

Chapter 9

Parasitoid Insects



Luis Cláudio Paterno Silveira, Ivana Lemos Souza, Vitor Barrile Tomazella, and Heisler Alexander Gomez Mendez

9.1 Introduction

The term parasitoid can be defined as an organism that develops at the expense of a single host, nurturing from it and leading to its death, directly or indirectly, as the cause of its development. In practical terms we will be restricted to parasitoid insects (to the detriment of other groups, such as some Nematoda and fungi that fit the same definition), and we will focus on insects as hosts, since it is known that they also use several other classes of the phylum Arthropoda as hosts, such as Chilopoda, Diplopoda and Arachnida, as well as other phyla, such as Platyhelminthes, Mollusca (mainly Gastropoda) and Annelida (Eggleton and Gaston 1990). Also we will not consider here the cases where the host suffers only castration by the “parasitoid”, nor the species that attack oothecae and feed on several embryos (considered predators), nor those species where a single individual is able to dominate the nest of a social insect, called “nest parasitoids”. Finally, in terms of terminology, we prefer to use the term parasitism rather than parasitoidism to refer to the action of a parasitoid, since theoretically the correct would be parasite/parasitism and parasitoid/parasitoidism. However, this term is rarely used in entomology publications.

It is very difficult to determine the exact number of insects that exhibit parasitoid behaviour at some point in their life, or during all of it, but it is accepted that today about 10% of the described species of insects show parasitoid behaviour (Eggleton and Belshaw 1992) which would result in more than 100 thousand species. Therefore, this behaviour or way of life is very important in terms of species irradiation, which results in the great adaptation of this group to the most diverse terrestrial and, in some cases, aquatic habitats (Hanson and Gauld 2006).

L. C. P. Silveira (✉) · I. L. Souza · V. B. Tomazella
Federal University of Lavras (UFLA), Department of Entomology, Lavras, MG, Brazil
e-mail: lcpsilveira@ufla.br

H. A. G. Mendez
Protección de Plantas Department, Universidad de San Carlos de Guatemala,
Guatemala, Guatemala

There are families with parasitoid representatives in five orders of Insecta: 1 family in Neuroptera, 2 in Lepidoptera, 11 in Coleoptera, 21 in Diptera and 65 in Hymenoptera. Diptera and Hymenoptera are the most important, with 16,000 and 95,000 species already identified, respectively. For some reasons the order Hymenoptera clearly stands out from the rest: first, by the number of species described, since Hymenoptera correspond to 78% of all species mentioned as parasitoids, the remaining 22% being concentrated in Diptera and Coleoptera. Second, they present a perforating ovipositor, allowing them to deposit the eggs inside hosts, even in hidden places, as galls, and to explore small resources such as eggs of other insects (Gauld and Bolton 1996). Third, they have venom accessory glands, which allow them to dominate and subdue very active hosts and control their physiology in favour of their progeny. Finally, hymenopteran parasitoids are haplodiploid, allowing females to control the sex ratio of their progeny, which leads to less competition and adjustment according to the size of the exploited resource (Godfray and Shimada 1999). Due to these characteristics, the importance of Hymenoptera parasitoid as regulators of agricultural pests in many biological control programs applied throughout the world is undeniable.

Despite this, Diptera parasitoids are important in the regulation of many relevant species of insect pests, and it is estimated that they represent about 20% of all species with this behaviour. This indicates that the group is possibly underutilized as a pest regulator when compared to the use of Hymenoptera (Feener Jr and Brown 1997). On the other hand, the order Diptera presents a much wider range of adaptations and behaviours to exert its parasitism, allowing much more advanced studies in terms of evolution of parasitic behaviour (Gullan and Cranston 2017). For example, in Diptera there are structural adaptations, as for oviposition, ranging from a false ovipositor, where the abdominal segments just extend, to a perforating ovipositor, there are also structures like the respiratory funnels made by the larvae inside the host to avoid encapsulation and death by asphyxia. There are also changes in behaviour, such as the existence of planid larvae in many species, which are responsible for actively penetrating the body of the host, and host location detection by sounds emitted by it. Therefore, it is a very rich group for several important studies to understand parasitoid behaviour.

As for the other orders with parasitoid representatives, their applied importance is lower, but its study has revealed interesting aspects regarding the evolution of the parasitoid behaviour that, unlike what occurred in Hymenoptera (this behaviour appeared only once during the evolution of the group), arose independently for each family where this lifestyle is found, that is, 21 times in Diptera and 11 in Coleoptera.

