

Parasitoid Wasps in Flower Heads of Asteraceae in the Brazilian Cerrado: Taxonomical Composition and Determinants of Diversity

AR NASCIMENTO^{1,5}, M ALMEIDA-NETO², AM ALMEIDA³, CR FONSECA³, TM LEWINSOHN⁴, AM PENTEADO-DIAS¹

¹Depto de Ecologia e Biologia Evolutiva, Univ Federal de São Carlos, São Carlos, SP, Brasil

²Depto de Ecologia, Univ Federal de Goiás, Goiânia, GO, Brasil

³Depto de Ecologia, Univ Federal do Rio Grande do Norte, Natal, RN, Brasil

⁴Lab de Interações Insetos-Plantas, Depto Biologia Animal, Instituto de Biologia, Univ Estadual de Campinas, Campinas, SP, Brasil

⁵Lab de Interações Ecológicas e Biodiversidade (LIEB), Depto de Ecologia, Univ Federal de Goiás, Goiânia, Goiás, Brasil

Keywords

Compositae, Hymenoptera Parasitica, microhymenoptera

Correspondence

AR Nascimento, Lab de Interações Ecológicas e Biodiversidade (LIEB), Depto de Ecologia, Univ Federal de Goiás, CP 131, CEP 74001-970 Goiânia, Goiás, Brasil; andre110479@gmail.com

Edited by Kleber del Claro – UFU

Received 24 October 2013 and accepted 5 April 2014

Published online: 13 May 2014

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Abstract

This study provides the first survey of the parasitoid fauna reared in flower heads of Asteraceae in the Brazilian cerrado. We investigated the relative importance of herbivore richness and plant species commonness to differences in parasitoid species richness among the plant species. A total of 15,372 specimens from 192 morphospecies belonging to 103 genera of Hymenoptera were reared from the flower heads of 74 Asteraceae species. Chalcidoidea and Ichneumonoidea were the most common superfamilies, with Eulophidae and Braconidae as the main families of parasitoid wasps. Singletons and doubletons accounted for 45% of total parasitoid species richness. The number of parasitoid species per plant species ranged from 1 to 67, and the variation in parasitoid species richness among plants was mainly explained by the number of sites in which the plants were recorded. This study shows that there is a highly diversified fauna of Hymenoptera parasitoids associated with flower heads of Asteraceae in the Brazilian cerrado. Our findings suggest that the accumulation of parasitoid species on plants is mainly determined by the regional commonness of plant species rather than the number of herbivore species associated with the plants.

Introduction

Plant diversity is a major predictor of insect diversity, especially of phytophages and their natural enemies (Ødegaard *et al* 2000, Lewinsohn *et al* 2005, Gering *et al* 2007). If the positive relationship between plant and insect diversity recorded at local scales also holds true at larger spatial scales, such as entire biomes or continents, then the Neotropical region probably harbors the world's most diverse entomofauna among all biogeographical domains. Considering that about 37% of all seed plant species are native to the neotropics (Antonelli & Sanmartín 2011), we could suppose that at least one third of all insect species should also be found in the same region. However, the Neotropical entomofauna is mostly unknown, and some of the most diverse insect groups are still poorly studied. This is especially true for parasitoid

wasps, for which only 11,000 species have been described for the neotropics (Fernández & Sharkey 2006). As a consequence of this knowledge gap, any extensive sample of Neotropical parasitoid assemblages usually contains a large proportion of undescribed species (Linnean shortfall) and many first occurrences of described ones (Wallacean shortfall; see Lomolino 2004). In addition, because parasitoid wasps are frequently sampled through attraction and trapping techniques (e.g., Malaise or yellow pan traps), there is little biological information about the plants and herbivore hosts used by the parasitoids. Insect-plant systems that allow the rearing of parasitoids directly on their hosts can help to overcome this information gap (Lewinsohn 1991). In this study, we present a taxonomic characterization of the parasitoid wasps reared from Asteraceae flower heads in remnants of the Brazilian cerrado.

