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ECOLOGY, BEHAVIOR AND BIONOMICS

Assemblages of Endophagous Insects on Asteraceae in São Paulo Cerrados

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A Comunidade de Insetos Endófagos de Asteraceae em Cerrados de São Paulo

RESUMO - No presente estudo foi realizado um levantamento da fauna de insetos endófagos de capítulos de Asteraceae (Compostas), de 2000 a 2002, em oito localidades de cerrados *sensu stricto* no estado de São Paulo. Foram obtidas 64 espécies de endófagos (dípteros e lepidópteros) de 49 espécies de hospedeiras. Aproximadamente metade das espécies foi obtida de apenas uma área, e destas uma grande proporção ocorreu em apenas uma amostra (unicatas). Trinta por cento das espécies foram consideradas "singletons" (apenas um indivíduo foi obtido). A grande quantidade de espécies raras sugere uma forte troca de espécies entre diferentes áreas. Lepidópteros foram registrados em mais espécies hospedeiras que dípteros, confirmando o já observado para o mesmo sistema de insetos e plantas em outros ambientes no Brasil e Europa. As áreas de cerrado *sensu stricto* estudadas no estado de São Paulo encontram-se isoladas, com uma grande parte da fauna de invertebrados composta por muitas espécies raras e exclusivas. Diante deste quadro, sugere-se que a manutenção da biodiversidade de Asteraceae e seus endófagos em seus níveis atuais depende da conservação de todo o conjunto de remanescentes de cerrado do estado.

PALAVRAS-CHAVE: Interação inseto-planta, biodiversidade, Diptera, Lepidoptera

ABSTRACT - A survey of the endophagous insects fauna associated to Asteraceae capitula was carried out from 2000 to 2002 in eight cerrado *sensu stricto* sites located in the Brazilian state of São Paulo. Sixty-four endophagous species of Diptera and Lepidoptera were recorded from 49 asteracean host plants. Approximately half of the species were obtained from a single locality, with a large proportion emerging from a single sample (unicates). Thirty percent of the species were singletons (i.e. only one individual was recorded). The large proportion of rare species suggests a high species turnover among localities. Lepidopteran species were recorded on more host species than dipterans, confirming their more polyphagous food habit, also observed in other Brazilian biomes and in Europe. We conclude that the studied cerrado localities, all within São Paulo State, are isolated with its invertebrate fauna composed of many rare and exclusive species. We suggest that the maintenance of Asteraceae biodiversity and their endophagous insects depend on the conservation of all cerrado remnants in the state.

KEY WORDS: Insect-plant interaction, biodiversity, Diptera, Lepidoptera

About 23% of the Brazilian territory (2 million km²) was originally covered by cerrado vegetation (Ratter *et al.* 1997). Its core area, situated on the Brazilian Central Plateau, is the most preserved and continuous (Ratter *et al.* 1997). In the state of São Paulo there are a number of outlying cerrado areas representing the southernmost

distribution of the biome. In the early 19th century an estimated 14% of its territory was covered with cerrados, but nowadays only 7% of its original cover remains, representing less than one percent of its territory (Kronka *et al.* 1998, Durigan *et al.* 2003).

Efforts have been made to study and describe cerrado

fragments in São Paulo state, mostly inventorying trees, or woody vegetation (e.g., Durigan 2003). Insect ecology in cerrados has not been sufficiently explored and studies tend to be restricted to its core area (e.g., Diniz & Morais 1997, Brown & Gifford 2002, Marquis *et al.* 2002), despite many recent studies in non-core areas (e.g. Ribeiro *et al.* 1998, Urso-Guimarães *et al.* 2003, Fernandes *et al.* 2005). Little is known about the insect fauna in São Paulo cerrados (but see Cytrynowicz 1991, Silveira & Campos 1995, Silva & Bates 2002). The study of insects in cerrado may bring surprises: information obtained so far shows that alternatively to accepted wisdom for vertebrates, the insect fauna in cerrados may be largely characteristic of the biome (MMA/SBF 2002, but see Camargo & Becker 1998).

The study of insect communities is often based on mass-collection methods such as insecticide fogging and light trapping. These methods provide a large number of individuals and species, but yield little or no information on the ecology of these species. It is uncertain which species are genuine members of the community and which are transient. An alternative approach in community ecology is the study of strongly interacting species, through resource-centered inventories, e.g. sampling live insects from host plants (Lewinsohn *et al.* 2001, Novotny *et al.* 2004).

Endophagous insects feed internally on host plants and can be borers, miners, or gall makers, and endophages are especially diverse and frequent in Asteraceae flower heads. Host plants act as microhabitat and food resource to herbivores (Southwood 1973). Surveys of endophagous insects yield more ecological information on the studied species, because once the endophages are sampled (in general as larvae), its trophic link to the host plant is ensured. This protocol provide a novel source of information on the structure of food webs and is very important in obtaining information on important and diversified groups that are not available if other sampling method is used (Lewinsohn *et al.* 2001, Novotny *et al.* 2004).