9.2 General Characteristics

The parasitoids developed different strategies of parasitism along the coevolution with their hosts. According to the preference for hosts and the way in which they explore them during their life, a possible classification is as follows:

(a) *Host diversity* (Marshall 1981; Jameson 1985; Hofstede et al. 2004)

Monoxenes – group of parasitoids whose development cycle is restricted to only one species of host

Oligoxenes – when they are restricted to more than one species, but within the same genus

Pleioxenes – restricted to hosts within a single host family

Polyxenes – use hosts belonging to two or more families

(b) *Manipulation of the host*

Coinobionts – group of parasitoids that partially paralyze the hosts for oviposition, in such a way that the target is considered sessile, but soon recover its movements. The host then continues its development and is killed when the parasitoid reaches maturity, which usually happens in a few days (Godfray and Shimada 1999). Parasitoids with this behaviour differ very little, in fact, from predators, who devour their prey usually immediately after the attack, leading to their instantaneous death (Gullan and Cranston 2017). They can be divided into: ectoparasitoids, developing externally to the host, and endoparasitoids (Fig. 9.1), which develop internally in the host (Gordh and Headrick 2001).

Idiobionts – a group of parasitoids that prevent the future development of the host after initial paralysis. They usually attack hosts in their naturally immobile stage (e.g. eggs, pupae, immobile larvae and nymphs) (Gordh and Headrick 2001).

(c) *Preference for hosts parasitized or not*

Primary parasitoid – individuals that seek out non-parasitized hosts and develop on them (Gullan and Cranston 2017). The species with this behaviour are almost always selected to compose biological pest control programs, since they are able to locate healthy hosts (usually species known as agricultural pests), discriminating those that are already hosting other parasitoids, evaluating their size, sanity and nourish condition for their progeny, to finally parasite them and regulate their population.

Fig. 9.1 Endoparasitoid *Palmistichus elaeisis* (Eulophidae) inserting its ovipositor inside the pupae of *Tenebrio molitor* (Tenebrionidae). (Photo: Silveira LCP 2018)



Primary parasites, however, often confront the immune defence system of the host and may undergo the process called encapsulation, when haemolymph cells (haemocytes), as well as the pigment melanin, clump together on the egg or larva of the parasitoid, suffocating them (Salt 1963; Nappi 1975; Blumberg 1997). However, by the process of coevolution, many parasitoids developed mechanisms to avoid these defences (Salt 1968), such as:

- *Evasion*, a typical case of ectoparasitoids, which are not involved in the haemolymph of the host, as well as egg parasitoids, since eggs have no immune response
- *Molecular mimicry*, when the larva of the parasitoid produces and is surrounded in substances similar to the proteins of the host, passing unnoticed
- *Viral suppression*, when the parasitoid introduces into the host one or more viruses that deactivate its immune system
- *Destruction*, which can occur through vigorous feeding of host tissues by the larva of the parasitoid, or by the engorgement of haemolymph and defence cells, leading to the rapid weakening of the host, making it impossible to defend itself
- *Subversion*, divided into two possibilities: first, when the parasitoid maintains the host cell coverage used in the encapsulation, and the larva only opens a food channel, nourishing itself without the host noticing, and second, when giant cells (teratocytes) arise from fragments of the parasitoid egg and disrupts the host's immune system

As we can see, there are several ways for parasitoids to avoid being encapsulated and, as a rule, the older the host (e.g. caterpillars in more advanced instars), the greater the encapsulation. Therefore, for the regulation of a particular pest, it is important that the female parasitoid correctly discriminate the species, size, nutritional condition and age of the host, so that its progeny are successful, and biological control is effective.

Secondary parasitoid – develop on a primary parasitoid. This type of preference is also called hyperparasitism, found in many species, which have adapted to explore not the primary host (the organism being biologically regulated), but rather its primary parasitoid, leading to its death and impairing biological control programs. The host will fatally die, but there will be no progeny of the primary parasitoid, allowing future generations of the insect pest to escape control. Hyperparasitoids may also place their eggs inside or outside the larva of the primary parasitoid, receiving the following denominations:

- *Endophagous*, when the hyperparasitoid places its eggs inside the primary parasitoid
- *Ectophagous*, when it deposits the eggs on the surface of the larva of the primary parasitoid within the host being regulated (Fig. 9.2)

Facultative parasitoids – may act as a primary parasitoid, attacking healthy hosts or, optionally, attack the primary parasitoid within the already parasitized host (Salt 1968)

Fig. 9.2 Example of an ectophagous hyperparasitoid, *Asaphes* sp. (Pteromalidae) ovipositing on the larva of a primary Braconidae parasitoid within a mummified aphid *Lipaphis erysimi*. (Photo: Silveira LCP 2012)



9.3 Families of Hymenoptera and Diptera Parasitoids

In Hymenoptera currently 63 families belonging to 15 superfamilies present insect or spider parasitoids. The total number is bigger because some families also have predatory or phytophagous behaviour. One is considered a predator, not a parasitoid, and one is considered completely phytophagous, included in Table 9.1. The order Diptera has 16 families with insect or spider parasitoid species, mentioned in Table 9.2 with their respective primary hosts. It is quite common to find Diptera as parasitoids of other animal groups, not included here.

