

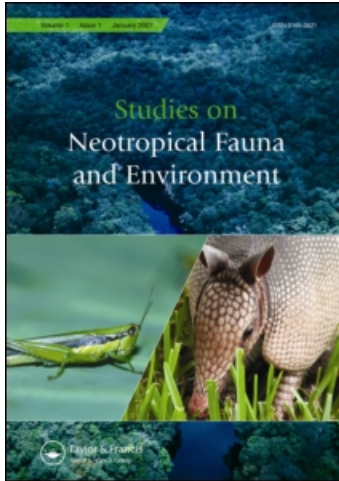
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Adriana Salvo^a; G. R. Valladares^a; L. Cagnolo^a

^a Centro de Investigaciones Entomológicas, Instituto Multidisciplinario de Biología Vegetal, CONICET, Córdoba, Argentina

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ORIGINAL ARTICLE

Parasitic assemblages on leafminers: a comparison of structure and function among host orders

Adriana Salvo*, G. R. Valladares & L. Cagnolo

Centro de Investigaciones Entomológicas, Instituto Multidisciplinario de Biología Vegetal, CONICET, Córdoba, Argentina

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In this study we ask whether parasitic complexes of leafminers display differences associated to host order, by comparing species number, taxonomic composition, parasitism rates and host ranges in parasitoid assemblages associated with lepidopteran and dipteran leafminers, in Chaco Serrano woodlands, central Argentina. Parasitoid assemblage size did not significantly differ between host orders, but dipteran hosts suffered higher parasitism rates. Lepidopteran hosts recruited a higher proportion of species and individuals of Braconidae, whereas dipteran leafminers were attacked by a higher proportion of Pteromalidae. We found clear effects of host taxonomic affiliation on the associated parasitoid fauna.

En este estudio preguntamos si las comunidades de parasitoides de minadores de hojas difieren según el orden del hospedador, analizando número de especies, composición taxonómica, tasas de parasitismo y rango de hospedadores en complejos parasíticos asociados a minadores de hojas de los órdenes Lepidoptera y Diptera en Chaco Serrano, Argentina Central. El tamaño de los complejos no difirió significativamente entre órdenes de hospedadores, pero los dípteros minadores sufrieron porcentajes de parasitismo más elevados. Lepidoptera mostró mayor proporción de especies e individuos de Braconidae, mientras que los dípteros minadores fueron atacados por una mayor proporción de Pteromalidae. Encontramos claros efectos de la afiliación taxonómica del hospedador sobre la fauna de parasitoides asociados.

Keywords: Argentina; Chaco Serrano; host assemblages; host order; parasitoid communities; parasitism

Introduction

Parasitoids are typically insects, mostly found in the orders Hymenoptera and Diptera, that use another insect to rear their own young and kill the host in the process (Godfray 1994). Species in this functional group represent a very important component of many terrestrial ecosystems, displaying a huge biological and ecological diversity (La Salle & Gauld 1991). Since parasitoids eliminate individuals from their host populations, they play a valuable role in maintaining the diversity of natural communities (Quicke 1997) and are frequently used in pest management programs.

Hundreds of species in at least 10 families of Apocrita (Hymenoptera) have evolved the ability to locate and parasitize leafminer larvae (Schauff et al. 1998; Gates et al. 2002). The leaf-mining habit, which consists of living and feeding inside a leaf by chewing tunnels in the mesophyll, has developed in more than 10,000 species of holometabolous insects belonging to 51 families in four orders (Diptera, Coleoptera, Hymenoptera and Lepidoptera) (Connor & Taverner 1997). Several leafminer species are considered important pests of cultivated plants, which they damage

mainly by impairing photosynthetic capacity, inducing early leaf abscission and facilitating the entrance of fungi and bacteria (Spencer 1973; Dempewolf 2004).

More diverse parasitoid assemblages and higher rates of parasitism are found in leafminers than in any other insect feeding niche (Hawkins et al. 1997). The high susceptibility of leafminers to parasitoids is attributed to lack of mobility, coupled with high visibility of the mines and scant physical protection offered by the leaf epidermis (Hawkins 1994). A high ecological homogeneity among leafminers, due to strong selection pressures resulting from feeding within a leaf lamina, is also regarded to increase their vulnerability to parasitoids (Godfray 1994). These features, added to relatively easy sampling and rearing methods, have promoted an array of ecological studies dealing with various aspects of leafminer–parasitoid interactions, from host searching (Dutton et al. 2000, Salvo & Valladares 2004), apparent competition (Memmott et al. 2000) or tritrophic interactions (Pincebourde & Casas 2006; Videla et al. 2006) to community assemblages in foodwebs (Memmott et al. 1994; Lewis et al. 2002; Morris et al. 2004; Hirao & Murakami 2008).

*Corresponding author. Email: asalvo@com.uncor.edu

The taxonomic composition of parasitic assemblages associated with leafminers has also been studied, mainly in the Holarctic and Nearctic regions, and in relation to particular species or groups of species (La Salle & Parrella 1991; Whitfield & Wagner 1991; Schauff et al. 1998; Gates et al. 2002). Some Neotropical assemblages of leafminer parasitoids have been described in the tropics (Memmott et al. 1994; Lewis et al. 2002), with emphasis on their ecological rather than taxonomic structure. Within southern temperate areas, only the parasitic assemblages of Agromyzidae (Diptera) leafminers in central Argentina have been extensively explored in terms of number of species, taxonomic composition and parasitism rates (Salvo 1996; Salvo & Valladares 1998, 1999; Valladares et al. 2001). Most of the parasitoid species involved in such assemblages belong to the families Eulophidae (Chalcidoidea) and Braconidae (Ichneumonoidea) (Salvo & Valladares 1998), several genera of which have radiated specifically on leafminers (Rott & Godfray 2000). Information on parasitoid assemblages on other leafminer groups in central Argentina is practically nonexistent.

Particular features of the leaf mines (Hering 1951), in conjunction with other possible phylogenetic effects, could be expected to determine differences in size, structure and composition of parasitic communities associated to leafminers belonging to different orders. For example, lepidopteran leafminers exhibit the widest variation in mine morphology (Hering 1951) and have also exclusive movement defense strategies against parasitoids (Djemai et al. 2000), both factors probably affecting parasitoid colonization (Salvo & Valladares 2004). However, the possibility of parasitic complexes of leafminers displaying differences related to host order has only marginally been analyzed (Askew 1994; Lewis et al. 2002).

Here, we compare species number, taxonomic composition and parasitism rates of parasitoid assemblages associated with leafminers in two insect orders, from a survey in Chaco Serrano woodland of central Argentina. Furthermore, we ask whether interactions between parasitoids and hosts are affected by their phylogeny, in the form of preferential associations among particular taxonomic groups of hosts and parasitoids, and finally, we compare host ranges and host similarity between the dominant families of parasitoids.