The present study used a resource-centered protocol to study the endophagous insect communities associated with asteracean flower heads in eight cerrado localities in the state of São Paulo. Flower heads are food resources with high structural diversity and are spatially and temporally fairly predictable. On the other hand, being restricted to a discrete structure, endophagous species face other competitor species and are easy and predictable targets for specialized natural enemies (Zwölfer 1983). From March to June for three years we sampled flower heads from 71 host species, belonging to different tribes (Almeida *et al.* 2005). In total, we found 64 endophagous species belonging to the orders Diptera and Lepidoptera, comprising 252 realized interactions. A high proportion of species was represented by one individual (singleton), and approximately half of the observed species of both hosts and endophages was restricted to a single locality.

In this paper we present a list of the species of flowerhead-feeding insects on cerrado Asteraceae, and an initial analyses on the occurrence and distribution across the studied localities in São Paulo. The following hypotheses were tested: 1. Is the total number of endophagous insect

species positively correlated with local richness of its host community? 2. Is the geographical range of a host plant positively correlated with the size of its associated endophagous assemblage?

Material and Methods

Field sampling and insect rearing. We conducted 23 field trips to sample flower heads from eight remnant cerrado localities in São Paulo state. All sampled areas were covered by cerrado *sensu stricto*, characterized by dense cover of herbs and shrubs, and scattered trees (Oliveira & Marquis 2002). Fieldwork was performed in March to June, 2000 to 2002 (autumn in the Southern hemisphere), the main flowering period of most Asteraceae in cerrados (see Almeida *et al.* 2005 and Fonseca *et al.* 2005, for details of host sampling). In general, each remnant was sampled once a year, although Pedregulho, Martinópolis and Pé de Gigante were not sampled in 2001 (Table 1 in Almeida *et al.* 2005). In Itirapina in the last year, two distinct remnants 13 km apart were sampled. Since we are concerned with larger-scale geographical patterns, these two remnants were grouped as a single locality (Almeida *et al.* 2005).

For the present purpose, one sample is defined as a group of flower heads sampled from a population of one host species, in one remnant, in each sampling period. Only mature flower heads were sampled to rear endophagous adults. In each remnant, we obtained a variable number of samples, up to the total number of flowering Asteraceae species at the time. Some hosts were so rare that they could only be sampled for voucher specimens, and consequently no samples of these species could be obtained to rear herbivores.

In the laboratory, each sample was kept in transparent plastic containers of 500 ml or 1000 ml covered with a fine mesh lid. Samples were kept in the lab for a minimum of two months and were checked every two days for the presence of adult insects. Emerged insects were sedated with CO₂ to facilitate manipulation.

After adult emergence, each sample (one host plant in one locality) dry weight was measured as an approximate measure of sampling effort.

Species identification. All insects were assigned to morphospecies based on their external morphology. Morphospecies were subsequently verified by specialist taxonomists (see acknowledgements) and identified as far as possible. Our morphospecies correspond to species that have often been matched to named species and are the subject of further taxonomic research. Voucher specimens are deposited in the "Museu de História Natural da Unicamp" (MZUEC, Campinas, Brazil). Approximately half of the obtained species could be assigned to named species (28 species, 44%).

A high proportion of the morphospecies is probably of undescribed species. One example is the family Tephritidae (Diptera) in which several species have been described (e.g., Prado *et al.* 2004, Abreu *et al.* 2005) and others await description from our material (Allen Norrbom, personal

Table 1. List of sampled localities with their geographical location, the species richness of Asteraceae in flower and of endophagous insects, and the TSS = total sample size (total flower-head dry weight) for the locality.

Locality code	Locality	County	Latitude	Longitude	S _{Hosts}	S _{Endophages}	TSS(g)
AGD	Reserva Ambiental da AMBEV	Agudos	22°28'20"S	48°53'49"W	30	26	569.53
ASB	Estação Ecológica de Águas de Santa Bárbara	Águas de Santa Bárbara	22°49'37"S	49°13'42"W	38	28	930.37
ASSIS	Estação Ecológica de Assis	Assis	22°35'58"S	50°22'17"W	25	19	710.26
ITI	Estação Experimental de Itirapina	Itirapina	22°13'22"S	47°55'11"W	42	42	1729.90
	Itirapina (Area 1)	Itirapina	22°15'58"S	47°47'49"W			
MART	Reserva Ambiental do Assentamento Nova Vida	Martinópolis	22°15'43"S	51°7'05"W	27	12	235.83
MOJ	Reserva Biológica de Moji-Guaçu	Mogi-Guaçu	22°15'22"S	47°10'43"W	23	20	990.71
PED	Particular Property	Pedregulho	20°14'21"S	47°23'50"W	36	23	797.55
SRP4	Gleba Pé-de-Gigante, Parque Estadual de Vassununga	Santa Rita do Passa-Quatro	21°38'34"S	47°38'35"W	10	14	379.44