9.4 Foraging and Oviposition Behaviour in Parasitoids

To parasitize the host, a parasitoid first locates the host's potential habitat, locates the appropriate host and finally oviposits (Doutt 1964; Vinson 1975). Females of many species of parasitoids can use resources for feeding or oviposition throughout adult life. Their choices are mediated by external stimuli such as odours, tastes, colours and shapes and the individuals can be continuously influenced as they learn these stimuli during foraging. Successful foraging can increase longevity and search ability and lead to increased fecundity (Baggen and Gurr 1998; Winkler et al. 2006). Female parasitoids need to detect and respond to sensory signals indicating the occurrence of both host and food resources to achieve reproductive success (Schroeder and Hilker 2008).

Plants provide a variety of defences, which help to reduce the damage of insect pests in agroecosystems. They produce different important substances in the foraging process, such as volatile organic compounds and plant volatiles induced by herbivory (De Moraes et al. 1998). Such substances act through the detection of plant odours by parasitoids and consequently increase their foraging efficiency. The response to external stimuli in host locations for oviposition or food depends on the physiological state in which each female is (Lewis and Takasu 1990). In this way, when well fed they expand their foraging and reproduction capacity (Wäckers 1994).

Table 9.1 Superfamilies and families of hymenopteran parasitoids and their primary hosts

Superfamily/family	Primary hosts
1. <i>Apoidea</i>	
1. Sphecidae	Araneae, Orthoptera, larvae of Lepidoptera and Hymenoptera
2. <i>Ceraphronoidea</i>	
2. Ceraphronidae	Diptera, Hemiptera, Neuroptera, Thysanoptera
3. Megaspilidae	Coccoidea, Neuroptera, pupae of many Diptera
3. <i>Chalcidoidea</i>	
4. Aphelinidae	Hemiptera Sternorrhyncha; eggs of Lepidoptera, Hemiptera and Orthoptera
5. Chalcididae	Pupae of Lepidoptera; larvae of Diptera
6. Elasmidae	Larvae of Lepidoptera
7. Encyrtidae	Hemiptera, Coleoptera, Diptera, Lepidoptera
8. Eucharitidae	Larvae of Formicidae (Heraty 2002)
9. Eulophidae	Lepidoptera, Coleoptera, Hymenoptera, Diptera
10. Eupelmidae	Larvae and pupae of Coleoptera, Diptera and Lepidoptera
11. Eurytomidae (PH/PA)	Larvae and pupae of Coleoptera, Diptera and Lepidoptera
12. Leucospidae	Larvae and pupae in nests of Apoidea, Vespidae and Sphecidae
13. Mymaridae	Eggs of Auchenorrhyncha, Heteroptera, Coleoptera, Orthoptera and Diptera
14. Ormyridae	In galls of Diptera and Hymenoptera (Hanson 1992)
15. Perilampidae	Larvae of Tachinidae, Ichneumonoidea and Coleoptera
16. Pteromalidae (PH/PA/PR)	Coleoptera, Diptera, Lepidoptera, Araneae, Blattodea, Dermaptera, Hemiptera, Neuroptera and Hymenoptera
17. Rotoitidae	Unknown, possibly insect eggs (Bouček 1987)
18. Signiphoridae	Coccidae, Aleyrodidae, Aphididae and Psyllidae
19. Tanaostigmatidae (PH/PA)	Larvae of Cynipidae
20. Tetracampidae (PH/PA)	Larvae of Diptera, eggs of Diprionidae and Coleoptera
21. Torymidae (PH/PA)	Larvae and pupae of Diptera, nests of Hymenoptera, larvae of Lepidoptera
22. Trichogrammatidae	Eggs of Holometabola and of Hemiptera, Orthoptera and Thysanoptera
4. <i>Chrysoidea</i>	
23. Bethylidae	Cryptic larvae of Coleoptera and microlepidoptera
24. Chrysididae	Larvae and prepupae of Symphyta, eggs of Phasmatodea
25. Scolebythidae	Larvae of woodborer Coleoptera
26. Sclerogibbidae	Nymphs and adults of Embioptera
27. Embolemidae	Nymphs of some of a few Auchenorrhyncha
28. Dryinidae	Nymphs of Auchenorrhyncha
5. <i>Cynipoidea</i>	
29. Austrocynipidae	Larvae of Lepidoptera in <i>Araucaria</i> sp.