Materials and methods

Study area

We studied leafminers and their parasitoids in Chaco Serrano woodlands within an area (31°10'–31°30'S,

64°00'–64°30'W) located in central Argentina, at an elevation of about 700 m a.s.l. The vegetation of Chaco Serrano is characterized by an open tree stratum up to 15 m high, 1–3 m high shrubs covering 10–80% of the ground, a herbaceous layer (up to 95% cover), and many vines and epiphytes (Cabido et al. 1991). Agricultural and urban development is increasing in the area, and forest species are now restricted to remnants of various sizes (Zak et al. 2004).

Sampling, rearing, identification

In November–December 2002 and February–March 2003, we collected all mined leaves found along 190 transects covering a total area of 19,000 m² (each 50 m long, 2 m wide and 2 m high) in remnants of Chaco Serrano. Given our previous knowledge of leafminer species bionomy in the study region, no biases were expected in the sampled species according to mine apparency (see Salvo & Valladares 2004). Samples were taken within the peak period of leafminer activity (Valladares et al. 2001). Mined leaves were incubated within transparent polyethylene bags in the laboratory, keeping them separately by plant and leafminer species, in order to rear adult leafminers and parasitoids. Special rearing techniques were developed for leaves with high water content or those that rapidly dried once excised. In the former case, either a box covered with gauze was used instead of a bag, or the mined portion of the leaf was cut off from the remaining leaf tissue to reduce the risk of the mine becoming infected with mould fungi. In the second case, either stems with several leaves were collected, thus slowing down desiccation on individual leaves, or humid cotton wool pieces were added to the bags. Adults of both leafminers and parasitoids were stored in glass vials; once emergence had ceased they were counted and identified. All individuals collected were sorted into species or morphospecies by the authors. Reference collections of both leafminers and parasitoids have been deposited in the collection of Catedra de Entomología, Facultad de Ciencias Exactas, Físicas y Naturales (Universidad Nacional de Córdoba, Argentina).

Data analyses

The following variables were calculated for the parasitoid assemblage associated with each leafminer species:

- (1) Parasitoid assemblage size: number of species attacking a host.

- (2) Parasitoid assemblage structure: number of species in Braconidae, Eulophidae and Pteromalidae on the total number of species in each assemblage.
- (3) Parasitism rates: we used apparent parasitism (McAuslane et al. 1993), calculated as total number of parasitoids over total number of adults reared from a particular host species or host order. This method of calculation, even if not providing an accurate evaluation of mortality caused by parasitism, allows comparisons between different groups (Girardo et al. 2007). In order to avoid overestimating the effect of gregarious parasitoids (*Copidosoma* sp.), we calculated the average number of individuals emerging from one host through previous rearings, and then considered that this number of parasitoids represented one parasitoid killing one host, in overall parasitism calculations. A data set restricted to hosts with sample size over 20 adults was used to reduce errors attributable to small samples.
- (4) Relative parasitism rates due to Braconidae, Eulophidae and Pteromalidae, calculated as the number of parasitoids of these families over total number of parasitoids reared from a particular host species.

Means and standard errors were calculated for the parasitoid assemblage size of each leafminer taxon and for host ranges of the parasitoid taxa. Data sets restricted to hosts with sample size ≥ 20 adults, or parasitoid species with sample size ≥ 10 specimens were used in statistical analyses in order to reduce errors attributable to small samples. Moreover, total parasitoid species load per host species and number of hosts attacked by each parasitoid species were corrected by rarefaction.

Parasitoid assemblage sizes of leafminers were estimated at the species and order levels, whereas the host ranges of parasitoid species were assessed at the species, family and order level of their hosts. The relationship between sample size and parasitoid assemblage size of hosts, and also on host ranges of parasitoid species was tested by regression analysis. Although the overall relationships must eventually be asymptotic, the nonlinear models tested did not show a better fit to the data. Parasitoid assemblage size, host ranges and sample sizes were previously log transformed. *Copidosoma* sp. 1 and *Dolichogenidea* sp. 2 were excluded from parasitoid host range calculations because these taxa were difficult to identify and may include more than one species.

The Mann–Whitney *U*-Test was used to compare size, structure and parasitism rates of parasitic complexes between host orders. These analyses were only performed for lepidopteran and dipteran leafminers given the low number of available species in Coleoptera (two) and Hymenoptera (one).

Potential differences in host ranges (as number of species, families or orders of hosts) among Braconidae and Eulophidae were examined with the Mann–Whitney *U*-Test. The specific composition of

Table 1. Hymenoptera reared from leafminers in Chaco Serrano woodlands, central Argentina.

Taxon	Species
Chrysoidea	
Bethylidae	Bethylidae sp.
Chalcidoidea	
Chalcididae	<i>Brachymeria</i> sp. <i>Conura</i> (11 spp.) Chalcididae sp.
Elasmidae	<i>Elasmus</i> sp.
Encyrtidae	<i>Copidosoma</i> sp.
Eulophidae	
Entedontinae	<i>Chrysocharis caribea</i> <i>C. flacilla</i> <i>C. vonones</i> <i>Chrysocharis</i> (8 spp.) <i>Chrysonotomyia</i> (7 spp.) <i>Closterocerus</i> (3 spp.) <i>Closterocerus tricinctus</i> <i>Horismenus</i> (6 spp.) <i>Necremmus</i> sp. <i>Proacrias thysanoides</i> <i>Proacrias xenodice</i>
Eulophinae	<i>Cirrospilus</i> near <i>submedialis</i> <i>Cirrospilus</i> near <i>vittatus</i> <i>Cirrospilus</i> (4 spp.) <i>Diaulinopsis</i> sp. <i>Diglyphus websteri</i> <i>Diglyphus</i> sp. <i>Elachertus</i> (7 spp.) <i>Pnigalio</i> (3 spp.) <i>Sympiesis</i> (3 spp.) <i>Aprostocetus</i> (2 spp.)
Tetrastichinae	Tetrastichinae (9 spp.)
Eupelmidae	<i>Eupelmus</i> (4 spp.)
Eurytomidae	<i>Eurytoma</i> (4 spp.)
Perilampidae	<i>Perilampus</i> sp.
Pteromalidae	
Miscogasterinae	<i>Halticoptera helioponi</i> <i>Halticoptera</i> sp. <i>Mauleus</i> sp. <i>Thinodytes</i> (5 spp.)
Pteromalinae	<i>Heteroschema</i> (2 spp.) <i>Leptomera porus</i> (2 spp.)
Herbertiinae	<i>Herbertia brasiliensis</i>
Unknown subfamily	Pteromalidae (6 spp.)
Trichogrammatidae	Trichogrammatidae (5 spp.)

(Continued)

Table 1. (Continued).

