

Composition and structure of the fig wasp community in Amazonia

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ABSTRACT

An understanding of the complex ecological interaction between fig wasps and their host plants in Amazonia requires previous knowledge of their distribution and diversity. The objective of this study was to describe the composition and structure of the wasp community associated with four species of *Ficus* in the municipal area of Manaus, Amazonas, Brazil. A total of 600 syconia from four species were collected. The study species were: *Ficus obtusifolia* Kunth; *Ficus citrifolia* Mill; *F. americana* subspecies *guianensis* Desv. form *mathewsii*; and *F. americana* subspecies *guianensis* Desv. form *parkeriana*. Statistical analyses were used to examine the relationship between fig wasp diversity and syconium diameter, and the effect of non-pollinating wasps on numbers of pollinators and seeds. Forty three species of fig wasp were identified, distributed across seven genera (*Pegoscapus*, *Idarnes*, *Aepocerus*, *Physothorax*, *Anidarnes*, *Heterandrium*, *Eurytoma*). *Idarnes* (*carne* group) was the wasps genus non-pollinator with greatest number of individuals with the greatest number of infested syconia (7409 wasps in 376 syconia). Analysing non-pollinating wasp diversity in relation to fig diameter, a significant difference was observed between the four fig species. *Ficus citrifolia* and *F. americana* subspecies *guianensis* form *mathewsii* had the smallest diameter but the greatest diversity of fig wasp. *Ficus obtusifolia* was the only species in which the non-pollinating wasps had a significant negative effect on the number of *Pegoscapus* sp. and on seed production.

KEYWORDS: Figs, diversity, Brazilian Amazon.

Composição e estrutura da comunidade de vespas-de-figo na Amazônia

RESUMO

A compreensão sobre as complexas interações ecológicas envolvendo vespas-de-figo e suas plantas hospedeiras na Amazônia depende do conhecimento prévio sobre a distribuição e diversidade dessas vespas. O objetivo deste estudo foi descrever a composição e estrutura da comunidade de vespas associadas a quatro espécies de *Ficus* no município de Manaus, Amazonas. Foram coletados e analisados 600 sicônios de quatro espécies: *Ficus obtusifolia* Kunth; *Ficus citrifolia* Mill; *F. americana* subspecies *guianensis* Desv. forma *mathewsii*; and *F. americana* subspecies *guianensis* Desv. forma *parkeriana*. Análises estatísticas foram usadas para analisar a relação entre a diversidade de vespas-de-figo e o diâmetro do sicônio, e o efeito das vespas não-polinizadoras em relação ao número de polinizadoras e sementes. Foram encontradas 43 espécies de vespas-de-figo distribuídas em sete gêneros (*Pegoscapus*, *Idarnes*, *Aepocerus*, *Physothorax*, *Anidarnes*, *Heterandrium*, *Eurytoma*). *Idarnes* grupo *carne* foi o gênero de vespas não-polinizadora com maior número de indivíduos com maior número de sicônios infestado (7.409 vespas em 376 sicônios). Ao analisar a diversidade de vespas não-polinizadoras em relação ao diâmetro do figo observou-se diferença significativa entre as quatro espécies de figueiras. *Ficus citrifolia* e *F. americana*, subespécie *guianensis*, forma *mathewsii* apresentaram o diâmetro menor, porém uma maior diversidade de vespas-de-figo. *Ficus obtusifolia* foi a única espécie em que as vespas não-polinizadoras exerceram efeito negativo significativo tanto no número de *Pegoscapus* sp. quanto na produção de sementes.

PALAVRAS-CHAVE: Figueiras, Diversidade, Amazônia Brasileira.

INTRODUCTION

Mutualistic interactions between plants and insects are of particular interest because the exchange of resources involved attracts a great variety of other organisms that benefit from the relationship (Bronstein 2001). A classic example is the relationship between the 750 species of the genus *Ficus* (Moraceae) and its pollinating wasps. The figs (syconia) are pollinated exclusively by specific wasps from the family Agaonidae (Chalcidoidea), which in turn reproduce by laying eggs in the fig's flowers (by preference the longer-styled flowers), where the larvae feed and develop (Kerdelhué and Rasplus 1996; Cook and Segar 2010). This mutualism is exploited by a number of other parasitic wasps - denominated non-pollinating wasps (Wiebes and Compton 1990) - and by innumerable species of ants, Homoptera, Coleoptera, Lepidoptera and Diptera (Yang *et al.* 2008; Bain *et al.* 2012).

Non-pollinating wasps are considered the main exploiters of the mutualism and they cover three ecological groups: gall-inducing wasps, parasites and cleptoparasites (Rasplus *et al.* 1998; Kjellberg *et al.* 2005). The gall inducers oviposit in flowers that have no existing galls and thus negatively affect both pollinating wasp production and fig seed production. The parasitic and cleptoparasitic wasps negatively affect only pollinator and other non-pollinator production (Kerdelhué e Rasplus 1996; West *et al.* 1996; Kerdelhué *et al.* 2000). However, the negative effects of non-pollinating wasps, whether in relation to seed production or pollinator production, can vary between fig trees and the regions in which they occur (Wei *et al.* 2005; Elias *et al.* 2007; Conchou *et al.* 2013). In the absence of any quantitative studies, it has not been possible until now to evaluate the effect of non-pollinating wasps on seed and pollinator production among Amazonian fig trees.

