Herbivore, parasitoid and hyperparasitoid insects associated with fruits and seeds of *Enterolobium contortisiliquum* (Vell.) Morong (Fabaceae)

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(With 3 figures)

Abstract

This study aimed to inventory the herbivore insects associated with *Enterolobium contortisiliquum* (Vell.) Morong (Fabaceae) fruits and seeds and their primary and secondary parasitoids. Six samples collected between May and October 2013 yielded 210 fruits, from which 326 insects of six orders emerged: Coleoptera, Hymenoptera, Lepidoptera, Diptera, Thysanoptera and Psocoptera. Coleoptera (five families) was represented by the seed consumers *Merobruchus bicoloripes* Pic, *Stator* sp. Bridwell (Chrysomelidae, Bruchinae), two species of Silvanidae, one species of Scolytinae (Curculionidae), one species of Nitidulidae and one species of Cerambycidae. The cerambycid was also observed forming galleries on fruit mesocarp. Immature individuals of Lepidoptera were observed consuming the fruits and seeds. From the seven Hymenoptera families, only two species were associated with Coleoptera, being *Horismenus* Walker sp. (Eulophidae) as parasitoid of *M. bicoloripes*, and *Neoheterospilus falcatus* (Marsh) (Braconidae) as parasitoid of Scolytinae. The Lepidoptera parasitoids represented four genera: *Pseudophanerotoma* Zetel, *Chelonus* Panzer (Braconidae), *Orgilus* Nees (Braconidae) and *Goniozus* Forster (Bethylidae). The host associations for the reared parasitoids *Bracon* Fabricius (Braconidae), Pimplinae sp. (Ichneumonidae) and *Perilampus* Forster (Perilampidae) were not confirmed. We obtained a single representative of Diptera (Tachinidae) associated with Lepidoptera hosts in this food web.

Keywords: endophytic insects, seed consumers, parasitism, trophic interactions.

Insetos herbívoros, parasitoides e hiperparasitoides associados a frutos e sementes de *Enterolobium contortisiliquum* (Vell.) Morong (Fabaceae)

Resumo

Este estudo teve como objetivo inventariar os insetos herbívoros associados a frutos e sementes de *Enterolobium contortisiliquum* (Vell.) Morong (Fabaceae) e seus parasitoides primários e secundários. De seis amostras coletadas entre maio e outubro de 2013, obteve-se 210 frutos, dos quais emergiram 326 insetos pertencentes a seis ordens: Coleoptera, Hymenoptera, Lepidoptera, Diptera, Thysanoptera e Psocoptera. Coleoptera (cinco famílias) foi representada pelos consumidores de sementes: *Merobruchus bicoloripes* Pic, *Stator* sp. Bridwell (Chrysomelidae, Bruchinae), Silvanidae sp. 1 e sp. 2, Scolytinae sp. (Curculionidae), Nitidulidae sp. e Cerambycidae sp. A última espécie também foi observada formando galerias no mesocarpo do fruto. Indivíduos imaturos de Lepidoptera também foram observados consumindo os frutos e sementes. Dos Hymenoptera (sete famílias), duas espécies foram associadas a Coleoptera, sendo *Horismenus* Walker sp. (Eulophidae) parasitoide de *M. bicoloripes* e *Neoheterospilus falcatus* (Marsh) (Braconidae) parasitoide de Scolytinae. Os parasitoides de Lepidoptera foram totalizados em quatro gêneros: *Pseudophanerotoma* Zetel e *Chelonus* Panzer (Braconidae), *Orgilus* Nees (Braconidae) e *Goniozus* Forster (Bethylidae). As interações para os parasitoides *Bracon* Fabricius (Braconidae), Pimplinae sp. (Ichneumonidae) e *Perilampus* Forster (Perilampidae) não foram confirmadas. Nós encontramos apenas um único representante de Diptera (Tachinidae) como parasitoide de Lepidoptera nesta rede trófica.

Palavras-chave: insetos endofíticos, consumidores de sementes, parasitismo, interações tróficas.

