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Diversity of native and exotic parasitoids attacking agricultural pests in Ecuador: are Ecuadorian biocontrol programs in decline?

Diversidad de parasitoides nativos y exóticos que atacan plagas agrícolas en Ecuador: ¿están en declive los programas de biocontrol ecuatorianos?

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ABSTRACT

In Ecuador, agriculture is an important economic activity. Crops are grown mainly in the regions of the continental area: Amazon, Andes and Coast. We conducted this study to elaborate a compendium about the diversity of parasitoids of agricultural insect pests and to estimate the trend of biocontrol by the use of these natural enemies. Approximately 200 taxa of parasitoids were found to be reported controlling various pests that affect cultivated crops in continental Ecuador. The major parasitoids referred in biological control in Ecuador are *Telenomus* spp. (Hymenoptera: Platygastridae), *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) and *Encarsia* spp. (Hymenoptera: Aphelinidae). The results suggest a decreasing trend in the use of parasitoids as biocontrol agents from 1980 to the present (R^2: 0.80, P<0.0001). In this paper, we discuss the probable explanations of this trend.

Keywords: Biological control, hymenopterans, natural enemies, insect pests, tachinid flies, wasps.

RESUMEN

En Ecuador, la agricultura es una actividad económica importante. Los cultivos se siembran principalmente en las regiones del área continental: Amazonia, Andes y Costa. Realizamos este estudio para elaborar un compendio sobre la diversidad de parasitoides de plagas insectiles agrícolas y estimar la tendencia del biocontrol mediante el uso de estos enemigos naturales. Se encontró que aproximadamente 200 taxa de parasitoides controlan varias plagas que afectan los cultivos en el Ecuador continental. Los principales parasitoides utilizados en el control biológico en Ecuador son *Telenomus* spp. (Hymenoptera: Platygastridae), *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) y *Encarsia* spp. (Hymenoptera: Aphelinidae). Los resultados sugieren una tendencia decreciente en el uso de parasitoides como agentes de control biológico desde 1980 hasta el presente (R^2: 0,80, P <0,0001). En este artículo, discutimos las posibles explicaciones de esa tendencia.

Palabras clave: avispas, control biológico, enemigos naturales, himenópteros, moscas taquínidas, plagas.

INTRODUCTION

Historically, agriculture constitutes one of the fundamental pillars of the economy in Ecuador, through export or local trade of a variety of crops, including banana, cacao, coffee, sugarcane, flowers, vegetables, corn and potato (Castillo *et al.* 2020, Peñalver-Cruz *et al.* 2019). These crops are mainly cultivated in the continental region of the country, which is geographically divided by the Andean Mountains into three zones: the Coast, the Andes and the Amazon (Fig. 1). Throughout the crop production process, biological competitors may appear, among which insect pests stand out, whose populations must be controlled to avoid adverse effects on productivity (Savary *et al.* 2012, Culliney 2014).

In integrated pest management programs the first pest control alternative that must be considered is biological control (Metcalf & Luckmann 1975). Although Ecuador has a high diversity of agricultural pest species, there is also a significant ecological richness, as well as a considerable abundance of natural enemies, among which parasitoids stand out. In fact, parasitoids have been used extensively for pest control in the coastal region since the 1980s (Castillo 2020). Additionally, in Ecuador, the existing information on biological control of insect pests is limited to conference reports, abstracts and proceedings (Castillo 2019). However, in certain cases such information is not readily available (Castillo 2019) and furthermore, the information on parasitoid inventories associated to natural biological control is difficult to access.

This study had two objectives: 1) to elaborate a compendium of information about the diversity of parasitoids involved in biocontrol in Ecuador, with emphasis on natural biological control and 2) to estimate the trend of biocontrol as a pest control strategy since 1937 in this country.

MATERIAL AND METHODS

Data selection

Studies involving parasitoids were obtained from the databases, Scielo, the repositories of the National Institute of Agricultural Research (INIAP) of Ecuador and Google Scholar. A literature search was carried out for papers published between 1937 and 2020 that included the keywords: agricultural pests, augmentative-, natural-, conservation-, classical biological control, crops, diversity,

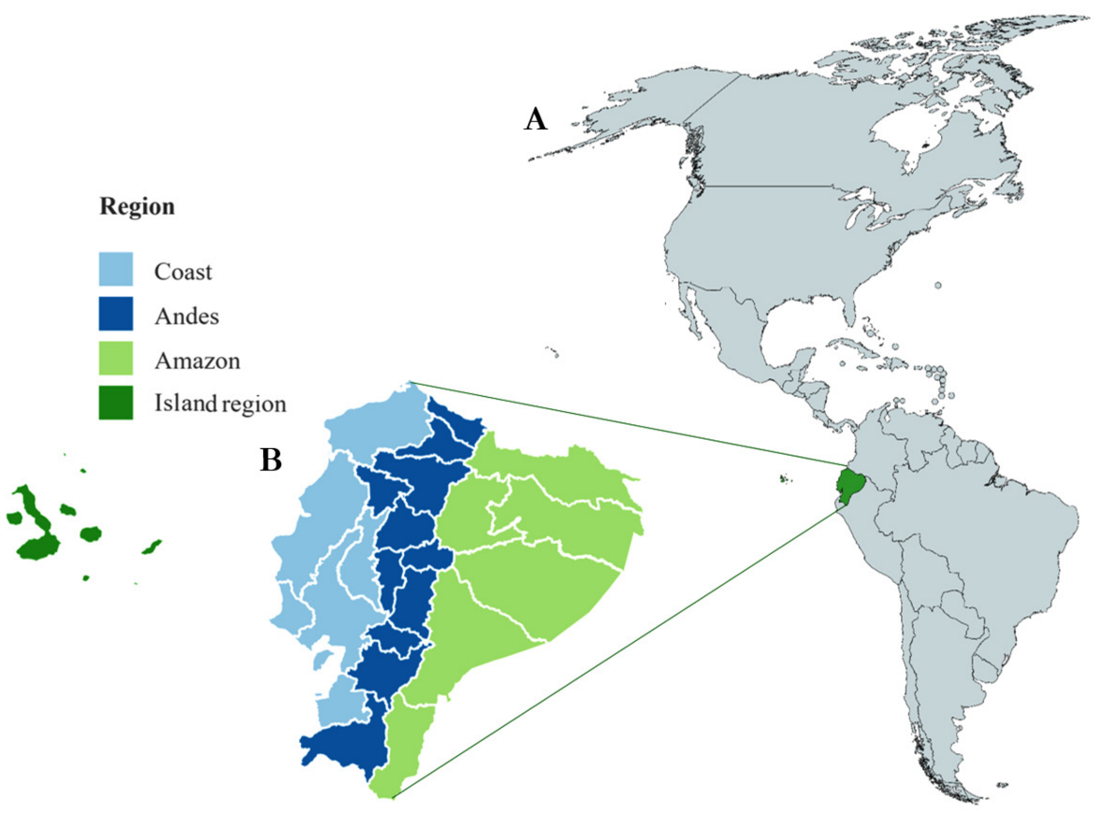

Figure 1. (A) Map of America illustrating the location of Ecuador (B) Map of Ecuador showing the regions: Andes, Amazon and Coast.

Ecuador, inventory of natural enemies, parasitism rates, parasitoids, and pest management. We included technical reports, conference abstracts, theses, book chapters, books and scientific papers.

Data recording

We recorded studies in classical biological control, augmentative biological control and natural biological control. In the cases of classical biological control, the following were included: crop name, insect host, parasitoid species, year of introduction, country of origin, region of Ecuador where the control was carried out and the positive or negative effect of the control. For studies on augmentative biological control, cases reported since the programs began, and the time of application were reviewed.

Analysis of data

Once the information was collected, we plotted the following: a) parasitoid species by insect host per crop, indicating the interactions between the trophic levels of each agroecosystem, b) number of parasitoid species for each of the geographical regions of continental Ecuador for those species with three or more reports. We also conducted a principal component analysis to associate the parasitoids reported by geographical region. To obtain the principal components, a standardization of the data was executed (mean 0 and standard deviation 1), to avoid that the variables with greater variance dominated the others. Finally, a regression model was estimated between the years of the studies (X) versus the number of parasitoids (Y), adjusting to a polynomial function ($P < 0.0001$).

Although the use of parasitoids began in 1937, only five studies with parasitoids were conducted in approximately five decades (1937-1979). Given that the substantial increase in biocontrol programs with parasitoids began in 1980, analyses were carried out evaluating the period 1980-2020.

RESULTS

Approximately 200 taxa of parasitoids were found to be controlling various pests that affect cultivated crops in continental Ecuador during the period 1937-2020. Among the referred parasitoids, 10% belonged to the Order Diptera, while 90% were found from the Order Hymenoptera. Within the latter, the most abundant group was the superfamily Chalcidoidea followed by Platygastroidea.

