townsend (Guimarães, 1971). These findings, along with observations of *Phytomyptera*, highlight important potential natural biological control agents for these lepidopteran pests in Colombia, warranting further research.

In the Department of Nariño in Colombia, where sugarcane is also cultivated to produce panela, *B. claripalpis* has been collected only from the larvae of *D. indigenella*. *Billaea claripalpis* is adapted to different environmental conditions, i.e., tropical premontane dry forest (TP-df), tropical premontane wet forest (TP-wf), and tropical lower montane wet forest (TLM-wf), with its highest parasitic activity found in drier environments (TP-df), where a natural parasitoidism rate of 17 % has been recorded, in comparison with the other two environmental conditions, with 10.7 % (TP-wf) and 4.3 % (TLM-wf), respectively (Igua Urbano, 2018). In this region of Colombia, it appears that *G. jaynesi* is more restricted to the tropical premontane dry forest (TP-df) and tropical premontane wet forest (TP-wf), with the highest control activity being observed in the drier environment (TP-df), with a parasitoidism rate of 16.6 % (Igua Urbano, 2018). These authors believed this latter parasitoid could control both *D. saccharalis* and *D. indigenella* larvae in the above environments (Igua Urbano, 2018). On the other hand, in the CRV, *G. jaynesi* is more aggressive against *D. indigenella* than *B. claripalpis*, with parasitoidism rates of approximately 10 % in *D. indigenella* in comparison to 7 % in *D. saccharalis*, based on field surveys during the first semester of 2006 in Southern CRV (Bustillo, 2013; Vargas et al., 2006).

Under the conditions of the panela-producing region of Nariño, populations of *L. minense* have not been recovered from the field despite the growers’ mass-release of *B. claripalpis* and *L. minense*. This may indicate a lack of adaptation of *L. minense* to the natural conditions of Nariño or the low density of its natural host (*D. saccharalis*) since, in this region, the share of *Diatraea* species is 80 % of *D. indigenella* and 20 % of *D. saccharalis* (Igua Urbano, 2018). *Diatraea indigenella* has been only identified in the panela production region of Nariño (Igua Urbano, 2018), and it seems that this species is endemic to the southwestern region of Colombia, being recorded in Cauca, Choco, Tolima, and Valle del Cauca (Gómez & Vargas, 2014).

Regarding these tachinid parasitoids and their host species relationships, Aya et al. (2019) found that parasitoidism rates by *L. minense* and *B. claripalpis* were reduced in *Diatraea tabernella* Dyar and *Diatraea busckella* Dyar & Heinrich compared to that found in *D. saccharalis* and *D. indigenella*, which in part would explain the outbreaks of *Diatraea* spp. stem borers that occurred in the CRV

between 2012 and 2014 (Vargas et al., 2018). The possibility of different resistance mechanisms amongst species of *Diatraea* to these parasitoids warrants further study.

In different sugarcane plantations in the CRV region, field surveys found that *G. jaynesi* causes between 10 and 40 % natural parasitoidism rates in different *Diatraea* species, which suggests that this tachinid is the primary larval parasitoid of *Diatraea* spp. in this region (Vargas et al., 2018). It is known that once adult females of *G. jaynesi* emerge, they must look for flowers that provide them with nectar and nutrients needed for the gestation period of their larvae, which also applies to other commercially released tachinid parasitoids. Further, Jiménez et al. (2018) reported the presence of adult flies of *G. jaynesi* in 16 morphotypes of broadleaf weeds in the alleys surrounding cultivated sugarcane fields. Thus, one of the strategies to maintain the populations of *G. jaynesi* and other natural enemies in sugarcane fields is to stimulate the establishment and proliferation of nectar plants around cultivated areas by implementing a conservation biological control strategy in sugarcane (Vargas et al., 2015). The benefits of landscape diversity on the increase of biological control of pests via parasitoidism and predation have been demonstrated in other economically important agroecosystems (Begg et al., 2017; Gardiner et al., 2009; Sendoya-Corrales & Bustillo, 2016). According to the above, the planting and conservation of broad-leaved weeds as plant refuges in the vegetation strips that surround the sugarcane crops and in the alleys that divide the cultivated lots could be complementary to the releases of beneficial insects currently used and can be incorporated into an integrated pest management program of the sugarcane borers.

Tachinid Flies for the Control of the Black Palm Weevil *Rhynchophorus palmarum* L. (Coleoptera: Dryophthoridae): A Case Study

Besides the sugarcane stem borers *Diatraea* spp., there is another lesser-known stem borer in Colombia that can reach very high populations, the black palm weevil *R. palmarum* (Coleoptera: Dryophthoridae), the primary insect vector of the nematode *Bursaphelenchus cocophilus* (Cobb) (Nematoda: Tylenchida), which causes Red Ring disease on coconut palm, *Cocos nucifera* L., and oil palm, *Elaeis guineensis* Jacq. (Griffith, 1987). Besides attacking palms, this weevil is also known as a pest of sugarcane (Griffith, 1987; Restrepo et al., 1982). Not much is known about the damage it causes in sugarcane, but many weevil adults are attracted to pheromone traps in sugarcane plantations. Löhr et al. (2015) reported the capture of more than 53,000 weevils in traps surrounding a seven-hectare sugarcane area in less than a year.

