ECOLOGY, BEHAVIOR AND BIONOMICS

Ant-Plant Associations in Different Forests in Venezuela

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Associações Formiga-Planta em Diferentes Florestas na Venezuela

RESUMO - Avaliou-se a hipótese de que a distribuição da abundância e o número de espécie de dois tipos diferentes de plantas mirmecófilas são influenciadas diferentemente pela diversidade e pela abundância de formigas. Em oito florestas naturais diferentes na Venezuela nós estimamos a riqueza de espécies e a abundância de plantas, de formigas no solo e no dossel, os danos às folhas e os nutrientes do solo. Os resultados mostram que as plantas com domácias para alojar formigas e plantas com nectários extraflorais (PEFN) têm relacionamentos diferentes com formigas e sofrem confinamentos ecológicos diferentes. As plantas com domácias atraem um grupo mais específico de formigas do que as PEFN. Os resultados são consistentes com a hipótese de que as domácias são adaptações que ajudam a planta a aumentar o acesso a nutrientes escassos para a defesa de herbívoros. PEFN atraem uma variedade maior da espécie de formigas do que as plantas com domácias, e a abundância de formigas parece limitar a escala ecológica de PEFN. A atração das formigas como mecanismo para reduzir a herbivoria, como feito por PEFN, não parece ser superior aos mecanismos alternativos de prevenção de herbivoria usados por outras plantas. Contrário a muitos estudos anteriores, as formigas mostraram-se geralmente mais diversas no solo comparado ao dossel.

PALAVRAS-CHAVE: Mirmecofita, mirmecófilo

ABSTRACT - We evaluated the hypothesis that the abundance and species distribution of two different kinds of myrmecophilous plants is influenced differently by the ant diversity and abundance. In eight different natural forests in Venezuela we estimated the species richness and abundance of plants, ants on the soil and on the canopy, the leaf damage of plants and soil nutrients. The main results of the study show that plants with domatia (PD) and plants with extrafloral nectaries (PEFN) have different relationships with ants and suffer from different ecological constraints. PD attract a more specific group of ants than PEFN. Our results are consistent with the hypothesis that domatia are adaptations that help plants to increase rare nutrient uptake rather than for herbivore defense. We found that PEFN attract a larger variety of ant species than PD, and ant abundance seems to limit the ecological range of PEFN. The attraction of ants as a mechanism to reduce herbivory, as done by PEFN, does not seem to be superior to alternative anti-herbivore mechanisms used by other plants. Contrary to many former studies, we found that ants are generally more diverse on the soil compared to canopies.

KEY WORDS: Myrmecophilous plant, Myrmecophyte

Plants and ants have been interacting during a long evolutionary history, probably starting at the mid Cretaceous when angiosperms became dominant among the terrestrial flora and the first ants in the fossil record appeared (Jolivet 1986, Hölldobler & Wilson 1990). At present, a complex variety of symbioses, associations and mutualisms between plants and ants are known. Some plants actively attract ants. Here we will call them myrmecophiles or myrmecophilous plants (MP). Several of these MP attract ants by using extra floral nectaries (EFN). We will call these plants PEFN. Another group of MP is characterized by myrmecophytes or plants possessing domatia (PD). The domatia in PD are commonly used or inhabited by ants. PD have been reported from over 90 genera in 40 families; of those, over a third of the families and genera are neotropical (Hölldobler & Wilson 1990, Davidson & McKey 1993, Jolivet 1996, Folgarait 1998). Some PD have adaptations in the interior of their domatia which allow them to absorb nutrients from the ant wastes deposited in them (Janzen 1974, Rickson 1979, Huxley 1980, Thompson 1981); although nutrient transfer from ants to the plant has been experimentally demonstrated only in few cases [see Cabrera & Jaffe (1994) for example]. Several of these associations are found in epiphytes growing on trees with an open canopy (Thompson 1981). Other PD are shrubs of the family Melastomataceae, especially from the genera *Maieta* (three spp.) and *Tococa* (ca. 50 spp.) (Schnell 1967, Roth 1976, Herre *et al* 1986, Cabrera & Jaffe 1994) and *Clidemia tococoidea* (Hölldobler & Wilson 1990), which have domatia at the base of their leaves hosting colonies of ants from the genera *Azteca*, *Pheidole*, *Crematogaster* and *Allomerus*, among others.

Bentley (1976) suggested that the abundance of PEFN in a given biotope depended on the abundance of ants present. This prediction has been experimentally supported by Keeler (1979, 1980), Barton (1986) and Oliveira (1997) among others (see review in Folgarait 1998). Experimental studies showed that the presence of ants enhances the growth of PEFN (Bently 1976, 1977a, b) mainly through a reduction of the herbivore pressure (Barton 1986). The ant-plant associations seem to be more frequent in the tropics compared to temperate habitats. Abundance of MP varies from zero to 80% in neotropical habitats (Bentley 1976, 1977a, b, Keeler 1979, Oliveira & Leitão 1987, Ibarra-Manríquez & Dirzo 1990, Morellato & Oliveira 1991) and zero to 8.3% in temperate areas (Keeler 1980).

In contrast to our understanding about ant species distribution, little is known about the distribution of MP in South-America (but see Morellato & Oliveira 1991, Oliveira & Freitas 2004, Díaz-Castelazo *et al* 2004). Even less is known about the distribution of PD. The aim of this study was to gain more insight into the ecological constraints affecting the distribution of MP, specifically of PEFN and PD. This might help us in understanding if abundance and species distribution of two different kinds of MP is influenced by the ant diversity and abundance. We measured the abundance and species richness of ants on the soil and in the canopies; and the abundance and species richness of plants, mainly MP, in diverse neotropical forests. In addition, the foliar damage on PD, PEFN and non-MP was evaluated in the various ecosystems and was correlated with the occurrence of ants.

Material and Methods

Study sites. The study sites were all closed canopy forest (canopies of trees touching each other) covering much over 1000 ha and had little human intervention, as assed visually by us and verbally by informants living in the neighborhoods, and were located in:

Cata - Parque Nacional Henri Pittier, Distrito Girardot, Municipio Ocumare, Estado Aragua , 10°30' N, 67 ° 44' W, very dry forest (following Huber and Alarcon 1988) at 0-30 m.a.s.l.

Cúpira - Distrito Paéz, Municipio Pedro Gual, Estado Miranda, 10 ° 10'N, 65 ° 43' W, dry forest at 25 m.a.s.l.

Uracoa - Morichal Río Uracoa, El Merey, Distrito Sotillo, Municipio Uracoa, Estado Monagas, 8° 45' N, 62° 47' W, humid gallery forest at 70 m.a.s.l.

Cupo - Distrito Acevedo, Estado Miranda, 10° 17'N, 66° 22'W, humid forest at 95 m.a.s.l.

San Ignacio - Distrito Roscio, Municipio El Callao, Estado Bolívar, 5° 2' N, 60° 57' W, humid premontane forest at 975 m.a.s.l.

San Francisco - Morichal San Francisco de Yuruani, Distrito Roscio, Municipio El Callao, Estado Bolívar, 5° 2' N, 60° 57' W, humid gallery forest at 980 m.a.s.l.

Sartenejas - Valle de Sartenejas, Distrito Baruta, Estado Miranda,10° 27' N, 66 ° 52' W, premontane humid forest at 1200 m.a.s.l.

Rancho Grande - Pico Guacamaya, Parque Nacional Henri Pittier, Distrito Girardot, Estado Aragua, 10° 23' N; 67° 44' W, montane cloud forest at 1660 m.a.s.l.

The selection of localities aimed at studying forests with different types of vegetation, growing at different altitudes and that were located at accessible sites.