The exploitation of fig/wasp mutualism can also be observed by examining species abundance and richness among non-pollinating wasps, which vary enormously and depend on the biology of both wasp and fig tree (Bronstein 1992; Wang *et al.* 2012), as well as on external factors (Elias *et al.* 2007; Ma *et al.* 2009). There are cases of fig trees being exploited by six (Conchou *et al.* 2013), sixteen (Segar *et al.* 2013) or up to 30 species of non-pollinating wasp (Bouček 1993). In some cases the diversity of non-pollinating wasps may be closely related to the plant's reproductive systems (monoecious or dioecious) (Kerdelhué and Rasplus 1996). Monoecious species, for example, possess a greater diversity of wasps because they provide a larger number of niches (flowers) - of at least four types (heterostyly) - on which non-pollinating wasps may oviposit, while the pollinating wasps associated with the dioecious species are limited to just one type of flower (longer-styled flowers).

It can also be seen that, at least among monoecious species, the diversity of non-pollinating wasps varies in relation to fig diameter. Figs diameter normally varies between 4,0 mm and 60 mm, and with 10 to 10,000 flowers respectively (Herre 1989; Berg and Wiebes 1992; Cook and Rasplus 2003). This potentially leads us to conclude that large-diameter figs will have the largest number of flowers and consequently a greater availability of locations for oviposition than figs of a smaller diameter. However, although this hypothesis has been proposed by Cook and Segar (2010), there are as yet no studies to corroborate the relationship. In the present study, we describe the composition and structure of the wasps community associated with four monoecious species of *Ficus* in the municipal area of Manaus, Amazonas, Brazil.

MATERIALS AND METHODS

The study was carried out in the urban area of the municipality of Manaus, Amazonas, Brazil (03°08'S 60°01'W), covering an area of 11,458.5 km² (Saraiva *et al.* 2009). The city is located in central Amazonia, on the left bank of the River Negro and near the confluence of the River Negro with the River Solimões. The climate is equatorial humid, with a mean annual temperature of 26.7°C. Relative humidity is 80% and average annual rainfall is 2,286 mm. The year has two distinct seasons: one humid, with significant rainfall from November to May; and one drier, between June and October (Alvares 2013).

Seven areas (districts) were selected for the study: Ponta Negra, Dom Pedro, São Geraldo, Cachoeirinha, Cidade Nova, Distrito Industrial and Flores. Four taxa were selected: *Ficus obtusifolia* Kunth; *Ficus citrifolia* Mill; *F. americana* subspecies *guianensis* form *mathewsii*; and *F. americana* subspecies *guianensis* form *parkeriana*. The latter two taxa according to the latest version of Berg (2007). All species and subspecies belonging to section *Americana* are pollinated exclusively by wasps of the genus *Pegoscapus*.

The choice of these taxa owes itself to their great abundance in urban fragments like squares and parks, and to their limited height (± 7 metres) in these areas which facilitates the collection of syconia in all reproductive phases. It was not possible to select individuals within ecological reserves or undisturbed areas, because the height of individuals in these environments (above 25m) made it difficult to gather syconia from these trees.

Six hundred syconia were collected at random from four individuals (150 syconia from each fig tree) between July 2011 and October 2012. We selected figs that we judged to be in male phase (D stage sensu Galil and Eisikowitch 1968), but which did not yet have wasp exit holes. Such figs are relatively large and are often slightly soft when pressed between thumb and forefinger.

The syconia were separated in plastic flasks covered with a voile type cloth, and kept for 48 hours to collect all the wasps. At the end of this time, the insects were killed by freezing, and subsequently a solution of 70% alcohol was added to the flasks, where the specimens were kept with their respective syconia before sorting (Costa and Gracioli 2010). The wasps that emerged from the syconia were sorted with the help of a stereoscopic magnifier (Nikon SMZ 645, Tokyo, Japan) and microscope (Primo Star; Carl Zeiss Microimaging, Jena, Germany), and identified at the level of morphospecies using Bouček's key for fig wasps of the New World (Bouček 1988; 1993; Farache *et al.* 2013). The wasp and *Ficus* specimens were deposited in the entomological collection and herbarium respectively at the Instituto Nacional de Pesquisa da Amazônia (INPA).

The largest diameter of 150 syconia (30 per fig tree) was measured using digital callipers. These syconia were dissected with the aid of a dissecting knife and stereoscopic magnifier in order to count the galls. Syconia of the species *F. obtusifolia* were divided in four separate equal parts, the galls counted for one of the parts, and the result multiplied by four. Syconia of the species *F. citrifolia* and *F. americana* subspecies *guianensis* form *parkeriana* were cut into two equal halves, the galls counted from one half and the result multiplied by two. For species *F. americana* subspecies *guianensis* form *mathewsii*, the total number of galls were counted individually (Kerdélhuc and Rasplus 1996).