The cerrado is the world's most species-rich savanna, harboring at least 11,600 plant species (Rezende *et al* 2008), of which almost 40% are endemic to this biome (Myers *et al* 2000). The cerrado biome is a biodiversity hot spot which was estimated to have lost 5,000 to 15,000 specialized insect herbivores due to the geographic contraction of the host plants (Fonseca 2009). These extinctions of insect herbivores are expected to generate a number of associated co-extinctions of their parasitoids, increasing the urgency of parasitoid inventories. Dias (1996) estimated the insect fauna at 90,000 species in the cerrado, and some studies have suggested a high level of endemism for some groups (e.g., Camargo & Becker 1999, Brown & Gifford 2002). There are very few studies on parasitoid wasps from the Brazilian cerrado, and these studies have focused on the description of only a few species (e.g., Flores & Penteado-Dias 2011, Nascimento & Penteado-Dias 2011).

Asteraceae is the second-largest plant family in the Brazilian cerrado (Warming 1973, Sano *et al* 2008), after Fabaceae. Both the density and richness of Asteraceae species are higher in more open types of cerrado vegetation, such as the *cerrado sensu stricto* and the *campo cerrado* (Figueiras 2002, Fonseca *et al* 2005, Almeida-Neto *et al* 2010). The inflorescences of Asteraceae, also known as flower heads, are an important resource for many herbivore insects (Lewinsohn 1991, Prado & Lewinsohn 2002, Almeida *et al* 2006). Many flower-head-feeding insects lay their eggs on the flower heads, where their larvae feed and develop (Zwölfer & Romstöck-Völkl 1991, Lewinsohn 1991, Gagné 1994, Prado & Lewinsohn 2002). The major taxonomic groups of flower-head-feeding insects are three Diptera families (Agromyzidae, Cecidomyiidae, and Tephritidae), several Lepidoptera families (Gelechiidae, Geometridae, Pterophoridae, Pyralidae, and Tortricidae), and Coleoptera (Apionidae) among the endophages (Almeida *et al* 2006, Almeida-Neto *et al* 2011). Although some studies have reported a large number of parasitoids reared in Asteraceae flower heads (e.g., Fonseca *et al* 2005, Dias *et al* 2010), no study has provided a comprehensive taxonomic characterization of the parasitoid wasps attacking flower-head-feeding herbivores.

The availability of food resources is the major bottom-up determinant of species richness (Kelly & Southwood 1999). The geographical range of resources plays a central role in how species are distributed, creating a cascade effect in the distribution of tritrophic interactions (Dyer 2007). Thus, one should expect that parasitoid wasps respond not only to changes in their insect hosts, but also to changes in herbivore host plants. In the plant-herbivore interactions in flower heads of the Asteraceae in the Brazilian cerrado, the abundance, geographical range, richness, and phylogeny of host plants are important factors in determining the richness of their associated herbivores (Prado & Lewinsohn 2004, Fonseca *et al* 2005, Almeida *et al* 2006).

In this study, we performed the largest systematic inventory of parasitoid wasps associated with Asteraceae flower heads in the Brazilian cerrado in an attempt to answer the following questions: (1) What is the taxonomic composition of flower head parasitoid fauna in terms of genera and higher taxa? (2) What is the species richness of parasitoid wasps associated with different Asteraceae taxonomic groups? and (3) What is the relative importance of plant commonness and insect herbivore richness to explain the variation in parasitoid species richness across host plant species?

Material and Methods

Study areas and sampling design

Asteraceae and their flower heads were sampled in 36 areas comprising distinct vegetation physiognomies of the Brazilian cerrado, which range from open grasslands (*Campo sujo*) to woodland vegetation (*Cerradão*). The sampled cerrado remnants are located in the state of São Paulo, Brazil, within the coordinates 51°06' to 47°09' W and 20°07' to 22°50' S (Fig 1). The regional climate is classified as Cwa according to Köppen (1948) and is characterized by rainy summers and dry winters.