Taxon	Species
Cynipoidea	
Figitidae	
Eucoilinae	<i>Ageseucoela grenadensis</i> <i>Ageseucoela</i> sp. <i>Agrostocynips clavatus</i> <i>Agrostocynips</i> sp. Eucoilinae (2 spp.)
Ichneumonoidea	
Braconidae	
Agathidinae	Agathidinae (11 spp.)
Microgasterinae	<i>Aleiodes</i> sp. <i>Apanteles</i> (2 spp.) <i>Cotesia</i> sp. <i>Diolcogaster</i> sp. <i>Dolichogenidea</i> (2 spp.) <i>Hypomicrogaster</i> sp. <i>Pseudapanteles</i> (3 spp.) <i>Rasivalva</i> sp.
Braconinae	<i>Bracon</i> (7 spp.)
Cheloninae	<i>Chelonus chelonus</i> (3 spp.) <i>C. microchelonus</i> (2 spp.)
Gnaptodontinae	<i>Gnaptodon</i> (3 spp.) <i>Pseudognaptodon</i> (3 spp.)
Hormiinae	<i>Hormius</i> (3 spp.) <i>Monitoriella</i> (3 spp.) Hormiinae (3 spp.)
Meteorinae	<i>Meteorus</i> sp.
Miracinae	<i>Mirax</i> (6 spp.)
Orgilinae	<i>Orgilus</i> (4 spp.)
Opiinae	<i>Phadedrotoma luteoclypealis</i> <i>P. angicypealis</i> <i>P. denticlypealis</i> <i>P. mesoclypealis</i> <i>P. scabriventris</i> <i>Phaedrotoma</i> (16 spp.) <i>Pholetesor</i> sp.
Rogadinae	<i>Polystenidea</i> (2 spp.) <i>Stiropius</i> (7 spp.)
Ichneumonidae	
Campopleginae	Campopleginae (4 spp.)
Cremastinae	Cremastinae (3 spp.)
Diplazontinae	Diplazontinae sp.
Geliinae	Geliinae sp.
Metopiinae	Metopiinae sp.
Pimplinae	Pimplinae sp.
Tersilochinae	Tersilochinae sp. Ichneumonidae (4 spp.)
Proctotrupoidea	
Diapriidae	Diapriidae (2 spp.)

assemblages was analyzed at order level for host assemblages and family level for parasitoid assemblages by using multivariate analysis of variance (MANOVA) and discriminant analysis (both based on Wilks's lambda statistics). These analyses were performed on a data matrix restricted to hosts with sample sizes with ≥ 50 adults and parasitoids with ≥ 20 adults. The variables used were the standardized

abundances of the parasitoid species and host species (previously log transformed).

Results

Leafminer-parasitoid community

Of the 14,100 specimens reared from sampled mined leaves, 9535 were parasitoids. Parasitoids were classified into 237 morphospecies (70% classified at least to the generic level) in 12 families and five superfamilies of Hymenoptera (Table 1). Most species were solitary parasitoids, with the exception of some Encyrtidae (e.g. *Copidosoma* sp.) and Elasmidae. Whereas obligatory hyperparasitism is rare among leafminer parasitoids, facultative hyperparasitoids are rather common (Askew & Shaw 1974), however this was not assessed in this study.

Hosts belonging to 117 species of leafminers in four insect orders, Lepidoptera (63 species in 18 families), Diptera (50 species of Agromyzidae), Coleoptera (three species of Chrysomelidae) and Hymenoptera (one species of Tenthredinidae) were reared from 115 plant species in the study area. Lepidoptera, mainly represented by Gracillariidae (21 species), Gelechiidae and Nepticulidae (10 species each); and Diptera accounted for 48 and 44% of total leafminer species reared, respectively. More information on leafminer assemblages will be provided elsewhere, as it is not the objective of this paper.

Eulophidae and Braconidae were the dominant families in the parasitoid community, together providing 79% of specimens and 71% of species. Braconidae was the most important component in parasitic complexes of lepidopteran leafminers considering both abundance and species richness, whereas parasitic complexes of dipteran and coleopteran leafminers were dominated by eulophids (Figure 1).

Two-thirds of the 188 parasitoid species attacking Lepidoptera were found attacking only this order, whereas less than half of the 61 parasitoid species were associated exclusively with Diptera. Only two species of parasitoids were restricted to coleopteran leafminers from the 29 species recorded on them (Figure 2A).

Parasitoid assemblage size, parasitism rates and taxonomic structure in relation to host order

There was a strong positive relationship between the number of parasitoid species in the assemblages and sample size (number of hosts reared), which was also evident when data were partitioned by host order (Table 2). A relationship between sample size and parasitoid species load was also observed at the host

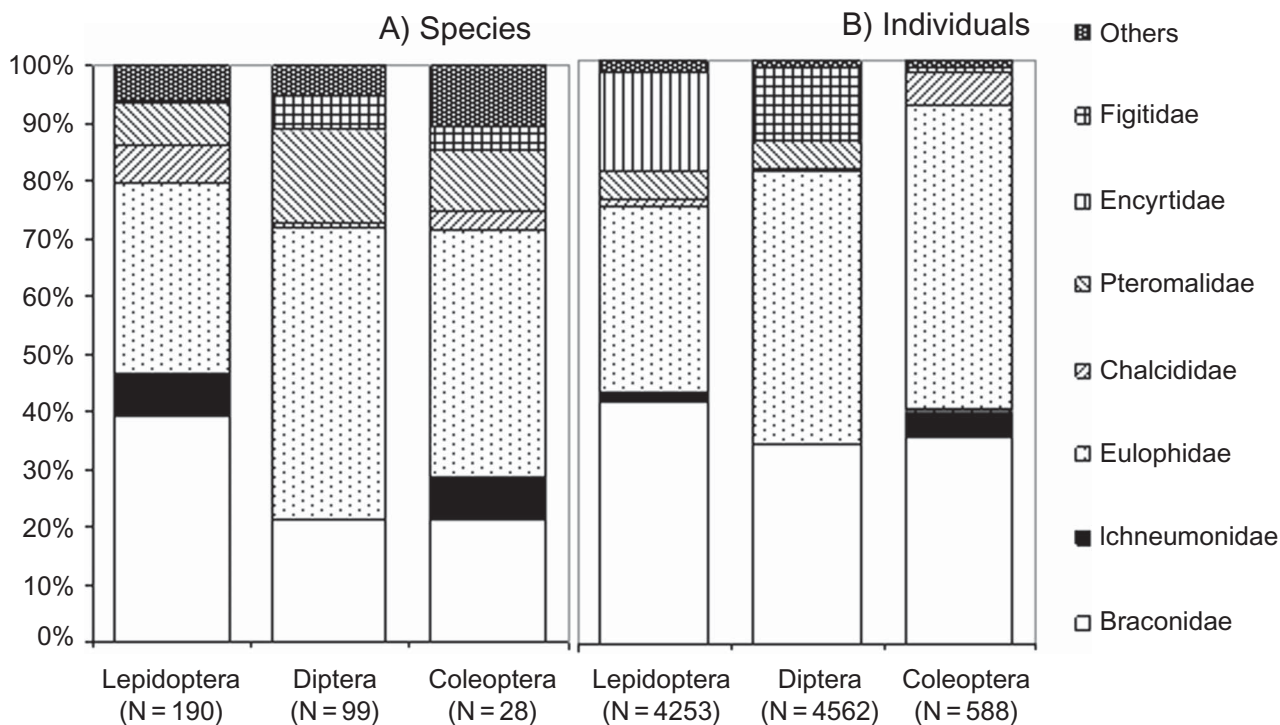


Figure 1. Relative contribution of each family to the total number of hymenopteran parasitoid species (A) and individuals (B) reared from lepidopteran, dipteran and coleopteran leafminers in Chaco Serrano woodlands, central Argentina.