The quantitative distribution of fig wasp species for each host was calculated using the formula proposed by Bush *et al.* (1997), where the frequency of occurrence corresponds to

$$\frac{\text{N}^{\circ} \text{ of infested syconia}}{\text{N}^{\circ} \text{ of syconia in sample}} \times 100$$

while the mean intensity of infestation (Number of individuals of fig wasp species in a single host) corresponds to

$$\frac{\text{N}^{\circ} \text{ of individuals in species } x}{\text{N}^{\circ} \text{ of syconia infested by species } x} \times 100$$

To identify the fig tree species with the greatest wasp diversity, Shannon's index was employed, where $H = -\sum P_i(\ln P_i)$, using the PAST 3.0 program. To analyse the relationship between fig wasp diversity and syconium diameter, Bioestat 5.0 was used. To define the type of statistic used - parametric or non-parametric - a normality test was performed *a priori*. To evaluate the relationship between syconium diameter and gall quantity, the Kruskal-Wallis Test was used, followed by the Dunn post-test. Spearman's correlation was used to examine the association between syconium diameter and gall quantity, as well as to estimate non-pollinating wasp species (male and female) richness and abundance in relation to syconium diameter. A 95% significance level was used for all tests ($p < 0.05$).

To analyse the effect of the non-pollinating wasp species on the numbers of *Pegoscapus* and seeds, a simple linear regression was used with the number of individual wasps by genus for each host. The non-pollinating wasps were divided in two groups: 1) wasps with large bodies; and 2) wasps with smaller bodies, in relation to the body size of pollinating wasps. This division was done on the basis that the size of the galls of non-pollinating large-bodied wasps reduces the available space in the lumen of the syconia (Conchou *et al.* 2013).

RESULTS

The fig wasp community associated with the four fig trees comprised 43 morphospecies of fig wasp. Twenty nine morphospecies were encountered in *F. citrifolia*, 24 in *F. americana* subspecies *guianensis* form *mathewsii*, 18 in *F. obtusifolia* and seven in *F. americana* subspecies *guianensis* form *parkeriana*. The 43 morphospecies of fig wasp belong to three families and seven genera, with *Aepocerus* and *Physothorax* being those with the largest number of morphospecies (Table 1). The genus *Idarnes* was notable for having the greatest abundance and the largest number of infested syconia (Table 2).

The distribution index of the fig wasps in the syconia showed that *Pegoscapus* was the most prevalent genus in all the fig trees. In *F. americana* subspecies *guianensis* form *parkeriana* the frequency of occurrence was 100% and mean intensity 120.7%. *F. americana* subspecies *guianensis* form *mathewsii* had a frequency of occurrence of 98.6% and a mean intensity of 22.8%; *F. citrifolia* a frequency of 94.6% and mean intensity 75.8%; and *F. obtusifolia* a frequency of 99.3% and mean intensity of 186.8% *Idarnes* had the

Table 1. Summary of the number of morphospecies, total individuals, and infested syconia for each wasp genus associated with species *Ficus* in the urban area of Manaus, Amazonas, Brazil.

Fig wasp Family/Subfamily	Wasp genus	Number of morphospecies	Number of individuals	Number of infested syconia
Agaonidae	<i>Pegoscapus</i>	04	60,101	589
Sycophaginae	<i>Idarnes</i> (<i>carne</i> group) ^a	06	7,409	376
Sycophaginae	<i>Idarnes</i> (<i>flavicollis</i> group) ^a	01	14	6
Sycophaginae	<i>Idarnes</i> (<i>incerta</i> group) ^a	01	49	27
	<i>Aepocerus</i> ^{b*}	08	164	133
Torymidae	<i>Physothorax</i> ^b	08	34	27
Sycophaginae	<i>Anidarnes</i> ^b	07	83	58
	<i>Heterandrium</i> ^{a*}	04	155	65
Eurytomidae	<i>Eurytoma</i> ^b	06	45	34

^aWasps of the same body size as pollinators; ^bWasps of larger body size than pollinators. *Genus with undefined family and/or subfamily

Table 2. Quantitative distribution of fig wasp species in 600 syconia present in four species of *Ficus* in the urban area of Manaus, Amazonas, Brazil. The numbers of figs collected are in parentheses under the plant taxon column.