Due to their development inside the stems, the larvae and pupae of *R. palmarum* are protected against attacks by natural enemies. An alternative for biological control that appears to be the most promising of all known natural enemies to date and which has not received due attention is the parasitoid fly *Billaea rhynchophorae* (Blanchard) (Diptera: Tachinidae) that attacks the larvae and pupae of the black palm weevil in Brazil (Guzzo et al., 2023; Moura et al., 1993, 2006). Most species of the genus *Billaea* Robineau-Desvoidy parasitize beetles from the families Cerambycidae, Dryophthoridae, Lucanidae, and Passalidae (Arnaud, 1978; Nihei & Pavarini, 2011), the only known exception being *B. claripalpis* which attacks Lepidoptera (Pyralidae/Crambidae) (Nihei & Pavarini, 2011), and, under laboratory conditions may also parasitize *R. palmarum* (Gaviria & Lohr, 2020).

To determine the parasitoidism capacity of *B. claripalpis* on *R. palmarum*, Gaviria and Löhr (2020) carried out manual inoculation experiments of planidia extracted from gravid flies on weevil larvae with a weight range between 100 and 2,000 mg, which have been reared in sugarcane cuttings and artificial diet. Larvae reared on the artificial diet exhibited distinct immune responses to those reared on sugarcane cuttings, with those on an artificial diet being less attacked by the planidia due to their better nutritional status, which enhanced their defenses against pathogens and parasitoids (Löhr, 2016; Löhr & Parra, 2014).

Encapsulation of the parasitoid larvae was observed across all weight ranges, a defense mechanism of the host that prevented full development of the parasitoid. In many cases of parasitoidism, the host's immune cell response is activated, generating a process of phagocytosis or entrapment of the parasitoid, which triggers the host's encapsulation mechanism (Lavine & Strand, 2002). Encapsulation can be followed by a melanization process, resulting in the death of the parasitoid by asphyxia or cytotoxicity (Reed et al., 2007). In semi-natural free-choice conditions, 50 % of the larvae were parasitized, but no parasitoid puparia were recovered. On the other hand, the larvae of *D. saccharalis* that functioned as positive controls presented a complete development of the parasitoid. The study by Gaviria and Löhr (2020) confirmed that *B. claripalpis* can parasitize *R. palmarum* larvae, but the tachinid planidia could not complete their development under the experimental conditions. Additionally, larval mortality of *R. palmarum* due to parasitoidism was much lower than that observed for sugarcane borers (Gaviria & Löhr, 2020). Despite the significant impact on *R. palmarum* larval development and behavior, most larvae completed their development, emerging as seemingly normal adult weevils.

Importation protocols and risk analysis studies associated with introducing the specialist tachinid parasitoid of *R. palmarum* reported in Brazil (i.e., *B. rhynchophorae*) must be conducted. No mass-rearing techniques have been developed in Brazil for *B. rhynchophorae*. Thus, the study by Gaviria and Löhr (2020) on the mass-rearing of *B. claripalpis* on *R. palmarum* should serve as a baseline.

Despite the existence of *B. rhynchophorae* in field conditions in Brazil, the importation of exotic parasitoids for use in classical biological control remains a challenge due to the complicated legislation in Colombia that impedes the import and use of exotic natural enemies (Bueno, 2005; Kondo et al., 2020). Overcoming these regulatory barriers could enable the importation of the specialist tachinid parasitoid, potentially improving the parasitoidism rates of *R. palmarum* in coconut palm, oil palm, and sugarcane crops in Colombia.

Tachinids in the Biological Control of the Solanaceous Fruit Borer *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae) in Colombia

The solanaceous fruit borer, *Neoleucinodes elegantalis* (Lepidoptera: Crambidae), is an important pest that attacks fruits of species of Solanaceae, including eggplant, *Solanum melongena* L., *S. quitoense* Lam. (a popular fruit locally known as “lulo” in Colombia or “naranjilla” in Ecuador), green and red peppers (*Capsicum annuum* L.), tomato, *S. lycopersicum* Lam., tree tomato, *S. betaceum* Cav., as well as a wide variety of solanaceous plants of the *Leptostemonum* clade (Dunal M-F.) (Diaz-Montilla et al., 2013). Numerous natural enemies attack the various stages of development of *N. elegantalis*, mostly hymenopteran parasitoids of the families Braconidae, Chalcididae, Encyrtidae, Eulophidae, Eupelmidae, Ichneumonidae, and Trichogrammatidae; a species of green lacewing of the genus *Chrysopa* Leach (Neuroptera: Chrysopidae); a parasitic fungus,

possibly of the genus *Beauveria* Vuillemin (Hyphomycetes); and a tachinid fly of the genus *Lixophaga* Townsend (Diaz-Montilla et al., 2013). The latter was subsequently described as *Lixophaga puscolulo* Carrejo & Woodley (Diptera: Tachinidae) by Carrejo et al. (2013). According to Carrejo et al. (2013), *L. puscolulo* is associated exclusively with *N. elegantalis* found on spiny Solanaceae of the *Leptostemonum* clade. In orchards of *S. quitoense*, the adults of *L. puscolulo* mate near fruits infested by *N. elegantalis* and are active from 9 a.m. to 5 p.m., with a natural parasitoidism rate of about 48 % when farmers reduce insecticide applications (Carrejo et al., 2013).