Classical biological control

The first classical biological control program was implemented in Ecuador by Luis Rodríguez Torres who introduced and established during 1937-1947 the aphelinid, *Aphelinus mali* Haldeman, 1851 (Hymenoptera: Aphelinidae) to control the woolly apple aphid, *Eriosoma lanigerum* Hausmann, 1802 (Hemiptera: Aphididae) (Merino 1984). Later, in 1955, the parasitoid, *Amitus hesperidum* Silvestri, 1927 (Hymenoptera: Platygastridae) was imported from Mexico with the intention of reducing the damage caused by the citrus blackfly, *Aleurocanthus woglumi* Ashby, 1915 (Hemiptera: Aleyrodidae) on citrus trees (Browning 1992, Merino 1984). Another pest of citrus trees, the purple scale, *Lepidosaphes beckii* (Newman, 1869) (Hemiptera: Diaspididae) was also the subject of classic biological control program, using the parasitic wasp, *Aphytis lepidosaphes* Compere, 1955 (Hymenoptera: Aphelinidae) (Merino & Vazquez 1962). Those programs were conducted in the Andean region with satisfactory results. Unfortunately, the obtained references do not present quantitative levels of parasitism and degrees of infestation before and after the programs were conducted.

The sugarcane borer, *Diatraea saccharalis* (Fabricius, 1794) (Lepidoptera: Crambidae) constitutes a major problem in the coastal region where most sugarcane is planted (Mendoza 2018). Although the parasitoid, *Billaea claripalpis* Wulp, 1896 (Diptera: Tachinidae) was known to occur in Ecuador as a biocontrol agent for this pest, its parasitism rates were very low (18%) (Gaviria 1981). For this reason, a biological control program was put into practice with a race of *B. claripalpis* introduced from Peru back in 1965. At the time, the Peruvian race was crossed with the native one, obtaining progeny that showed a parasitism rates as high as 87.9%, which significantly reduced the infestation levels of the sugarcane borer (Gaviria 1981).

Approximately 15 years later, two additional parasitoids of *D. saccharalis* were imported from Venezuela, the parasitic flies, *Lydella minense* (Townsend, 1927) and *Lixophaga diatraeae* (Townsend, 1916) (Diptera: Tachinidae) (Mendoza *et al*. 2005). However, none of those species adapted to the Ecuadorian coast's environment. At the same time, the parasitic wasp, *Cotesia flavipes* (Cameron, 1891) (Hymenoptera: Braconidae), was introduced from Colombia, which together with *B. claripalpis* has been able to regulate the populations of *D. saccharalis* (CINCAE 2013, Mendoza 2018).

Castillo *et al*. (2020) refer several imports of egg parasitoids made from Colombia in 1983 with different levels of success. *Telenomus* sp. (Hymenoptera: Platygastridae) resulted in an effective control of the South American white borer, *Rupela albina* Becker & Solis, 1990 (Lepidoptera: Crambidae) in rice. However, it is unknown if *Trichogramma semifumatum* (Perkins, 1910) and *Tricho-*

gramma pretiosum Riley, 1871 (Hymenoptera: Trichogrammatidae), which were imported to control the borers, *D. saccharalis* and *Diatraea lineolata* (Walker, 1856) (Lepidoptera: Crambidae), have had any effect controlling the pests.

Between the years 1970 and 1990, cotton was produced on the Ecuadorian coast (FAO: Food and Agriculture Organization of the United Nations 2017) and in 1988 the parasitoid *Bracon kirkpatricki* (Wilkinson, 1927) (Hymenoptera: Braconidae) was imported from Colombia to control the pink bollworm, *Pectinophora gossypiella* (Saunders, 1844) (Lepidoptera: Gelechiidae), with unsatisfactory results (Castillo *et al.* 2020). That same year, the species *Diachasmimorpha longicaudata* Ashmead (Wharton, 1987) (Hymenoptera: Braconidae), *Psyttalia concolor* (Szépligeti, 1910) and *Aganaspis daci* (Weld, 1951) (Hymenoptera: Figitidae), were imported from the U.S.A. for the biocontrol of fruit flies, *Anastrepha* spp. (Diptera: Tephritidae) in cherimoya (Castillo *et al.* 2020). However, those introductions did not show conclusive results. In the Guayas province in the Ecuadorian coast, a classical biological control program using the parasitoid *D. longicaudata*, introduced from Peru to control *Anastrepha* spp. on various fruit trees was carried out in various locations (Arias *et al.* 2009).

The coffee berry borer, *Hypothenemus hampei* (Ferrari, 1867) (Coleoptera: Curculionidae) was detected in the Zamora Chinchipe province (Amazon region) in 1981, spreading to all other coffee-producing areas of Ecuador (Mendoza *et al.* 1994). In an effort to the control this destructive pest, during 1987-1988, two parasitoids, *Prorops nasuta* Waterston, 1923 and *Cephalonomia stephanoderis* Betrem, 1861 (Hymenoptera: Bethylidae) were introduced by INIAP from Kenya and Togo in coffee-producing provinces belonging to the three regions of continental Ecuador (Mendoza *et al.* 1994). After the quarantine process and laboratory rearing, the species were released (Klein Koch *et al.* 1988, Mendoza *et al.* 1994). Out of the two parasitoids, *C. stephanoderis* was the best adapted (82.0% parasitism) than *P. nasuta* (22.5%) (Klein Koch *et al.* 1988).

A decade later, the parasitoid, *Phymastichus coffea* La Salle, 1990 (Hymenoptera: Eulophidae) was introduced from Colombia, mediated by the Integrated Management of Coffee Berry Borer Project, and conducted by the National Association of Coffee Exporters of Ecuador (ANECAFE), together with the International Institute for Biological Control (Delgado *et al.* 2002). The wasps were released during 2000 and 2001 in six Ecuadorian provinces, reporting averages of parasitism that varied from 20 to 30% (Delgado *et al.* 2002).

Augmentative biological control

Some introduced parasitoid species were mass reared and released during 1980-1990. *Trichogramma* sp. was extensively released in the coastal region for the control of eggs of various lepidopterous pests on cotton, soybean, corn, as well as for the control of *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) in tomato (Arias *et al.* 1992). In addition, there are also reports of releases of the species *Trichogramma fasciatum* (Perkins, 1912) and *T. pretiosum* in tomatoes grown in the Andes to control *T. absoluta* (Castillo *et al.* 2020). *Telenomus* sp. was also used in 1980 in an augmentative biological control program of *Diatraea* spp. in corn (Arias *et al.* 1996). Subsequently, the parasitoid, *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae) was used in biocontrol programs of whitefly species (Hemiptera: Aleyrodidae) on tomato in the Chimborazo province of the Andean region (Castillo *et al.* 2020).

Most of the augmentative biological control programs carried out since the 1980s were not sustainable over time. However, the species *B. claripalpis* and *C. flavipes* continue to be released in sugarcane fields in the coastal region because they are considered the most effective methods for controlling the sugarcane borer, *D. saccharalis* (CINCAE 2013, Mendoza 2018).

Currently, parasitoids are used as one of the pest management strategies in flower crops due to international requirements. An example of this is the release of the parasitic wasp *Diglyphus isaea* (Walker, 1838) (Hymenoptera: Eulophidae) for the control of the leafminer, *Liriomyza huidobrensis* (Blanchard, 1926) (Diptera: Agromyzidae) that causes losses in *Gypsophila* sp. summer flowers (Prado *et al.* 2018). Reported results of releases of *D. isaea* indicate its important role as a biological control agent because of the high percentages of parasitism (90%) associated with low infestations of *L. huidobrensis* (Prado *et al.* 2018).

Parasitoids by crop and geographical region

The parasitoids reported for Ecuador are shown in Tables 1-12 and Figures 2-8. Each figure illustrates the interconnections, crop-insect host-parasitoid. Associated with four important maize pests, 34 taxa of parasitoids have been reported, four identified up to family, 11 at generic level and 19 to species level (Table 1, Fig. 2).

On bananas and plantains, 22 genera and eight species of parasitoids have been recorded as biocontrol agents for fourteen phytophagous insects and one of those genera is a hyperparasitoid (Table 2, Fig. 3). Interestingly, 77% of the referred parasitoids associated with bananas and plantains attack defoliator caterpillars. Attacking five pests on *Citrus* spp., 20 parasitoids have been reported belonging to eight

Table 1. Parasitoids reported in association with pests on corn, *Zea mays* L.