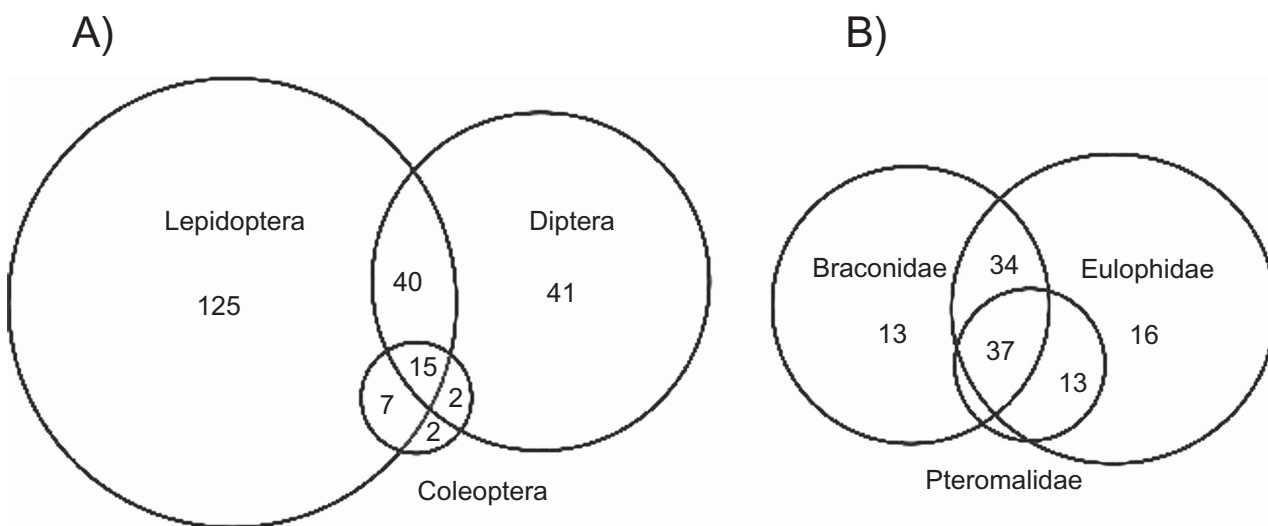


Figure 2. Venn diagrams displaying (A) the number of parasitoid species associated to insect orders that comprise leafminers and (B) the number of host species associated to the main families of hymenopteran parasitoids collected in Chaco Serrano woodlands, central Argentina. The number of species shared between groups is indicated in the area where the circles overlap. Circle size is proportional to the total number of species in each order or family.

family level ($R^2 = 0.87$, $n = 20$, $P < 0.0001$, Model: $\log(y + 1) = 0.202 + 0.505 \times \log(x + 1)$).

All species of leafminers were associated with at least one parasitoid species, up to a maximum parasitic load of 42 species. On average, each host species was

attacked by 10.62 ± 1.09 ($n = 115$) species of parasitoids in the study area.

Total size of parasitic assemblages on Lepidoptera and Diptera leafminers (Figure 3A) did not significantly differ when either observed or estimated

Table 2. Relationship between (A) size of parasitic complex and (B) parasitoid host ranges (total and for each category) with sample size, defined as (A) total adults reared (host + parasitoids) and (B) total parasitoids reared.

	Category	Number of cases	<i>P</i>	<i>R</i> ²	Model
(A) Parasitoid assemblage size	Total	117	<0.0001	0.88	$\log(y + 1) = 0.181 + 0.505 \times \log(x + 1)$
	Lepidoptera	63	<0.0001	0.86	$\log(y + 1) = 0.163 + 0.528 \times \log(x + 1)$
	Diptera	50	<0.0001	0.90	$\log(y + 1) = 0.185 + 0.497 \times \log(x + 1)$
(B) Host ranges	Total	235	<0.0001	0.74	$\log(y + 1) = 0.152 + 0.453 \times \log(x + 1)$
	Braconidae	93	<0.0001	0.73	$\log(y + 1) = 0.172 + 0.387 \times \log(x + 1)$
	Eulophidae	75	<0.0001	0.79	$\log(y + 1) = 0.126 + 0.515 \times \log(x + 1)$
	Pteromalidae	19	<0.0001	0.83	$\log(y + 1) = 0.093 + 0.566 \times \log(x + 1)$