Table 9.1 (continued)

Superfamily/family	Primary hosts
30. Cynipidae (PH)	Gall formers or invaders
31. Figitidae	In galls of Cynipidae and Chalcidoidea, larvae of Chrysopidae, Hemeroibiidae and Diptera
32. Ibaliidae	Larvae of Siricidae
33. Liopteridae	Larvae of Buprestidae and Cerambycidae
6. <i>Evanioidae</i>	
34. Aulacidae	Larvae of Buprestidae, Cerambycidae and Xiphydriidae
35. Evaniidae (PRE)	Ootheca of Blattodea
36. Gasteruptionidae (PAR/PRE)	Nests of Apoidea and solitary wasps
7. <i>Ichneumonoidae</i>	
37. Braconidae (FI/PAR)	Larvae of Lepidoptera, Coleoptera, Diptera and Hymenoptera, nymphs and adults of Aphididae
38. Ichneumonidae	Eggs, larvae and pupae of Lepidoptera, Coleoptera, Diptera, Hymenoptera, Symphyta, Raphidioptera and Trichoptera, eggs and adults of Araneae
39. Apozygidae	Host unknown
8. <i>Megalyroidae</i>	
40. Megalyridae	Larvae of Bostrichidae, Buprestidae and Cerambycidae
9. <i>Mymarommatoidea</i>	
41. Mymaromatidae	Polyporales fungi (shelf fungi), possibly insect eggs (unconfirmed)
10. <i>Platygastridae</i>	
42. Platygastridae	Eggs of Orthoptera, Mantodea, Coleoptera, Hemiptera and Arachnida, Cecidomyiidae larvae, Psodococcidae nymphs and Aleyrodidae
11. <i>Proctotrupoidae</i>	
43. Austroniidae	Host unknown
44. Diapriidae	Larvae of Formicidae, terrestrial and aquatic Diptera
45. Heloridae	Larvae of Neuroptera
46. Maamingidae	Host unknown
47. Mesoserphidae	From Mesozoic fossils only
48. Monomachidae	Larvae of Stratiomyidae (Chironomyzinae) and Muscidae
49. Peleciniidae	Larvae of Scarabaeidae
50. Proctorenyxidae	Host unknown
51. Peradeniidae	Host unknown
52. Proctotrupidae	Larvae of Coleoptera and Mycetophilidae
53. Roproniidae	Symphyta pupae
54. Vanhorniidae	Larvae of Eucnemidae
12. <i>Stephanoidea</i>	
55. Stephanidae	Several woodborers Coleoptera and Siricidae

(continued)

Table 9.1 (continued)

Superfamily/family	Primary hosts
13. <i>Trigonaloidea</i>	
56. Trigonalidae	Larvae of Vespidae, Ichneumonidae and Tachinidae
14. <i>Vespoidea</i>	
57. Bradynobaenidae	Solifugae adults (Arachnida)
58. Mutillidae	Aculeate Hymenoptera (Apidae, Halictidae, Crabronidae, Megachilidae, Sphecidae, Pompilidae)
59. Pompilidae	Adults of Araneae
60. Rhopalosomatidae	Adults of Gryllidae
61. Sapygidae	Larvae of Vespidae, Apoidea
62. Scoliidae	Larvae of Scarabaeidae
63. Sierolomorphidae	Host unknown
64. Tiphiidae	Larvae of Cerambycidae, Carabidae, Curculionidae and Scarabaeidae in the soil
15. <i>Orussoidea</i>	
65. Orussidae	Larvae and pupae of woodborers (Buprestidae, Cerambycidae, Xiphytriidae) and Siricidae

Some families are parasitoids and predators, indicated by the acronym PA/PR, others are phytophagous and parasitoids (PH/PA), and one is considered predator (PR) and other phytophagous (FI). Host information without reference in the right column refers to Goulet and Huber (1993) and Hanson and Gauld (2006)

Table 9.2 Diptera families with insect or spider parasitoid representatives and their primary hosts