The known geographical distribution of *L. puscolulo* includes the Departments of Caldas, Cauca, Cundinamarca, and Valle del Cauca in Colombia, which fit into the premontane wet forest (bh-PM) and premontane very wet forest (bmh-PM) (Carrejo et al., 2013). However, *L. puscolulo* is probably found in other areas of Colombia and Ecuador where *S. quitoense* is grown. Despite *N. elegantalis* being known to attack many plant species of the family Solanaceae, so far, *L. puscolulo* has been reared only from larvae of *N. elegantalis* collected from fruits of *S. quitoense* and *S. birtum* Vahl, a wild solanaceous plant (Carrejo et al., 2013).

Carrejo et al. (2013) proposed the implementation of simple practices to increase natural populations of *L. puscolulo* in orchards of *S. quitoense* as follows: (i) pesticides should be used after 5 p.m. (when the tachinids are not active), applying active ingredients that act on *N. elegantalis* by ingestion and not by contact, (ii) collect infested fruits to recover parasitoids for their subsequent release, and (iii) conserve weed plants that provide nectar and pollen to *L. puscolulo* populations. Hence, *L. puscolulo* can be incorporated into an integrated pest management program under a conservation biological control framework.

Lixophaga puscolulo can be mass-reared in the laboratory using the larvae of the greater wax moth, *Galleria mellonella* L. (Lepidoptera: Pyralidae), as a factitious host (Diaz Montilla, 2014). Adults of *L. puscolulo* do not mate in the laboratory, and thus, gravid females need to be collected in the field to extract their planidia. Each larva of *G. mellonella* can be inoculated with five to seven planidia of the parasitoid, and 33 days after larviposition, an average of three *L. puscolulo* flies emerge from each parasitized larva (Diaz-Montilla, 2014). The reared tachinid flies are then released in the orchards to mate, reproduce, and parasitize *N. elegantalis*, allowing a satisfactory increase in the tachinid populations (Villada et al., 2012).

Other Dipterans as Natural Enemies in Colombia

Many dipteran families include predators and/or parasitoids, i.e., Anthomyiidae, Asilidae, Calliphoridae, Cecidomyiidae, Chamaemyiidae, Chironomidae (Tanypodinae), Chloropidae, Culicidae, Dolichopodidae, Drosophilidae, Empidae, Lonchaeidae, Otitidae, Rhagionidae, Syrphidae, and Tipulidae (Nicholls, 2008). However, most studies that mention dipterans with a potential as biological control agents, e.g., Dolichopodidae, Muscidae (*Coenosia* sp.), Syrphidae, Tachinidae, only identify them to the genus or family levels (e.g., Aristizábal et al., 2013; Ballestas-Álvarez et al., 2023; Sáenz et al., 2023). Here, we present additional dipteran taxa identified at the species or genus level that are currently used or have potential for use as biocontrol agents.

Montes-Rodríguez et al. (2024) recently described a new species, *Leucopina nyiaybsa* Gaimari & Montes (Diptera: Chamaemyiidae), which acts as a natural enemy of the pink hibiscus mealybug, *Maconellicoccus hirsutus* (Green) (PHM) (Hemiptera: Coccothraupidae: Pseudococcidae), a quarantine pest in Colombia. The larvae of this species feed on the eggs within the mealybug's ovisac, the first potential biological control agent of PHM to originate from the Neotropics (Montes-Rodríguez et al., 2024). Additionally, the tachinid parasitoid *Trigonospila unicaldasi* Vinasco, Vallejo & Soto (Diptera: Tachinidae) shows promise as a biological control agent for the citrus weevil, *Compsus* sp. (Coleoptera: Curculionidae) (Soto-Giraldo & Oliveira, 2018; Vinasco et al., 2017).

Löhr et al. (2018), in a study of natural enemies of the cassava hornworm, *Erinnyis ello* (L.) (Lepidoptera: Sphingidae), reported that the larvae of *E. ello* are attacked by flies of the families Sarcophagidae and Tachinidae, but gave no further details. Besides Tachinidae, very few other dipterans are used in augmentative biological control programs in Colombia. In countries like Brazil, tachinid flies appear to be the most significant parasitoids attacking *E. ello* larvae. For example, *Belvosia* sp. lays microtype eggs on cassava leaves, which the caterpillars then ingest, while the larviparous *Drino* sp. targets the larvae (Winder, 1976).

Furthermore, in scientific literature there are frequent reports of species of hoverfly larvae (Diptera: Syrphidae) found carrying out natural control on soft-bodied insects, e.g., *Dioprosopa clavatus* (Fabricius) has been reported as an efficient natural enemy of *Aphis craccivora* (Koch) (Hemiptera: Aphididae) on cowpea, *Vigna unguiculata* (L.) Walp. (Fabaceae), in the Department of Magdalena (De la Pava & Sepulveda-Cano, 2015); *Salpingogaster nigra* Schiner has been reported as a natural enemy of the pasture spittlebug, *Zulia carbonaria* (Lallemand) (Hemiptera: Cercopidae), in the Cauca River Valley (Castro et al., 2005); and *Allograpta* (Fazia) aff. *bians* (Enderlein) and a species of the genus *Leucopodella* Hull (Diptera: Syrphidae) have been reported as natural enemies of the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae) in Valle del Cauca (Kondo et al., 2015).