Study area. In each site, a 1 x 180 m transect covering an area of 180 m^2 was marked with colored tape. In these transects, at 10 m intervals, we marked eighteen 10 m^2 areas. The plant and ant samples in these marked transects were used to estimate abundance and diversity indices.

In each site, we searched for additional plant specimens outside the marked area of the transect, so as to locate at least 10 MP specimens of each morpho-type, and 10 non-MP that served as controls. These specimens were used to better quantify ant abundance and diversity, and leaf damage, on rare plants, and were called "extra samples".

In each site we localized 30 trees which were at least 10 m high. These trees could be inside the marked transect or outside it. We called these specimens the "tall trees" and used them for hand collecting ants in the canopy, by climbing into the canopy with ropes.

Sampling of plants. Along the transect, at each 10 m^2 we counted the number of plant morph-types, based on leaf morphology and on structures that attract or host ants, such as Mullerian bodies, extrafloral nectaries, domatia or other structures with ants. Leaves and flowers, if present, were sampled for identification of the plants. The presence of honeydew-producing hemipterans was not considered as a plant structure and plants hosting them were not studied here, although these hemipterans also attract ants.

Sampling of ants. Each site was sampled twice, once in the wet season (August-November 1992) and again in the dry season (February-May 1993). Samples were taken along a 180 m transect, placing at each 10 m a pitfall trap on the soil and one on the tree canopy (Figs 1, 2). Pitfall traps placed on the soil consisted of a plastic beaker of 210 ml capacity as described by Romero & Jaffe (1989). The beaker contained 50 ml of 1% formaldehyde for trapping ants. Baits consisting of a mix of honey, tuna, cake and jam were placed on a small iron tripod located inside the beaker. Traps were protected with a metal mesh with holes of 1 cm^2 to avoid feeding by rodents and other animals, and with a plastic roof to avoid rain filling the traps. Along the transect, at each 10 m, a pitfall trap was placed on the largest tree available in a radius

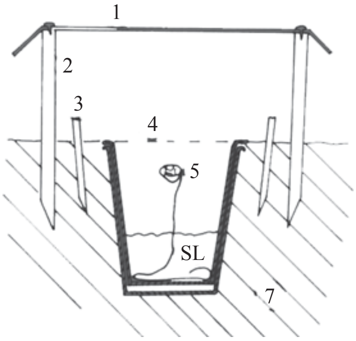

Fig 1 Pitfall traps used for collection of soil ants. 1: plastic roof, 2: support for roof, 3: anchor for the metallic grid, 4: metallic grid, 5: attractant bait, 6: soil, SL: solution of 1% formaldehyde in water.

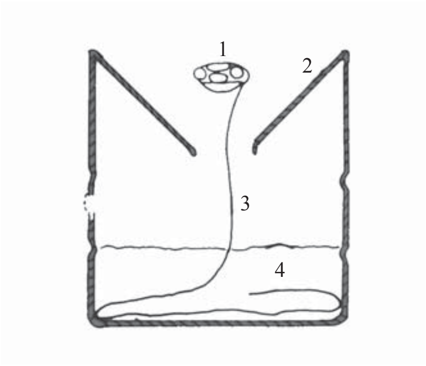

Fig 2 Pitfall traps used for collecting ants in the canopy. 1: bait, 2: funnel, 3: iron wire, 4: solution of 1% formaldehyde in water.

of 1.5 m from the point in the transect. The traps consisted of plastic beakers of 200 ml capacity with the same bait and formaldehyde solution as described above. The beaker had an inverted plastic cylinder covering the entrance serving as a funnel. The surface of the funnel was covered with deodorized talk powder, to favor the gliding of ants into the beaker. The traps were fixed to a rope and were hung from a branch and elevated until reaching the lower branches of the canopy, which depending on the plant was 3 m to 20 m above the ground. All traps were collected and replaced every two days during six days.

In each site, in addition to the samples taken along the transect, other sampling efforts were performed. These samplings aimed at focusing on ants not captured by pitfall traps and those foraging and living on MP. These "extra samples" were studied for their ants by direct sampling. For each extra plant specimen, we spent five minutes collecting ants in the morning (8-11 am) and five in the afternoon (3-6 pm). Direct sampling of ants in the site was performed by slowly walking in the forest, near the transect, collecting ants seen on the soil and the vegetation during 10h at each site distributed with 5h collecting on the soil and 5h on the "tall trees" (not counting the time taken to climb the trees). For this sampling we used forceps and entomological nets. The "tall trees" were climbed with the help of static ropes (Perry 1978). On each tree climbed, ants were collected by direct sampling for 10 min. Thus, total sampling time in the canopy by direct sampling, on each site was 5h (in Cata and Cúpira, no or very few tall trees could be found and thus, the total number of tall trees climbed was zero and three, respectively). This sampling effort aimed at collecting ants that are normally not captured with pitfall traps. The behavior of the ants found was observed and recruitment behavior and feeding on plant structures was noted. Ant samples were deposited at the Museo de Entomologia MIZA and plant samples at the Herbarium MY-FAGRO, both at Universidad Central de Venezuela in Maracay, Venezuela.

Assessing leaf damage. In order to quantify leaf-damage on plants and correlate it with the ant species found on the plants, we proceeded as follows: On each tree we selected four branches, one on each axis of an imaginary horizontal cross. On each branch we selected at random two groups of 10 old leaves and two of young leaves and visually examined them for damage (defoliation, spots, fungi, deformations, sclerosis), estimating the total damage as a percentage of the total leaf surface, by placing the leaves on a grid and visually estimating the damaged area. In the case of tall trees, we climbed to the lower part of the canopy using the method of Perry (1978).

Calculating the indices (frequency of occurrence and diversity). Species richness was estimated as the total number of ant or plant species captured or found in the area defined by the transect. Ant and plant abundance were estimated using the frequency index for the transect $FI = \Sigma fi / k$, where fi is the frequency of capture of species i, k is the total number of sample units examined. FI was calculated as the sum of all fi of each ant species found. Sample units k for ants corresponded to 36 traps, and for plants k corresponded to eighteen $10\ m^2$ plots. This index estimated the average of the frequency of occurrence of a species in each site. This frequency index, a proxy for true abundance, allows for comparisons between ant abundances and that of other non social species, such as plants. The reason we used this index, and not ant abundance assessed by the number of workers captured in traps, was due to the fact that ants recruit to baits and thus, the amount of ants captured in a trap depends largely on the recruiting habits of the specific species (for details see Romero & Jaffe 1989). The FI index, thus, gives a relative estimate of the likelihood of finding plant specimens or ant workers of any species in a sampling unit.

In addition, Margalef's diversity index was calculated as $D_{Mg} = S\text{-}1/\ln N$, were S = number of species, N = total number of individuals (frequency in our case). The Berger-Parker index was calculated as $d = N_{max}/N$, were N_{max} is the number of individuals of the most abundant species (frequency in our case). The similarity coefficient of Sorensen was calculated as $I_S = 2c/a+b$, were "a" is the number of species in site 1, "b" is the number of species in site 2 and "c" is the number of species shared between both biotopes (Moreno 2001).

Soil analysis. We collected soil samples on three different points of each transect; at each extreme and in the center of the transect. For each sample a 10 cm hole was excavated and then, three shovels of soil were placed into a plastic bag. The three soil samples for each transect where mixed and 1 kg of the mix was used for analysis at the Laboratorio de Suelos, FONAIAP, Maracay using the methods indicated in Gilabert *et al* (1990). That is, the distribution of particles was assed by Zouyuco's method, phosphor and potassium by Olsen's method, organic material by humid combustion, the pH and electric conductivity were assessed with a conductometer, and magnesium and calcium using Morgan's method.