Family	Primary host
1. Acroceridae	Araneae (Schlinger 1987)
2. Anthomyiidae	Nymphs and adult Orthoptera
3. Asilidae	Scarabaeidae and Xylocopidae (Knutson 1972)
4. Bombyliidae	Hymenoptera, Coleoptera, Diptera, Neuroptera, Orthoptera and Lepidoptera (Davis 1919, Hull 1973)
5. Cecidomiidae	Hemiptera: adult of Aphididae and Psyllidae, nymphs of Tingidae (Eggleton and Belshaw 1992)
6. Chloropidae	Chrysomelidae eggs, larvae of Coleoptera and Tortricidae
7. Conopidae	Hymenoptera (Askew 1971)
8. Cryptochetidae	Coccoidea nymphs (Eggleton and Belshaw 1992)
9. Empididae	Trichoptera (Eggleton and Belshaw 1992)
10. Nemestrinidae	Acrididae and Scarabaeidae (Richter 1997)
11. Pipunculidae	Auchenorrhyncha (Waloff 1975) and Tipulidae (Skevington 2005)
12. Phoridae	Hymenoptera, Diptera, Coleoptera, Isoptera (Disney 1994)
13. Pyrgotidae	Scarabaeidae (Davis 1919)
14. Rhinophoridae	Isoptera (Sutton 1980)
15. Sarcophagidae	Lepidoptera, Auchenorrhyncha, Sternorrhyncha, Coleoptera, Orthoptera, Diptera and Hymenoptera (Pape 1990, Eggleton and Belshaw 1992)
16. Tachinidae	Hymenoptera, Coleoptera, Hemiptera (Wood 1987)

Although some parasitoids feed on host larvae for protein, most of them feed also on carbohydrate and protein sources as floral pollen, nectar and honeydew harvested from Hemiptera (Jervis et al. 1996). In the case of nectar and pollen, diversified agricultural landscapes could provide these food resources to parasitoids, through an ecological engineering plan in order to have plant diversification within and around the crops. The ingestion of carbohydrates derived from flowers allows the parasitoids to deposit more eggs in the hosts while feeding freely in the fields (Lee and Heimpel 2008).

In contrast, in the absence of carbohydrate sources, females reabsorb the eggs and redirect energy for survival, thus reducing fertility (Rivero and Casas 1999). In a study carried out in Brazil, the females of the parasitoid *Aphidius platensis* Bréthes (Braconidae) parasitized a larger number of aphids *Myzus persicae* Sulzer or *Schizaphis graminum* Rondani (Aphididae) when the flowers of the yellow marigold *Tagetes erecta* L. (Asteraceae) were present. The lack of these flowers as food source led to a lower rate of parasitism, and females spend most of their time walking or remaining immobile (Souza et al. 2018a).

9.5 Influence of Plant Diversification on Parasitoids

Conservation biological control through plant diversification has been a subject of exploration in agricultural production. Several studies evaluate different spatial arrangements, such as vegetation corridors, plant strips and consortium between plants in general. In addition, it is important to assess the impact of plant diversification on the increase of biological control. The maintenance of vegetation adjacent to crops is important as a strategy of natural enemies' conservation, since it promotes the flow of energy, genes, plants and animals among the elements of the landscape (Altieri et al. 2003). For example, many plants have morphological structures such as hairs, domatia and floral and extrafloral nectaries that provide shelter and food sources for many entomophagous arthropods, many of which are effective in controlling various pests (Marquis and Whelan 1996; Agrawal et al. 2000).

Márquez et al. (2017) registered the beneficial entomofauna in Guatemala on the edges of sugarcane fields, in vegetation corridors among the fields and in the interior of the crop. They found that some families were more abundant in the vegetation corridor while others were more abundant inside the sugarcane fields, indicating that the presence of some landscape attributes was important in terms of abundance of parasitoid families.

In Colombia the major sugarcane pest *Diatraea saccharalis* Fabr. (Crambidae) is controlled using the tachinid fly *Jaynesleskia jaynesi* Aldrich (Tachinidae) which locate and find the borer by the hole left in the stems (Williams et al. 1969). Vargas et al. (2006) found that the weed *Bidens pilosa* L. (Compositae) were suitable as a nectar source for these parasitoids, recommending its maintenance within sugarcane fields as a tactic of conservation biological control.

According to Haro et al. (2015) important parasitoids of various vegetable pests, for example, of several aphid pests, were found in plants of the family Apiaceae as coriander (*Coriandrum sativum* L.) and dill (*Anethum graveolens* L.). In each of these plants, eight different species of parasitoids were found while the sweet fennel (*Foeniculum vulgare* Mill.) were suitable for four species. The main genus of parasitoids found were *Aphidius* and *Lysiphlebus* (Braconidae), *Copidosoma* (Encyrtidae), *Pediobius* and *Sympiesis* (Eulophidae) and *Trichogramma* sp. (Trichogrammatidae). Thus, these surveys are important to elucidate the role of different plants to attract and conserve natural enemies of horticultural pests and can be used in different spatial arrangements as a component to increase biological control and pest regulation in the tropics.