Besides hover flies, the larvae of the predatory phorid fly *Syneura cocciphila* (Coquillett) (Diptera: Phoridae) have been reported as an efficient biological control agent of the Colombian fluted scale, *Crypticerya multicatrides* Kondo & Unruh (Hemiptera: Monophlebidae: Iceryini), in Valle del Cauca, but it has not been possible to mass-rear this insect under laboratory conditions (Gaimari et al., 2012; Muñoz et al., 2018).

Kondo et al. (2022) reported the association of the predatory fly *Pseudiasata* sp. (Diptera: Drosophilidae) with the pineapple mealybug *Dysmicoccus brevipes* (Cockerell, 1893) (Hemiptera: Pseudococcidae) in pineapple, *Ananas comosus* (L.) Merr. (Bromeliaceae) orchards in the department of Valle del Cauca, Colombia. Future research is needed to determine the fly to the species level, and conduct studies on its biology, predation rates and mass rearing techniques.

Colombia's only known dipteran predator used in augmentative biological control programs is the aphid midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). This species is mass-released to control several species of aphids (Hemiptera: Aphididae) that attack flowers and ornamental plants in greenhouses (Kondo et al., 2018). The larvae of *A. aphidimyza* are sold by an unregistered laboratory in Valle del Cauca (Kondo et al., 2020).

Tachinidae as Biological Control Agents in Ecuador

In Ecuador, there are approximately 88 genera reported within the family Tachinidae (O'Hara et al., 2020; Stireman et al., 2009, 2024), and although they constitute parasitoids of several groups of arthropods, studies about host-parasitoid interactions on some plants or crops are limited (Figure 1).