communication). In every insect family, however, some groups show identification problems: (1) *Xanthaciura* sp.n.01 is undescribed and at present would be considered a morph of *Xanthaciura chrysur* S.G. Thomson (Allen Norrbom, pers. comm.); there are however some subtle differences in the puparium and adult external characters that will probably enable this morph to be described as a new species. (2) All agromyzids were aggregated as a single entity of *Melanagromyza* because species differentiation in this genus is based only on male genitalia, except for the individuals obtained in Mogi Guaçu, which were identified as *Melanagromyza minimoides* Spencer. (3) The microlepidopterans also have identification problems; the taxonomy of the genera and species groups represented on Asteraceae is based on small and scattered series of specimens, lacking almost any biological and host information. This group is comprised of small and fragile species that usually lose wing characters still in the sample container, hindering even more their identification. (4) The family Cecidomyiidae (Diptera) was excluded from the species list due to the difficulty in identifying species based only on adult characters; reliable identification in most important genera requires series of matched adults and immature stages, which are impossible to ensure with our rearing methods. Cecidomyiidae in flower heads can live freely or in floret-tube galls, and some are known to be predators of other larvae. The herbivorous species may present a high diversity, and some species are known to have a high potential impact on their hosts' populations and have been evaluated as potential biological control

agents (e.g., Hinz 1998).

Data analyses. We performed path analyses to evaluate the importance of different variables in determining endophagous species richness per locality and per host species. Path analysis is a statistical analysis technique used primarily to test the fit of data to an a priori causal hypothesis about the functioning of a system (McIntire 2004). This analysis is a generalized form of multiple regression, where the causal model is tested for consistency with the correlation structure among variables (Lewinsohn 1991, Wilkinson *et al.* 1996). To analyze local endophagous species richness we tested the effects of Asteraceae richness (potential hosts) and of the total flower head dry weight collected in each locality (a proxy of aggregate sampling effort). An additional analysis was performed to test a causal model for endophage richness on each plant species. Variables tested were the total sample dry weight and the number of localities where that host occurs (as a rough estimate of geographical distribution within the state). In both analyses, flower head dry weight was used as an estimate of sampling effort, but it is also directly affected by flower head availability in the field (Fonseca *et al.* 2005).

Results and Discussion

Occurrence and distribution along sampled localities. In all we recorded 89 Asteraceae species in the São Paulo cerrado remnants (Almeida *et al.* 2005). In total, we collected

358 flower head samples from 71 Asteraceae species throughout the three years of study (not all species could be sampled for rearing adult insects, see methods). The year with most samples was 2002 with 151 samples, followed by 136 samples in 2000 and 71 samples in 2001 (Almeida *et al.* 2005)

We identified 64 endophagous insect species or morphospecies from 229 samples from 49 host plants. No endophagous emerged from 129 samples from 22 plant species (32% of species). Itirapina had the highest species richness, with 42 species, whereas Martinópolis presented the lowest richness with 12 species (Table 1). Itirapina, where two remnants were sampled in 2001, was the locality with highest plant richness and total sample volume (Table 1).

Forty endophagous species of Diptera (Tephritidae and Agromyzidae; Table 2) and 24 of Lepidoptera (Blastobasidae, Gelechiidae, Pterophoridae, Pyralidae, Tortricidae, Geometridae and Lycaenidae; Table 3) were reared from flower heads. Among dipterans, only *X. chrysur* and *Melanagromyza* spp. occurred in all sampled localities, and three other species occurred in seven localities (*Xanthaciura* sp.n.01, absent only from Martinópolis, and *Neomyopites paulensis* Steyskal and *Cecidochares connexa* Macquart absent from Pedregulho, Table 2). Among lepidopterans, *Adaina bipunctata* Möschler and *Phalonidia squalida* Raz. & Becker emerged from samples from all localities, and *Lioptilodes parvus* Walsingham was absent only in Pé de Gigante and *Unadilla erronella* Zeller was absent only in Assis (Table 3).

As already noted and described from Asteraceae host plants (Almeida *et al.* 2005), a high proportion of endophagous insects was restricted to one locality (45% of Diptera and 46% of Lepidoptera species; Fig. 1). All dipteran species restricted to one locality emerged from a single sample (unicates), except for *M. minimoides*, which is recorded only in Mogi Guaçu, because till now was only identified to species from this locality (see Methods). One study in progress (Marina R. Braun, unpublished data) found that *M. minimoides* presents a broad geographical distribution. Among lepidopterans, species that occurred in one locality were also obtained from a single sample (unicates), with only one exception (Table 3).

Singletons. Thirty percent of the species were singletons, that is, represented by only one individual. We found proportionally more singletons among the Lepidoptera (10 species, 41.6%) than among the Diptera (9 species, 22.5%). Seven species (all Tephritids) were unicates (occurring in one sample) but not singletons (Table 2).

The occurrence of a great proportion of singletons is usually cited for herbivorous insects in tropical regions (Robinson & Tuck 1993, Novotny & Basset 2000), including previous studies in cerrados (Price *et al.* 1995, Diniz & Morais 1997). Diniz & Morais (1997) studied caterpillars from three host plant species in four cerrado *sensu stricto* areas in central Brazil. They reared 107 lepidopteran species, of which 46% were singletons. The authors conclude that Lepidoptera species in cerrados have a high incidence of rare species. Price *et al.* (1995) studied Lepidoptera larvae in three

congeneric host plants in a cerrado near Brasília, and also found a high richness of rare species.