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1. Introduction

Insects have a key role in terrestrial environments, since they are the most abundant organisms in the world. In terrestrial ecosystems, herbivore insects are frequently parasitized by other insects (May, 1988). On average, 10% of insect species are parasitoids and, among the known parasitoid species, 80% belong to Hymenoptera, followed by Diptera (Van Driesche and Bellows, 1996). The order Hymenoptera is one of the most diverse in nature (Hanson and Gauld, 2006), comprising on average 115 thousand known species and 300 thousand to three million species still undescribed in the Neotropical region. (Hanson and Gauld, 2006; Melo et al., 2012).

Hymenoptera insects are present in roughly 50% of all terrestrial food webs (Lasalle and Gauld, 1991). The parasitized hosts are very diverse and include galls, seed consumers, spiders and thrips. However, the majority of Hymenoptera are parasitoids of herbivore Coleoptera, Diptera, Lepidoptera and Hymenoptera (Quicke, 1997a). Parasitoids are known to control herbivore populations by laying eggs when the host is still in its larval stage (Gómez and Zamora, 1994). The high number of parasitoids and their ability to increase their populations as the host population increases provides the important ecological balance that contributes to species diversity (Gauld and Bolton, 1988; La Salle and Gauld, 1991; Scatolini and Penteado-Dias, 1997). The ecological balance occurs when parasitoids reduce the host population, facilitating the coexistence of other species that compete with their hosts, increasing the local richness (La Salle, 1993; Monmany and Aide, 2009).

In some cases, parasitoids can enhance plant fitness by parasitizing herbivores that damage the seeds by feeding on them (Gómez and Zamora, 1994; Traveset, 1991). Insect interactions in fruits have an important role in ecological communities (Herrera, 1982; Lawton, 1986) due to their impacts on seed survival and consequently plant recruitment success, which is directly related to seed damage by herbivores (Kursar and Coley, 2003). Studies of parasitoids reared directly from their hosts on plants are very important because they can reveal new interactions and important relationships in community webs (Lewinsohn, 1991; Nascimento et al., 2014).

The parasitoid studies are mostly conducted by attraction techniques and other trapping methods. However, few studies have explored the parasitoids based on their hosts and plants in natural conditions (Nascimento et al., 2014). Also, host-parasitoid interactions can change spatially (Reigada et al., 2014), demonstrating the importance of this study for food web approaches. Thus, this study aimed to take an inventory of the endophytic insect consumers of fruits and seeds of *Enterolobium contortisiliquum* (Vell.) Morong (Fabaceae: Mimosoideae) and their associated parasitoid insects.

2. Material and Methods

2.1. Study area

The fruits of *E. contortisiliquum* were collected in a savannah area comprising different phytophysiognomies such as gallery forests, *sensu stricto* savannah, *campo sujo,* and *campo cerrado* (Couto Júnior et al., 2010). The trees are located in a fragment edge near Serra da Canastra National Park in southwestern Minas Gerais state, in the municipalities of São Roque de Minas, Delfinópolis, and Sacramento (20° 32' 38.1" S; 46° 32' 19.7" W).

2.2. Host plant

Enterolobium contortisiliquum fruits present a brownish color and are ear-shaped, which is the reason for its common name, *orelha-de-macaco* (lit. Portuguese for "monkey ear") (Lorenzi, 2002; Silva et al., 2012). This tree occurs in five Brazilian states in rainforests and semidecidual forests where presents fast growth, reaching 20-35 meters (Lorenzi, 2002). This species is used for reforestation and in intercropping (Araújo and Paiva-Sobrinho, 2011).

2.3. Fruit sampling and insect rearing

Ten fruits per *E. contortisiliquum* individual were collected monthly during its fructification period between May and October, 2013 (six months). The number of trees sampled varied between the months according to availability of fruits. Overall, a total of 210 *E. contortisiliquum* fruits were collected (Table 1).