Results

Plant diversity. All sites explored had MP (myrmecophilous plants) (Tables 1, 2). We found a total of 64 plant species of MP from 17 different families. Some of these plants possessed only extra floral nectaries (PEFN: 57 species from 12 families), whereas others (PD: seven species from five families) were true myrmecophytes possessing domatia. The PEFN species most frequently encountered were from the families Leguminoceae, Passifloraceae, and the PD species most frequently encountered were from the family Cecropiaceae.

The most common MP was *Cecropia peltata* (Cecropiaceae), found in four out of eight localities. No PD, but only PEFN were found in Cata and Uracoa. In Cúpira we found *Triplaris caracassana* which was associated with Pseudomyrmex symbioticus (Forel) and *C. peltata* with *Azteca ovaticeps* (Forel), which was also predominant in Cupo. In San Ignacio and San Francisco we found the largest number of MP: *Tococa guianensis* associated with *Azteca* spp. and *Crematogaster* sp12, *Cordia nodosa* with *Azteca* sp. 1, and *Cecropia* spp. with *Azteca xanthochroa* (Roger). In Sartenejas *Cecropia* spp. - *A. ovaticeps* associations were common in addition to *Tillandsia pruinosa* associated with *Strumigenys usbensis* Latke & Goitia and *Crematogaster* spp. In Rancho Grande, *Cecropia* spp. were associated with *Azteca*

Table 1 Myrmecophiles and their associated ants in different sites.

Families of myrmecophilous plants	Plant species	Plant trait	Ants[1]	Sites
Apocynaceae	*Plumeria alba*	EFN	5[2] *Camponotus crassus* 5 *Crematogaster* sp. 9	C
Bignonaceae	Bignonaceae 1	EFN	2 *Azteca foreli* 3 *Cephalotes atratus* 2 *Cephalotes pusillus* 2 *Leptothorax* sp. 3 2 *Pseudomyrmex* sp. 5	Cu
Boraginaceae	*Cordia nodosa*	Domatia	0; 8 *Azteca* sp. 2 0; 2 *Crematogaster* sp. 18 8; 0 *Myrmelachysta* sp. 1 3; 0 *Solenopsis* sp. 7 2; 0 *Wasmannia auropunctata*	SI, SF
Bromeliaceae	*Tillandsia pruinosa*	Domatia	2 *Crematogaster* sp. 7 2 *Crematogaster* sp. 18 5 *Strumigenys usbense*	S
Cactaceae	*Hylocereus venezuelensis*	EFN	4 *Crematogaster* sp. 9 2 *Dolichoderus debilis*	C
	Opuntia caracasana	EFN	2 *Camponotus* sp. 7 3 *Crematogaster* sp.9	C
Capparidaceae	*Capparis hastata*	EFN	5 *Camponotus crassus* 7 *Camponotus* sp. 7 3 *Dolichoderus debilis*	C
	Capparis sp.	EFN	6 *Camponotus crassus* 3 *Cephalotes atratus* 4 *Solenopsis* sp. 5	Cu

Continue

Table 1 Continuation.

Families of myrmecophilous plants	Plant species	Plant trait	Ants¹	Sites
Convolvulaceae	*Ipomoea batatoides*	EFN	3 *Camponotus* sp. 7	C
			2 *Crematogaster* sp. 3	
			8 *Crematogaster* sp. 9	
Euphorbiaceae	*Croton xanthochloros*	EFN	3 *Crematogaster* sp. 7	S
			6 *Pseudomyrmex pallens*	
	Croton sp.	EFN	1 *Solenopsis* sp. 1	RG
Fabaceae	*Acacia glomerosa*	EFN	8 *Azteca foreli*	Cu
			8 *Cephalotes atratus*	
			4 *Ectatomma ruidum*	
	Acacia sp.	EFN	7 *Azteca foreli*	Cu
			4 *Cephalotes minutus*	
			4 *Leptothorax* sp. 3	
			3 *Pseudomyrmex gracilis*	
	Crotalaria incana	EFN	1 *Pseudomyrmex oculatus*	C
	Inga laurina	EFN	1 *Myrmelachysta* sp. 3	RG
	Inga oerstediana	EFN	2 *Pseudomyrmex pallens*	S
	Inga panaensis	EFN	1 *Solenopsis* sp. 7	SI
			1 *Wasmannia auropunctata*	
	Inga tribaudina	EFN	5 *Brachymyrmex* sp. 3	SI
			3 *Solenopsis* sp. 7	
			3 *Wasmannia auropunctata*	
	Inga vera	EFN	0,2 *Crematogaster* sp. 1	SI,U
			2,0 *Ectatomma tuberculatum*	
			3,0 *Solenopsis* sp. 7	
	Inga villosissima	EFN	1 *Camponotus crassus*	RG
			1 *Myrmelachysta* sp. 3	
	Inga sp.1	EFN	2 *Azteca* sp. 2	SF
	Inga sp.2	EFN	3 *Azteca foreli*	Cp
			3 *Brachymyrmex* sp. 2	
			4 *Crematogaster* sp. 2	
			2 *Ectatomma tuberculatum*	
			2 *Wasmannia auropunctata*	
	Inga sp.3	EFN	3 *Azteca foreli*	Cp
			4 *Brachymyrmex* sp. 2	
			2 *Pseudomyrmex boopis*	
			2 *Wasmannia auropunctata*	
	Inga sp. 4	EFN	2 *Azteca foreli*	Cp
			2 *Brachymyrmex* sp. 2	
			2 *Ectatomma tuberculatum*	
			2 *Wasmannia auropuctata*	
	Piptadenia flava	EFN	5 *Camponotus crassus*	C
			6 *Crematogaster* sp. 9	

Continue

Table 1 Continuation.

Families of myrmecophilous plants	Plant species	Plant trait	Ants¹	Sites
	Pithecellobium lingustrinum	EFN	4 *Azteca foreli*	Cu
			2 *Camponotus crassus*	
			2 *Cephalotes minutus*	
			3 *Ectatomma ruidum*	
			2 *Pseudomyrmex* sp. 4	
			5 *Solenopsis* sp. 5	
	Pithecellobium unguiscati	EFN	8 *Camponotus crassus*	C
			8 *Crematogaster* sp. 9	
	Pithecellobium sp. 1	EFN	3 *Azteca* sp. 3	U
			4 *Camponotus crassus*	
			3 *Paratrechina* sp. 1	
	Pithecellobium sp. 2	EFN	1 *Azteca foreli*	Cp
	Papilionoideae 1	EFN	2 *Camponotus* sp. 22	C
			5 *Crematogaster* sp. 9	
	Papilionoideae 2	EFN	2 *Camponotus* sp. 7	C
			5 *Crematogaster* sp. 9	
	Papilionoideae 3	EFN	2 *Azteca foreli*	Cu
			2 *Camponotus crassus*	
	Papilionoideae 4	EFN	7 *Brachymyrmex* sp. 3	SI
			2 *Solenopsis* sp. 7	
	Papilionoideae 5	EFN	1 *Azteca* sp. 2	SF
			1 *Pheidole* sp. 5	
	Papilionoideae 6	EFN	4 *Azteca* sp. 3	U
			3 *Camponotus crassus*	
			2 *Wasmannia auropunctata*	
Mimosoideae		EFN	5 *Azteca foreli*	Cp
			3 *Brachymyrmex* sp. 2	
			2 *Crematogaster* sp. 2	
			2 *Wasmannia auropunctata*	
Fabaceae species 1		EFN	1 *Crematogaster* sp. 2	Cp
Malvaceae	*Gossypium hirsutum*	EFN	3 *Azteca* sp. 2	C
			4 *Camponotus crassus*	
			2 *Camponotus* sp. 7	
			5 *Camponotus* sp. 22	
			3 *Crematogaster* sp. 9	
Cecropiacea	*Cecropia palmatisecta*	Domatia	2 *Azteca austrialianus*	RG
			3 *Azteca coeruleipennis*	
	Cecropia peltata	Domatia	3,1,0 *Azteca ovaticeps*	S, Cu, Cp, SF
			0,0,3 *Azteca* sp. 2	
	Cecropia sp.	Domatia	1 *Azteca xanthochroa*	SI

Continue

Table 1 Continuation.