One of the most promising plants to promote vegetable diversification in horticultural systems in Latin America is the yellow marigold *Tagetes erecta*. In Brazil the maintenance of lines of *T. erecta* near the onion cultivation promoted a greater amount of parasitoids, specially from the families Braconidae, Mymaridae, Figitidae, Trichogrammatidae, Eulophidae and Scelionidae, resulting in a lower presence of phytophagous insects in the plants, helping to regulate the natural pests of the crop (Silveira et al. 2009).

In Guatemala studies by Gomez (2017) on corn (*Zea mays*) associated with *T. erecta* at different distances from the field showed that this attractive plant influences the composition of the parasitoid species found in the crop. The abundance and richness of parasitoids associated with the fall armyworm *Spodoptera frugiperda* (J.E. Smith) was higher near the *T. erecta* strips, resulting in a better biological control of the pest. The presence of representatives of the genus *Apanteles*, *Chelonus*, *Cotesia*, *Trichospilus*, *Anomalon*, *Telenomus* and *Trichogramma*, all directly associated with all stages of the pest, was found in the marigold strips and on corn near these strips, proving that the diversification with this plant was efficient.

In Brazil Silva et al. (2016) observed that plants of kale *Brassica oleracea* L. (Brassicaceae) associated with coriander (*Coriandrum sativum*), dill (*Anethum graveolens*), yellow marigold (*T. erecta*) and calendula (*Calendula officinalis*) influenced the abundance, species richness and diversity of parasitoids of the aphid pest *Lipaphis erysimi* (Kaltenbach) (Aphididae). The aphid parasitoid species *Diaeretiella rapae* (McIntosh), *Aphidius colemani* (Viereck) and *Praon volucre* (Haliday) were attracted to the entomophagous plants and disperse to kale beds, helping to control the aphids.

A survey of Souza et al. (2018b) in sweet pepper (*Capsicum annuum* L.) fields associated with *T. erecta* and basil (*Ocimum basilicum* L.) revealed a greater abundance of parasitoids when the crop was next to these attractive plants (abundance of 98 versus 130 parasitoids for marigold and basil, respectively). In sweet pepper alone (monoculture), the number of parasitoids was reduced to 40 individuals. Among the parasitoids that contributed to increase abundance, the genera *Didyctium* sp. (Figitidae), *Polynema* sp. (Mymaridae) and *Apanteles* sp. (Braconidae) stood out. The diversification of sweet pepper fields with basil and marigold increases the number of parasitoids who benefits the culture and it is, therefore, recommended.

Haro et al. (2018) observed that the presence of marigold flowers within lettuce *Lactuca sativa* L. fields mediate shifts in arthropod food webs. The presence of marigold flowers in the field successfully increased richness, body size and the numerical and biomass abundance of natural enemies in the lettuce arthropod community, which affected the number of links, vulnerability, generality, omnivory rate and food chain length in the community. These are key factors for the stability of relationships between species in food webs. In conclusion, this reinforces the need of having flowers distributed, i.e. within horticultural fields, as a tool for regulation of pests via conservation biological control.

Wyckhuys et al. (2013) made a survey about conservation biological control at developing countries and have found 390 papers related to the topic about a variety of things regarding the method. Many of them were from Brazil, Cuba, Mexico and Philippines. They found that despite being a method of control not highly supported by the government nor the industries, it is growing every year with more and more researches. By the time of the survey there were more than 50 plants already studied (cultivated or not), and they attested that this method has a great importance and impact at developing countries' agriculture and even to help minimize the greenhouse effect.

9.6 Final Considerations

Parasitoids are individuals of great importance as part of the ecosystem itself and as part of agroecosystems, where they stand a role as insect regulators. Most of those insects regulated by parasitoids are serious pests, so the ecological service made by them contribute to enhanced production. Since they offer this service, the need of chemical sprays on crops tends to minimize, bringing benefits to the environment. There is still a lot to be known about parasitoids in diversified agroecosystems, especially at the tropics, where the utilization of biological control as a tool is still a small portion of pest control. Recent research, however, has shown that habitat diversification with flowering plants increases the abundance, richness and survival of parasitoids in tropical agroecosystems and, therefore, must be increased over the next few years.