Novotny & Basset (2000) made an exhaustive survey of herbivorous insects associated with 30 species of trees and shrubs in New Guinea and found that 30% of the insect species were represented by singletons. The average proportion of singleton herbivores per plant species was 45%, while an average of 8% were unique singletons (i.e., that did not occur on other hosts). They observed that a species could be a singleton in a particular host whilst being more common on other, often related, host species, or even relatively rare on numerous other host plants, so that its aggregate population was high. They hypothesized that the large number of singletons is due to the mass effect of Shmida & Wilson (1985). According to this effect, singleton species occur in “marginal” host plants, with its populations maintained by a constant influx of immigrants from the “main” host plants.

The tephritids studied here are usually restricted to one or few tribes within Asteraceae (Prado *et al.* 2002). We have also no information of our endophagous microlepidoptera species, but it is very unlikely that they would be able to use resources from families other than Asteraceae. The present study sampled flower heads from all asteracean flowering species that could be found in the area, so all known potential hosts were represented in our sample and the “mass effect” hypothesis among Asteraceae host plants is less likely to apply.

Host specificity is one of the most relevant traits influencing species rarity, since the patterns of host use determine the abundance and dynamics of resources available to herbivorous species (Novotny & Basset 2000). Nonetheless, Diniz & Morais (1997) found no relation between lepidopteran species frequency and abundance or specialization: the most frequent species can be either restricted to one plant genus or be generalist.

Abundance and specialization. *X. chrysur* was the most abundant species with 2,585 reared individuals, followed by *Xanthaciura* sp.n.01 with 1,760 individuals, *Tetreauresta obscuriventris* Loew, with 782 individuals and *Melanagromyza* spp. with 505 individuals (Table 2). The most abundant Lepidoptera species was *U. erronella* with 125 individuals (Table 3).

More frequent endophagous species (i.e., that occurred in more samples) were also more abundant, both for Diptera (freq = 0.037 inds + 4.962; $r^2 = 0.73$; $F_{1,38} = 102.0$; $P < 0.001$; $n = 40$) and Lepidoptera (freq = 0.271 inds + 1.956; $F_{1,22} = 87.1$; $r^2 = 0.80$; $P < 0.001$; $n = 24$). Diniz & Morais (1997) found no such relationship between abundance and frequency in a local survey of cerrado leaf-feeding caterpillars.

Host plant number explained 57% of dipteran log-transformed abundance per species (loginds = 0.15 nhosts + 0.66; $F_{1,38} = 51.7$; $r^2 = 0.57$; $P < 0.001$; Fig. 2). Lepidoptera showed a similar pattern – species recorded on more hosts were most abundant (loginds = 0.09 nhosts + 0.46; $F_{1,22} = 45.8$; $r^2 = 0.68$; $P < 0.001$; Fig. 2), although the slope was significantly shallower (analysis of covariance,

Table 2. Endophagous Diptera reared from Asteraceae capitula sampled in eight cerrado areas in São Paulo. We present species occurrence per locality and total number of localities, samples, individuals and hosts for each species. See Table 1 for locality codes. Family codes are AG – Agromyzidae and TEP – Tephritidae.