Families of myrmecophilous plants	Plant species	Plant trait	Ants[1]	Sites
Melastomataceae	*Tococa guianensis*	Domatia	0,3 *Azteca* sp. 2 0,2 *Azteca* sp. 8 0,3 *Crematogaster* sp. 12	SI, SF
Passifloraceae	*Passiflora serrulata*	EFN	4 *Camponotuscrassus* 7 *Crematogaster* sp. 9	C
	Passiflora sp.1	EFN	3 *Azteca* sp. 2 3 *Azteca* sp. 8 2 *Camponotus* sp. 4 9 *Crematogaster* sp. 18 4 *Ectatomma tuberculatum*	SF
	Passifloraceae 1	EFN	3 *Camponotus crassus* 2 *Daceton armigerum* 2 *Pseudomyrmex* sp. 1 3 *Wasmannia auropunctata*	U
	Passifloraceae 2	EFN	1 *Azteca* sp. 3 1 *Wasmannia auropunctata*	U
	Passifloraceae 3	EFN	2 *Camponotus crassus* 2 *Cephalotes minutus* 2 *Ectatomma tuberculatum* 2 *Pheidole* sp. 5 3 *Wasmannia auropunctata*	SF
Polygonaceae	*Triplaris caracassana*	Domatia	3 *Azteca foreli* 9 *Pseudomyrmex symbioticus*	Cu
Rosaceae	*Licania pittieri*	EFN	1 *Camponotus* sp. 7 1 *Myrmelachysta* sp. 3 1 *Solenopsis* sp. 1	RG
Verbenaceae	*Aegiphila fendleri*	EFN	2 *Solenopsis* sp. 10	RG
Zingiberaceae	*Costus* sp.(C)	EFN	1 *Azteca* sp. 8 1 *Camponotus crassus*	SF
Non identified families				
A		EFN	7 *Camponotus* sp. 7 4 *Lepthotorax asper*	C
B		EFN	1 *Crematogaster* sp. 9	C
C		EFN	4 *Azteca* sp. 4 3 *Camponotus crassus* 2 *Crematogaster* sp. 1 3 *Pseudomyrmex* sp. 1	U
D		EFN	4 *Azteca* sp. 4 2 *Brachymyrmex* sp. 1 2 *Camponotus crassus* 3 *Crematogaster* sp. 1	U

Continue

Table 1 Continuation.

Families of myrmecophilous plants	Plant species	Plant trait	Ants[1]	Sites
			3 *Daceton armigerum* 2 *Pseudomyrmex* sp. 1 3 *Wasmannia auropunctata*	
E		EFN	2 *Crematogaster* sp. 1 1 *Lepthotorax* sp. 2	U
F		EFN	1 *Azteca* sp. 5 1 *Camponotus* sp. 9	U
G		EFN	4 *Brachymyrmex* sp. 3 3 *Solenopsis* sp. 7	SI
H		EFN	1 *Azteca* sp. 8	SF
I		EFN	3 *Wasmannia auropunctata*	SF
J		EFN	4 *Camponotus crassus*	SF
K		EFN	2 *Crematogaster* sp. 18 5 *Pseudomyrmex pallens*	S
L		EFN	1 *Camponotus crassus*	RG
M		EFN	1 *Solenopsis* sp. 1	RG

[1] Only ant species found on more than one plant per site are given; [2] Number of plants on which the ant species was collected.

EFN = Extra floral nectaries; Domatia = Adaptations of plants on leafs or inside trunk or branches to house ants, including hollow trunks and other structures housing ans. Some plants with domatia had also EFN

Sites: C = Cata, Cu = Cúpira, U = Uracoa, Cp = Cupo, SI = San Ignacio, SF = San Francisco, S = Sartenajas, RG = Rancho Grande

Table 2 Frequency index (FI: plant number per 10 m^2) and species richness (SR) of plants along transect and total (transect plus direct sampling) in each locality.

Locality	Collected on transect										Total collections			
	All plants		PEFN				PD				PEFN		PD	
	FI	SR	FI	SR	FI as % of all	SR as % of all	FI	SR	FI as % of all	SR as % of all	FI	SR	FI	SR
Cata	1.3	64	0.23	10	17.7	15.6	0.00	0	0.0	0.0	0.63	14	0.00	0
Cúpira	1.3	71	0.11	2	8.5	2.8	0.05	2	3.8	1.4	0.31	6	0.07	2
Uracoa	1.2	73	0.14	7	11.6	9.6	0.00	0	0.0	0.0	0.36	9	0.00	0
Cupo	1.8	108	0.14	6	7.6	5.6	0.00	1	0.0	0.0	0.21	6	0.01	1
S.Ignacio	2.8	153	0.04	2	1.4	1.3	0.03	3	1.0	0.7	0.18	5	0.07	3
S.Francisco	2.6	173	0.08	5	2.9	2.9	0.14	3	5.5	1.2	0.22	8	0.13	3
Sartenejas	1.5	88	0.08	2	5.1	2.3	0.02	2	1.1	2.3	0.14	3	0.17	2
Rancho Grande	1.6	86	0.06	1	3.9	4.7	0.00	1	0.0	0.0	0.23	7	0.03	1

australis Wheeler and *Azteca coeruleipennis* Emery.

The field data for plants with diversity and frequency indices (Table 2) reveal that sites with high percentage of PEFN [both measured as species richness (SR) or frequency of occurrence (FI)], Cata and Uracoa, were also among the sites with the lowest proportion of PD. The opposite was also true. That is, sites with the highest proportion of PD were among the sites with the lowest amount of PEFN, such as Cúpira and San Francisco. Plant diversity increased with altitude just below 1000 masl and then decreased. This trend was not evidenced among PD and PEFN. PEFN were most common in sites with the lowest altitude.

Some general trends were evident among the data. The higher the FI index for all plants (i.e. more plant specimens per square meter), the higher the diversity of plant species found. That is, plant species richness correlated strongly and positively with FI for all plants (r = 0.87, P = 0.0045).

The ant fauna. In the eight biotopes explored we found a total of 352 ant species, listed in Table 3. We found 197 ant species foraging on plants, captured 151 ant species in pitfall traps, and counted 105 ant species from direct collections. On the soil, 208 ant species were collected (pitfall traps and direct collection on the soil). Regarding comparisons between biotopes, 83.2% of ant species were found in only one of the biotopes studied, 10.5% in two, 3.1% in three, 0.9% in four, 0.6% in five, 1.1% in six and 0.6% in seven. The species most frequently encountered in the different biotopes were: *Camponotus crassus* Mayr (7), *Camponotus abdominalis* (Fabricius) (7), *Ectatomma tuberculatum* (Olivier) (6), *Wasmannia auropunctata* (Roger) (6), *Pseudomyrmex boopis* (Roger) (6), *Crematogaster* sp. 18 (6), *Pseudomyrmex gracilis* (Fabricius) (5), *Ectatomma ruidum* (Roger) (5).