The parasitoid wasps analyzed here were sampled in two studies focusing on interactions between Asteraceae and herbivorous insects in cerrado remnants in the state of São Paulo (Fonseca *et al* 2005, Almeida-Neto *et al* 2011). In the first study (Fonseca *et al* 2005), the flower heads were sampled from April to May 2001, a major reproductive period for the Eupatorieae and Vernonieae tribes; the second study sampled flower heads during three periods from 2001 to 2002, including the same period cited above (April to May 2001) and two other major reproductive periods for other Asteraceae tribes (August to September 2001 and January to February 2002). In both studies, all sites were sampled within 45 days. A distinction between the two studies is that the first one (Fonseca *et al* 2005) was undertaken in 16 cerrado remnants relatively distant from each other (mean distance=198.27 km), whereas the second one (Almeida-Neto *et al* 2011) was conducted within a smaller geographic area containing 20 cerrado remnants in the counties of São Carlos and Itirapina (mean distance=14.89 km). Both Fonseca *et al* (2005) and Almeida-Neto *et al* (2011) used 15 randomly placed transects of 5 m×30 m to determine the species richness of Asteraceae in each cerrado remnant. The number of sampled flower heads per plant species correlated highly with the local density of Asteraceae populations and the mean number of flower heads per individual plant (Pearson's correlation coefficients >0.85 and $p<0.001$ for all correlations).

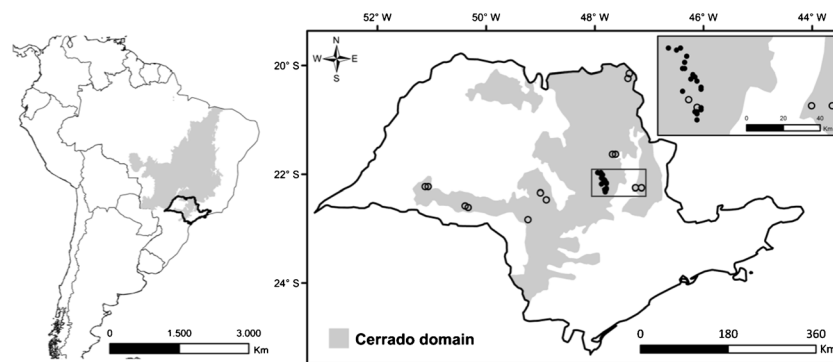


Fig 1 Distribution of the cerrado biome in Brazil and sampled cerrado localities in the state of São Paulo. *Open circles* indicate sites sampled in Fonseca *et al* (2005), and *solid black circles* represent the sites sampled in Almeida-Neto *et al* (2011).

In each remnant of cerrado, the study of Fonseca *et al* (2005) kept the flower head samples in plastic containers of 500 ml, while in the study conducted by Almeida-Neto *et al* (2011), the flower head samples were kept in plastic containers of 80 ml (or less, if that amount was not available). In both studies, the containers were covered with mesh lids and kept in the laboratory with no control of air temperature or humidity. The flower head samples were checked for the presence of adult insects once or twice weekly for a period of 2 months or until the emergence rate of adult insects became insignificant. Most insects were reliably identified at least to the genus level.

Some herbivore groups feed externally on Asteraceae flower heads (beetles, caterpillars, grasshoppers, bugs, and thrips), but these insects seem to be less common and less specialized than the endophagous herbivores whose larvae feed on plant tissue within the flower heads (Lewinsohn 1988). Exophagous insects were not kept or recorded in either Fonseca *et al* (2005) or Almeida-Neto *et al* (2011); consequently, the insects recorded in this study emerged from internal parts of the flower heads. Based on the visual inspection of host remains found inside the flower heads (about 3,000 flower heads were individually inspected) and based on the known biology of the genus and subfamilies (Gibson *et al* 1997, Wharton *et al* 1997, Fernández & Sharkey 2006), we ascertain that the majority of microhymenoptera are parasitoids of the endophytic herbivores. Some species of microhymenoptera probably are hyperparasitoids while a few ones have no apparent host, thus meaning that they can be herbivores.

Almost all plants were identified to the species level (see Fonseca *et al* 2005, Almeida-Neto *et al* 2010). Among the insects, many endophagous herbivore species could be identified to the species level, but most of the parasitoid wasps and microlepidoptera herbivores were identified to the genus or subfamily level and then sorted into operational taxonomic units. Herbivore insects from the families Cecidomyiidae (Diptera) and Apionidae (Coleoptera) were not included in the analysis because they were identified to the genus level

and then separated into morphospecies only in Almeida-Neto *et al* (2011). More details regarding the sampling and identification of plants and herbivore insects can be found in Fonseca *et al* (2005) and Almeida-Neto *et al* (2011).