Pest	Parasitoid	Region	Reference
Diatraea spp.	*Billaea claripalpis* *Cotesia flavipes* *Lixophaga spherophori* *Palpozenilla diatraeae* *Palpozenilla* sp. *Pediobius furvus*	Coast	Arias 2021, Páliz & Mendoza 1999
Dalbulus maidis	*Gonatopus bartletti*	Coast	Valarezo *et al*. 2009
Heliothis spp.	*Glyptapanteles militaris* *Lespesia* spp. *Campoletis argentiflora* *Chelonus texanus* *Cotesia marginiventris* *Encarsia* spp. *Gonia* sp. *Hyposoter albipes* *Hyposoter exiguae* *Conura igneoides* *Therion californicum* *Whinthemia* sp.	Coast	Mendoza 1994a, 1994b
Mocis latipes	Diptera: Sarcophagidae Diptera: Tachinidae Hymenoptera: Braconidae Hymenoptera: Chalcididae	Coast	Arias *et al*. 1996, Páliz & Mendoza 1999
Spodoptera frugiperda	*Chelonus* sp. *Eiphosoma* sp. *Euplectrus* sp. *Meteorus* sp. *Rogas* sp. *Telenomus alecto* *Telenomus remus*	Coast	Arias 2021, Mendoza 1994a, 1994b
Various Lepidoptera	*Telenomus* spp. *Trichogramma fasciatum* *Trichogramma pretiosum* *Trichogramma* spp.	Andes Coast	Benzing *et al*. 1997, Crespo & Ramakrishna 1989, Páliz & Mendoza 1999

genera and 12 species (Table 3, Fig. 4). Two important pests of cassava in Ecuador are controlled by 17 primary parasitoids (seven genera and ten species), and one associated hyperparasitoid has been reported (Table 4, Fig.5A). Eleven parasitoids (six genera and five species) parasitize two relevant pests associated with coffee (Table 5, Fig. 5B).

On vegetables, 13 taxa of insect pests have been recorded, which are controlled by 20 parasitoids classified in eight genera and 12 species (Table 6). On the other hand, 17 parasitoids (11 genera and six species) are reported parasitizing several species of phytophagous insects on various fruit trees (Table 7). In rice agroecosystem, there are five major pests, which are controlled by 22 parasitoids (17 genera and five species) (Table 8, Fig. 6A). Four phytophagous species that feed on sugarcane are attacked by ten taxa of parasitoids, six identified to the genus level and four to species level (Table 9, Fig. 6B).

Reports of parasitoids associated with eight phytophagous insects in cacao date from 1980. In this agroecosystem, 13 primary parasitoids (one species and 12 genera) and one hyperparasitoid, were detected (Table 10, Fig. 7A). Additionally, two taxa of parasitoids were reported attacking Neuroptera and Araneae (taxa with predatory habits). In legumes (Fabaceae), 14 taxa of parasitoids were mentioned (one species and 13 genera) that parasitize ten insect hosts (Table 11, Fig. 7B).

Of the 12 phytophagous insects reported on palms, two species belong to the family Chrysomelidae (Coleoptera) and the rest to different families of Lepidoptera, from which parasitoids belonging to six genera and seven

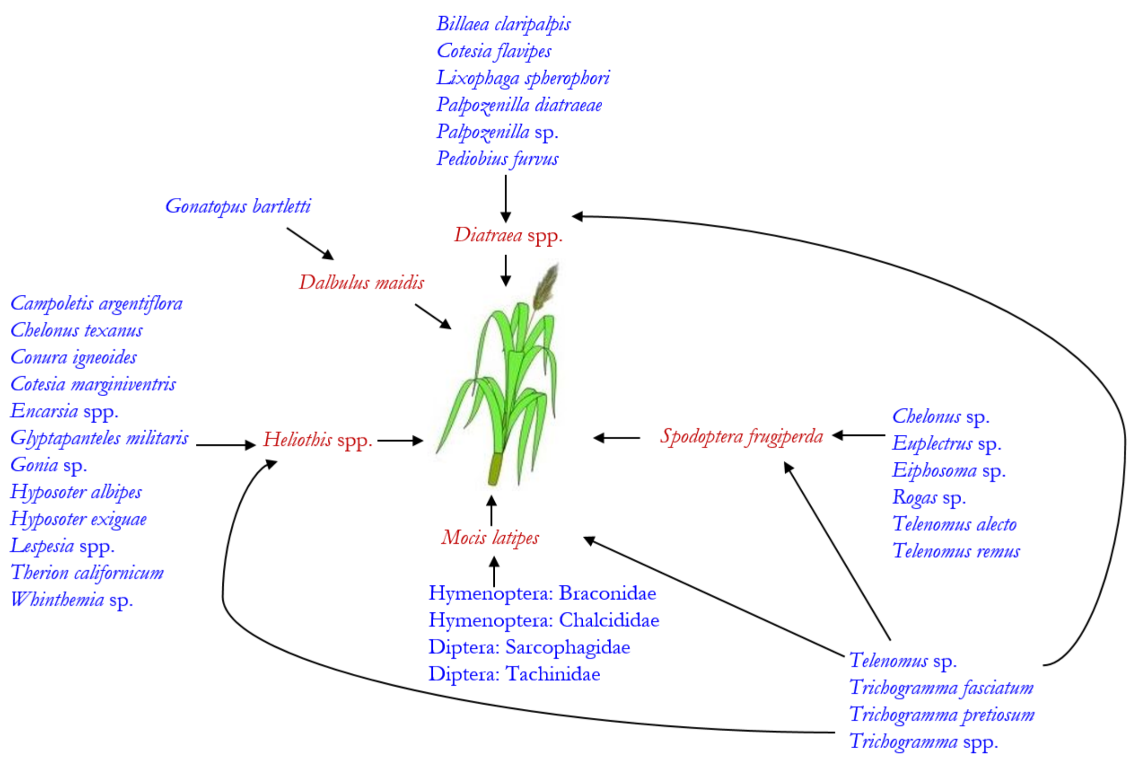

Figure 2. Parasitoids associated with pests that attack corn, *Zea mays* L. The arrows show the interconnections in the agroecosystem. Pests are indicated in red letters and parasitoids in blue.

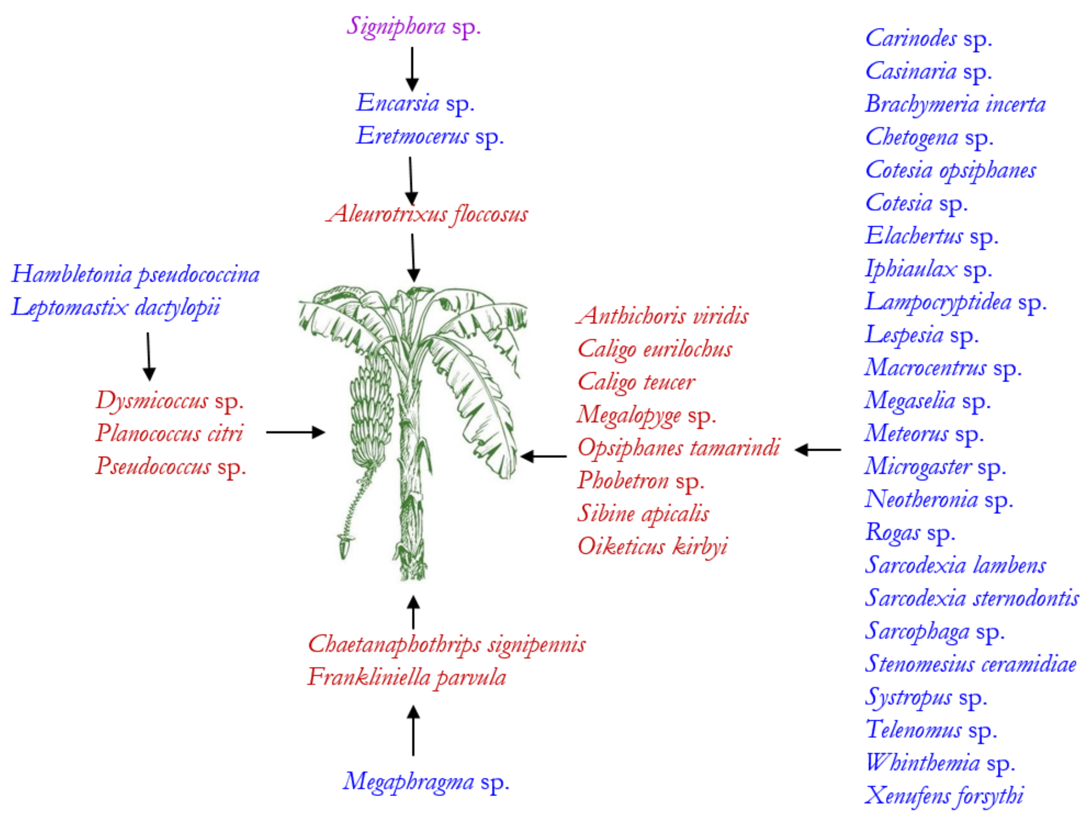

Figure 3. Parasitoids associated with pests that attack bananas and plantains. The arrows show the interconnections in the agroecosystem. Pests are indicated in red letters, parasitoids in blue and hyperparasitoids in purple.