The ripe and unripe fruits were collected from both high and low regions of the plant. The fruits were then taken to the laboratory, stored individually in plastic containers, covered by voile fabric to enable air circulation and to prevent insects from escaping, and kept at 23 °C. The samples were checked daily, and the emerged adult insects were collected and stored in labeled Eppendorf microcentrifuge vials, containing ethanol at 70%. Insects were identified based on identification keys and some insects were sent to specialists for confirmation. Only the herbivores were sorted through morphospecies. The voucher specimens were deposited in the Entomological Collection of Universidade Estadual de Minas Gerais, Passos, Minas Gerais, Collection of the Coleoptera Bioecology and Systematics Laboratory at Federal University of Paraná, Curitiba, Paraná and Entomological Collection of Biological Institute of Campinas, São Paulo.

2.4. Statistical analysis

We used species-accumulation curves to evaluate the sampling efficiency for each month of fruit collection. The accumulation curves are used to evaluate sampling effectiveness by associating the sampling effort

Table 1. Number of consumed and non-consumed *Enterolobium contortisiliquum* fruits (Vell.) Morong (Fabaceae).

Sampled month	May	June	July	August	September	October	Total
Number of fruits	40	20	60	40	40	10	210
Consumed	11	10	34	20	21	6	102
Non-consumed	29	10	26	20	19	4	108

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(number of fruits) to the accumulated species richness. Accumulation curves were prepared using the *vegan* package (Oksanen et al., 2007) with the rarefaction method and non-parametric bootstrapping based on 1000 randomizations to display the confidence intervals (±95% CI). To check the sampling efficiency, we use the function s*pecpool* to extrapolate the species richness and to compare with the observed species richness. For each month, we tested whether the increase in parasitoid population was correlated to herbivore population increase, then we built GLM models according to its adequate error distribution. All analyses were made using R (R Development Core Team, 2011).

3. Results and Discussion

From the total of *E. contortisiliquum* fruits collected, only 102 fruits (48.57% of the total) yielded associated insects (Table 1). The 326 reared insects belong to six orders: Coleoptera, represented by 178 individuals (54.60% of the total insects); Hymenoptera (102 individuals/ 31.29%); Lepidoptera (38 individuals/ 11.66%); Diptera (5 individuals/ 1.53%); Thysanoptera (2 individuals/ 0.61%) and Psocoptera (1 individual/ 0.31%) (Table 2, Figure 1). Overall, species-based accumulation curves demonstrated an adequate sampling effort since in most months the curve reached a plateau, except for October (Figure 2). The sampling efficiency was around 77% and 83%. Additionally, the increase in the herbivore abundance was
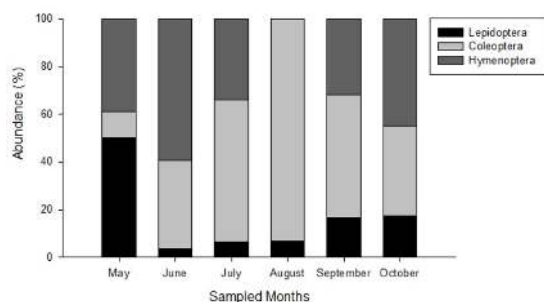
Figure 1. Abundance of the main insect orders associated with *Enterolobium contortisiliquum* fruits, reared between May and October of 2013.
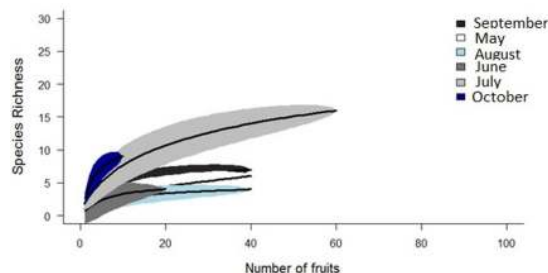
Figure 2. Sample-based species accumulation curves. Rarefaction curve comparing the number of fruits in each sampled month. The 95% CIs are shown in grey and blue scales according to sampled months.

not correlated to an increase in parasitoid abundance in any of the sampled months (p>0.05).