Family	Species	ASB	AGD	ASSIS	ITI	MART	MOJ	PED	SRP4	Localities	Samples	Individuals	Hosts
AG	<i>Melanagromyza minimoides</i> Spencer						x			1	6	62	6
AG	<i>Melanagromyza</i> spp.	x	x	x	x	x	x	x	x	8	71	505	21
TEP	<i>Caenoriata pertinax</i> Bates			x	x		x			3	3	3	1
TEP	<i>Cecidochares connexa</i> Macquart	x	x	x	x	x	x		x	7	34	89	6
TEP	<i>Cecidochares fluminensis</i> Lima	x	x	x	x		x			5	14	40	4
TEP	<i>Cecidochares</i> sp.n.e	x	x		x			x		4	22	219	9
TEP	<i>Dictyotrypeta</i> sp.06	x			x					2	2	3	2
TEP	<i>Dictyotrypeta</i> sp.24				x					1	1	3	1
TEP	<i>Dioxyna</i> cf. <i>thomae</i>				x					1	1	12	1
TEP	<i>Dyseuaresta</i> sp.n.	x								1	1	1	1
TEP	<i>Dyseuaresta</i> sp.b						x			1	1	1	1
TEP	<i>Euarestoides</i> sp.01						x			1	1	1	1
TEP	<i>Euarestoides</i> sp.05				x					1	1	4	1
TEP	<i>Neomyopites paulensis</i> Steyskal	x	x	x	x	x	x		x	7	31	139	7
TEP	<i>Tetreuaresta obscuriventris</i> Loew	x			x			x		3	4	782	4
TEP	<i>Tetreuaresta</i> sp.b		x		x					2	2	3	2
TEP	<i>Tomoplagia achromoptera</i> Prado Norrbon & Lewinsohn			x	x		x	x	x	5	7	45	2
TEP	<i>Tomoplagia</i> aff. <i>heringi</i>				x					1	1	2	1
TEP	<i>Tomoplagia</i> aff. <i>fiebrigi</i>		x							1	1	1	1
TEP	<i>Tomoplagia costalimai</i> Aczel				x					1	1	4	1
TEP	<i>Tomoplagia formosa</i> Aczel			x						1	1	1	1
TEP	<i>Tomoplagia incompleta</i> Williston	x			x			x		3	4	4	4
TEP	<i>Tomoplagia minuta</i> Hering							x		1	1	4	1
TEP	<i>Tomoplagia reimoseri</i> Hendel				x	x		x		3	3	108	2
TEP	<i>Tomoplagia</i> n.i.		x							1	1	1	1
TEP	<i>Tomoplagia</i> sp.01	x	x	x	x		x			5	9	102	1
TEP	<i>Tomoplagia</i> sp.03	x	x							2	2	5	1
TEP	<i>Tomoplagia</i> sp.05				x					1	1	1	1
TEP	<i>Tomoplagia trivittata</i> Lutz & Lima				x				x	2	2	3	1
TEP	<i>Trupanea</i> sp.02				x					1	1	1	1
TEP	<i>Trupanea</i> sp.10	x	x		x	x	x	x		6	13	40	6
TEP	<i>Trupanea</i> sp.11				x					1	2	13	2
TEP	<i>Trypanaresta</i> aff. <i>imitatrix</i>				x					1	1	1	1
TEP	<i>Trypanaresta</i> sp.14				x					1	1	16	1
TEP	<i>Xanthaciura</i> sp.n.01	x	x	x	x		x	x	x	7	67	1760	10
TEP	<i>Xanthaciura biocellata</i> S.G.Thomson	x			x		x	x	x	5	19	48	10
TEP	<i>Xanthaciura chrysur</i> S.G.Thomson	x	x	x	x	x	x	x	x	8	100	2585	15
TEP	<i>Xanthaciura insecta</i> H.Loew				x			x		2	4	15	2
TEP	<i>Xanthaciura mallochi</i> Aczel	x			x		x			3	5	14	2
TEP	<i>Xanthaciura quadrisetosa</i> F. Hendel	x	x							2	3	8	2

Table 3. Endophagous Lepidoptera reared from Asteraceae capitula sampled in eight cerrado areas in São Paulo. We present species occurrence per locality and total number of localities, samples, individuals and hosts for each species. See Table 1 for locality codes. Family codes are BLAST – Blastobasidae, GEL – Gelechiidae, GEO – Geometridae, LYC – Lycaenidae, PTER – Pterophoridae, PYR – Pyralidae and TORT – Tortricidae.

Family	Species	ASB	AGD	ASSIS	ITI	MART	MOJ	PED	SRP4	Localities	Samples	Individuals	Hosts
BLAST	<i>Blastobasidae</i> sp.01			x	x					2	5	6	5
BLAST	<i>Blastobasidae</i> sp.03		x			x		x		3	5	25	5
BLAST	<i>Blastobasidae</i> sp.04		x	x		x				3	7	12	7
BLAST	<i>Blastobasidae</i> sp.06				x					1	1	1	1
GEL	<i>Recurvaria</i> sp.01	x	x	x	x		x	x		6	17	28	9
GEL	<i>Recurvaria</i> sp.02		x					x	x	3	5	6	4
GEO	<i>Eupithecia</i> sp.01				x					1	1	1	1
GEO	<i>Eupithecia</i> sp.02								x	1	1	1	1
GEO	<i>Eupithecia</i> sp.03				x					1	1	1	1
GEO	<i>Eupithecia</i> sp.07	x								1	1	1	1
GEO	<i>Synchlora rufilineata</i> Warr.	x								1	1	1	1
LYC	<i>Lycaenidae</i> sp.09	x								1	1	1	1
LYC	<i>Lycaenidae</i> sp.10							x		1	1	1	1
PTER	<i>Adaina bipunctata</i> Möschler	x	x	x	x	x	x	x	x	8	22	34	11
PTER	<i>Adaina fuscahodias</i> Möschler	x	x							2	2	18	1
PTER	<i>Lioptilodes parvus</i> Walsingham	x	x	x	x	x	x	x		7	16	99	7
PYR	<i>Phycitinae</i> sp.05		x							1	2	6	2
PYR	<i>Unadilla erronella</i> Zeller	x	x		x	x	x	x	x	8	39	125	24
TORT	<i>Cochylini</i> sp.15		x		x			x		3	5	13	4
TORT	<i>Cochylis cf. sagittigera</i>			x	x			x		3	7	13	6
TORT	<i>Epinotia</i> sp.								x	1	1	1	1
TORT	<i>Phalonidia squalida</i> Raz. & Becker	x	x	x	x	x	x	x	x	8	27	69	14
TORT	<i>Phalonidia unguifera</i> Raz. & Becker	x	x		x			x		4	6	8	6
TORT	<i>Platphalonidia fusifera</i> Meyrick	x								1	1	1	1

test for homogeneity of slopes, $F_{1,60} = 5.58$; $P = 0.02$). Lepidoptera larvae require several flower heads to complete their development, while more than one dipteran individual can develop in a single flower head (Almeida 1997, Almeida *et al.* unpublished). Moreover, the frequency of Diptera in flower heads is higher than of Lepidoptera (Almeida *et al.* unpublished). These two observations explain at least in part why more dipteran individuals are obtained than lepidopterans.