Plant taxon	Wasp taxon	Total individuals	Total number of infested syconia	Frequency of occurrence (%)	Mean intensity (%)
form <i>parkeriana</i> (150)	<i>Pegoscapus</i> sp.4	18,107	150	100.000	120.713
	<i>Idarnes</i> sp.2 (carne group)	47	14	9.333	3.357
	<i>Idarnes</i> sp.7 (carne group)	25	7	4.667	3.571
	<i>Aepocerus</i> sp.8	6	3	2.000	2.000
	<i>Heterandrium</i> sp.2	8	4	2.667	2.000
	<i>Eurytoma</i> sp.1	1	1	0.667	1.000
form <i>mathewsii</i> (150)	<i>Pegoscapus</i> sp.3	3,380	148	98.667	22.838
	<i>Idarnes</i> sp.1 (carne group)	201	43	28.667	4.674
	<i>Idarnes</i> sp.2 (carne group)	36	11	7.333	3.273
	<i>Idarnes</i> sp.5 (carne group)	23	7	4.667	3.286
	<i>Idarnes</i> sp.3 (flavicolis group)	9	2	1.333	4.500
	<i>Idarnes</i> sp.4 (incerta group)	3	1	0.667	3.000
	<i>Aepocerus</i> sp.1	3	3	2.000	1.000
	<i>Aepocerus</i> sp.3	14	9	6.000	1.556
	<i>Aepocerus</i> sp.5	3	2	1.333	1.500
	<i>Aepocerus</i> sp.6	1	1	0.667	1.000
	<i>Aepocerus</i> sp.7	10	8	5.333	1.250
	<i>Anidarnes</i> sp.2	6	2	1.333	3.000
	<i>Anidarnes</i> sp.4	15	12	8.000	1.250
	<i>Anidarnes</i> sp.5	5	5	3.333	1.000
	<i>Anidarnes</i> sp.6	4	3	2.000	1.333
	<i>Heterandrium</i> sp.1	93	33	22.000	2.818
	<i>Eurytoma</i> sp.2	5	4	2.667	1.250
	<i>Eurytoma</i> sp.3	1	1	0.667	1.000
	<i>Eurytoma</i> sp.4	5	2	1.333	2.500
	<i>Eurytoma</i> sp.5	2	2	1.333	1.000
<i>F. citrifolia</i> (150)	<i>Pegoscapus</i> sp.2	10,767	142	94.667	75.824
	<i>Idarnes</i> sp.1 (carne group)	1,145	48	32.000	23.854
	<i>Idarnes</i> sp.2 (carne group)	259	20	13.333	12.950
<i>F. obtusifolia</i> (150)	<i>Idarnes</i> sp.5 (carne group)	185	14	9.333	13.214
	<i>Idarnes</i> sp.6 (carne group)	118	40	26.667	2.950
	<i>Idarnes</i> sp.7 (carne group)	166	19	12.667	8.737
	<i>Idarnes</i> sp.8 (carne group)	425	26	17.333	16.346
	<i>Idarnes</i> sp.4 (incerta group)	42	23	15.333	1.826
	<i>Aepocerus</i> sp.1	22	14	9.333	1.571
	<i>Aepocerus</i> sp.2	1	1	0.667	1.000
	<i>Aepocerus</i> sp.3	3	3	2.000	1.000
	<i>Aepocerus</i> sp.4	3	3	2.000	1.000
	<i>Aepocerus</i> sp.7	49	31	20.667	1.581
	<i>Physothorax</i> sp.1	2	2	1.333	1.000
	<i>Physothorax</i> sp.5	2	2	1.333	1.000
	<i>Physothorax</i> sp.6	2	1	0.667	2.000
	<i>Physothorax</i> sp.7	2	2	1.333	1.000
	<i>Physothorax</i> sp.8	7	6	4.000	1.167
	<i>Anidarnes</i> sp.4	1	1	0.667	1.000
<i>Anidarnes</i> sp.7	8	6	4.000	1.333	
<i>Anidarnes</i> sp.8	1	1	0.667	1.000	
<i>Heterandrium</i> sp.1	45	20	13.333	2.250	
<i>Heterandrium</i> sp.2	1	1	0.667	1.000	
<i>Heterandrium</i> sp.3	6	6	4.000	1.000	
<i>Heterandrium</i> sp.4	2	1	0.667	2.000	
<i>Eurytoma</i> sp.2	8	7	4.667	1.143	
<i>Eurytoma</i> sp.3	16	12	8.000	1.333	
<i>Eurytoma</i> sp.6	7	5	3.333	1.400	
<i>F. obtusifolia</i> (150)	<i>Pegoscapus</i> sp.1	27,847	149	99.333	186.893
	<i>Idarnes</i> sp.1 (carne group)	2,294	46	30.667	49.870
	<i>Idarnes</i> sp.2 (carne group)	2,466	77	51.333	32.026

Table 2. Continuation

Plant taxon	Wasp taxon	Total individuals	Total number of infested syconia	Frequency of occurrence (%)	Mean intensity (%)
<i>F. obtusifolia</i> (150)	<i>Idarnes</i> sp.5 (<i>carne</i> group)	19	4	2.667	4.750
	<i>Idarnes</i> sp.3 (<i>flavicolis</i> group)	5	4	2.667	1.250
	<i>Idarnes</i> sp.4 (<i>incerta</i> group)	4	3	2.000	1.333
	<i>Aepocerus</i> sp.5	21	13	8.667	1.615
	<i>Aepocerus</i> sp.6	5	3	2.000	1.667
	<i>Aepocerus</i> sp.7	2	2	1.333	1.000
	<i>Physothorax</i> sp.1	6	4	2.667	1.500
	<i>Physothorax</i> sp.2	1	1	0.667	1.000
	<i>Physothorax</i> sp.3	1	1	0.667	1.000
	<i>Physothorax</i> sp.4	1	1	0.667	1.000
	<i>Anidarnes</i> sp.1	16	9	6.000	1.778
	<i>Anidarnes</i> sp.2	22	15	10.000	1.467
	<i>Anidarnes</i> sp.3	2	2	1.333	1.000
	<i>Eurytoma</i> sp.1	1	1	0.667	1.000