3.1. Coleoptera

Coleoptera was the most abundant order, represented by five families: Chrysomelidae (92.13% of total Coleoptera), Silvanidae (3.37%), Curculionidae (1.68%), Nitidulidae (1.12%) and Cerambycidae (1.68%). Chrysomelidae presented 164 individuals of *Merobruchus bicoloripes* Pic (148 individuals/ 83.15% of total Chrysomelidae) and *Stator* sp. (Bridwell) (16 individuals/ 8.99% of total Chrysomelidae), both from the subfamily Bruchinae (93.71% of total Coleoptera). The Bruchinae were responsible for most of the seed consumption and for the holes observed in the fruits. In their larval phase they consume seeds from many plant families, although 84% of their host plants are Fabaceae (Bondar, 1936; Johnson, 1981; Johnson et al., 1995; Kingsolver, 2004). *M. bicoloripes* and *Stator limbatus* Horn were also obtained in other studies on the insects associated with fruits and seeds of *E. contortisiliquum* in Pernambuco, Brazil (Meiado et al., 2013). Meiado et al. (2013) described a strict relationship between the number of holes in the fruits and the number of *M. bicoloripes* individuals, with seven as the maximum number of individuals feeding on *E. contortisiliquum* fruits. We found a maximum of nine holes per fruit, thus indicating there may be up to nine individuals.

The family Silvanidae was represented by six individuals of two species (indicated in Table 2 as Silvaninae sp. 1 and Silvaninae sp. 2), represented by 3 individuals each. Other individuals belonged to Curculionidae (three Scolytinae) and Nitidulidae (two individuals). These insects are generally known to consume seeds after their dispersal, seeds previously consumed by other insects, or decomposing matter (Sari and Ribeiro-Costa, 2011).

The number of Cerambycidae (3 individuals/ 1.69%) was low compared to the results obtained by Meiado et al. (2013). This family can be found in different habitats during development and most species are wood-borers (Marinoni et al., 2001). However, the Cerambycidae larvae found in this study are confirmed to develop inside the *E. contortisiliquum* fruits, feeding from their seeds (Di Iorio 1995; Santos et al., 1994). In addition to the seed predation, we observed that these insects formed galleries in the mesocarp of the fruit, as also noted by Meiado et al. (2013).

3.2. Lepidoptera

In this study, lepidopteran larvae were observed consuming both the seeds and fruit mesocarp of *E. contortisiliquum*, forming galleries. This behavior was also observed in other leguminous plants such as *Stryphnodendron adstringens* (Mart.) Coville and *Piptadenia gonoacantha* (Mart.) Macbr. (Sari and Ribeiro-Costa, 2011; Morales-Silva and Modesto-Zampieron, 2016; Morales-Silva et al., 2018). According to our data and laboratory observations we can hypothesize that the lepidopterans are the first herbivores to occupy the fruits of *E. contortisiliquum* (Table 2, Figure 1).

Table 2. List of insects emerged insects from *Enterolobium contortisiliquum* fruits collected in different phytophysiognomies of savannah between May and October 2013.