When comparing species richness and FI of ants

Table 3 Frequency of capture of ant species in pitfall trap; on MP (number after & sign); and species collected by hand (*) in eight different forest sites.[1]

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	R
Myrmicinae																
Acromyrmex octospinosus			3							*	3	1				
Acromyrmex coronatus														1		
Apterostigma urichi											3	4	4			
Apterostigma sp.2														1		
Basiceros militaris														1		
Cephalotes atratus		9&10		2&1	*					1						
Cephalotes clypeatus	1&2		3			1		1								
Cephalotes minutus		5&10			1&1	&3										
Cephalotes spinosus					4&1	2										
Cephalotes umbraculatus					1	3&1										
Cephalotes sp. 2			2&1													
Cephalotes sp. 3				*												
Cephalotes sp. 4			1&2													
Cephalotes sp. 5				*												
Cephalotes sp. 6	3															
Cephalotes sp. 7		&2														
Cephalotes sp. 8						&1										
Cephalotes sp. 9		2&5														
Cephalotes sp. 10					1											
Crematogaster sp.1			10&9													
Crematogaster sp.2				5&8												
Crematogaster sp.3	&4															
Crematogaster sp.4		1&2														
Crematogaster sp.5					5&1											
Crematogaster sp.6						&1										
Crematogaster sp.7							6&6									
Crematogaster sp.8	11							3	1							
Crematogaster sp.9		12&59														
Crematogaster sp.10		&1														
Crematogaster sp.11					3&2											

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Crematogaster sp.12						3&3										
Crematogaster sp.13			1													
Crematogaster sp.14												2				
Crematogaster sp.15	9															
Crematogaster sp.16					4								5			
Crematogaster sp.17						1&1										
Crematogaster sp.18		4	5	&2		8&12	6&4				5	2	4		8	
Crematogaster sp.19					1								1			
Crematogaster sp.20																
Crematogaster sp.21		1														
Crematogaster sp.22														1		
Crematogaster sp.23													1			
Crematogaster sp.24													1	10		
Crematogaster sp.25													1			
Cyphomyrmex sp.1												1				
Cyphomyrmex sp.2									1		5					
Cyphomyrmex sp.3										1				3		
Cyphomyrmex sp.4																
Cyphomyrmex sp.5																1
Daceton armigerum			&8								1					
Hylomyrma sp. 1													1			
Leptothorax asper	2&6															
Leptothorax sp.2			1													
Leptothorax sp.3		1&10	1&1													
Leptothorax sp.4					1											
Leptothorax sp.5						*										
Leptothorax sp.6															*	
Megalomyrmex sp.1											2					
Mycetarotes sp. 1											4					
Mycetarotes sp. 2														1		
Mycocepurus sp. 1														1		
Myrmecocrypta sp.1										*						
Pheidole sp. 1			*													
Pheidole sp. 2	&1							1&2	3							
Pheidole sp. 4					&1											
Pheidole sp. 5						&6										
Pheidole sp. 6																
Pheidole sp. 7			1						7		7					
Pheidole sp. 8					&1								12			
Pheidole sp. 9							1									
Pheidole sp. 10								1								9
Pheidole sp. 11							2									
Pheidole sp. 12											3					

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Pheidole sp. 13		1		3												
Pheidole sp. 14		1&1								12						
Pheidole sp. 15	1				1&1				6			9				
Pheidole sp. 16			1													
Pheidole sp. 17				1												
Pheidole sp. 18		&2								12						
Pheidole sp. 19					2&1								6			
Pheidole sp. 20							1									
Pheidole sp. 21		1&9									1	3				
Pheidole sp. 22				1												
Pheidole sp. 23													1			
Pheidole sp. 24																4
Pheidole sp. 25																
Pheidole sp. 26												1				2
Pheidole sp. 27						1										
Pheidole sp. 28							1									
Pheidole sp. 29															11	
Pheidole sp. 30			1													
Pheidole sp. 31												1				
Pheidole sp. 32					3											
Pheidole sp. 33																5
Pheidole sp. 34											*					1
Pheidole sp. 35														2		
Pheidole sp. 36															8	
Pheidole sp. 37															1	
Pheidole sp. 38											1					
Pheidole sp. 39					1							15				
Pheidole sp. 40																
Pheidole sp. 41											7					
Pheidole sp. 42					1								5		6	
Pheidole sp. 43																
Pheidole sp. 44															2	
Pheidole sp. 45											2					
Pheidole sp. 46														2		
Pheidole sp. 47														5		
Pheidole sp. 48															1	
Pheidole sp. 49															1	
Pheidole sp. 50														1		
Pheidole sp. 51												2				
Pheidole sp. 52													5			
Pheidole sp. 53											7					
Pheidole sp. 54													1			
Pheidole sp. 55											13					

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Pheidole sp. 56													2			
Pheidole sp. 57														1		
Pheidole sp. 58											4					
Pheidole sp. 59											1					
Pheidole sp. 60											5					
Pheidole sp. 61													6	4		
Pheidole sp. 62														2		
Pheidole sp. 63																
Pheidole sp. 64													1			
Pheidole sp. 65													1			
Pheidole sp. 66													6			
Pheidole sp. 67														2		
Pheidole sp. 68														5		
Pheidole sp. 69														2		
Pheidole sp. 70												13				
Pheidole sp. 71													2			
Pheidole sp. 72													3			
Pheidole sp. 73													2			
Pheidole sp. 74													1			
Pheidole sp. 75													3			
Pheidole sp. 76													13			
Pheidole sp. 77											6					
Pheidole sp. 78										17						
Pheidole sp. 79										1						
Pheidole sp. 80																
Procryptocerus sp. 1						*										
Procryptocerus sp. 2							&2									
Rogeria sp.1																1
Solenopsis sp. 1								4&7								17
Solenopsis sp. 2						11									1	
Solenopsis sp. 3			2													
Solenopsis sp. 4				5								13			9	
Solenopsis sp. 5		5&9														
Solenopsis sp. 6							1								2	
Solenopsis sp. 7	1					16&19							10			
Solenopsis sp. 8	13&2								6							
Solenopsis sp. 9		1&1								1						
Solenopsis sp. 10								1								
Solenopsis sp. 11			3													
Solenopsis sp. 12		24&1								17						
Solenopsis sp. 13																4
Solenopsis sp. 14															1	
Solenopsis sp. 15											1					

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Solenopsis sp. 16												1				
Solenopsis sp. 17									4							
Solenopsis sp. 18		&1								4						
Solenopsis sp. 19											3					
Solenopsis sp. 20												1				
Solenopsis sp. 21									3							
Solenopsis sp. 22		5														
Solenopsis sp. 23					1											
Solenopsis sp. 24														6		
Solenopsis sp. 25															1	
Solenopsis sp. 26															1	
Solenopsis sp. 27														1		
Solenopsis sp. 28											1					
Solenopsis sp. 29											11					
Solenopsis sp. 30					1								3			
Solenopsis sp. 31														10		
Solenopsis sp. 32														4		
Solenopsis sp. 33													5			
Solenopsis sp. 34											14					
Solenopsis sp. 35											4					
Solenopsis sp. 36													9			
Solenopsis sp. 37														1		
Solenopsis sp. 38														5		
Solenopsis sp. 39													13			
Solenopsis sp. 40													8			
Solenopsis sp. 41													4			
Solenopsis sp. 42														2		
Solenopsis sp. 43														1		
Solenopsis sp. 44													6			
Solenopsis sp. 45														3		
Solenopsis sp. 46														4		
Solenopsis sp. 47										11						
Solenopsis sp. 48										5						
Solenopsis sp. 49													3			
Solenopsis sp. 50					&3											
Strumigenys usbensis							&5									
Strumigenys eggersi											1					
Strumigenys cordovensis										1						
Tetramorium sp. 1									3							
Trachymyrmex sp. 1												4				
Trachymyrmex sp. 2									2							
Trachymyrmex sp. 3													2			
Wasmannia auropunctata	3	3&2	1&10	2&8	&5	2&10			1	14	14	14	6			