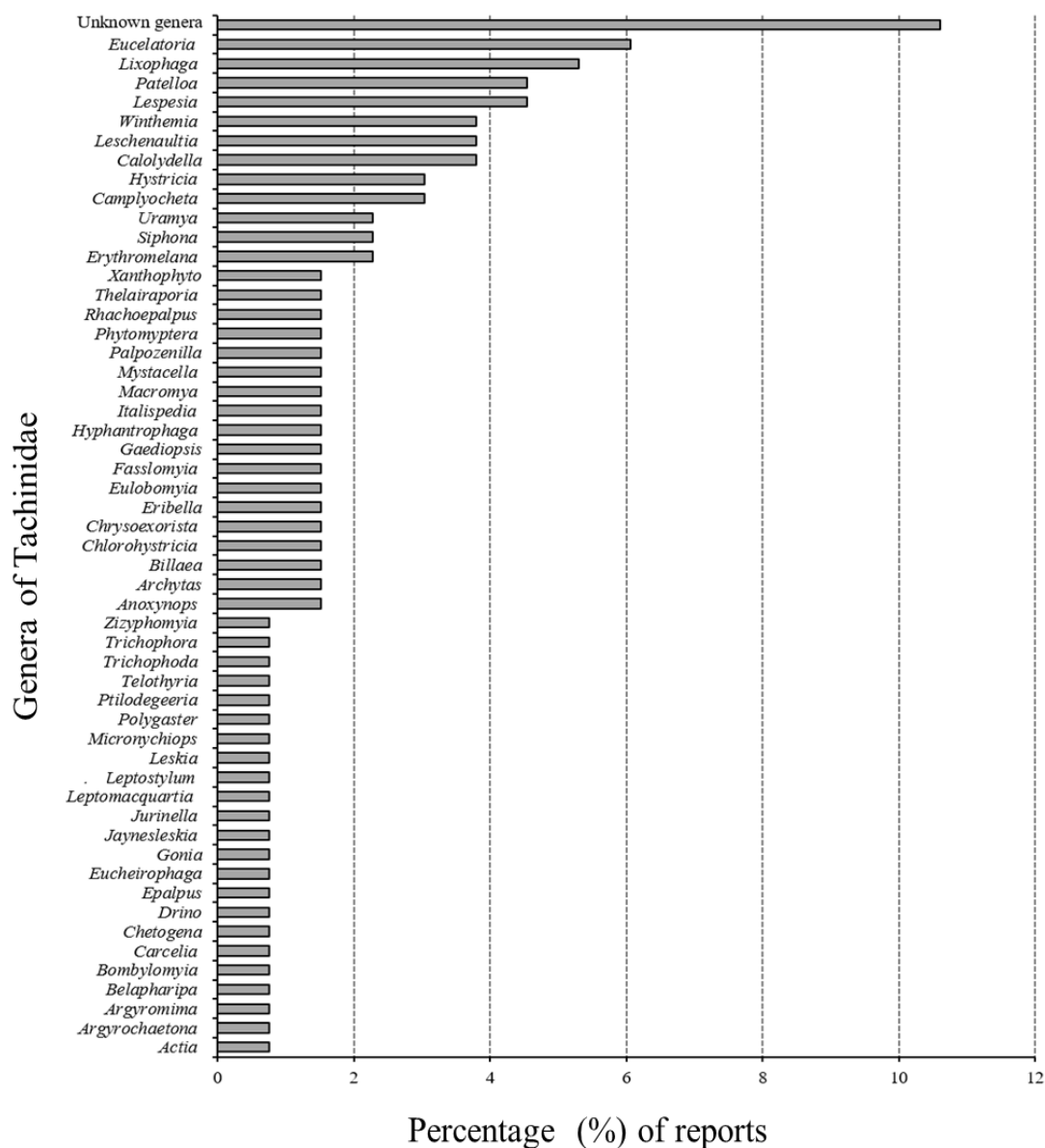


Figure 1. Percentage of reports of tachinid genera found in studies conducted in Ecuador. Source: Compiled from Arias (2021), Chirinos et al. (2024), Falcón Reibán and Padrón Martínez (2019), Hinostroza García et al. (2014), Malo and Willis (1961), Mazón et al. (2020), Mendoza et al. (2005), Padrón et al. (2020), Páliz and Mendoza (1999), Seifert et al. (2015), and Stireman et

al. (2009, 2024). $N = 132$ reports of genera associated with insect hosts. Illustration by Dorys T. Chirinos.

Genera of Tachinidae have been observed in continental Ecuador in the Amazon (82.6 %), Coastal (12.9 %), and Andean (4.5 %) regions, attacking mainly Lepidoptera, both in natural ecosystems (Mazón et al., 2020; Stireman et al., 2009, 2024) and in agroecosystems (Chirinos et al., 2021; Malo & Willis, 1961; Noboa et al., 2017), but also parasitizing Mantodea (Falcón Reibán & Padrón Martínez, 2019), Hemiptera (Andreocci, 2020), and Hymenoptera (Stireman et al., 2009) (Figure 2).

Of the tachinids reported, 10.6 % consisted of undetermined genera, whereas, of the 53 identified genera, the most common were *Eucelatoria* Townsend, *Lixophaga* Townsend, *Patelloa* Townsend, *Lespesia* Robineau-Desvoidy, *Winthemia* Robineau-Desvoidy, *Leschenaultia* Robineau-Desvoidy and *Calolydella* Townsend (Figure 1). These genera constitute larval or pupal parasitoids of hosts included in 20 families, but especially Crambidae/Pyralidae, Geometridae, Noctuidae, Nymphalidae, Erebiidae and Saturniidae (Figure 2). Although there are insect catalogs in which the taxa of Tachinidae in Ecuador are reported, they generally do not include information on the host-parasitoid relationships on the host plant. For this reason, in this review, we selected studies that provided information on the parasitoid, its associated host plant, and the region where it was found.

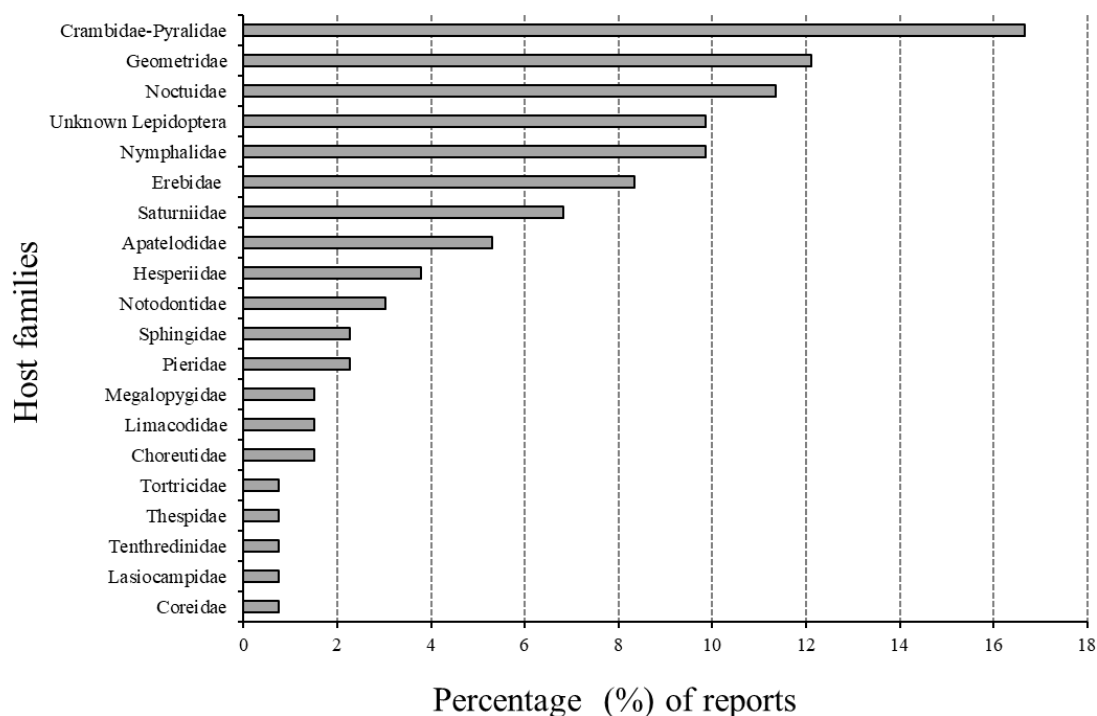


Figure 2. Insect host families attacked by Tachinidae genera found in studies carried out in Ecuador.