Table 2. Parasitoids reported in association with pests on bananas and plantains.

Pest	Parasitoid	Reference
Aleurotrixus floccosus	*Encarsia* sp. *Eretmocerus* sp. *Signiphora* sp.	Arias 2021
Anthichoris viridis, *Caligo eurilochus, Caligo teucer*, *Megalopyge* sp., *Opsiphanes tamarindi*, *Phobetron* sp., *Sibine apicalis, Oiketicus kirbyi*	*Carinodes* sp. *Casinaria* sp. *Brachymeria incerta* *Chetogena* sp. *Cotesia opsiphanes* *Cotesia* sp. *Elachertus* sp. *Iphiaulax* sp. *Lampocryptidea* sp. *Lespesia* sp. *Macrocentrus* sp. *Megaselia* sp. *Meteorus* sp. *Microgaster* sp. *Neotheronia* sp. *Rogas* sp. *Sarcodexia lambens* *Sarcodexia sternodontis* *Sarcophaga* sp. *Stenomesius ceramidiae* *Systropus* sp. *Telenomus* sp. *Whinthemia* sp. *Xenufens forsythi*	Arias 2021, Arias *et al*. 1992, Armijos 2008, Boucek 1962, Malo & Willis 1961, Ramon 2010
Chaetanaphothrips signipennis, *Frankliniella parvula*	*Megaphragma* sp.	Arias 2021
Dysmicoccus sp., *Pseudococcus* sp.	*Hambletonia pseudococcina*	Arias 2021, Contreras-Miranda *et al*. 2021
Planococcus citri	*Leptomastix dactylopii*	

species have been reported (Table 12, Fig. 8). Using the data reported in these studies, we estimated that the lowest percentage of parasitoid taxa were found in sugarcane and coffee (4.8%), whereas the highest proportion of parasitoids is found in corn crop (14.8%), followed by those observed in Musaceae (13.5%).

The major parasitoids used in biological control in Ecuador are *Telenomus* spp., *Trichogramma* spp., and *Encarsia* spp. (Tables 1-12). Of the total of studies that involve parasitoids, 69.1, 19.6 and 11.3% have been carried out on the Coast, Andes and Amazon, respectively. Principal Component Analysis shows that parasitoids are conspicuously associated with geographical regions, in the Coast and the Andes. *Doryctobracon crawfordi* (Viereck, 1911) (Hymenoptera: Braconidae) is associated to the Andes while *Telenomus* spp. and *Trichogramma* spp. are closely associated with the Coast (Fig. 9). These differences are likely to be associated to the different crops grown in these regions.

Although *Telenomus* spp. and *Trichogramma* spp. are the most noted parasitoids in biocontrol, most of the programs using parasitoids of these genera were conducted in the 1990s (Arias *et al.* 1996, INIAP, 1996, Benzing *et al.* 1997, Mendoza 1994a, 1944b, Páliz & Mendoza 1999). In the case of species of the genus *Encarsia*, studies indicate its greater importance as a natural biological control, from 1990 to the present (Mendoza 1994a, 1994b Valarezo *et al.* 2011, Dueñas *et al.* 2018, Zambrano *et al.* 2021).

Parasitoids in biocontrol: a declining strategy?

Despite the diversity of parasitoid species recorded in Ecuador, the data seem to indicate a decreasing trend in their use as a pest control strategy. The regression model calculated between the number of parasitoids used in biocontrol (Y) versus the years of study (X) shows an increase beginning in the 1980s reaching its maximum inflection in

Table 3. Parasitoids reported in association with pests on citrus, *Citrus* spp.

Pest	Parasitoid	Region	Reference
Aleurocanthus woglumi	*Amitus hesperidum*	Andes	Browning 1992, Merino 1984
Aleurothrixus floccosus	*Amitus spinifera* *Cales noacki* *Encarsia* sp. *Eretmocerus* sp.	Andes, Coast	Arias *et al*. 1992, Cañarte-Bermúdez & Navarrete-Cedeño 2019, Valarezo 2011, Valarezo *et al*. 2011
Anastrepha fraterculus, *Anastrepha striata*	*Aganaspis pelleranoi*	Coast	Valarezo 2011
Ceratitis capitata	*Diachasmimorpha longicaudata*	Andes	Valarezo *et al*. 2011
Diaphorina citri	*Diaphorencyrtus aligarhensis* *Tamarixia radiata*	Andes, Coast	Chávez *et al*. 2019, 2017, Cuadros *et al*. 2020, Erráez *et al*. 2020, Portalanza *et al*. 2017, Valarezo *et al*. 2011
Lepidosaphes beckii	*Aphytis lepidosaphes*	Andes	Merino & Vázquez 1962
Phyllocnistis citrella	*Ageniaspis citricola* *Cirrospilus* sp. *Elasmus tischeriae* *Galeopsomyia* sp. *Horismenus* sp.	Andes, Coast	Cañarte-Bermúdez *et al*. 2020, Cañarte-Bermúdez & Navarrete-Cedeño 2019, Valarezo *et al*. 2004
Toxoptera aurantii	*Aphelinus flavipes* *Aphidius matricariae* *Aphidius* sp. *Diaeretus* sp. *Lysiphlebus* sp.	Andes, Coast	Cañarte-Bermúdez & Navarrete-Cedeño 2019, Cañarte-Bermúdez *et al*. 2020, Valarezo *et al*. 2011

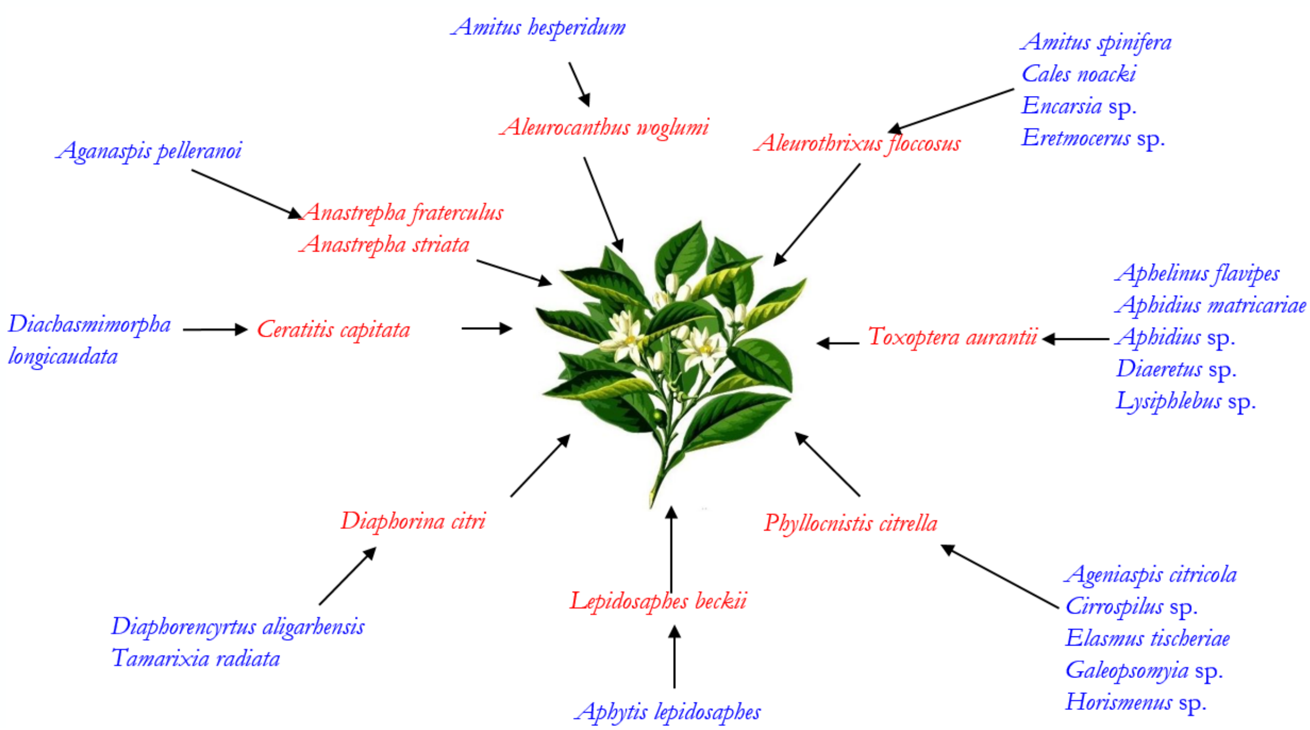

Figure 4. Parasitoids associated with pests that attack citrus, *Citrus* spp. The arrows show the interconnections in the agroecosystem. Pests are indicated in red letters and parasitoids in blue.

Table 4. Parasitoids reported in association with pests on cassava, *Manihot esculenta* Crantz.