Identification of the parasitoid wasps was undertaken using specialized literature for the Neotropical, Nearctic, and Gondwanic genera of the parasitoid superfamilies. To identify Chalcidoidea families, we used Gibson *et al* (1997) and Boucek (1988) and Hayat (1983) for Aphelinidae, Boucek & Delavare (1992) for Chalcididae, Noyes (1980) for Encyrtidae, Burks (1971) for Eurytomidae, Gibson (1995) for Eupelmidae, Lin *et al* (2007) and Triapitsyn (2006) for Mymaridae, and Fernández & Sharkey (2006) and Gibson *et al* (1997) for Perilampidae. For Ichneumonidea, we used Gauld (1997, 2000) and Fernández & Sharkey (2006) for most genera. Sandonato *et al* (2010) was used for the subfamily Campopleginae, and Wharton *et al* (1997) was used as a complementary reference for Braconidae. Dichotomous keys in Fernández & Sharkey (2006) were used for the superfamilies Cynipoidea, Ceraphronoidea, Platygastroidea, and Chrysidoidea. For some genera of Cynipoidea, we also used Quinlan (1986), Diaz & Gallardo (2000), Buffington (2004), Guimarães *et al* (2005), and Ovruski *et al* (2007).

Data analysis

We used path analysis (Shipley 2000, Grace 2006) to investigate the relative importance of plant commonness (i.e., the number of sites where the plant species occurs) and the number of herbivore species on plants in order to explain the variation of the number of parasitoid species reared in each plant species. Only plants with one or more parasitoids were included in the path analysis. The path analysis was based on the following rationale: (1) plant commonness was considered an exogenous variable that potentially affects all other variables; (2) the species richness of herbivore species associated with each plant species entered the model both as an exogenous variable that explains differences in parasitoid species richness among the plant species and as an

endogenous variable influenced by plant commonness; and (3) sampling effort (the weight of sampled flower heads) entered the model as a mediator variable because it increased with the number of sites where the plant species were found and thus could affect the number of parasitoid species through a passive sampling effect. For each plant species, the total weight of sampled flower heads was calculated as the sum of the dry weights (g) of flower heads (after insect emergence) across the sites. In order to evaluate if differences of sampling periods between Fonseca *et al* (2005) (only April–May) and Almeida-Neto *et al* (2011) (Jan–Feb, Apr–May, Aug–Sep) have any influence on the results, we also performed an alternative path analysis using only the species recorded during the April–May sampling period.

Model fit was assessed through a chi-squared test and by examining the Tucker-Lewis fit index (TLI), the comparative fit index (CFI), and the root mean square error of approximation (RMSEA). We used the approach introduced by MacCallum *et al* (1996) to verify the statistical power of the path model. Statistical power was calculated using RMSEA through the R code developed by Preacher & Coffman (2006). Normality was checked using Mardia's test, and outliers were inspected using Mahalanobis distance. Normality requirements were checked, and a logarithmic transformation was used for the weight of the sampled flower heads. The path analyses were constructed and analyzed using AMOS 5.0 (Arbuckle 2003).

Results

Overall, we reared 15,372 specimens of hymenopterans from flower heads of 74 Asteraceae species in 36 genera (Online Resource 1). We found a total of 192 morphospecies of parasitoid wasps, comprising 103 genera from 42 subfamilies, 18 families, and 6 superfamilies (Online Resource 2). Ninety-five percent of the parasitoid morphospecies were identified to the genus level, and the other 5% were identified to the subfamily level. Singletons (species represented by only one individual) and doubletons (species represented by two individuals) accounted for 56 and 20 of the parasitoid morphospecies (40% of total richness), whereas the five more abundant parasitoid wasps represented 52% of the total sampled specimens. The sampled parasitoid wasps from Asteraceae flower heads were dominated by a few species of Eulophidae (*Horismenus* sp. 1 and *Aprostocetus* sp. 2), Pteromalidae (*Heteroschema* sp. 1), and Braconidae (*Bracon* sp. 2).