Only eight percent (252) of the 3,136 possible interactions between 49 host and 64 endophagous species were recorded. The three most frequently observed interactions were *X. chrysur* with *Chromolaena*

pedunculosa (Hook & Arn.) K&R (28 records), *Xanthaciura* sp.n.01 with *C. pedunculosa* (19), and *X. chrysur* with *Chromolaena squalida* (DC.) K&R (15). Among lepidopterans, the most frequent interaction occurred between *Lioptilodes parvus* (Pterophoridae) and *Baccharis dracunculifolia* DC. (9 records). The community was dominated by rare interactions that were recorded once, and represented 65.5% of the total (Fig. 3).

The number of samples from which each herbivore species emerged was a good predictor of its number of host plants. Interestingly, among lepidopterans the increase in host plants with sample number is steeper ($y = 0.54x + 0.86$;

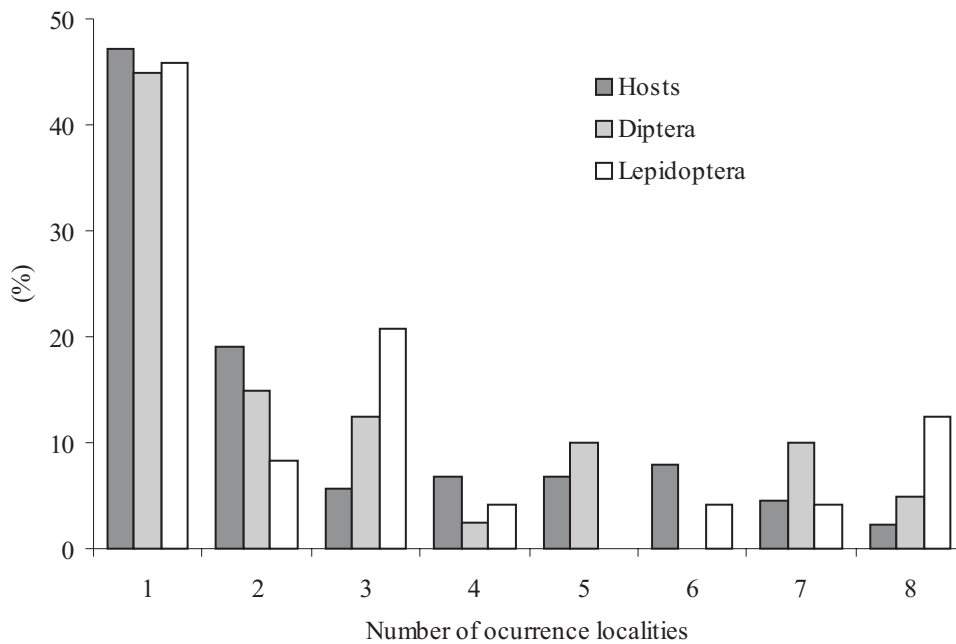


Figure 1. Proportion of species of Asteraceae and endophagous Diptera and Lepidoptera in flower heads according to the number of sampled cerrado localities in São Paulo.

$F_{1,22} = 414.1$; $r^2 = 0.95$; $P < 0.001$; $n = 24$) than among dipterans ($y = 0.18x + 1.48$; $F_{1,38} = 138.4$; $r^2 = 0.78$; $P < 0.001$; $n = 40$; Fig. 4); the difference among slopes is significant (covariance test for slope homogeneity, $F_{1,60} = 82.3$; $P < 0.001$). This means that each new sample is more

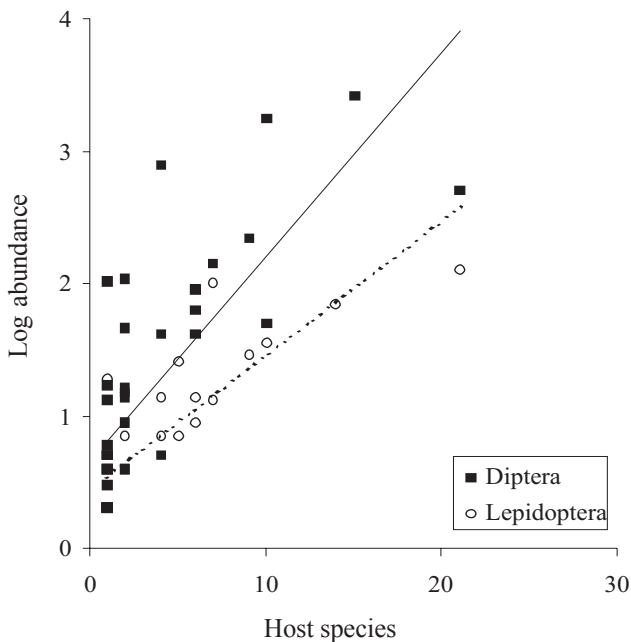


Figure 2. Log-transformed abundance of endophagous individuals per species, according to the number of their host plants. Diptera - closed squares and continuous line; Lepidoptera - open circles and pointed line. See text for regressions.

prone to reveal an additional host for a lepidopteran than for a dipteran species.