References

- Agrawal AA, Karban R, Colfer RG (2000) How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance. *Oikos* 89:70–80
- Altieri MA, Ne S, Nicholls CI (2003) O papel da biodiversidade no manejo de pragas. Holos, Ribeirão Preto. 226p
- Askew RR (1971) Parasitic insects. Elsevier, New York. 316 p
- Baggen LR, Gurr GM (1998) The influence of food on *Copidoso makoehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biol Control* 11:9–17

- Blumberg D (1997) Encapsulation of parasitoids. In *World Crop Pests*, Elsevier 7:375–387
- Bouček NJ (1987) Rotoitidae, a curious new family of Chalcidoidea (Hymenoptera) from New Zealand. *Syst Entomol* 12(4):407–412
- Davis JJ (1919) Contributions to knowledge of the natural enemies of Phyllophaga. III *Nat Hist Surv Bull* 13:53–133
- Disney RHL (1994) *Scuttle flies: the Phoridae*. Chapman & Hall, London. 467p
- De Moraes CM, Lewis WJ, Paré PW, Alborn HT, Tumlinson JH (1998) Herbivore-infested plants selectively attract parasitoids. *Nature* 393:570–573
- Doutt RL (1964) Biological characteristics of entomophagous adults. In: De Bach P (ed) *Biological control of insects pests and weeds*. Reinhold, New York, pp 145, 844 p–167
- Eggleton P, Belshaw R (1992) Insect parasitoids: an evolutionary overview. *Philos Trans Biol Sci* 337:1–20
- Eggleton P, Gaston KJ (1990) “Parasitoid” species and assemblages: convenient definitions or misleading compromises? *Oikos* 59:417–421
- Feener DH Jr, Brown BV (1997) Diptera as parasitoids. *Annu Rev Entomol* 42(1):73–97
- Gauld ID, Bolton B (1996) *The Hymenoptera*, 2nd edn. Oxford University Press, Oxford
- Godfray HCJ, Shimada M (1999) Parasitoids as modelorganisms for ecologists. *Popul Ecol* 41(1):3–10
- Gomez H (2017) *Vegetação de entorno e sua influência sobre insetos praga e parasitoides em cultivos de cana e milho na Guatemala*. (Tesis de doctorado). Universidad Federal de Lavras, Brasil
- Gordh G, Headrick D (Eds.) (2001). *A dictionary of entomology*. Cabi
- Goulet H, Huber JT (1993). *Hymenoptera of the world: an identification guide to families*. Research Branch, Agriculture Canada. 668p
- Gullan PJ, Cranston OS (2017) *Insetos - Fundamentos da Entomologia – 5a Ed*. Guanabara Koogan, 460p
- Hanson P (1992) The Nearctic species of *Ormyrus* Westwood (Hymenoptera: Chalcidoidea: Ormyridae). *J Nat Hist* 26(6):1333–1365
- Hanson PE, Gauld ID (2006). *Hymenoptera de la Región Neotropical*. Gainesville: American Entomological Institute. (Memoirs of the American Entomological Institute, 77). 994 p
- Haro MM, Resende ALS, Silva VF, Souza B, Silveira LCP (2015) Parasitoids of horticultural pests associated to commercial development stages of Apiaceae plants. *Entomotropica* 30:174–180
- Haro MM, Silveira LCP, Wilby A (2018). Stability lies in flowers: Plant diversification mediating shifts in arthropod food webs. *PLOS ONE* | <https://doi.org/10.1371/journal.pone.0193045> February 16, 2018.
- Heraty JM (2002) Revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the world. *Mem Entomol Soc Can* 68:1–359
- Hofstede HM, Fenton MB, Whitaker JO Jr (2004) Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) on Neotropical bats (Chiroptera). *Can J Zool* 82:616–626
- Hull FM (1973) *Bee flies of the world: the genera of the family Bombyliidae*. Smithsonian Institution Press, Washington, DC
- Jameson EW (1985) Pleioxenous host-restriction in fleas. *J Nat Hist* 19:861–876
- Jervis M, Hawkins B, Kidd NAC (1996) The usefulness of destructive host feeding parasitoids in classical biological control: theory and observation conflict. *Ecol Entomol* 21(1):41–46
- Knutson LV (1972) Pupa of *Neomochtheru sangustipennis* (Hine), with notes on feeding habits of robber flies and a review of publications on immature stages (Diptera: Asilidae). *Proc Biol Soc Wash* 85:163–178
- Lee JC, Heimpel GE (2008) Floral resources impact longevity and oviposition rate of a parasitoid in the field. *J Anim Ecol* 77:565–572
- Lewis WJ, Takasu K (1990) Use of learned odours by a parasitic wasp in accordance with host and food needs. *Nature* 348:635–636
- Márquez JM, Reyes E, Lemus JM, López E, Torres L, Duarte R, Leal S, Arroyo LC, Pec M, López E (2017) Entomofauna benéfica (Hymenoptera: Parasitica) en caña de azúcar, asociada a las áreas con infestación del barrenador del tallo. *Cengicaña* 16:223–241