Source: Compiled from Arias (2021), Chirinos et al. (2024), Falcón Reibán and Padrón Martínez (2019), Hinostroza García et al. (2014), Malo and Willis (1961), Mazón et al. (2020), Mendoza et al. (2005), Padrón et al. (2020), Páliz and Mendoza (1999), Seifert et al. (2015), and Stireman et

al. (2009, 2024). $N = 132$ reports of tachinid genera associated with insect hosts. Illustration by Dorys T. Chirinos.

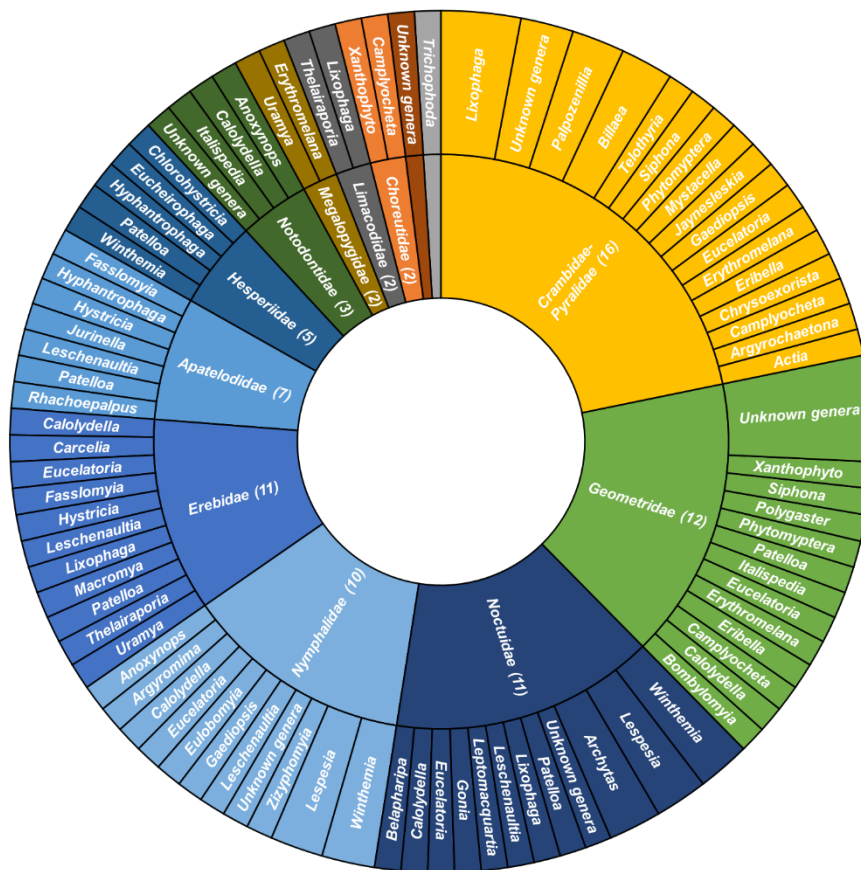


Figure 3. Insect host families parasitized by Tachinidae taxa found in Ecuador. The outer circle displays the genera of Tachinidae, while the inner circle shows the corresponding host families. The numbers in parentheses indicate how many genera are associated with each host family. Source: Illustration by Dorys T. Chirinos.

Some insect hosts were more strongly associated with specific genera of Tachinidae. Specifically, Crambidae and Pyralidae have been primarily associated with the genera *Billaea*, *Lixophaga*, and *Palpozenillia* (Townsend). In contrast, *Lespesia* and *Winthemia* are notable in Noctuidae and Nymphalidae (Figure 3). The tachinid genus *Archytas* Jaennicke is also commonly associated with the family Noctuidae.

In Ecuador, many Tachinidae taxa are typically identified only at the genus level, with some classified only at the family level (Figures 1-3). This highlights the importance of identifying tachinid taxa at the species level, as it significantly impacts biological control programs. Therefore, conducting more studies on Tachinidae taxonomy is a priority in Ecuador and other Neotropical countries.

Tachinid species have been found in natural ecosystems and agroecosystems as part of multitrophic chains along with Hymenoptera, including, among others, members of the family Braconidae (Mazón et al., 2020; Noboa et al., 2017; Stireman et al., 2017).

In January 1965, a lineage of *B. claripalpis* from Peru was introduced to Ecuador to control *D. saccharalis* at the San Carlos sugar mill in Guayaquil. This pest control strategy was a great success, which was attributed to the hybridization of the Peruvian and Ecuadorian lineages of *B. claripalpis*, which resulted in an improved lineage that inherited genetic characteristics, such as a shorter life cycle and more active searching behavior (Risco-Briceño, 1996). In Ecuador, sugarcane growers maintain laboratories to mass-produce and release individuals of *B. claripalpis* and the parasitic wasp *C. flavipes* (Mendoza, 2018). These parasitoids are mass-released, resulting in the effective control of the sugarcane borer, *D. saccharalis*, at a rate of 12 to 24 fly pairs and 2 to 4 wasps for each caterpillar of *D. saccharalis* estimated per hectare (Mendoza, 2018).