greatest frequency and mean intensity in all the fig trees. In *F. obtusifolia* the morphospecies *Idarnes* sp.2 (*carne* group) had the greatest frequency (51.33%) and *Idarnes* sp.1 (*carne* group) the greatest mean intensity (49.8 %, Table 2).

Regarding the diversity of non-pollinating wasps in relation to fig diameter (in millimeters), a significant difference was observed among the four fig species. *Ficus americana* subspecies *guianensis* form *mathewsii* and *F. citrifolia* were the species with the smallest figs, mean (\pm SD) of 4.62 ± 0.52 and 9.61 ± 1.91 respectively, but had the largest Shannon index at $H=1.829$ and $H=1.835$ respectively (Table 3). In *F. obtusifolia* (figs with a diameter almost 4 times larger than that of *F. americana* subspecies *guianensis* form *mathewsii*) the Shannon index was $H=0.828$. It was also found that species richness of wasps is not correlated with fig diameter in *F. Americana* subspecies *guianensis* form *mathewsii* and *F. citrifolia*, although there is a correlation between wasp species abundance and fig diameter in both fig trees. For *F. americana* subspecies *guianensis* form *parkeriana*, species richness is correlated with fig diameter, mean (\pm SD) of 12.0 ± 1.25 , while species abundance is not. In species *F. obtusifolia* both richness and

abundance are correlated with fig diameter, mean (\pm SD) of 16.57 ± 2.62 (Table 3).

In relation to the effect of non-pollinating wasps on the number of pollinating wasps and seeds, in *F. citrifolia* wasps of the genus *Idarnes* represented 92.37% of all individuals. Among large-bodied non-pollinating species, *Aepocerus* was the most abundant with 54.48% of the individuals. In *F. americana* subspecies *guianensis* form *mathewsii*, 76.92% of non-pollinating wasps were represented by *Idarnes* and *Heterandrium* (wasps with the same body size as the pollinating wasps). In *F. americana* subspecies *guianensis* form *parkeriana*, 82.6% of non-pollinating wasps were represented by *Idarnes*. For these three species of *Ficus*, the total number of non-pollinating wasps did not correlate negatively with either the number of *Pegoscapus* or the number of seeds (Figures 1-3 A, B).

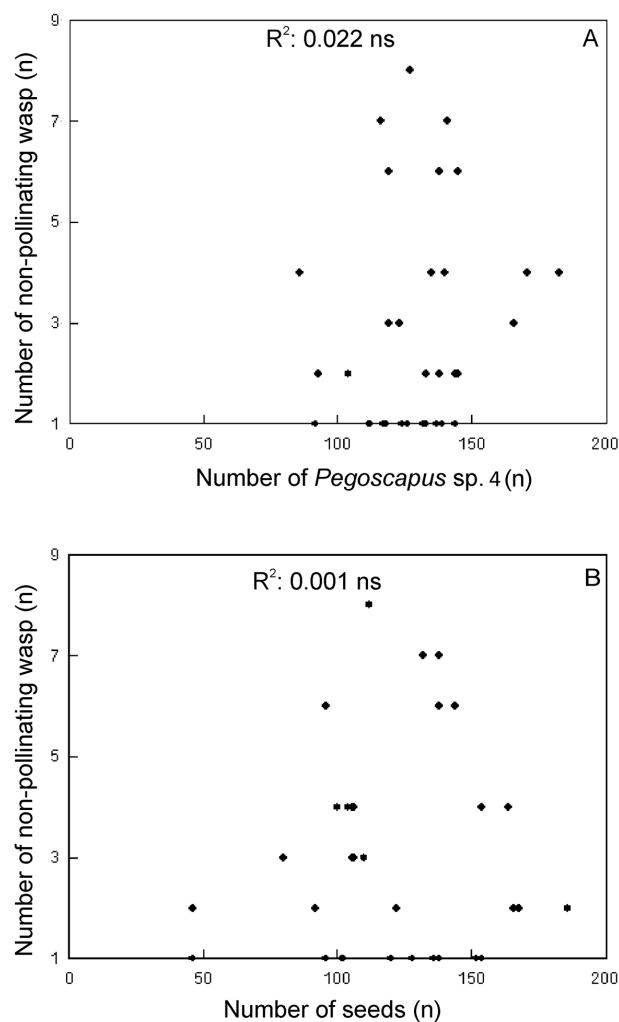


Figure 1. Number of non-pollinating fig wasps as a function of the number of *Pegoscapus* sp. 4 (A), and the number of seeds (B) in *F. americana* subspecies *guianensis* form *parkeriana*.