Continue

Table 3. Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Pseudomyrmecinae																
Pseudomyrmex acanthobius					1								1			
Pseudomyrmex boopis	1	&2	1	1&2		1		3	2		1	1				
Pseudomyrmex eduardi					1											
Pseudomyrmex elongatus	1&1															
Pseudomyrmex filiformis					&1											
Pseudomyrmex flavidulus	&3		&1								1					
Pseudomyrmex gracilis	14&5	1&10		10&1	2	3										
Pseudomyrmex maculatus						&1										
Pseudomyrmex oculatus	3&2															
Pseudomyrmex pallens							18&5									
Pseudomyrmex symbioticus		&10								2						
Pseudomyrmex tenuissimus	1&3			1		1										
Pseudomyrmex sp.1			2&11													
Pseudomyrmex sp.2				2												
Pseudomyrmex sp.3				1												
Pseudomyrmex sp.4		&5														
Pseudomyrmex sp.5							2								1	
Pseudomyrmex sp.6		&2	3													
Pseudomyrmex sp.7																
Formicinae																
Brachymyrmex sp.1			1&2								5					
Brachymyrmex sp.2				1&13								2				
Brachymyrmex sp.3					&17											
Brachymyrmex sp.4	3															
Brachymyrmex sp.5						&2										
Brachymyrmex sp.6							&1								1	
Brachymyrmex sp.7						&2										
Brachymyrmex sp.8				2												
Brachymyrmex sp.9				1												
Camponotus abdominalis	10	19	10			14	1	1	1	8	6	1		7		
Camponotus crassus	7&33	5&12		17&15	2	2&4	&4	2&4		1	7				1	
Camponotus latangulus					3								1			
Camponotus lindigi	&4															
Camponotus sericeiventris					6											
Camponotus sp.1				&1												
Camponotus sp.2						&1										
Camponotus sp.3							5									
Camponotus sp.4						&2										
Camponotus sp.5			2													
Camponotus sp.6				13												
Camponotus sp.7	2&18							1	2							

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Camponotus sp.8				1												
Camponotus sp.9			&1													
Camponotus sp.10		3														
Camponotus sp.11																
Camponotus sp.12												1				
Camponotus sp.13					3											
Camponotus sp.14						3										
Camponotus sp.15						1								1		
Camponotus sp.16					1											
Camponotus sp.17			*													
Camponotus sp.18							1									
Camponotus sp.19							4									
Camponotus sp.20					1											
Camponotus sp.21																
Camponotus sp.22	&18															
Camponotus sp.23					1											
Camponotus sp.24			6													
Camponotus sp.25					1											
Camponotus sp.26					2											
Camponotus sp.27	6				1	1			2		5		11			
Camponotus sp.28	2															
Camponotus sp.29													1			
Camponotus sp.30																
Camponotus sp.31							6									
Camponotus sp.32			&1													
Camponotus sp.33								1								
Gigantiops destructor														*		
Myrmelachista sp.1					&8			3&3								
Myrmelachista sp.2	1															
Myrmelachista sp.3																
Myrmelachista sp.4					1											
Myrmelachista sp.5					2											
Myrmelachista sp.6							&1									
Paratrechina sp.1					&1											
Paratrechina sp.2			1&4			3&3					16					
Paratrechina sp.3														8		
Paratrechina sp.4																
Paratrechina sp.5				1												
Paratrechina sp.6		2														
Paratrechina sp.7													2			
Paratrechina sp.8													10			
Paratrechina sp.9																
Paratrechina sp.10							1&2									

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Dolichoderinae																
Azteca alfari							&2									
Azteca australianus								&2								
Azteca coeruleipennis								&3								
Azteca foreli		14&27		27&16			8&1								3	
Azteca ovaticeps		&4		&2												
Azteca xanthochroa					&1											
Azteca sp. 1					5&1											
Azteca sp. 2	4&4															
Azteca sp. 3			7&20													
Azteca sp. 4						6&18										
Azteca sp. 5			3&1													
Azteca sp. 6	2&1															
Azteca sp. 7					2											
Azteca sp. 8						4&14										
Azteca sp. 9						3										
Azteca sp. 10			*													
Azteca sp. 11							1									
Azteca sp. 12											2					
Azteca sp. 13						2										
Azteca sp. 14						1										
Azteca sp. 15														2		
Azteca sp. 16							1									
Dolichoderus bispinosa	1&1	2							1		1					
Dolichoderus debilis	4&12	&3														
Dolichoderus lobicornis					8					10						
Dolichoderus lutosus			2													
Dolichoderus sp. 1			1													
Dolichoderus sp. 2																
Dolichoderus sp. 3		1			1											
Dolichoderus sp. 4					1											
Dolichoderus sp. 6	1															
Dolichoderus sp. 7						1										
Dolichoderus sp. 9		&1				2										
Dolichoderus sp. 10		4&2														
Dolichoderus sp. 11		1														
Dolichoderus sp. 12								1								
Dolichoderus sp. 13							2									
Tapinoma sp. 1									1							
Tapinoma sp. 2				3								5				
Tapinoma sp. 3													2			
Ponerinae																

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Anochetus diegensis												*				
Anochetus striatulus												*				
Anochetus sp. 1										1						
Anochetus sp. 2													3			
Anochetus sp. 3														2		
Anochetus sp. 4											2					
Ectatomma ruidum	1&3	2&7							10	18		1	9	6		
Ectatomma tuberculatum		&4	&3	3&4	&5	3&6		1				5		1		
Gnamptogenys sp. 1											1			1		
Gnamptogenys sp. 2																
Gnamptogenys sp. 3													4			
Hypoponera puctatissima											1					
Hypoponera sp. 1												*	1			
Hypoponera sp. 2																
Leptogenys sp. 1												2				
Leptogenys sp. 2										2						
Pachycondyla apicalis													1	10		
Pachycondyla villosa					4	5								1		
Odontomachus bauri										12	11	15		17		
Odontomachus chelifer												*	10	1		
Odontomachus haematodus												*				
Odontomachus sp.1									1							
Pachycondyla bucki												*				
Pachycondyla commutata									4				4			
Pachycondyla crassinoda												*				
Pachycondyla harpax					3							*	10			
Pachycondyla impressa										3						*
Pachycondyla metanotalis								1	2							
Pachycondyla stigma										4						
Pachycondyla unidentata		2														
Pachycondyla sp. 1											*					
Pachycondyla sp. 2											*					
Pachycondyla sp. 3														1		
Pachycondyla sp. 4											*					
Pachycondyla sp. 5											14					
Pachycondyla sp. 6														1		
Pachycondyla sp. 7														9		
Pachycondyla sp. 8											3					
Pachycondyla sp. 9														1		
Pachycondyla sp. 10														8		
Ecitoninae																
Eciton burchelli												2			*	*

Continue

Table 3 Continuation.

Ants	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
Labidus praedator										4						*
Neivamyrmex emersoni												*				
Neivamyrmex postcarinatus										1						
Nomarmyrmex hartigi									4							

Sites: C = Cata, Cu = Cúpira, U = Uracoa, Cp = Cupo, SI = San Ignacio, SF = San Francisco, S = Sartenajas, RG = Rancho Grande

among strata in different sites (Table 4), only in the sites with the lowest altitude (Cata and Cúpira) and the highest altitude (Sartenejas and Rancho Grande) did the canopy harbor more ants than the soil. In the intermediate sites, more ants were found on the soil than in the canopy. If only ants found exclusively in the canopy or on the soil are taken into account (Table 5), then in all localities soil ants were more diverse than canopy ants. The same data show that ants are more common on MP than on non-MP. In general, ant species richness and FI of ants on the soil correlated positively with the ant species richness in the canopy (Spearman's correlation r = 0.73, P = 0.039; and r = 0.74, P = 0.037 respectively); and FI and SR correlated very strongly among ants on the soil (r = 0.92, P = 0.0013).