On the other hand, an inventory of natural enemies of *N. elegantalis* carried out by Noboa et al. (2017) in the Amazon and Andean regions of Ecuador showed high rates of parasitoidism (up to 82 %) by several natural enemies, including wasp (Hymenoptera) parasitoids in the genera, *Copidosoma* Ratzeburg (Encyrtidae), *Bracon* Fabricius, and *Chelonus* Panzer (Braconidae), and tachinid species of the genus *Lixophaga* (Diptera: Tachinidae), suggesting that they may have a high potential for biological control of this important pest. As sugarcane growers practice, augmentation of tachinid and hymenopteran parasitoids could be used as a control strategy for Solanaceae pest species and to reduce insecticide sprays. Such a strategy would require evaluations of the effectiveness of these parasitoids in regulating insect host populations.

Complementing the action of the Tachinidae, taxa belonging to other families in the Order Diptera can act as biological control agents for some important insect pests. Species of *Sarcodexia* Townsend and *Sarcophaga* Meigen (Diptera: Sarcophagidae) represent important parasitoids of Lepidoptera larvae in banana, plantain, and maize (Chirinos et al., 2021, 2024). The larvae of a hoverfly, *Ocyptamus dimidiatus* (Fabricius) (Diptera: Syrphidae), have been reported preying on *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae) in maize (Centeno et al., 2022).

Tachinidae as Biological Control Agents in Peru

Tachinids are often reported in Peru as parasitoids of various lepidopterans, but very few identify them to the genus or species level. Nevertheless, several tachinid flies have been reported carrying out natural control in the field, e.g., *Phytomyptera* sp. has been reported as the main parasitoid of the quinoa moth, *Eurysacca melanocampta* (Meyrick) (Lepidoptera: Gelechiidae), in the Department of Cusco (Costa et al., 2009). A more recent study found *Phytomyptera* sp. in eight departments, namely Anta, Calca, Canchis, Cusco, Urubamba, where quinoa is grown, with different levels of parasitoidism rates among the regions (Yábar-Landa & Costa, 2020); and a species of the genus *Chrysodoria* Townsend (Diptera: Tachinidae) was reported from the pupae of the avocado seed moth, *Stenoma catenifer* Walsingham (Lepidoptera: Depressariidae), in the Departments of Junín and Huánuco (Hoddle & Hoddle, 2012).

A study conducted in the Department of Ucayali, Peru, to identify natural enemies of agricultural pests in that region reported the presence of two species of tachinid flies, namely, *Archytas marmoratus* (Townsend) as a parasitoid of maize lepidopteran pests and *Gonia* sp. in cotton,

without mentioning its insect pest host (Espinoza & Tenazoa, 2007). The same authors reported a species of the genus *Ocyptamus* Macquart (Diptera: Syrphidae) as a predator of *Tutbillia cognata* Hodkinson, Brown and Burckhardt (Hemiptera: Psyllidae) on camu-camu, *Myrciaria dubia* (Kunth) McVaugh (Myrtaceae) (Espinoza & Tenazoa, 2007).

As in Colombia and Ecuador, augmentative biological control with Tachinidae in Peru has been focused on controlling *Diatraea* spp. According to Risco-Briseño (1996), in 1952, during a visit to Iquitos, Peru, the entomologist Harold Edmund Box (1898–1973) found *D. saccharalis* developing abundantly on the stems of *Echinochloa polystachya* (Kunth) Hitchc. (Poaceae) and reported that it was heavily parasitized by *L. minense* and *Miobiopsis diadema* (Wiedemann) [as *Leskia diadema*].

According to Mujica and Whu (2020), augmentative biological control of *D. saccharalis* in Peru is conducted with mass releases of *B. claripalpis* over about 44,000 hectares. In 2015, it was estimated that nearly 1,504,000 pairs of *B. claripalpis* were released in sugarcane crops in Peru to control *D. saccharalis* (Mujica & Whu, 2020).

Conclusions and Future Perspectives

Dipteran natural enemies, especially tachinid flies, play a crucial role in biological control across various crops in Colombia, Ecuador, and Peru. For example, biological control in sugarcane crops in these countries involves Augmentative Biological Control (ABC) using a combination of parasitoids that target different developmental stages of sugarcane borers, *Diatraea* spp., where the wasp parasitoid *Trichogramma exiguum* is used to control the egg stage. In contrast, the braconid parasitoid *C. flavipes* and the tachinid flies *B. claripalpis* and *L. minense* target the larval stages. Additionally, in Colombia, the tachinid fly *G. jaynesi* exerts a Natural Control (NC) on *Diatraea* spp. by parasitizing their larval stages in sugarcane fields (Figure 4).

For tomatoes and lulo, *Lixophaga puscolulo* can be successfully mass-reared to target the solanaceous fruit borer, *Neoleucinodes elegantalis*. For palms such as coconut, oil palm, and peach palm, *Billaea rhynchophorae* is being explored to control the black palm weevil, *Rhynchophorus palmarum*. Additionally, *Archytas* and *Gonia* species are important parasitoids found naturally in corn fields that could be used in biocontrol programs. Furthermore, species from the families Cecidomyiidae, Chamaemyiidae, Muscidae, Phoridae, Sarcophagidae, and Syrphidae are natural enemies of various insect pests.