Pest	Parasitoid	Region	Reference
Erinnyis ello	*Cotesia americanus* *Cotesia congregata* *Cotesia* sp. *Chetogena scutellaris* *Euplectrus* sp. *Oencyrtus submetalicus* *Telenomus dilophonotae* *Telenomus sphingis* *Thysanamyia* sp. *Trichogramma exiguum* *Trichogramma fasciatum* *Trichogramma minitum* *Trichogramma* sp.	Amazon, Coast	Hinostroza *et al.* 2014, Rogg 2000
Hemiptera: Aleyrodidae	*Amitus macgowni* *Encarsia* sp. *Eretmocerus* sp. *Euderomphale* sp. *Signiphora aleyroidis* *	Andes, Coast	Trujillo *et al.* 2004

* Hyperparasitoid.

Table 5. Parasitoids reported in association with pests on coffee, *Coffea arabica* L.

Pest	Parasitoid	Region	Reference
Hypothenemus hampei	*Prorops nasuta*	Amazon, Andes	Klein Koch *et al.* 1988 Mendoza *et al.* 1994
	Cephalonomia stephanoderis	Andes, Coast	Mendoza *et al.* 1994b, Klein Koch *et al.* 1988
	Phymastichus coffea	Coast	Delgado *et al.* 2002
Perileucoptera coffeella	*Catolaccus* sp. *Cirrospilus* sp. *Horismenus cupreus* *Mirax* sp. *Prigalio* sp. *Tetrastichus* sp. *Viridipyge letifer* *Zagrammosona* sp.	Coast	Anchundia 1994, Mendoza *et al.* 1994, Sotomayor & Duicela 1995

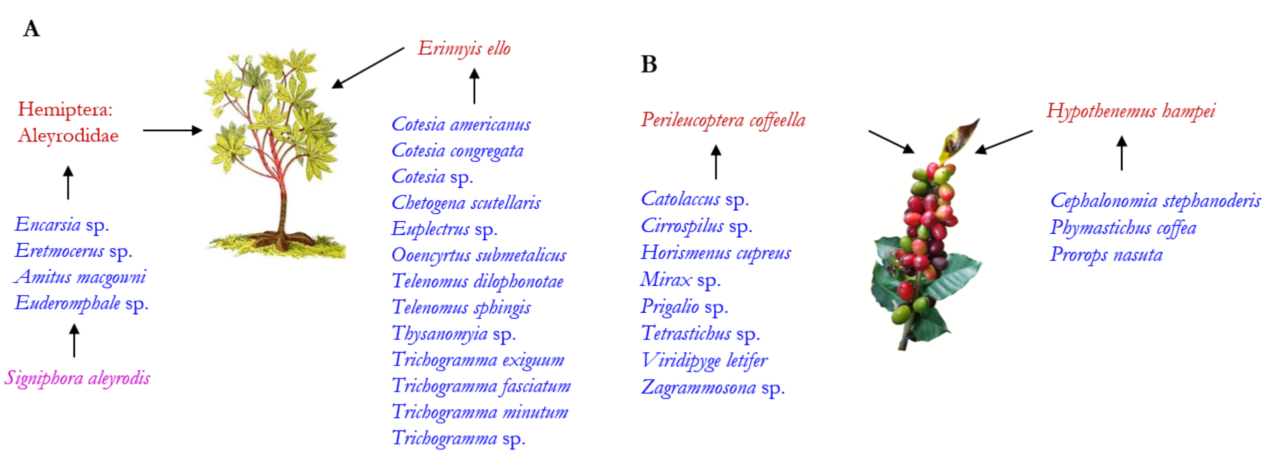

Figure 5. Parasitoids associated with pests that attack A: cassava, *Manihot esculenta* Crantz, B: coffee, *Coffea arabica* L. The arrows show the interconnections in the agroecosystem. Pests are indicated in red letters, parasitoids in blue and hyperparasitoids in purple.

Table 6. Parasitoids reported in association with pests on vegetables and other transitory crops.

Crop	Pest	Parasitoid	Region	Reference
Crucifers	*Plutella xylostella*	*Diadegma insulare* *Diadegma majale* *Diadegma* sp. *Oomyzus* sp.	Andes	Gavilanes 2018, Lalangui & Caicedo 2018
	Brevicoryne brassicae	*Diaeretiella rapae*	Andes, Coast	Zamorano 2012
Summer flowers	*Liriomyza huidobrensis*	*Diglyphus isaea*	Andes, Coast	Prado *et al*. 2018
Melon, pepper, tobacco	Hemiptera: Aleyrodidae	*Amitus fuscipennis* *Amitus* sp. *Encarsia nigricephala* *Encarsia* sp. *Eretmocerus* sp.	Andes, Coast	Arias *et al*. 2008, Dueñas *et al*. 2018, Navarrete *et al*. 2017, Valarezo *et al*. 2008
	Aphis gossypii *Myzus persicae*	*Aphidius* spp. *Lysiphlebus testaceipes*	Coast	Arias 2021, Dueñas *et al*. 2018, Paredes 2011, Toledo *et al*. 2018
Potato	*Phthorimaea operculella* *Symmetrischema tangolias* *Tecia solanivora*	*Copidosoma koehleri*	Andes	Báez & Gallegos 2011
Tomato	*Prodiplosis longifila*	*Synopeas* sp.	Coast	Arias 2021, Valarezo *et al*. 2011
	Spodoptera sunia	*Telenomus remus*	Coast	Arias 2021
	Tuta absoluta	*Encarsia porteri*	Andes	Benzing *et al*. 1997
Unidentified plants, cotton	*Bemisia* spp.	*Encarsia lanceolata* *Encarsia pergandiella*		Schuster *et al*. 1998, Zambrano *et al*. 2021
Unidentified vegetables	Unidentified Lepidoptera	*Incamyia chilensis* *Trichogramma* sp.	Andes	Andrade 1990

Table 7. Parasitoids reported in association with pests on various fruit trees.

Crop	Pest	Parasitoid	Region	Reference
Avocado	*Caloptilia azaleella*	*Telenomus* sp.	Andes	Venegas *et al*. 2018
Cherimoya Guava, Fruit trees	*Anastrepha* spp. *Ceratitis capitata*	*Aceratoneuromya indica* *Aganaspis pelleranoi* *Coptera haywardi* *Diachasmimorpha longicaudata* *Doryctobracon crawfordi* *Sycophila* sp. *Utetes anastrephae*	Andes, Coast	Arias 2021, Arias & Carrasco 2004, Feicán *et al*. 1999, León & Larriva 2019, Minga *et al*. 2020, Tigrero 2007, Valarezo 2011
Little orange	*Neoleucinodes elegantalis*	*Bracon* sp.	Andes, Amazon	Noboa *et al*. 2017
		Chelonus sp.	Andes, Amazon	Noboa *et al*. 2017
		Copidosoma sp.	Andes, Amazon	Sosa 2009, Noboa *et al*. 2017
		Lixophaga sp.	Amazon, Andes	Noboa *et al*. 2017
		Lymeon sp.	Andes	Sosa 2009
		Meteorus sp.	Andes	Sosa 2009
Mango	*Dysmicoccus brevipes*	*Aenasius* sp. *Cheiloneurus* sp. *Metaphycus* sp.	Coast	Arias 2021
Fruit trees	*Aleurothrixus floccosus*	*Encarsia* sp.	Coast	Valarezo *et al*. 2011

Table 8. Parasitoids reported in association with pests on rice, *Oryza sativa* L.