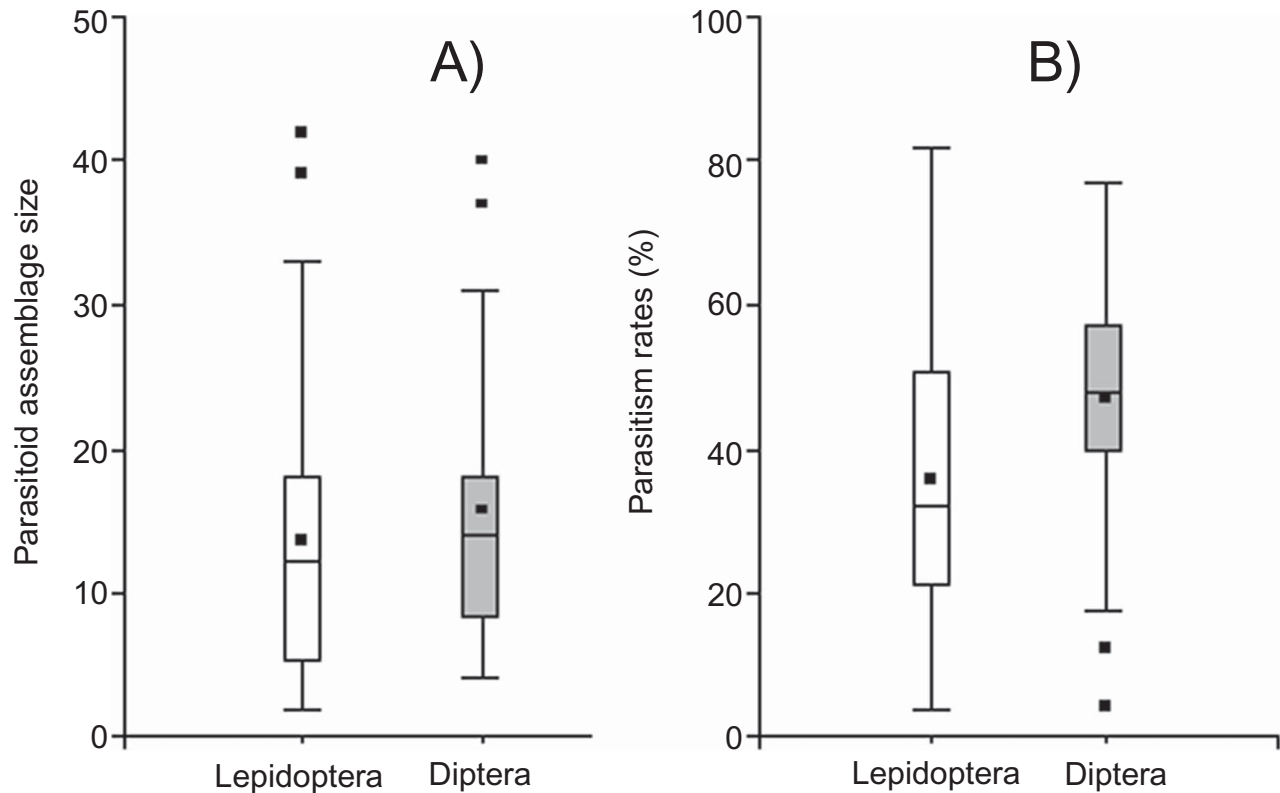


Figure 3. Box plots of the number of species in hymenopteran parasitoid assemblages (A) and parasitism rates (B) for lepidopteran and dipteran leafminers (only hosts with sample size >20 were considered) collected in Chaco Serrano woodlands, central Argentina.

through rarefaction data were used (Mann–Whitney $P > 0.05$). However, a significantly higher proportion of Braconidae species on lepidopterans (Mann–Whitney $W = 762$, $P = 0.02$) and a higher proportion of Pteromalidae on dipterans (Mann–Whitney $W = 208$, $P < 0.0001$) were recorded, whereas no differences were observed regarding the relative proportion of eulophid species richness (Figure 4A).

Leafminers suffered an average parasitism of 40.19% (SE = 2.25, $n = 70$, host restricted data set). Species in Diptera experienced significantly higher mortality by parasitism than those in Lepidoptera (Mann–Whitney $P < 0.01$) (Figure 3B). The relative

parasitism rates due to eulophids were similar for lepidopteran and dipteran leafminers (Mann–Whitney $P > 0.05$), whereas Braconidae and Pteromalidae caused marginally higher parasitism in Lepidoptera and Diptera, respectively (Mann–Whitney Braconidae $W = 734$, $P = 0.04$; Pteromalidae $W = 241$, $P < 0.0001$) (Figure 4B).

Host order had a significant effect on the quantitative specific composition of parasitic assemblages associated with leafminer species (MANOVA Wilks's $\lambda < 0.0001$, $F = 47.36$, $df = 2.74$, $P = 0.008$). The degree of divergence among assemblages was shown by discriminant analysis in which all three

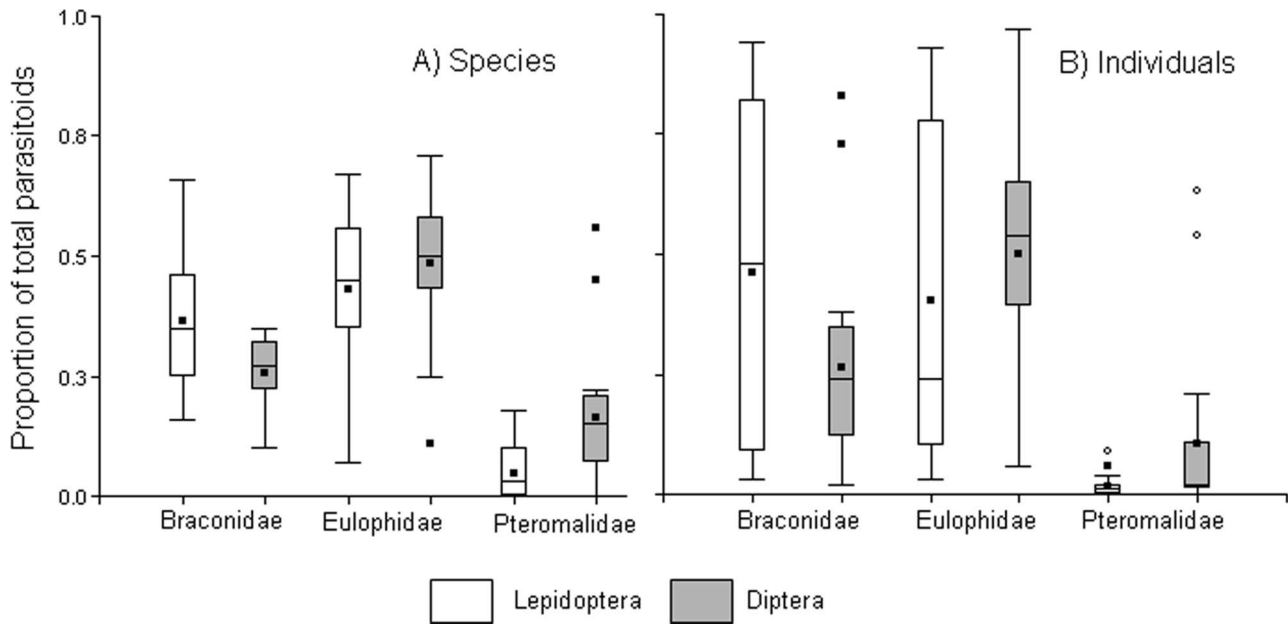


Figure 4. Box plots of the relative contribution of braconids, eulophids and pteromalids to the total number of species (A) and individuals (B) in the parasitic assemblages associated with lepidopteran and dipteran leafminers (only hosts with sample size >20 were considered) collected in Chaco Serrano woodlands, central Argentina.

orders were separated on the first axis (Function 1: Eigenvalue = 113.47, variance explained = 92%, canonical correlation = 0.996, Wilks's λ = 0.0008, χ^2 = 139.80, df = 72, P < 0.00001; Function 2: Eigenvalue = 10.34, variance explained = 8%, canonical correlation = 0.955, Wilks's λ = 0.0882, χ^2 = 47.36, df = 35, P = 0.079) (Figure 5).

Parasitoid host ranges and taxonomic structure of host assemblages

A strong positive relationship between sample size (as number of parasitoids reared) and number of attacked host species was observed for the total parasitoid species (R^2 = 0.74, P < 0.0001, n = 235) and also for the most important families when they were separately considered (Table 2).