- Marquis RJ, Whelan C (1996) Plant morphology and recruitment of third trophic level: subtle and little recognized defenses? *Oikos* 75:330–334
- Marshall AG (1981) The sex ratio in ectoparasitic insects. *Ecol Entomol* 6:155–174
- Nappi AJ (1975) Parasite encapsulation in insects. In: Maramorosch K, Shope RE (eds) *Invertebrate immunity*. Academic Press, New York, NY, pp 293–326
- Pape T (1990) Revisionary notes on American Sarcophaginae (Diptera: Sarcophagidae). *Tijdschr Voor Entomol* 133:43–74
- Richter VA (1997) Family Nemeritidae. In: Papp L, Darvas B (eds) *Contributions to a manual of Palearctic Diptera*, vol 2. Science Herald, Budapest, pp 459–468
- Rivero A, Casas J (1999) Incorporating physiology into parasitoid behavioral ecology: the allocation of nutritional resource. *Res Popul Ecol* 41:39–45
- Salt G (1963) The defence reactions of insects to metazoan parasites. *Parasitology* 53:527–642
- Salt G (1968) The resistance of insect parasitoids to the defence reactions of their hosts. *Biol Rev* 43:200–232
- Schlinger EI (1987) The biology of Acroceridae (Diptera): true endoparasitoids of spiders. In: Nentwig W (ed) *Ecophysiology of spiders*. Springer, Berlin, Heidelberg
- Schroeder R, Hilker M (2008) The relevance of background odor in resource location by insects: a behavioral approach. *Bioscience* 58:308–316
- Silva V, Silveira L, Santos A, Santos AJN, Tomazella VB (2016) Companion plants associated with kale increase the abundance and species richness of the natural-enemies of *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae). *Afr J Agric Res* 11(29):2630–2639
- Silveira LCP, Berti-Filho E, Pierre LSR, Peres SC, Louzada JL (2009) Marigold (*Tagetes erecta* L.) as an attractive crop to natural enemies in onion fields. *Sci Agric* 66:780–787
- Skevington JH (2005) Revision of Nearctic *Nephrocerus* Zetterstedt (Diptera: Pipunculidae). *Zootaxa* 977:1–36
- Souza IL, Marucci RC, LCP S, de Paulo NCP, Lee JC (2018a) Effects of marigold on the behavior, survival and nutrient reserves of *Aphidius platensis*. *BioControl* 63(4):543–553
- Souza IL, Tomazella VB, AJN S, Moraes T, LCP S (2018b) Parasitoids diversity in organic Sweet Pepper (*Capsicum annum*) associated with Basil (*Ocimum basilicum*) and Marigold (*Tagetes erecta*). *Braz J Biol (AHEAD)*
- Sutton SL (1980) *Woodlice*, 2nd edn. Pergamon Press, Oxford. 144 p
- Vargas GA, Obando V, Gómez LA (2006) *Jaynesleskia jaynesi*: otra alternativa para el manejo de *Diatraea* spp. *Carta Trimestral. Cenicafía* 28(2):3–5
- Vinson SB (1975) Biochemical coevolution between parasitoids and their host. In: Price PW (ed) *Evolutionary strategies of parasitic insects and mites*. Plenum Press, New York, pp 14–48. 224p
- Wäckers FL (1994) The effect of food deprivation on the innate visual and olfactory preferences in the parasitoid *Cotesia rubecula*. *J Insect Physiol* 40:641–649
- Waloff N (1975) The parasitoids of the nymphal and adult stages of leafhoppers (Auchenorrhyncha: Homoptera) of acidic grassland. *Trans R Entomol Soc Lond* 126(4):637–686
- Wood, D.M. 1987. Tachinidae. In: *Manual of Nearctic Diptera*. Vol. 1. Research Branch, Agriculture Canada, Monograph No. 27, pp 549–573
- Winkler K, Wackers F, Bukovinszkyne-Kiss G, van Lenteren J (2006) Sugar resources are vital for *Diadegma semiclausum* fecundity under field conditions. *Basic Appl Ecol* 7:133–140
- Wyckhuys KAG, Lu Y, Morales H, Vazquez LL, Legaspi JC, Eliopoulos PA, Hernandez LM (2013) Current status and potential of conservation biological control for agriculture in the developing world. *Biol Control* 65(1):152–167
- Williams JR, Metcalfe JR, Mungomery RW, Mathes RW (1969) *Pests of sugarcane*. Elsevier publishing company, Amsterdam-London-New York, p 367