As noted above, endophagous dipterans are more specialized than lepidopterans, both in Brazil and in Europe. In the Mantiqueira Range, southeast Brazil, dipterans are associated to fewer host species than lepidopterans (Almeida 2001 Almeida *et al.* unpublished). An analysis of the main endophagous Tephritidae in Brazil revealed that 80% of species are oligophagous, found in host plants belonging to one genus or to related genera (Prado *et al.* 2002). In Europe, endophagous dipterans in Cynaroideae flower heads have a maximum host range of two genera, a quite high degree of specialization (Frenzel & Brandl 2000).

High specialization increases the risk of coextinctions in communities. When a host species is removed from its habitat, some associated species may become extinct, and this effect is more evident among specialists (Koh *et al.* 2004). This is a relevant concern for cerrado areas in São Paulo, which are already quite reduced (in area and number of remnants) and subject to major disturbances.

Factors influencing endophagous richness. We performed a path analysis in order to investigate whether local insect richness is affected by local host plant richness and by the total flowerhead sample size per locality (Fig. 5). The analysis revealed that total sample size had a significant direct effect on determining the number of endophagous species recorded per locality. The total effect of plant richness on insect richness (i.e., their correlation coefficient) is significant; however, each of its components – neither the direct path, nor the indirect one by way of its effect on sample size – is not significant by itself.

A second path analysis evaluated differences in

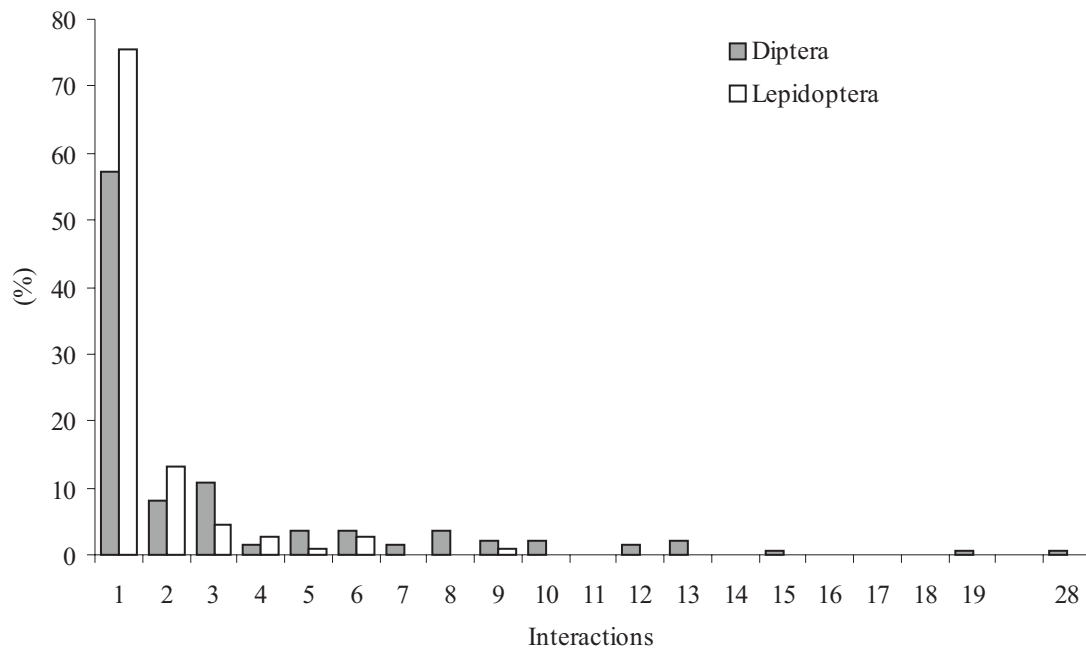


Figure 3. Proportion of interactions among endophagous Diptera and Lepidoptera and their host plants in cerrado remnants in São Paulo, according to their frequency. Note that two thirds of the interactions were observed only once.

endophaga insect richness recorded on each host plant, rather than in each locality as in the preceding analysis. Potential factors included in this analysis were the number of localities, and the total sample size (i.e., flowerhead volume) for each host species. This analysis revealed that the sample size of flower heads was as important as the hosts' geographical spread within São Paulo cerrados in determining the size of

their associated faunas (Fig. 6); however, since total sample size was highly correlated with geographical range, range can be identified as a prime factor in setting total endophagous species richness (i.e., insect gamma diversity)