On average, parasitoid species in the study area fed on nearly five leafminer species (4.52 ± 0.46 , n = 235). The average host range estimated through rarefaction (samples of 20 adults) was $5.63 (\pm 0.40)$, n = 62). *Chrysocharis vonones* Walker (Eulophidae) displayed the widest host range, with 72 host species in the area, followed by two other eulophids, *Proacrius xenodice* (Walker) and *P. thysanoides* (De Santis), with host ranges of 40 and 33 leafminer species, respectively.

A Venn diagram (Figure 2B) depicts the high overlap of hosts among parasitoids: nearly three-quarters

of the species in each of the main parasitoid families shared hosts with at least another parasitoid family.

Braconid species were more specialized than eulophids (Figure 6). Host ranges of 10 or more species were found in 17% of eulophids but only in 7% of braconids. Also, when the host ranges were estimated through rarefaction for samples of 20 individuals, host ranges of braconids were significantly smaller than those of the eulophids at the species level of host taxonomy (Mann-Whitney W = 611, P < 0.0001).

Parasitoids belonging to the most abundant families (Braconidae, Ichneumonidae, Eulophidae, Pteromalidae and Figitidae) differed in their assemblages of host leafminer species (MANOVA Wilks's λ = 0.0001, F = 2.90, df = 4,50, P < 0.0001) as shown in a scatter plot of Functions 1 and 2 from a discriminant analysis (Function 1: Eigenvalue = 41.48, variance explained = 70%, canonical correlation = 0.988, Wilks's λ = 0.0001, χ^2 = 300.60, df = 160, P < 0.00001; Function 2: Eigenvalue = 10.53, variance explained = 18%, canonical correlation = 0.956, Wilks's λ = 0.004, χ^2 = 178.76, df = 117, P = 0.0002; Function 3: Eigenvalue = 5.24, variance explained = 9%, canonical correlation = 0.916, Wilks's λ = 0.047, χ^2 = 99.28, df = 76, P = 0.04). Pteromalidae species were not grouped with Eulophidae despite belonging to the same superfamily. Instead, their host assemblages appeared closer to those of the more distantly related Braconidae (Figure 7).

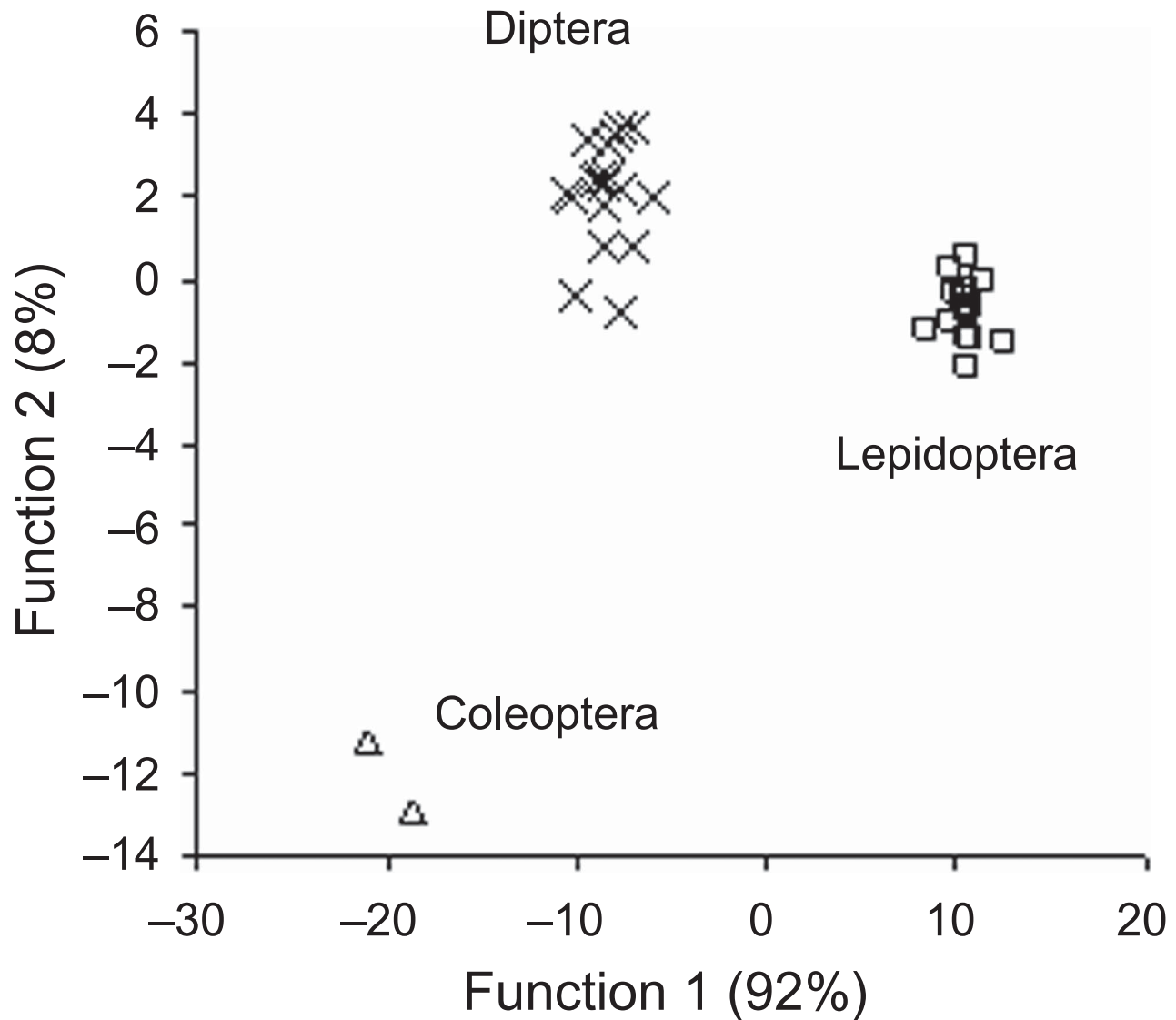


Figure 5. First two functions from a discriminant analysis of parasitic assemblages of 40 leafminer species ($n > 50$) based on order of the host species, using the abundance of well-represented parasitoids ($n > 20$).

Discussion

Parasitoid assemblages of leafminer species in Chaco Serrano at central Argentina were remarkably diverse and on average, each host supported four times more parasitoid species than those in a comparable system in Costa Rica (Memmott et al. 1994). As observed in other studies (e.g. Hawkins 1994; Memmott et al. 1994; Salvo & Valladares 1999; Stireman & Singer 2003), there was a strong relationship between sample size and parasitoid species load, with no evidence of reaching an asymptote. Such a trend suggests that many more host–parasitoid associations could have gone unrecorded.