Order/ Fam./Subf./Gen.	Months /2013						Total	RF(%)*
	May	June	July	August	September	October		
COLEOPTERA	**2**	**10**	**73**	**42**	**37**	**11**	**178**	**54.60**
Chrysomelidae	1	10	66	42	37	8	164	92.13
Bruchinae	1	10	63	35	37	2	148	83.15
Merobruchus bicoloripes								
Stator sp.	0	0	3	7	0	6	16	8.99
Silvanidae	0	0	3	0	0	3	6	3.37
Silvaninae sp.1	0	0	3	0	0	0	3	1.69
Silvaninae sp. 2	0	0	0	0	0	3	3	1.69
Curculionidae	1	0	2	0	0	0	3	1.69
Scolytinae	1	0	2	0	0	0	3	1.69
Cerambycidae	0	0	3	0	0	0	3	1.69
Nitidulidae	0	0	2	0	0	0	2	1.12
DIPTERA	**4**	**0**	**0**	**0**	**1**	**0**	**5**	**1.53**
Tachinidae	0	0	0	0	1	0	1	20
N.ID.**	4	0	0	0	0	0	4	80
HYMENOPTERA	**7**	**16**	**43**	**0**	**23**	**13**	**102**	**31.29**
Braconidae	7	12	24	0	11	8	62	60.78
Braconinae	6	12	10	0	9	2	39	38.24
Bracon sp.								
Cheloninae	0	0	8	0	2	6	16	15.69
Chelonus sp.								
Pseudophanerotoma sp.	1	0	0	0	0	0	1	0.98
Orgilinae	0	0	5	0	0	0	5	4.90
Orgilus sp.								
Doryctinae	0	0	1	0	0	0	1	0.98
Neoheterospilus falcatus								
Bethylidae	0	0	16	0	11	4	31	30.39
Bethylinae	0	0	16	0	11	4	31	30.39
*Goniozus*sp.								
Eulophidae	0	4	0	0	0	0	4	3.92
Entedoninae	0	4	0	0	0	0	4	3.92
Horismenus sp.								
Perilampidae	0	0	1	0	0	1	2	1.96
Perilampinae	0	0	1	0	0	1	2	1.96
Perilampus sp.								
Ichneumonidae	0	0	1	0	0	0	1	0.98
Pimplinae	0	0	1	0	0	0	1	0.98
Encyrtidae	0	0	1	0	0	0	1	0.98
Formicidae	0	0	0	0	1	0	1	0.98
LEPIDOPTERA	**9**	**1**	**8**	**3**	**12**	**5**	**38**	**11.66**
PSOCOPTERA	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0.31**
THYSANOPTERA	**0**	**0**	**1**	**1**	**0**	**0**	**2**	**0.61**
TOTAL	**22**	**27**	**128**	**46**	**73**	**30**	**326**	**100**

*RF = Relative frequency; **N.ID = non-identified insects.

Although the Lepidoptera were not the most abundant herbivores of this study, they played an important role in the sustainment of this food web. In this study we confirmed four parasitoid species associated with Lepidoptera hosts: *Pseudophanerotoma* sp., *Chelonus* sp., *Orgilus* sp. (Braconidae) and *Goniozus* sp. (Bethylidae), (which represented 51.96% from all Hymenoptera collected), and another two potential parasitoids of Lepidoptera hosts (*Bracon* sp. and an unidentified species of Pimplinae). These parasitoids were considered potential parasitoids of Lepidoptera because the specimen of Pimplinae and most *Bracon* specimens were found in fruits where no

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predation by Coleoptera was observed. However, the possibility of these parasitoids to also use Coleoptera hosts is not excluded, since there are records of them in the literature (Whitehead, 1975; Gagnepain and Rasplus, 1989). In contrast, other studies have shown the importance of bruchine beetles in the sustainment of leguminous plant food webs, such as *Senegalia tenuifolia* (L.) Britton and Rose, *S. adstringens* and *P. gonoacantha* (Sari and Ribeiro-Costa, 2011; Tuller et al., 2015; Morales-Silva and Modesto-Zampieron, 2016; Maia et al., 2018; Morales-Silva et al., 2018). *Horismenus* Walker (Eulophidae) was the only parasitoid found associated with Bruchinae in the present study. Figure 3 was developed to demonstrate the general food web associated to this plant, including the parasitoid potential interactions we described here.

3.3. Hymenoptera

Regarding the emerged adult Hymenoptera, we identified seven families: Braconidae, Bethylidae, Encyrtidae, Eulophidae, Formicidae, Ichneumonidae and Perilampidae.