Table 3. Syconium diameter (mm), number of galls, richness and abundance of non-pollinating fig wasps, and Shannon diversity index for different species of *Ficus* in the urban areas of Manaus, Amazonas, Brazil. Acronyms: **SD** standard deviation; **P*** represent significant differences; **rs** are Spearman's correlation; **df** degrees of freedom.

Plant taxon	Diameter mean ± SD	P*	Galls mean ± SD	Shannon index (H)	Richness			Abundance		
					P*	df	rs*	P*	df	rs
<i>parkeriana</i> ¹	12.0 ± 1.25	B	128.3 ± 23.89	1.146	=0.0079	148	=0.2161	=0.6505	148	=0.0379
<i>mathewsii</i> ²	4.62 ± 0.52	A	29.3 ± 14.10	1.829	=0.6252	148	=0.0735	=0.2125	148	=0.1018
<i>F. citrifolia</i>	9.61 ± 1.91	C	105.0 ± 55.03	1.835	=0.9587	148	=0.0042	=0.0123	148	=0.2028
<i>F. obtusifolia</i>	16.57 ± 2.62	D	252.9 ± 87.48	0.828	=0.0051	148	=0.2289	<0.0001	148	=0.4815

*Dunn test, 95% significance level. Letters in column **P*** represent significant differences in mean values between fig diameters of the fig tree species. Forms belonging to ¹*F. americana* subspecies *guianensis* form *Parkeriana*, ²*Ficus americana* subspecies *guianensis* form *mathewsii* according to Berg (2007).

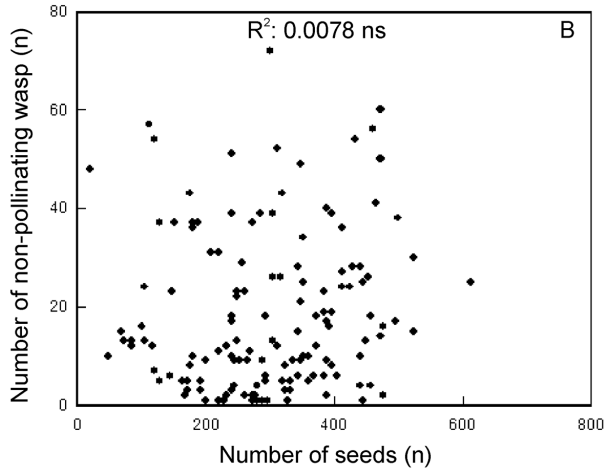
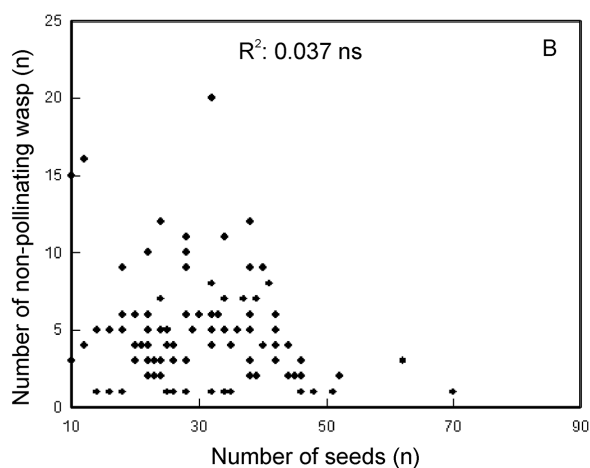
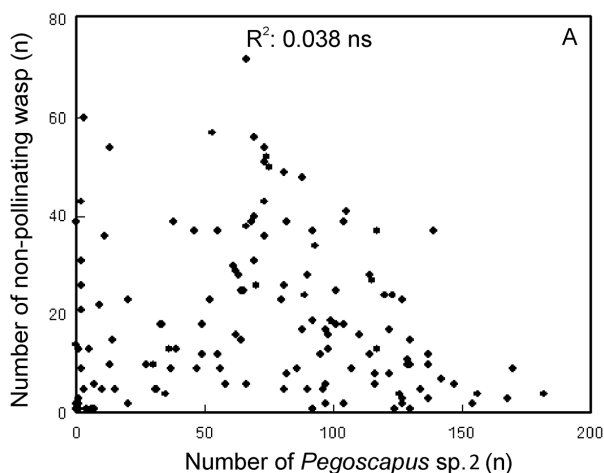
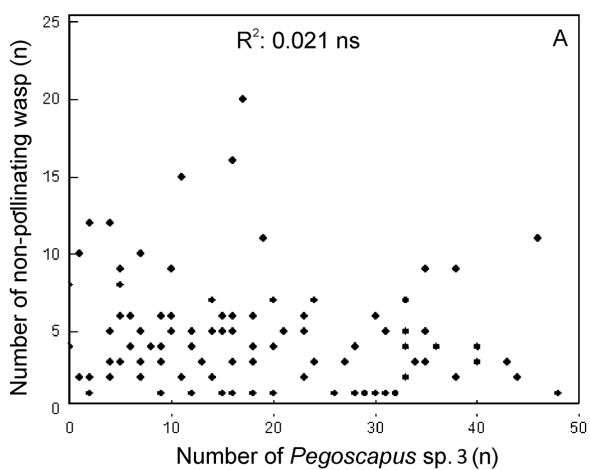


Figure 2. Number of non-pollinating fig wasps as a function of the number of *Pegoscapus* sp. 3 (A), and the number of seeds (B) in *F. americana* subspecies *guianensis* form *mathewsii*.