Despite tachinids and other dipterans being promising biological control agents, limitations on their use and implementation persist, including fragmented research, challenges in mass-rearing certain species, regulatory barriers for importing effective parasitoids and predators, the presence of different “races” and probably cryptic species with differences in rates of parasitoidism or predation, and host resistance among target pests. Future efforts should prioritize comprehensive research to enhance the understanding of these dipterans, develop effective mass-rearing techniques, advocate for regulatory changes, and implement integrated pest management strategies emphasizing biological control. By addressing these challenges, the effectiveness of biological control can be significantly improved in the region. Additionally, more

studies are needed to improve conservation biological control strategies to enhance the performance of tachinid flies in the field.

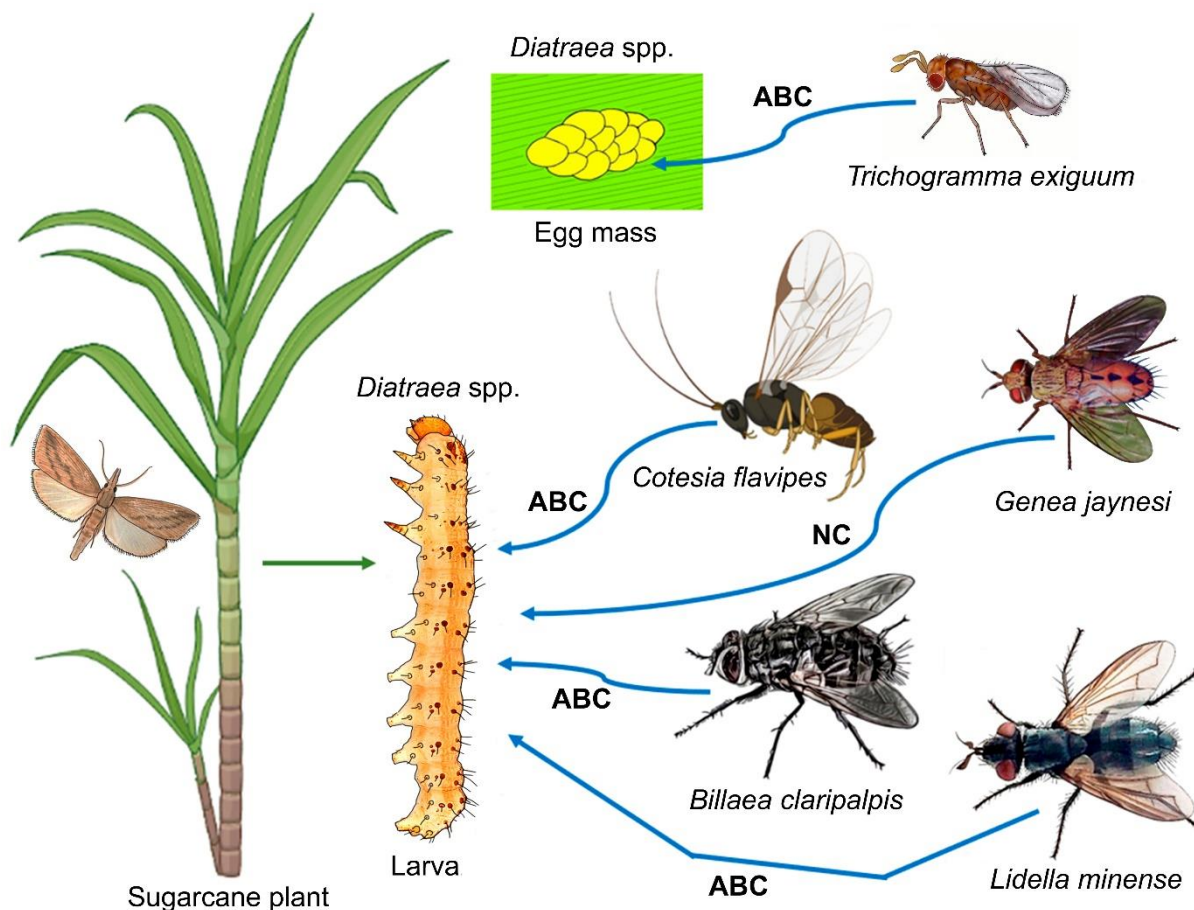


Figure 4. Representation of the main parasitoids of the sugarcane borer, *Diatraea* spp. Abbreviations: **ABC** = Augmentative Biological Control; **NC** = Natural Control. Source: Illustration by Takumasa Kondo.

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Authors' Contributions

JGV: data collection and analysis, editing the final manuscript, writing of the manuscript; GV: data collection and analysis, writing of the manuscript and revision of the English language; DTCT: data collection and analysis, writing of the manuscript, preparation of tables and figures;

AEDM: data collection and analysis, writing of the manuscript; TK: development and supervision of the methodology and analytical methods, data collection and analysis, writing of the manuscript, preparation of figures and revision of the English language and editing the final manuscript.

Ethical implications

This article has no ethical implications.

Conflict of Interest

The authors declare no conflicts of interest in this study.

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