The Braconidae were the most abundant, represented by 62 individuals (60.78% from all Hymenoptera collected). This family is considered the second most diverse in Hymenoptera (Van Achterberg, 1988; Fernandez and Sharkey, 2006), and four subfamilies and five genera were found: Braconinae (*Bracon* sp.

with 39 individuals / 38.24% of all Hymenoptera); Cheloninae (*Chelonus* sp., 16 individuals/ 15.69% and *Pseudophanerotoma* sp.,1 individual/ 0.98%); Orgilinae (*Orgilus* sp., 5 individuals/ 4.90%); and Doryctinae (one individual of *Neoheterospilus falcatu*s (Marsh)). Among Braconidae, *Bracon* was the most abundant genus (38.24%). The individuals of this genus can be larval parasitoids of Lepidoptera, Coleoptera and Diptera, mainly parasitoids of larvae found in the plant tissues, and are thus considered generalist parasitoids (Quicke, 1997b; Shaw, 2006; Shaw and Huddleston, 1991). *Bracon* parasites various genera of Bruchinae (Whitehead, 1975; Gagnepain and Rasplus, 1989). In addition, the phytophagous habit was also described for *Bracon*. The phytophagous species *Bracon zuleideae* Perioto and Lara, 2011 was described from Brazil associated with fruits of *Protium ovatum* Engl. (Burseraceae) (Perioto et al., 2011). Therefore, it was not possible to determine the precise food web role for *Bracon* sp. (Figure 3).

Chelonus and *Pseudophanerotoma* genera are solitary endoparasitoids of larval and egg stages of Lepidoptera (Shaw, 1997). Additionally, *Orgilus* is a cenobiont endoparasitoid of Lepidoptera larvae and consume endophytic Lepidoptera larvae (Van Achterberg, 1997). The *Neoheterospilus falcatus* specimen obtained in this study was putatively a parasitoid of Scolytinae, based
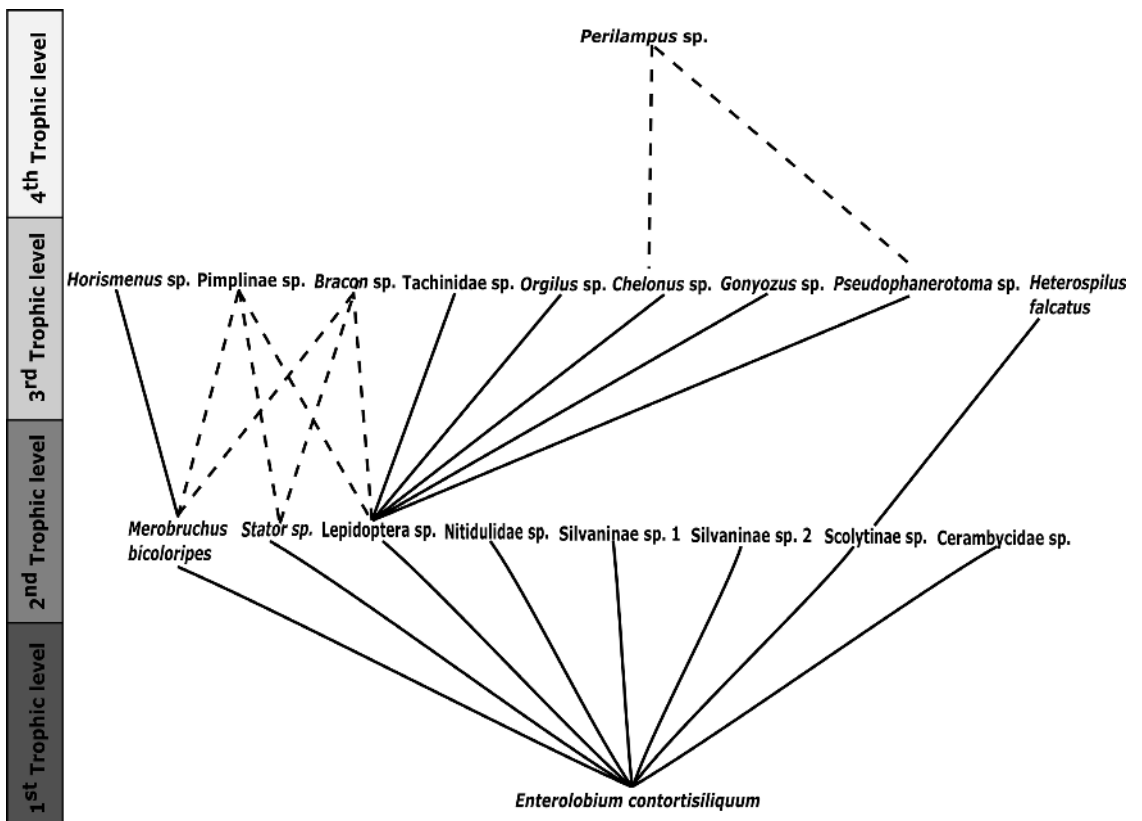