Chalcidoidea was the largest superfamily, both in terms of species richness and abundance (Fig 2a, b), being represented by 11 families. Within Chalcidoidea, the Eulophidae family stands out in terms of abundance and species richness (Fig 3a, b). The Ichneumonoidea superfamily accounted for 19% of parasitoid richness and for 9.7% of the total abundance

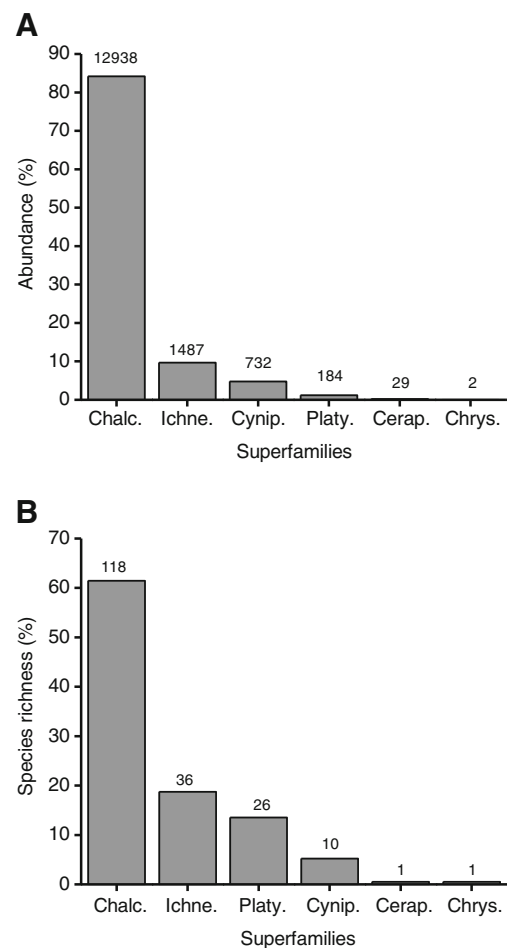


Fig 2 Taxonomic characterization of the parasitoid fauna reared in Asteraceae flower heads in cerrado remnants in São Paulo as percentages of total abundance (a) and total species richness (b) of the Hymenoptera superfamilies. *Chalc.* Chalcidoidea, *Ichne.* Ichneumonoidea, *Cynip.* Cynipoidea, *Platy.* Platygastridae, *Cerap.* Ceraphronidae, *Chrys.* Chrysoidea).

(Fig 2), being mostly represented by the Braconidae family both in terms of species richness (80.6%) and abundance (97%). The superfamilies Platygastridae and Cynipoidea accounted for 14% (26 morphospecies) and 5% (10 morphospecies) of the parasitoid species, respectively. However, while Platygastridae represented only 1.2% (184 individuals) of the reared parasitoid individuals, Cynipoidea accounted for 4.8% (732 individuals) of the total abundance of parasitoid wasps. The other two superfamilies (Ceraphronidae and Chrysoidea) were represented by only one species each, which together comprised 31 parasitoid individuals.

About 63% of the parasitoid species were found on three or fewer species of Asteraceae, with a mean number of 5.5 (± 7.7 SD) plant species per parasitoid. The commonness pattern of the parasitoid wasps indicates that the distribution of most species is restricted to a few sites. While 59.9% (136 morphospecies) of the parasitoid species were sampled in three or fewer areas, only 13.7% (31 morphospecies) of the