Table 4 Abundance index (FI) and species richness (SR) of ants in the soil and the canopy (captured with pitfall traps) and percentages of PEFN, PD, and non-myrmecophilous plants (non-MP) plants occupied by ants (assessed with direct sampling of ants).

Locality	Altitude	Soil ants		Canopy ants		% of PEFN with ants	% of PD with ants	% of non-MP with ants
	masl	FI	SR	FI	SR			
Cata	15	1.8	21	3.5	32	89	*	10
Cúpira	25	4.5	25	3.3	26	96	100	80
Uracoa	70	6.7	42	2.6	29	77	*	70
Cupo	95	3.4	27	2.4	21	89	100	80
S. Ignacio	975	6.3	51	2.8	39	81	83	-
S. Francisco	980	4.7	47	2.5	30	92	91	-
Sartenejas	1200	1.6	18	1.9	20	65	40	40
Rancho Grande	1660	1.2	9	0.7	15	26	67	10

* No PD plants were found; - Missing data

Table 5 Number of ant species (% of ant species respect to the total in the biotope) in different forests.

Biotope	Altitude masl	Exclusively found in			Found in		
		Canopy	Soil	MP	Canopy & soil	MP & soil	MP, soil & canopy
Cata	15	7 (16)	9 (21)	3 (7)	10 (23)	1 (2)	4 (9)
Cúpira	25	10 (18)	16 (29)	9 (16)	8 (15)	2 (4)	7 (13)
Uracoa	70	15 (21)	35 (49)	3 (4)	8 (11)	1 (1)	4 (6)
Cupo	95	11 (20)	29 (53)	2 (4)	6 (11)	2 (4)	4 (7)
San Ignacio	975	21 (24)	39 (44)	8 (9)	8 (9)	2 (2)	2 (2)
San Francisco	980	16 (20)	42 (53)	9 (11)	3 (4)	0 (0)	1 (1)
Sartenajas	1200	11 (28)	15 (39)	3 (8)	4 (10)	1 (3)	2 (5)
Rancho Grande	1660	9 (33)	10 (37)	3 (11)	1 (4)	0 (0)	1 (4)

Table 6 Frequency index (FI), species richness (SR), Margalef's diversity index (DiI), Berger-Parker's dominance index (DoI) of ants in the canopy, soil and in all pitfall traps, MP, total, and percentages of PEFN, PF and non-myrmecophilous plants (non-MP) plants occupied by ants (assessed with direct sampling (DS) of ants).

Locality	Altitude masl	Pitfall traps in												SR of ants on MP			Total SR
		Soil				Canopy				Total							
		FI	SR	DiI	DoI	FI	SR	DiI	DoI	FI	SR (A)	DiI	DoI	Total (B)	+ canopy	+ soil	A+B+DS
Cata	15	1.8	21	4.8	0.2	3.5	29	5.8	0.1	5.2	39	7.3	0.1	20	15	5	44
Cúpira	25	4.5	25	4.7	0.1	3.3	27	5.4	0.2	7.9	44	7.6	0.1	28	16	10	55
Uracoa	70	5.7	42	7.7	0.1	2.6	28	6.0	0.1	8.3	60	10.4	0.1	16	11	6	71
Cupo	95	3.4	27	5.4	0.1	2.4	21	4.5	0.3	5.8	42	7.7	0.1	11	8	5	55
S. Ignacio	975	6.3	51	9.3	0.1	2.8	39	8.3	0.2	9.1	80	13.7	0.1	18	8	4	89
S. Francisco	980	4.5	46	8.9	0.1	2.5	28	6.0	0.2	6.9	70	12.5	0.1	19	10	1	80
Sartenejas	1200	1.6	18	4.2	0.2	1.9	19	4.3	0.3	3.5	33	6.6	0.1	11	5	4	39
Rancho Grande	1660	1.2	9	2.1	0.4	0.7	14	4.1	0.2	1.9	21	4.7	0.3	6	3	1	27

In the forests studied, a very low percentage of ant species was found exclusively on MP (Table 5).

When the ants in the different sites were compared using various indices (Tables 6 and 7), San Ignacio and San Francisco had the highest ant diversity and the lowest indices for dominance. Most dominant species there were tree dwellers. Exceptions were *Paratrechina* sp2 in Uracoa and *Pachycondyla villosa* (Fabricius) in San Francisco, which were dominant on the soil. Most dominant species in one stratum are rarely found on the other stratum, except *Solenopsis* sp12 and *C. crassus* in Uracoa and *Solenospis* sp7 in San Ignacio.

Regarding similarities (Table 8) in the myrmecofauna between biotopes, the values obtained for the indices were low. Slightly higher similarity indices were obtained for canopy ants in the proximate localities, Cata and Rancho Grande (0.28) and for the biotopes in Morichal Uracoa and Morichal San Francisco (0.29). Surprisingly, the similarity index for ant diversity between distant San Francisco and Cata (0.28) was relatively high, despite the fact that these habitats are very different. This might be explained by the fact that both sides consists of sandy savannas bordering woodland.

Ecological interactions between ants and plants. Direct sampling of MP and their ants on and outside the transect (Table 4) showed that PEFN were visited by ants more than non-MP ($P < 0.05$, binomial test). Although MP were visited by ants found on the soil and in the canopies, the highest number of visits was from canopy ants (Table 1). Few species were abundant in a biotope. In Cata: *Crematogaster* sp. 2 (on 38 PEFN), and *C. crassus* (23); in Cúpira: *Azteca foreli* Emery (21); in Uracoa: *C. crassus* (14) and *Azteca* sp.1 (13); in Cupo: *Azteca* sp. 1 (14); San Ignacio: *Solenopsis* sp. 2 (12) and *Brachymyrmex* sp. 1(15); in San Francisco: *W. auropunctata* (10) and *Azteca* sp. 3 (13). In Sartenejas and Rancho Grande none of the ants found on PEFN could be called dominant. PD maintained associations with a reduced number of ant species (mean: 2.75, range: 0 - 5) compared to PEFN which were associated with a larger number of ant species (mean: 14.5, range: 3 - 28). The Frequency Index (FI) of PEFN correlated strongly with the Species Richness (SR) of the ants present in the site (Spearman Rank Order Correlation $R = 0.83$, $P = 0.01$). In contrast, the FI of PD correlated only with the SR of ants found only on PD ($R = 0.81$, $P = 0.01$), and not with the SR of all ants in the site ($R = -0.2$, $P > 0.5$). The altitude of the site correlated negatively with AI of ants in the canopy ($r = -0.88$, $P = 0.004$) and AI of PEFN ($r = -0.77$, $P = 0.025$); but positively with ant species richness on PD ($r = 0.79$, $P = 0.02$).

The soil characteristics of the different sites are given in Table 9. When these soil characteristics are correlated with data on ant and plant diversity and abundance, some

Table 7 Shanon's diversity index (H`), equity (E) and dominance (d) for ants captured in pitfall traps in eight biotopes in Venezuela.

Locality	H	E	d	Dominant ant
Cata	3.26	0.080	0.13	*Solenopsis* sp. 8
Cúpira	3.23	0.075	0.14	*Solenopsis* sp. 12
Uracoa	3.74	0.058	0.08	*Camponotus crassus*
Cupo	3.12	0.078	0.14	*Azteca foreli*
S. Ignacio	3.97	0.051	0.08	*Solenopsis* sp. 7
S. Francisco	3.79	0.057	0.093	*Camponotus abdominalis*
Sartenejas	2.85	0.084	0.25	*Pseudomyrmes pallens*
Rancho Grande	2.43	0.122	0.31	*Solenopsis* sp. 1

Table 8 Similarity of myrmecofauna between localities, base on Sorence's index.