Pest	Parasitoid	Region	Reference
Diatraea spp.	*Telenomus alecto*	Coast	INIAP 1996
Rupela albinella	*Telenomus rowanii* *Strabotes* sp.	Coast	INIAP 1996, Arias 2021
Spodoptera sp.	*Euplectrus* sp.	Coast	INIAP 1996
Syngamia sp.	*Bracon* sp. *Conura* sp.	Coast	INIAP 1996
Oebalus spp., *Tibraca limbativentris*	*Telenomus* sp. *Trichopoda* sp. *Trissolcus basalis*	Coast	Arias 2021, Arias *et al*. 1996
Tagosodes orizicolus	*Anagrus* sp. *Elenchus* sp. *Gonatopus* sp. *Haplagonatopus hernandenze* *Paranagrus perforator*	Coast	Arias 2021
Various Lepidoptera	*Conura* sp. *Euplectrus* sp. *Goniozus* sp. *Hormius* sp. *Pseudochaeta* sp. *Stantonia* sp. *Telenomus* sp. *Trichogramma* sp.	Coast	Arias 2021, Arias *et al*. 1996, Castillo *et al*. 2020

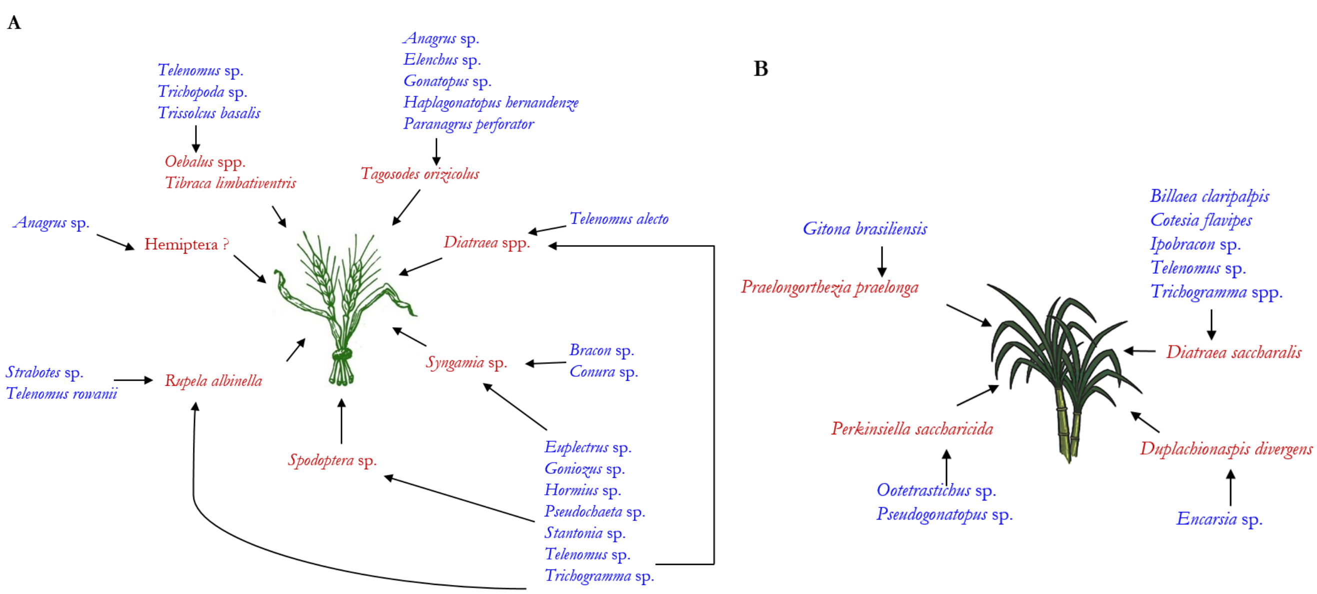

Figure 6. Parasitoids associated with pests that attack A: rice, *Oryza sativa* L. B: sugarcane, *Saccharum officinarum* L. The arrows show the interconnections in the agroecosystem. Pests are indicated in red letters and parasitoids in blue.

Table 9. Parasitoids reported in association with pests on sugarcane, *Saccharum officinarum* L.

Pest	Parasitoid	Region	Reference
Diatraea saccharalis	*Billaea claripalpis*	Coast	CINCAE 2013, Gaviria 1981, Mendoza 2018, Risco 1960
	Ipobracon sp.	Coast	Mendoza *et al*. 2005, Mendoza 2018
	Cotesia flavipes	Coast	CINCAE 2013, Mendoza 2018
	Telenomus sp.	Coast	Mendoza *et al*. 2005, Mendoza 2018
	Trichogramma spp.	Coast	Mendoza *et al*. 2005, Mendoza 2018
Duplachionaspis divergens	*Encarsia* sp.	Coast	Mendoza *et al*. 2013, Mendoza *et al*. 2005
Perkinsiella saccharicida	*Anagrus optabilis* *Aprostocetus* sp. *Ootetrastichus* sp.	Coast	Mendoza *et al*. 2005, Arias 2021
	Pseudogonatopus sp.	Coast	Mendoza *et al*. 2005, 2018
		Coast	Mendoza *et al*. 2005
Praelongorthezia praelonga	*Gitona brasiliensis*	Coast	Mendoza *et al*. 2005, Mendoza 2013

Table 10. Parasitoids reported in association with pests on cacao, *Theobroma cacao* L.

Pest	Parasitoid	Region	Reference
Aphid or Lepidoptera	*Ceraphron* sp.*	Coast	Páliz *et al.* 1982
Cecidomyiids	*Laptacis* sp. *Platygaster* sp. *Synopeas* sp.		
Unidentified larvae and pupae	*Brachymeria cominator*		
Unidentified Aranae**	*Trimorus* sp.		
Unidentified Diptera	*Trichopria* sp.		
Unidentified Lepidoptera and Coleoptera	*Cotesia* sp. *Asobara* sp. *Chelonus* sp. *Dissomphalus* sp. *Meteorus* sp.		
Unidentified Lepidoptera, Hemiptera, Coleoptera, Neuroptera**	*Bothriothorax* sp. *Tachinaphagus* sp.		

* Hyperparasitoid, **Predator.

the following decade (1990), and subsequently decreased from the 2000s to the present. The estimated model explains this trend with a high and significant coefficient of determination ($R^2 = 0.8093$, $P < 0.0001$) (Fig. 10). The use of parasitoids have probably been replaced by other pest control strategies.

We emphasize that in Ecuador there is an extensive legislation that regulates the importation and use of biocontrol agents whose responsibility is assigned to the Agency for the Regulation of Control and Phytosanitary Control (AGROCALIDAD). This agency also regulates chemical pesticides, restricting the use of highly toxic molecules and the indiscriminate applications of pesticides.

However, surveys carried out with farmers in recent years have diagnosed an excessive use of insecticides to control arthropod pests in different crops (Bravo-Zamora *et al.* 2020, Chirinos *et al.* 2020, Reinoso 2015, Valarezo *et al.* 2008). Additionally, the adverse effects of insecticides on the health of farmers and consumers have also been documented in Ecuador in the last decade (González-Andrade *et al.* 2010, Guevara *et al.* 2016, Lindao *et al.* 2017). With respect to the environment, insecticide residues

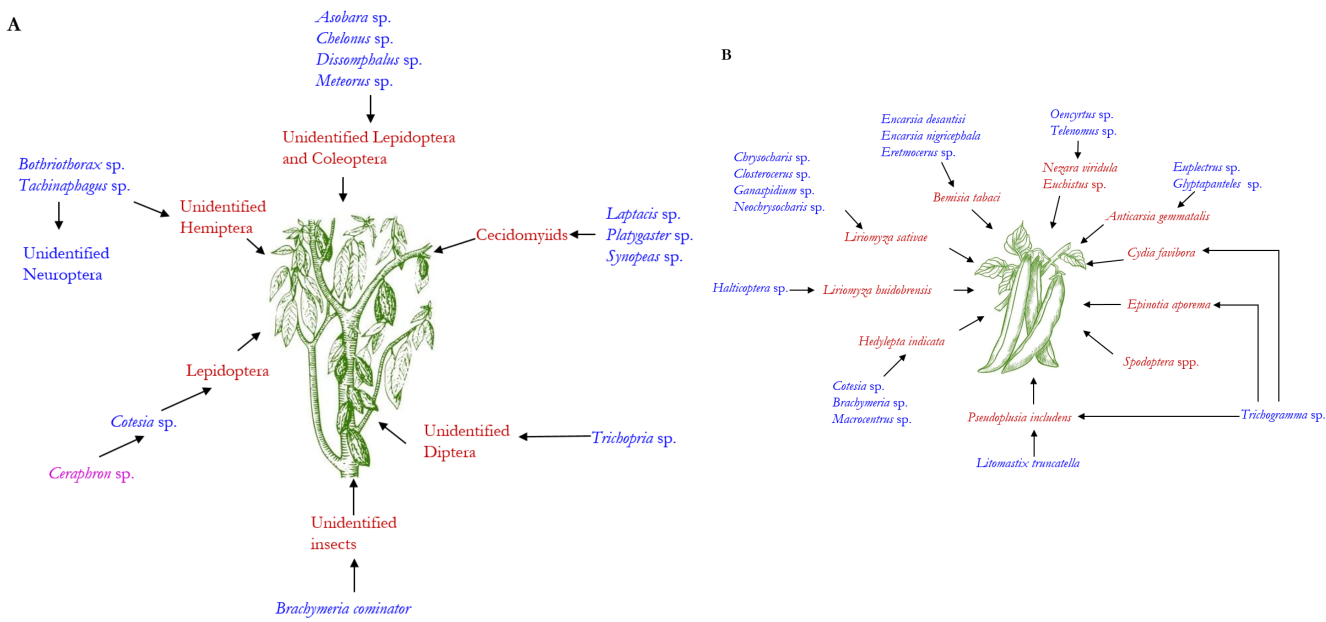

Figure 7. Parasitoids associated with pests that attack A: cacao, *Theobroma cacao* L., B: legumes The arrows show the interconnections in the agroecosystem. Pests are indicated in red letters, parasitoids in blue and hyperparasitoids in purple.