Determinants of endophagous richness per locality

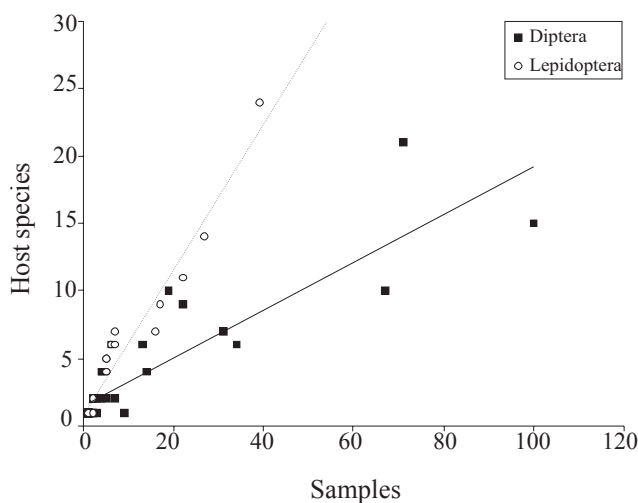


Figure 4. Number of host plants and number of samples in which each endophagous species was recorded. Diptera - closed squares and continuous line; Lepidoptera - open circles and pointed line. See text for regressions.

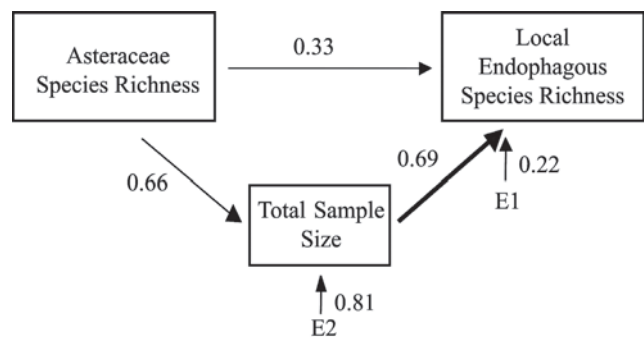


Figure 5. Path analysis model for endophaga richness in eight cerrado localities in São Paulo. Variables are: Asteraceae Species Richness in each locality; Total Sample Size = total flower head dry weight (a measure of sampling effort) obtained in each locality. A path model sets a priori causal effects, or correlations, among all included variables. The arrows indicate direction of influence from causal to response variables; numbers are path coefficients, which range from zero to one. Arrows in bold are significant direct paths ($P < 0.05$). E1 and E2 are the fraction of variance of each response variable that is not explained by the causal paths. N (number of localities) = 8. See Methods for more details.

Determinants of endophagous richness per host plant

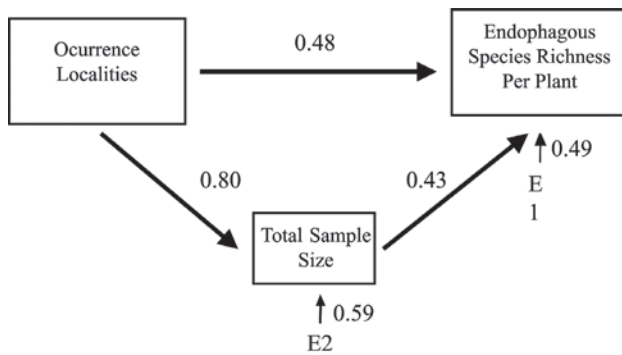


Figure 6. Path analysis model for endophagous richness host plants in cerrado *sensu stricto* in São Paulo. Variables are: Occurrence Localities = number of localities where each species was found (a measure of its geographical range); Total Sample Size = total flower head dry weight per host plant species (estimate of sampling effort). N (number of host species) = 71. See Fig. 5 and Methods for more details.

on different host plants.

Lewinsohn (1991) also found a strong relation between total sample size and asteracean endophagous species richness in southeastern Brazil. The effect of sample size can be ascribed to at least two main effects. The first one is that bulk sample reflects flower head abundance in the field (Fonseca *et al.* 2005). A greater resource pool should support more species (MacArthur 1972, Straw & Ludlow 1994). The second is the great number of rare species. Novotny and Basset (2000) found that a sizeable proportion of singletons in herbivore insects still occur even with a huge fieldwork effort. The greater the bulk sampled, the more the chance of finding rare species, increasing species richness. In the cerrado remnants studied, both effects are probably influencing the increase in endophagous richness with increase in total sample size per host.

Half of the endophagous insect species (Diptera or Lepidoptera) as well as their asteracean host plants (Almeida *et al.* 2005) were restricted to only one of the surveyed cerrado localities. We cannot estimate how many of these current singletons might eventually have been found with further sampling in each site but, given our highly focused and fairly effective sample scheme, there is undoubtedly a majority of scarce and infrequent species. This in turn leads us to infer that each sampled area bears not only unique plant or insect communities, but also unique insect-plant interaction webs (Lewinsohn *et al.* 2006). We cannot ascertain temporal turnover in species or in interaction links from our present data. However, if reciprocal colonization among cerrado areas has ever contributed to establish and maintain both local and regional diversity (see Thompson 2005), the current reduction of the cerrados in São Paulo to ever decreasing, scattered and isolated remnants is bound to threaten the future of this distinctive component of the neotropical biota.

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