Figure 3. Number of non-pollinating fig wasps as a function of the number of *Pegoscapus* sp. 2 (A), and the number of seeds (B) in *F. citrifolia*.

In *F. obtusifolia* the non-pollinating wasps were present in 124 of the 150 syconia, represented principally by wasps of the genus *Idarnes* (98.92%). Due to the low number of non-pollinating large-bodied wasps, simple regression analysis was performed only for wasps of the genus *Idarnes*. The results showed that the total number of non-pollinating wasp correlated negatively and significantly with both the number of *Pegoscapus* sp. 1 ($r^2: 0.44, p < 0.0001$), (Figure 4A), and the number of seeds ($r^2 = 0.44, p < 0.0001$) (Figure 4B).

DISCUSSION

The present study is the first to provide quantitative and qualitative data on fig wasp fauna in the Amazon region. In comparison with studies in the southeast and centre-west of Brazil, it was found that the wasp fauna associated with

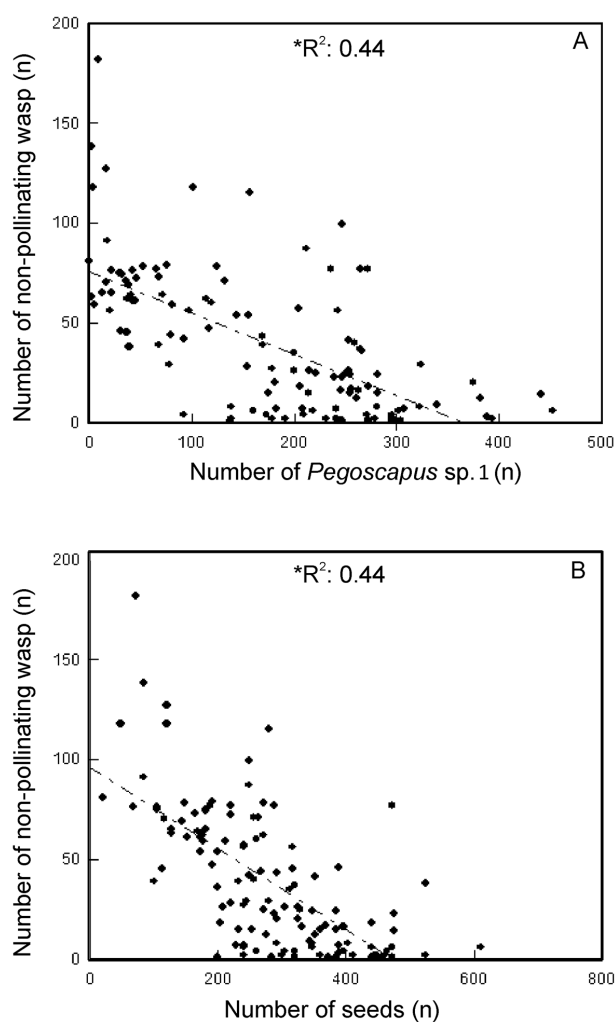


Figure 4. Number of non-pollinating fig wasps as a function of the number of *Pegoscapus* sp. 1 (A), and the number of seeds (B) in *F. obtusifolia*.

Amazonian fig trees is more diverse. The wasp community in *F. citrifolia* in this study comprised 29 species, while in Mato Grosso do Sul (Costa and Graciolli 2010), São Paulo and Londrina (Pereira *et al.* 2000), 12 and 15 species were registered respectively. The same was confirmed for *F. americana* subspecies *guianensis* form *mathewsii* which here contained 22 species in comparison with those in the study by Conchou *et al.* (2013) in French Guiana, with just six species. This is the first study, in which such a large number of non-pollinating wasp species has been registered, and given the diversity of fig trees in the neotropics (140 species) it is likely that there are many more species of fig wasp in the Amazon yet to be described.

The results showed that the morphospecies *Pegoscapus* and *Idarnes* (*carne* group) were the most frequently occurring and abundant. Among the non-pollinating wasps, *Idarnes* is commonly regarded as the most abundant and diverse in Central and South America (West and Herre 1994; Elias *et al.* 2007; Costa and Graciolli 2010). In the case of *Idarnes* (*carne* group) (cleptoparasites), success in exploiting the mutualism is evidenced partly by the fact that the species in this group oviposits during phase C - the plant's interfloral phase (Murussich and Machado 2007; Elias *et al.* 2008). This phase, being the longest (18 to 20 days depending on the species of *Ficus*), gives an advantage to wasps from the *carne* group in ovipositing in a larger number of galls. In addition, the larvae of the males of this group have been observed feeding on the seeds, which broadens the spectrum of alimentary resources and the chances of increasing the progeny (Pereira *et al.* 2007).