Table 11. Parasitoids reported in association with pests on legumes.

Pest	Parasitoid	Region	Reference
Anticarsia gemmatalis	*Euplectrus* sp. *Glyphapanteles* sp.	Coast	Mendoza 1994a
Bemisia tabaci	*Encarsia desantisi* *Encarsia nigricephala* *Eretmocerus* sp.	Coast	Arias 2005, 2021
Hedylepta indicata	*Cotesia* sp. *Brachymeria* sp. *Macrocentrus* sp.	Coast	Mendoza 1994a
Liriomyza sativae	*Chrysocharis* sp. *Closterocerus* sp. *Ganaspidium* sp. *Neochrysocharis* sp.	Coast	Chirinos *et al.* 2017
Liriomyza huidobrensis	*Halticoptera* sp.	Andes	Chirinos *et al.* 2020
Pseudoplusia includens	*Litomastix truncatella*	Coast	Mendoza 1994a
Euchistus sp. *Nezara viridula*	*Oencyrtus* sp. *Telenomus* sp.	Coast	Arias 2005
Anticarsia gemmatalis *Pseudoplusia includens* *Spodoptera* spp. *Epinotia aporema* *Cydia favibora*	*Trichogramma* sp.	Coast	Arias *et al.* 1992, Arias 2005, Mendoza 1994a

Table 12. Parasitoids reported in association with pests on palms (Arecaceae).

Pest	Parasitoid	Region	Reference
Brassolis astyra *Peleopoda arcanella* *Herminodes insulsa* *Opsiphanes cassina* *Opsiphanes sophorae* *Oiketicus kirbyi*	*Brachymeria* spp. *Conura* sp. *Xanthozona melanopyga*	Amazon	Rogg 2000
Euprosterna elaeasa	*Brachymeria* sp.	Amazon	Mexzón & Chinchilla 1996
Hispoleptis subfaciata	*Conura hispinephaga*	Amazon	Mexzón & Chinchilla 1996
Hispoleptis subfaciata	*Zaommomyia* sp.	Amazon	Mexzón & Chinchilla 1996
Oiketicus kirbyi	*Conura elaeisis*	Amazon	Mexzón & Chinchilla 1996
Saliana severus	*Brachymeria annulata*	Amazon	Mexzón & Chinchilla 1996
Opsiphanes cassina	*Xenufens forsythi*	Coast	Yoshimoto 1976
Saliana severus	*Trissolcus urichi*	Amazon	Mexzón & Chinchilla 1996
Sibine nesea	*Cotesia* sp.	Amazon	Mexzón & Chinchilla 1996
Spaethiella tristis	*Horismenus* sp.	Amazon	Mexzón & Chinchilla 1996
Spodoptera spp.	*Telenomus remus*	Amazon	Rogg 2000

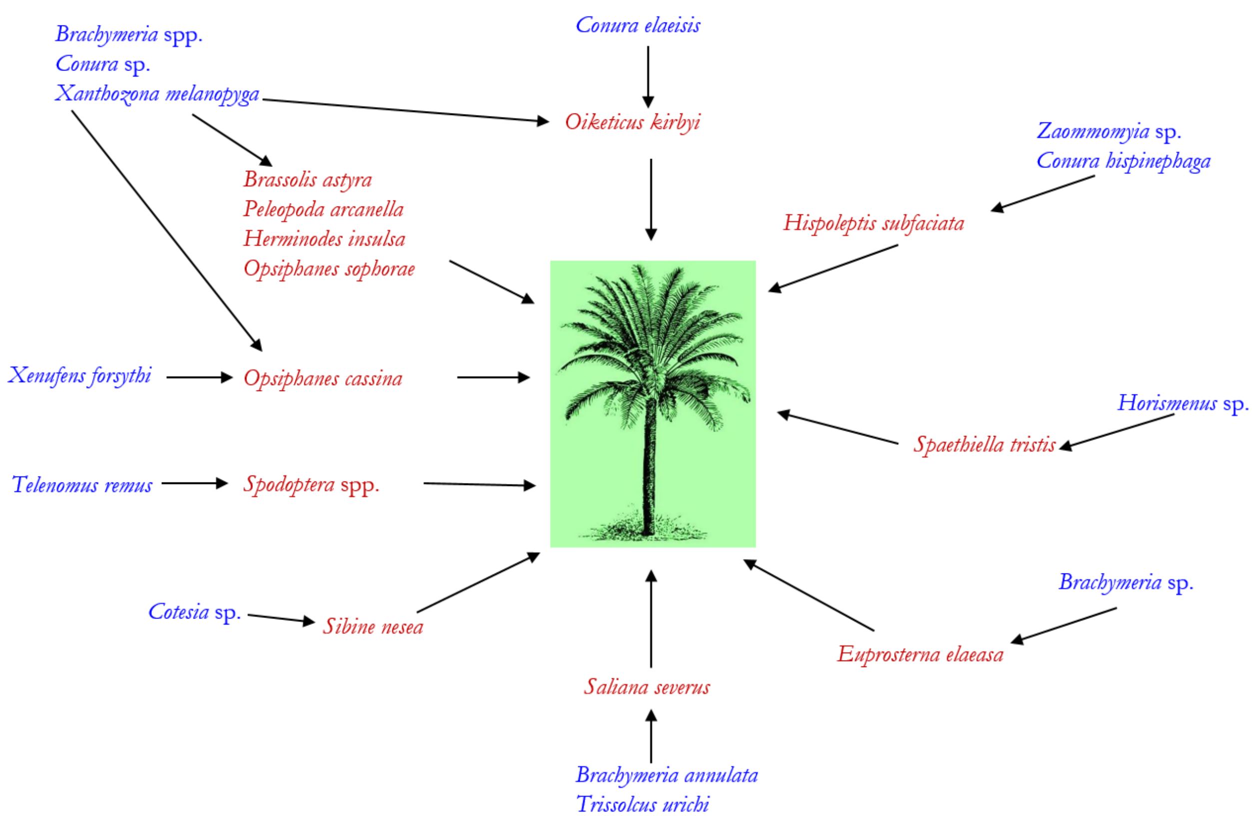

Figure 8. Parasitoids associated with pests that attack palms (Arecaceae). The arrows show the interconnections in the agroecosystem. Pests are indicated in red letters and parasitoids in blue.

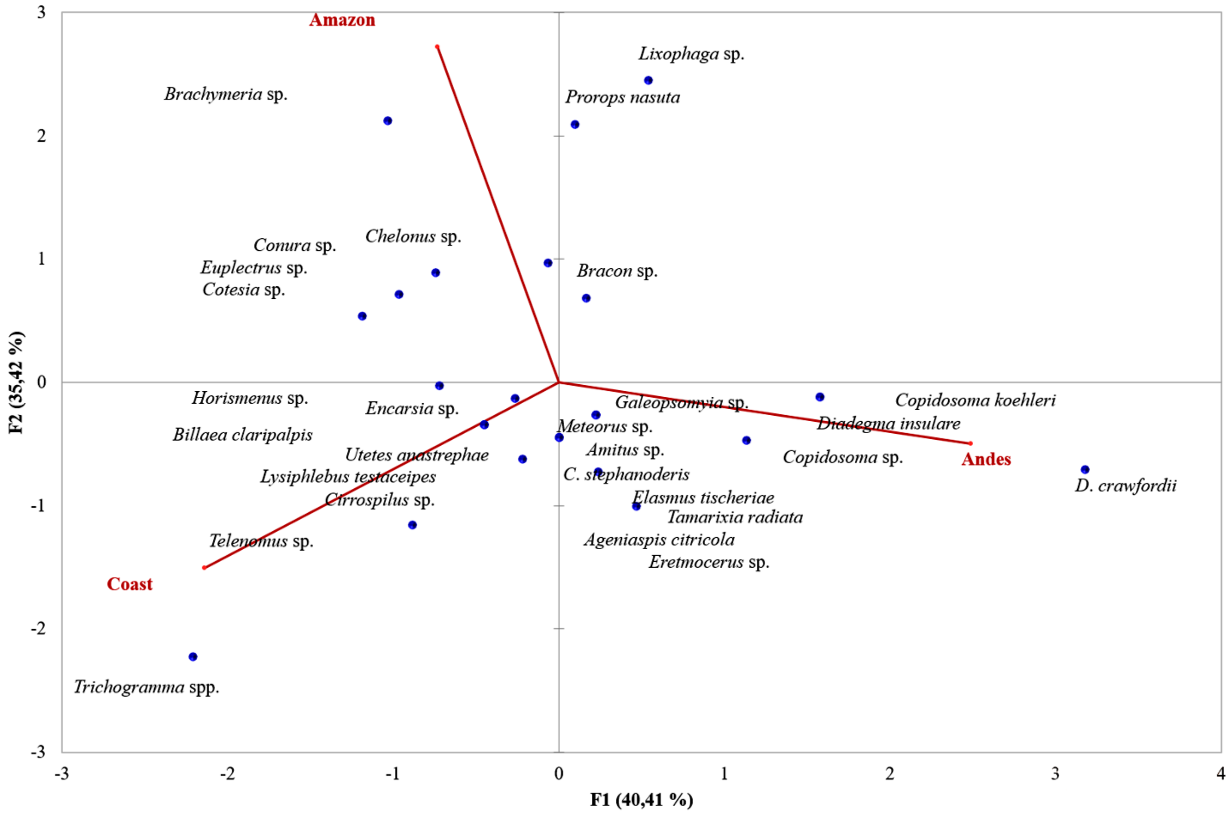

Figure 9. Principal component analysis between the geographical areas of continental Ecuador and the most studied parasitoids. Period 1980-2020.