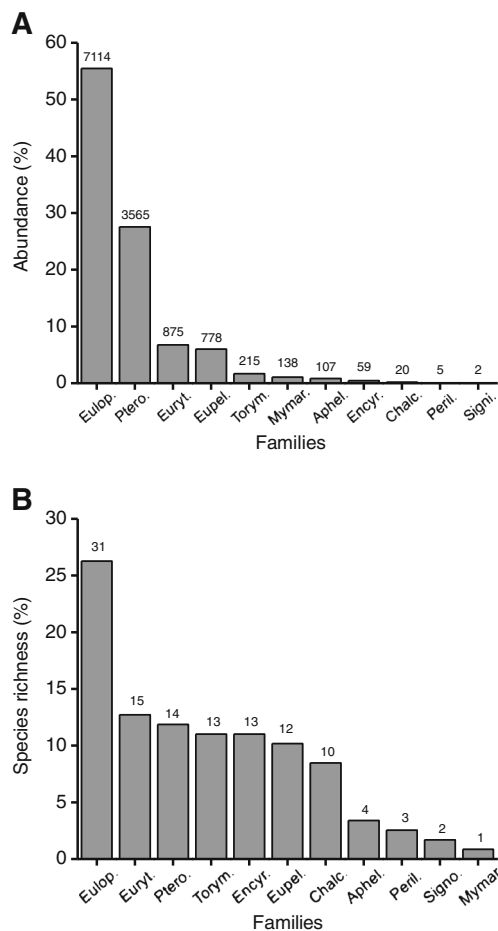


Fig 3 Taxonomic characterization of the chalcidoid wasps reared in Asteraceae flower heads in cerrado remnants in São Paulo as percentages of total abundance (**a**) and total species richness (**b**) of the Chalcidoidea families. *Eulop.* Eulophidae, *Ptero.* Pteromalidae, *Euryt.* Eurytomidae, *Eupel.* Eupelmidae, *Torym.* Torymidae, *Mymar.* Mymaridae, *Aphel.* Aphelinidae, *Encyr.* Encyrtidae, *Chalc.* Chalcididae, *Signi.* Signiphoridae.

parasitoid wasps were recorded in more than half of the sites (Fig 4).

The mean number of parasitoid wasps per plant species was 14.3 (± 16.1 SD), ranging from 1 (in 10 plant species) to 67 (in *Vernonanthura membranacea*) species. The path model explained 89% of the variation in parasitoid species richness among the plant species (Fig 5). Overall, there was a good fit between the model and the observed data ($\chi^2=0.41$, $df=1$, $p=0.520$; CFI=1.000; TLI=1.016; RMSEA<0.001; p value for the test of close fit=0.544). Both herbivore richness and plant commonness had positive direct effects on the number of parasitoid wasps recorded in the plant species. We found that the effect of the plant commonness variable was almost twice as high as the effect of the herbivore richness (standardized regression weights 0.324 and 0.602). Plant commonness also showed positive direct effects on the total weight of a sampled flower head and on the herbivore richness per plant species (Fig 4). Thus, plant commonness

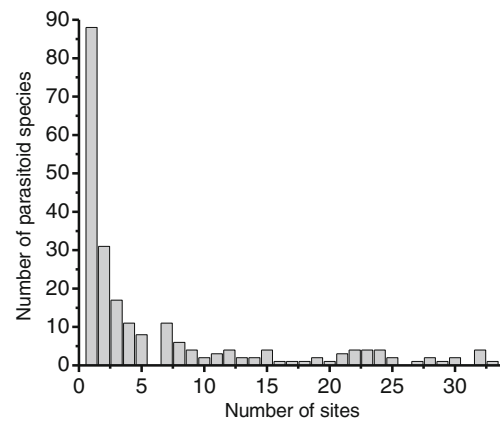


Fig 4 Total incidence of 192 parasitoid species associated with flower heads of Asteraceae in 36 remnants of cerrado in the state of São Paulo, Brazil.

determined the number of parasitoid species associated with each plant species both directly (through the spatial turnover of parasitoids) and indirectly (mediated by the number of herbivore species on each host plant species). Our findings, using only the species recorded during the April–May sampling period, produced qualitatively identical results (Online Resource 3).

Discussion

Taxonomic composition

This is the first extensive survey of Hymenoptera in flower heads of Asteraceae in the Neotropical region. In the last two

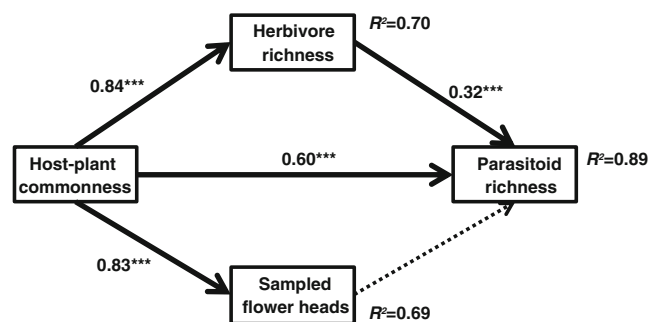


Fig 5 Path analysis model for parasitoid species richness associated with 49 Asteraceae species in cerrado remnants in São Paulo. *Host plant commonness*: number of localities (square-root-transformed) where each Asteraceae species was found. *Sampled flower heads*: total dry weight (log-transformed) of flower head per plant species. *Herbivore richness*: species richness (square-root-transformed) of endophagous herbivores reared in flower heads of Asteraceae. *Parasitoid richness*: species richness (square-root-transformed) of parasitoid wasps reared in flower heads of Asteraceae. R^2 values indicate the proportion of variation explained by the path model. The dotted arrow represents no significant relationship ($***p<0.0001$). See “Methods” for further details.