This study presents the first comparison of parasitoid assemblages on dipteran, lepidopteran and

coleopteran leafminer species in a temperate neotropical system. Braconidae and Eulophidae dominated the parasitic assemblages in this system and in other studies considering either leafminers of Diptera (Askew & Shaw 1986; Kato 1994; Salvo & Valladares 1998), Lepidoptera (Rott & Godfray 2000; Sato et al. 2002; Hirao & Murakami 2008) or mixed communities (Memmott et al. 1994; Gates et al. 2002; Lewis et al. 2002). Thus, the dominance of these families seems to be a characteristic trait of parasitoid assemblages on leafminers, although their relative importance can vary.

It has been proposed that a high ecological homogeneity could have promoted the recruitment of a large number of parasitoid species, all of them with the

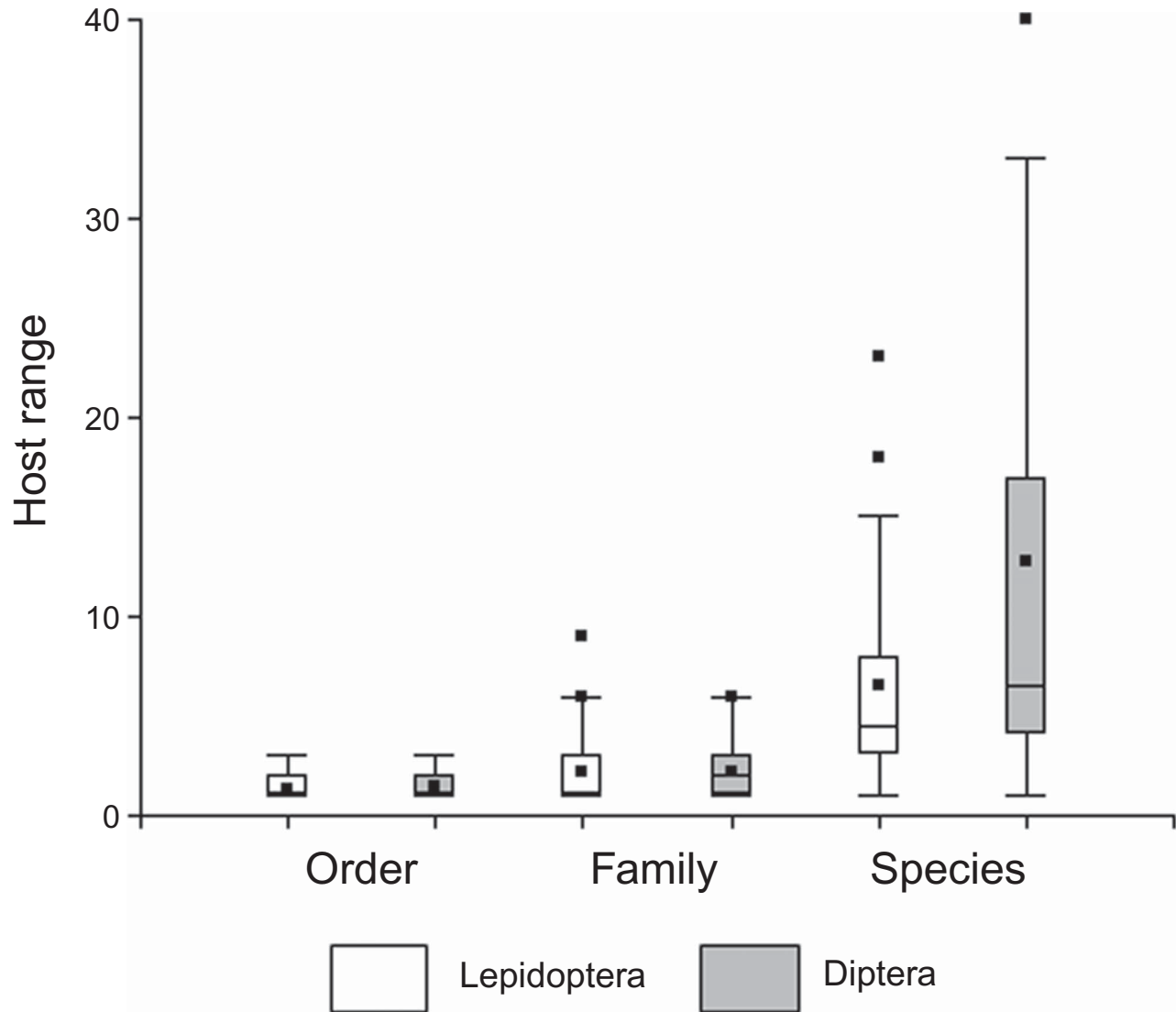


Figure 6. Box plots of host ranges of braconid and eulophid parasitoid species at three levels of host taxonomy (only parasitoid species with sample size > 10).

potential to attack many species in the leafminer guild (Godfray 1994; Memmott et al. 1994). The uniform assemblage size observed here across leafminers in different orders supports this hypothesis, although other mechanisms, such as the poor protection obtained from host plant, highly visible feeding cues and low host mobility could also contribute to the high diversity of parasitoids on leafminers (Hawkins 1994).

Not all parasitoids seem to be indifferent to host taxonomic affiliation: lepidopteran leafminers showed a higher proportion of braconids whereas dipterans had richer assemblages of pteromalids. Several interesting patterns, probably determined by phylogenies of hosts and parasitoids, emerged from these analyses. Dipterans were the only leaf-mining group attacked by Figitidae (Cynipoidea), whereas neither ichneumonids

nor chalcidids were present in their parasitic complexes. Only a few ichneumonid species evolved to parasitize leaf-mining insects and most of them tend to have wide host ranges and may include leaf-mining insects accidentally or very unusually in their diets (Shaw & Askew, 1976). Dipteran leafminers were not attacked by ichneumonids, possibly due to their small size (Hespenheide 1991), which might also be true for chalcidids and polyembryonic encyrtids. The species of the latter taxon found in this study tend to be exclusively associated to lepidopteran leafminers.