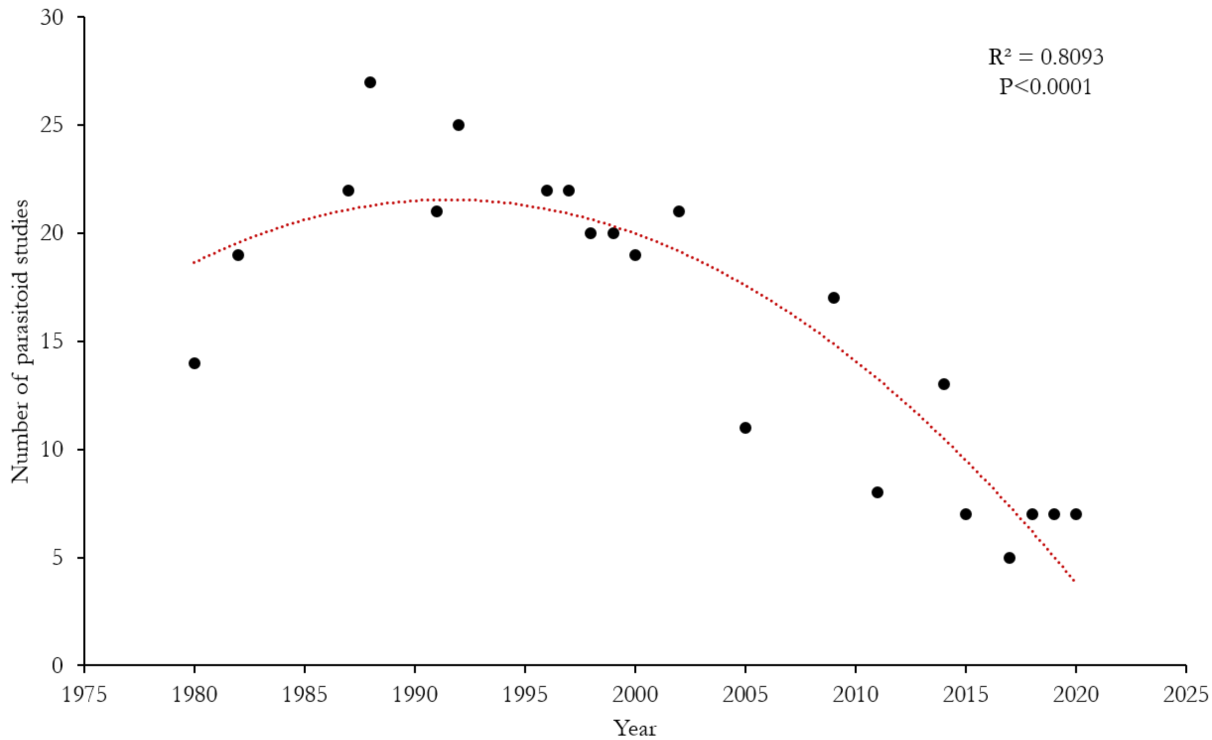

Figure 10. Regression model between the number of parasitoids studied and the years of study. Period 1980-2020.

have been detected in the Guayas river basin in the coastal region in areas close to banana and pineapple producing farms (Deknock *et al.* 2019).

Regarding ecological imbalances, several studies report the suppressive effect of insecticide applications on parasitoids. Chirinos *et al.* (2017) recorded parasitoids associated with the leafminer fly *Liriomyza sativae* Blanchard on beans, *Phaseolus vulgaris* L. and observed population outbreaks of this phytophagous species, caused by the interference with parasitism due to weekly sprays of lambda cyhalothrin + thiamethoxam. In a fieldwork conducted on melon, *Cucumis melo* L. in the coastal region, Navarrete *et al.* (2017) found lower rates of parasitism (3 to 7%) when formulations based on imidacloprid and neem (*Azadirachta indica* Juss.) were applied. A field assay determined the adverse effects of applications of insecticides based on neem on the parasitism rates of *Ageniaspis citricola* Logvinovskaya, 1983 (Hymenoptera: Encyrtidae) on *Citrus aurantifolia* (Christm.) Swingle (Cañarte-Bermúdez *et al.* 2020).

The frequent spraying of insecticides could be the consequence of several factors, among which stand out a disconnection between research and crop production, the farmer's perception of the damage caused by pests, the lack of knowledge about biological control and the excessive reliance on pesticides as a method of control. The report made by Delgado *et al.* (2002) analyzed the results of the introductions of parasitoids to control *H. hampei* in coffee. This study pointed out that biological control could be potentially effective and reduce the use of insecticides and lower production costs. However, they refer to the importance of a greater sociological interaction between the links in the researcher - producer chain to achieve these objectives (Delgado *et al.* 2002).

Citrus farmers from the Coast indicated that they mainly use chemical control due to the lack of knowledge of the importance of the use and action of parasitoids in pest management (Sornoza-Robles *et al.* 2020). Mendoza *et al.* (2005) reported that the establishment of integrated pest management programs in sugarcane are limited by the alarming perception that farmers have about the damage caused by a pest, as well as the excessive confidence they place on pesticides to control pests, which leads to their dependence and abuse of these products. Thus, insecticide applications seem to prevail in the control of agricultural pests in Ecuador. Cañarte-Bermúdez & Navarrete-Cedeño (2019) mentioned that 62% of citrus growers use chemical insecticides. All the vegetable farmers surveyed in five provinces of the Andean and coastal regions reported spraying insecticides to control the main pests with a range of 1 to 3 weekly sprays (Chirinos *et al.* 2020).

Since the late 1990s, some studies have focused at reducing the use of pesticides in Ecuador and conserving the action of natural enemies, including parasitoids. Feicán *et al.* (1999) reported that one of the strategies for the integrated management of fruit flies is the action of the parasitoid *D. crawfordi*, and that it is essential for its preservation to avoid the indiscriminate use of pesticides. The introduction of *D. longicaudata* in 2005 for the control of fruit flies was aimed at encouraging fruit growers to contribute to a production with less pesticide residues (Arias *et al.* 2009). In an inventory of parasitoids associated with the fruit borer, *Neoleucinodes elegantalis* Guenée, 1854 (Lepidoptera: Crambidae) in *Solanum quitoense* Lamarck, Noboa *et al.* (2017) reported that the parasitoid species detected in that study could be used in the biological control of this pest to reduce the use of pesticides in this crop.

The use of parasitoids in biological control programs has great potential in the Neotropical region due to their natural occurrence, considering that natural enemies have probably co-evolved within the plant-herbivore system, forming part of the ecosystem (Colmenarez *et al.* 2018). The structural and functional analysis of beneficial entomofauna could form the basis for conservation biological control programs (DeBach 1974). The two main strategies of conservation biological control consist of: 1) habitat modification to improve survival, longevity and reproduction of natural enemies and, 2) reducing the exposure of natural enemies to pesticides (Löhr *et al.* 2018). In the neighboring country, Colombia, studies on conservation biological control in crops such as sugarcane, chili, oil palm, coffee and ornamental plants have been conducted (Kondo *et al.* 2020). On the other hand, in Ecuador, unfortunately, with the synthesis of pesticides from 1945 onwards, the use of biological control decreased (Dangles *et al.* 2009) due to the simplistic perspective in which this alternative was framed. The bias in the use of this strategy has resulted in ecological imbalances, environmental crises and adverse economic and social effects (Metcalf & Luckmann 1975).

CONCLUSIONS

This review represents a compendium of about 200 taxa of parasitoids reported attacking agricultural pests in continental Ecuador with an emphasis on natural biological control. The major parasitoids reported are: *Telenomus* spp. (Hymenoptera: Platygastridae), *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) and *Encarsia* spp. (Hymenoptera: Aphelinidae), being the first two parasitoids mainly referred in biological control programs conducted between the 1980s and 1990s. The results suggest a decreasing trend in the use of parasitoids as biocontrol agents from 1980 to the present.

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