decades, different ecological and evolutionary aspects of the trophic system consisting of Asteraceae and flower head endophages have been studied in the neotropics (Lewinsohn 1991, Prado & Lewinsohn 2004, Fonseca *et al* 2005, Almeida *et al* 2006, Diniz *et al* 2010, Almeida-Neto *et al* 2011, Perre *et al* 2011). In the present study, we show that there is a rich fauna of parasitoid wasps associated with the flower heads of Asteraceae. The parasitoid fauna associated with Asteraceae flower heads was comprised of insects from six superfamilies, dominated by Chalcidoidea, the largest superfamily of parasitoid wasps in the world, as well as Ichneumonoidea. This dominance by chalcidoid wasps has been found in other guilds of endophagous herbivores in the Brazilian cerrado (Urso-Guimarães *et al* 2003, Araújo *et al* 2011), as well as in other biomes (Rott & Godfray 2000, Valladares & Salvo 2001).

Among the chalcidoid families, Eulophidae was the most speciose, comprising one third of all chalcidoid species. Species from the Eulophidae family were recorded in flower heads of 19 genera of Asteraceae, comprising almost half of the total abundance of parasitoids. According to Araújo *et al* (2011), Eulophidae is the most abundant parasitoid family among galling hosts in the Brazilian cerrado. Eulophids have also proven to be a dominant parasitoid family among leaf miners (Salvo & Valladares 1998, Rott & Godfray 2000, Salvo *et al* 2013). Pteromalidae was the second most representative family of Chalcidoidea, comprising about one quarter of all sampled individuals. Because this family is one of the least-studied taxonomic groups of parasitoids in the neotropics (Fernández & Sharkey 2006), the occurrence of unidentified Pteromalidae genera is common in Neotropical parasitoid assemblages (e.g., Salvo & Valladares 1998, Lewis *et al* 2002, Salvo *et al* 2013).

Ichneumonoidea was the second-largest superfamily recorded in the flower heads of Asteraceae, being largely represented by the Braconidae family. In all, we found 15 subfamilies of Ichneumonoidea (12 Braconidae and 3 Ichneumonidae), indicating that many lineages of this superfamily are able to exploit the rich host fauna in Asteraceae flower heads. The braconids were, indeed, the second-richest family of parasitoid wasps recorded in the flower heads. Through observation of individual flower heads, we noted that many braconids are primary parasitoids, mainly of Tephritidae (Diptera) and microlepidoptera species.

Although not as abundant as other parasitoid groups, the superfamily Platygastroidea placed third in species number (26 morphospecies). Many species of the Platygastriinae subfamily are parasitoids of Cecidomyiidae (Masner 1993), and this is probably the case here because the cecidomyiids are one of the most species-rich families of herbivores associated with flower heads of Asteraceae in the Brazilian cerrado (Almeida-Neto *et al* 2011). However, the genus *Trissolcus* (Scelionidae), the most abundant and species-rich within

Platygastroidea, according to the literature (Johnson 1987), is mostly comprised of parasitoids of Pentatomidae and a few other Heteroptera groups. In addition, many species within the subfamilies Scelioninae, Teleasinae, and Telenominae are egg parasitoids of insects and spiders (Masner 1993). Therefore, we suspect that some Platygastroidea species recorded here are not associated with the typical groups of flower head endophagous herbivores, but instead with external sap-sucking insects and even spiders.

The superfamily Cynipoidea was less speciose than Platygastroidea, but we recorded four times more parasitoids from the former than from the latter. All cynipoid species in flower heads were from the subfamily Eucilinae. According to Buffington & Ronquist (2006), these cynipoids are predominantly larval endoparasitoids of Diptera, attacking mainly Tephritidae, Agromyzidae, Anthomyiidae, and Chloropidae inside live plant tissues. The species *Nordlandiella* aff. *semirufa* (Kieffer) comprises more than one half of all Cynipoidea specimens. Buffington (2004) recorded *N. aff. semirufa* as a parasitoid of *Melanagromyza* spp. Hendel (Diptera: Agromyzidae), species infesting flower heads of *Bidens pilosa* L. and *Bidens* sp.