For the morphospecies of *Idarnes* of the group *incerta* and *flavicollis* (gall-inducers and phytophagous competitors), one of the factors that may influence the low frequency and/or abundance of the species is the short time available (seven to eight days) for oviposition. As they oviposit a little before or at the same time as the pollinators (Elias *et al.* 2008), they compete for location and thus reduce the chances of ovipositing due to the limited availability of resources (flowers) for larvae development. The same may be happening with morphospecies of the genus *Aepocerus* and *Heterandrium* (gall inducers), which oviposit approximately seven to twelve days prior to pollination (Rasplus and Soldati 2006). The genera *Physothorax* (Hanson 2006) and *Eurytoma*, (Burks 1971) are the last to colonise the syconia and are parasites of the larvae of the phytophagous species (West *et al.* 1996; Murussich and Machado 2007; Cruaud *et al.* 2011). Therefore, even though no data have been presented with respect to the feeding habits of the wasps, it is possible to infer that the period of ovipositing (during the reproductive phase of the fig) and the presence of the wasp host in the syconia could be influencing the frequency and/or abundance of the parasitoid wasp species.

In relation to fig wasp species diversity, *F. citifolia* and *F. americana* subspecies *guianensis* form *mathewsii* (syconia

of smaller diameter) contained the greatest diversity, while *F. obtusifolia* (syconia of larger diameter) had a low Shannon index. Consequently, our data failed to support the hypothesis postulated by Cook and Segar (2010) which predicted that larger diameter syconia would have a greater range of niches and the greatest wasp species richness. However, the timing difference in fig production (the interval between harvests) among species observed during our fieldwork, allows us to suggest that phenological aspects may be, in part, influencing normal fig wasp diversity. Individuals of *F. obtusifolia* and *F. americana*, subspecies *guianensis* form *parkeriana* were observed to fruit just twice a year. For *F. citrifolia* and *F. americana* subspecies *guianensis* form *mathewsii* fruiting occurred four times a year. Twice yearly fig production for *F. obtusifolia* was also observed in the studies of Ballestrini *et al.* (2011) in Venezuela and Panama. In the same way, Cerezini *et al.* (2007) observed that fig production in *F. citrifolia* may occur continuously throughout the year.

Considering that the greater the frequency of availability of the flowers, the greater the probability of an available niche suitable for reproduction, it appears that *F. americana* subspecies *guianensis* form *mathewsii* and *F. citrifolia*, are being selected by non-pollinating wasps as preferred species for the development of their larvae because both species flower up to four times per annum (personal observation). The limited period of time available for wasps to identify figs in which to lay eggs, the impact of adverse weather conditions and the effects of predation on the chances of successful reproduction (Kjellberg *et al.* 1988), are other factors which might tend to encourage such selection. In addition, even though there is a certain degree of specificity between non-pollinating wasps and host plants (Cook and Rasplus 2003), the wasps will select the fig species that are available in the period when they are ready for laying. For this to occur, it is necessary that the figs have at least some similar morphological characteristics. Phenotypic diversity with respect to syconium size indirectly causes the restriction of a considerable number of non-pollinating wasps, since large figs have a thicker receptacle wall which does not allow some species to reach the flower ovules during oviposition (Dunn *et al.* 2008).

With respect to the negative effect of the non-pollinating wasps on the numbers of *Pegoscapus* sp. 1 and seeds, *F. obtusifolia* was the only species that indicated a significant negative effect, caused specifically by *Idarnes* (*carme* group, wasps with the same body size as the pollinating wasps). According to Conchou *et al.* (2013), at least in small figs the development of large galls inside recently pollinated figs may reduce the amount of space available for the development of pollinator galls and seeds. Based on this premise, it is

suggested that the presence of a smaller number of large-body non-pollinating wasps in *F. obtusifolia*, may explain the significant negative effect of the species of *Idarnes* (*carme* group) on this species and not on *F. americana* subspecies *guianensis* form *mathewsii* and *F. citrifolia*. This is because the absence of large galls makes viable not only the production of a larger number of small galls, but also of seeds, which are the two resources used in gall development in *Idarnes* (*carme* group). However, caution is necessary in accepting this relationship since the effects on mutualism vary according to the ecology and biology of each one of the non-pollinating wasps involved (Bronstein 1992).

CONCLUSION

Our study provides significant evidence that wasp fauna associated with the figs of Amazonia is more diverse than in other regions of Brazil. It has also shown that non-pollinating fig wasp diversity varies in relation to fig diameter, but that figs of a large diameter are not necessarily those which host the greatest wasp diversity.

The interval between harvests - shorter in fig species with smaller figs - may influence the structure of the non-pollinating wasp community. Although non-pollinating wasps affect seed and pollinator production in one of the four fig species, our study suggests that the probably of the mutualism being negatively affected by the parasitic wasps can be considered low in the urban Amazonian environment. This work will provide a foundation for other studies on Amazonian fig wasp species.

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