Figure 3. Food web of insects associated with *Enterolobium contortisiliquum*. Solid lines represent the potential interactions while the dashed lines represent confirmed interactions.

on the records of Quicke and Marsh (1992). Scolytinae individuals were observed on *E. contortisiliquum* fruits in July and certainly they are hosts as this parasitoid was also found coexisting in the same month.

Bethylidae was the second most abundant family in fruits of *E. contortisiliquum.* We found 31 individuals, all from the genus *Goniozus* (30.39% of all Hymenoptera). These species are gregarious ectoparasitoids of microplepidopteran larvae (Melo and Evans, 1993).

For Eulophidae we found four *Horismenus* individuals. Species of *Horismenus* were previously observed as Bruchinae parasitoids in many studies with leguminous plants (Hetz and Johnson, 1988; Tuller et al., 2015; Wood et al., 2017; Morales-Silva et al., 2018). Thus, in this study we can hypothesize that *Horismenus* individuals are *Merobruchus bicoloripes* parasitoids due to the absence of other herbivorous hosts in the fruits from which these individuals emerged. The genus *Horismenus* was also recorded as a parasitoid of *Merobruchus* in *Senegalia tenuifolia* fruits in Brazil (Tuller et al., 2015).

For Perilampidae, we found only two individuals of *Perilampus* Forster (1.96% of all Hymenoptera collected). This genus is a hyperparasitoid of Lepidoptera via Braconidae (Darling, 2006).

The families Ichneumonidae (Pimplinae), Encyrtidae and Formicidae were represented only by one individual each (0.98% of all Hymenoptera).

The ichneumonids found in this study belongs to the subfamily Pimplinae (0.98% of all parasitoids). This subfamily has a broad association with different hosts and can behave as an ectoparasitoids or endoparasitoids, idiobionts or cenobionts, in cryptic or non-cryptic hosts (Gauld, 2006). Some species are endoparasitic idiobionts in Lepidoptera pupae (Gauld and Shaw, 1995). Pimplinae can also be Coleoptera parasitoids (Gauld, 2006).

Encyrtidae was also represented by a single individual. They are considered parasitoids from a range of arthropods and their role in this web remains unknown. (Noyes and Hanson, 2006).

3.4. Diptera

A single specimen of Tachinidae was reared during these observations. This group is known to be parasitoid of spiders, scorpions and caterpillars (Vincent, 1985; Williams et al., 1990). Therefore, this parasitoid can be associated with Lepidoptera hosts in this food web.

3.5. General observations

The most abundant families of Hymenoptera vary according to the areas and phytophysiognomies sampled, demonstrating the importance of this study and the relevance of improving the knowledge on interactions and biodiversity (Morais et al., 2011; Azevedo et al., 2003).

The most abundant species of our system, *Bracon* sp., can be considered generalist according to Quicke (1997b). Regarding the plant-host-generalist parasitoid interaction, a study in two savannah areas showed that, although the host similarity between these areas was low, but, parasitoid similarity was high (Caldas and Passos, 1996; Araújo, 2011). Thus, the generalist parasitoids have an advantage in the absence of the preferable host. The insect distribution, in general, depends on plant, local climatic conditions and distribution (Fine et al., 2006; Marquis et al., 2001). Herbivore and parasitoid species distributions are associated to the plant species (Lewinsohn et al., 2005) since most herbivores tend to specialize on a family plant. The present work encourages and contributes to the understanding of new species interaction in the Brazilian savannahs.

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