Fewer than 7% of parasitoid species were shared among the main three orders of leafminers, and parasitic assemblages associated with species of those orders differed significantly on the basis of relative abundance of common parasitic species. These results

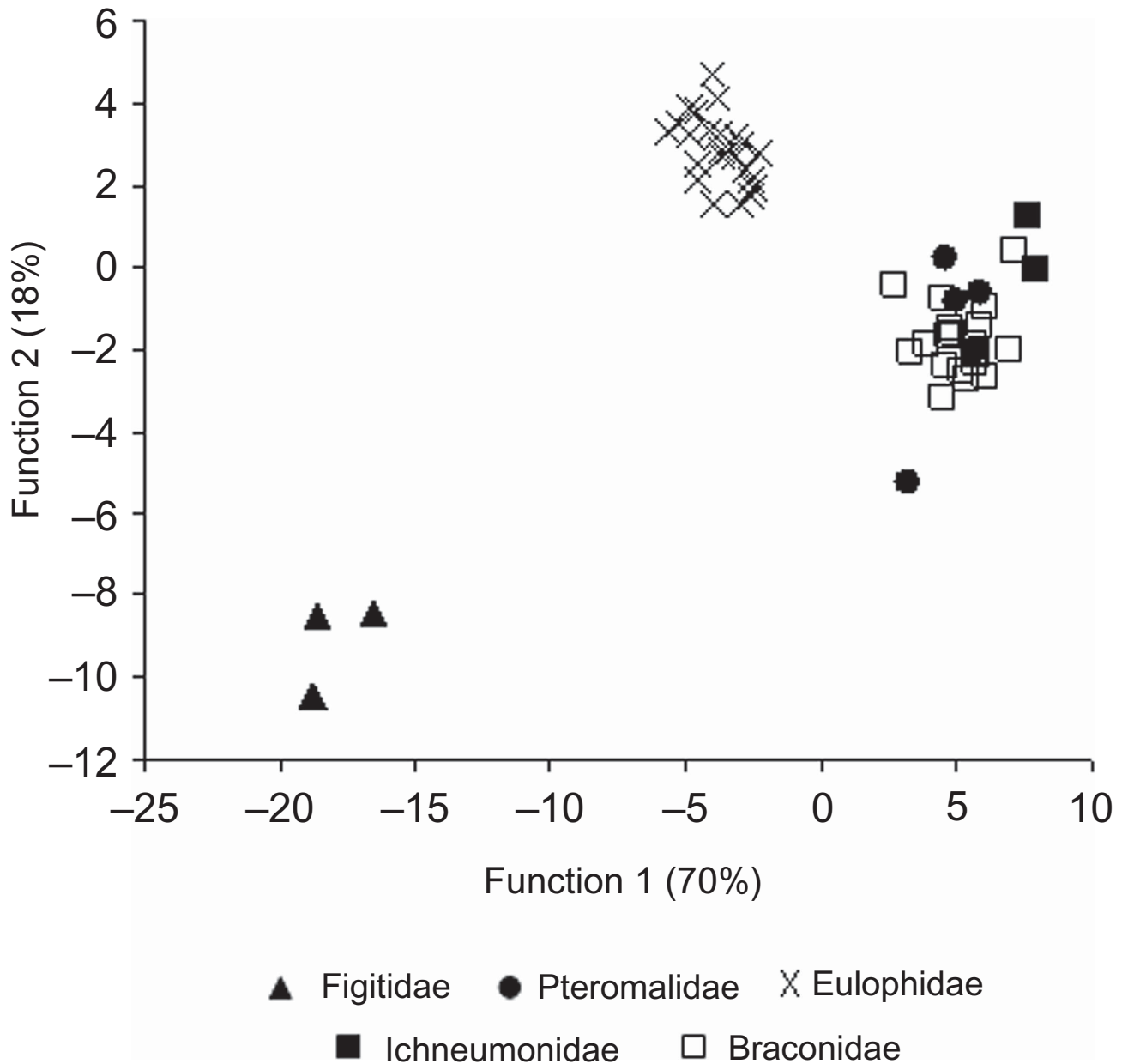


Figure 7. Discriminant analysis of host assemblages for parasitoid species ($n > 20$) based on the identity and abundance of their leafminer hosts ($n > 50$). All species were correctly classified.

suggest that even if parasitoids of leafminers are ecologically specialized (Godfray 1994) and tend to attack a broad range of species within the leafminer feeding guild, host taxonomic affiliation may still have a strong effect on the associated parasitoid fauna.

The parasitism rates observed in this study (nearly 45%) fell within the expected values for the leaf-mining guilds (Askew & Shaw 1979; Cornell & Hawkins 1993; Hawkins 1994; Grabenweger et al. 2005) and were slightly higher than in Costa Rica (38%). According to Hawkins (1994), levels of parasitism are similar in tropical and temperate systems or slightly higher in the

former, despite the fact that for some parasitoid groups diversity is lower and assemblage sizes are smaller in the tropics (Dyer & Coley 2001).

Host species of Diptera suffered significantly higher mortality rates by parasitism than those of Lepidoptera, whereas Coleoptera (albeit with only two species), showed the lowest rate of parasitism. This trend has also been observed in tropical parasitoid–leafminer communities (Memmott et al. 1994; Lewis et al. 2002). Host location strategies may contribute to explain the higher parasitism rates on dipterans observed in our study. The host plant seems to be

the first step in host localization, then the mine and lastly the larvae inside the mine (Sugimoto et al. 1988). Visual clues offered by the mine, such as shape and color, have been shown to affect the taxonomic structure of parasitic assemblages of leaf-mining Agromyzidae (Salvo & Valladares 2004). Once a parasitoid has detected a mine, hosts might deploy escape behaviors reducing the probability of successful parasitization (Dejmai et al. 2000). Escape movements, facilitated by wide voluminous mines, have been recorded for lepidopteran leafminers, particularly in the genus *Phyllonorycter* (Lepidoptera: Gracillariidae) (Meyhofer et al. 1997; Dejmai et al. 2000). With a less mobile foraging behavior within their mines, dipteran leafminers would be more susceptible to parasitoids, which might explain their higher parasitism rates.

Host taxonomy and shared ecology have been mentioned as the main determinants of parasitoid host ranges (Godfray 1994). Most leafminer parasitoids are highly polyphagous, with broad host ranges that include hosts on a variety of food plants (Askew & Shaw 1986; Askew 1994). A few more specific parasitoids can often be found in a stable parasitoid complex among the majority of polyphagous species (Pschorn-Walker & Altenhofer 1989; Askew 1994). These previous findings are fully supported by our data. Parasitoids of leafminers in central Argentina were even more generalists than those in tropical systems (Memmott et al. 1994; Lewis et al. 2002).

In this study, braconid parasitoids showed a higher degree of specialization than those of Eulophidae, at least at the specific level of their hosts. Taxonomic specialization at a variety of levels has been demonstrated for some Dacninae (Braconidae) parasitizing agromyzids (Griffiths 1964). In this group, some parasitoid species attack nearly all hosts in an area whilst others are restricted to single host species (Godfray 1994).

Our results show that even highly polyphagous parasitoids utilize the host resource base differentially, suggesting different host preferences in particular families of parasitoids. The fact that all host assemblages of Eulophidae were similar, as were those of Figitidae, and different from those of parasitoids in other families, suggest phylogenetic constraints on host ranges. On the other hand, the host assemblages of Pteromalidae were most similar to those of Braconidae and Ichneumonidae, instead of the taxonomically closer Eulophidae, suggesting that ecological factors might be also important. Future analysis of host-parasitoid associations based on host ecology could provide further insights on the relative importance of ecology versus phylogeny in these interactions.

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