The superfamilies Ceraphronoidea and Chrysidoidea were especially scarce in our samples, with only one species found in each one and a total of 29 and 2 individuals, respectively. The biology of the Ceraphronoidea is mostly unknown, but among the species with known hosts, there are many hyperparasitoids or primary parasitoids of Cecidomyiidae, Coleoptera, Lepidoptera, and Thysanoptera (Masner 1993, 2006). Thus, it is likely that the *Aphanogmus* sp. recorded in this study is a parasitoid of an herbivore or a parasitoid species associated with the flower heads. The genus of the only Chrysidoidea we found, *Goniozus* sp., is known to be an ectoparasitoid of immature stages of microlepidoptera (e.g., Gelechiidae, Pyralidae, and Tortricidae) (Gordh & Moczar 1990). Therefore, despite the rarity of this species in our samples, it is also likely to belong to the tritrophic system formed by Asteraceae, flower head endophages, and parasitoids.

While a few abundant species from just three families (Eulophidae, Pteromalidae, and Braconidae) made up more than half of the parasitoid individuals in our study, the majority of the parasitoid wasps were represented by only one or two individuals. This highly unequal abundance distribution is common among terrestrial insects in tropical ecosystems (Novotny & Bassett 2000). However, the presence of so many singletons and doubletons raises questions about the role of rare parasitoid species in this tritrophic system. The rare parasitoid species can be either truly specialist species whose hosts are locally rare or generalist parasitoid species that opportunistically parasitize herbivores in flower heads. The occurrence of rare herbivore species in

Asteraceae flower heads does not explain why there were so many rare parasitoid species. The less abundant herbivores are not necessarily attacked by less abundant parasitoids. Only a detailed study of the biological aspects of the parasitoids in flower heads could elucidate the trophic pattern of rare parasitoid species.

Why does parasitoid species richness vary so much among plant species?

At first glance, the answer to this question might be that because parasitoids depend on herbivores, and the more herbivore species are associated with a given plant species, the more parasitoid species will be found on that host plant. Ultimately, this answer would also imply that the predictors of herbivore richness on plants would be basically the same for the parasitoid richness on plants. However, our findings show that the answer is more complex. Using a path model that accounted for the effect of herbivore richness, we found that plant commonness is the main predictor of differences in parasitoid species richness among plant species.

A likely explanation for our findings is that the species composition of parasitoids in Asteraceae flower heads varies greatly from site to site, meaning that plant species accumulate parasitoid species mostly across their geographical range rather than through the average local richness of the herbivore insects associated with them. Plant species occurring in more sites tend to live in more diverse environments. Consequently, if a fraction of the insect species is restricted to certain environmental conditions, the plants will be exposed to different insect faunas of both herbivores and parasitoids.

Our findings thus suggest that the accumulation of parasitoid species on plant species is mainly determined by the regional commonness of the plants rather than the number of herbivore species associated with the plants. Whether the same pattern holds true for other plant-herbivore-parasitoid systems is an open question. Because the magnitude of the among-site heterogeneity will determine the relative importance of local environmental filters to the occurrence of species, we suspect that similar patterns are likely to be found in biomes or regions characterized by high habitat heterogeneity, such as the Brazilian cerrado.

Acknowledgments We are grateful to various colleagues for their valuable help with field work and to Marina R. Braun, Sérgio Vanin, José R. Mermudes, João Semir, Roberto L. Esteves, and Mara Magenta for providing or confirming identification of insects and plants. This study was supported by FAPESP grant no. 98/05085-2 to TML within the BIOTA-FAPESP Program, no. 04/15482-1 to T.M. Lewinsohn, and no. 03/02541-0 and 06/56889-2 to M. Almeida-Neto. A.R. Nascimento was supported by the CAPES Grant. MAN, CRF, TML, and APD received research productivity grants from CNPq.

Electronic Supplementary Material The online version of this article (doi:10.1007/s13744-014-0218-9) contains supplementary material, which is available users.

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