Strata		CU	UR	CP	SI	SF	SA	RG
Canopy	Cata	0.21	0.21	0.16	0.15	0.28	0.04	0.28
	Cúpira		0.22	0.21	0.13	0.18	0.13	0.10
	Uracoa			0.08	0.03	0.29	0.09	0.20
	Cupo				0.03	0.20	0.05	0.14
	S. Ignacio					0.18	0.00	0.04
	S. Francisco						0.08	0.24
	Sartenejas							0.06
Soil	Cata	0.12	0.21	0.17	0.11	0.06	0.00	0.00
	Cúpira		0.14	0.16	0.05	0.11	0.04	0.10
	Uracoa			0.20	0.08	0.06	0.06	0.03
	Cupo				0.16	0.12	0.11	0.08
	S. Ignacio					0.10	0.06	0.00
	S. Francisco						0.00	0.00
	Sartenejas							0.6
Total	Cata	0.16	0.17	0.14	0.12	0.15	0.05	0.23
	Cúpira		0.19	0.25	0.4	0.18	0.09	0.15
	Uracoa			0.14	0.08	0.15	0.05	0.12
	Cupo				0.17	0.15	0.11	0.12
	S. Ignacio					0.18	0.05	0.05
	S. Francisco						0.07	0.09
	Sartenejas							0.09

interesting relations are found. A Spearman rank correlation analysis of these data was filtered, following the method advised by Rice (1989), and only the most statistically significant results are given in Table 10. These results show that the ant species richness on MP plants correlated positively with the amount of phosphor in the soil. That is, high phosphor containing soils favored ants on MP. Phosphor (P) and potassium (K^+) content in the soils was cross-correlated. The frequency of occurrence of PD however was more correlated to the amount of organic material in the soil, as assessed by the amount of carbon (C). In addition, the proportion of PD relative to total plants correlated positively with phosphorus ($r = 0.85$, $P < 0.05$), potassium ($r = 0.82$, $P < 0.05$) and organic material as indicated by C ($r = 0.86$, $P < 0.05$). This last correlation was also evidenced when using the FI index of PD ($r = 0.84$, $P < 0.05$). The pH of the soil decreased with altitude. This decrease in pH and altitude was accompanied by a decrease in ants found exclusively

Table 9 Soil characteristics of the various sites.

Locality	Sand %	Silt %	Clay %	Conduc. (mmohs/cm)	K ppm	Ca ppm	P ppm	C %	pH
Cata	74.6	16	9.4	0.17	380	695	20	2.55	6.5
Cúpira	42.6	34	23.4	0.16	456	1500	33	6.01	6.5
Uracoa	64.6	20	15.4	0.13	88	55	16	5.64	4.4
Cupo	70.6	18	11.4	0.12	108	375	15	3.25	4.3
S. Ignacio	48.8	18	32.2	0.3	112	75	18	6.39	3.6
S. Francisco	88.6	4	7.4	0.72	340	355	32	6.99	4.2
Sartenejas	73.6	14	12.4	0.34	212	155	27	6.59	3.4
Rancho Grande	63.6	22	14.4	0.11	80	115	16	5.12	3.8

Table 10 Spearman correlation indices (Bold values indicate P < 0.01).

	K	Ca	P	C	pH
Altitude	-0.523810	-0.476190	-0.131739	0.476190	-0.874267
Ant SR exclusively on canopy	-0.730552	-0.754505	-0.349398	0.311383	-0.843373
Ants SR exclusively on MP	0.595238	0.261905	0.886243	0.714286	-0.227549
Ant FI on PD	0.596132	0.215622	0.803870	0.837121	-0.172258
Ant SR on MP	0.862291	0.550908	0.698795	0.107786	0.638554
% of PD visited by ants	0.318874	0.753702	0.115954	-0.376851	0.927634
K	1.000000	0.761905	0.850315	0.214286	0.419169

in the canopy, as discussed above. Increased pH correlated strongly with the percentage of plants with domatia visited by ants (see Table 10) and with FI and SR of all ants. The SR of ants found exclusively in the canopy increased with increasing altitude.

The data on leaf damage is given in Table 11. No meaningful correlation between leaf-damage and ant diversity and frequency of abundance could be found. MP and non-MP showed similar leaf damage. Yet, foliar damage between leafs of different ages differed (Table 11), showing that our method was sensitive enough to detect differences in leaf-damages.

Table 11 Foliar damage (mean % of foliar surface) on MP and non-MP in each locality and % of MP classes visited by ants.

Locality	Leaves on PEFN				Leaves on PF		Leaves on non-MP		% of plants visited by ants		
	Ants +		Ants -		Mature	Young	Mature	Young	PEFN	PF	Non-MP
	Mature	Young	Mature	Young							
Cata	8.2 (27)	4.6*** (27)	17.3 (6)	11.3 (6)	&	&	10.7 (10)	12.7 (10)	89	&	10
Cúpira	17.2 (44)	14.2*** (44)	24.2 (5)	8.2*** (5)	17.5 (13)	11.9*** (13)	11.2 (10)	9.0* (10)	96	100	80
Uracoa	13.9 (42)	8.2*** (42)	15.6 (7)	6.5*** (7)	&	&	25.8 (10)	8.7*** (10)	77	&	70
Cupo	16.0 (29)	14.0*** (29)	13.3 (6)	11.2 (6)	&	&	14.1 (10)	10.8** (10)	89	100	80
S.Ignacio	11.9 (14)	9.0** (14)	5.7 (5)	4.4 (5)	5.6 (10)	4.1** (10)	---	---	81	83	---
S.Francisco	14.3 (25)	11.8** (25)	9.4 (7)	5.7 (7)	17.8 (26)	13.5** (26)	---	---	92	91	---
Sartenejas	40.2 (10)	29.0*** (10)	30.4 (1)	25.4 (1)	15.9 (20)	11.3** (20)	7.4 (10)	7.9 (10)	65	40	40
Rancho Grande	18.3 (9)	9.6*** (9)	25.3 (23)	10.7*** (23)	32.2 (3)	15.9* (3)	20.0 (10)	11.0*** (10)	26	67	10

*: P < 0.05, **: 0.01, ***: P < 0.001, using Wilcoxon´s matched pairs test comparing young with mature leaves.
--- : no data available. &: no plants present. Ants +: ants captured on plant. Ants -: no ants detected on plant.
( ) : number of plants examined.

Discussion

The number of families represented in the sample of PEFN represents 25% of the families with PEFN reported for the world (Elias 1983). The families Passifloraceae and Fabaceae had the most Mp species in our samples. The MP that possessed domatia PD represented 29% of the families of PD reported by Hölldobler and Wilson (1990) for the neotropics. Thus, this study seems to cover a representative fraction of the MP of the neotropics. The large number of variables assessed allows for a very large number of comparisons and correlations. Yet, we studied only eight different sites. Although eight sites are much more than most previous studies have accomplished, it is still a small number. Thus, our conclusions should be taken more as trends, or suggestions, and we will focus here only on the most conspicuous results.

The main finding of our study is that ecological conditions (soil, altitude, ant diversity, etc) that favor PD plants differ from that favoring PEFN. The abundance of organic material seem to favor PD plants; whereas PEFN rather seem to require high P and K^+ content in the soil. This result confirms the claim that domatia are more likely adaptation to favor nutrient transfer from plants than devices to reduce herbivore pressure (Cabrera & Jaffe 1994). The lack of certain nutrients, in fast growing plants competing with other secondary vegetation growing nearby, might be the strongest adaptive pressure that has driven PD to evolve and maintain devices to attract ant colonies rather than foraging ants, in order to secure more of the scare nutrients. Good data on nutrient transfer from ants to plants is needed and certainly, this possibility should be studied in more PD species.

Comparing ant faunas on the soil and in the canopy. Ecological differences and differences in feeding habits between soil and canopy ants are known to exist (Tobin 1995, Brühl *et al* 1998). Our results confirm this finding. The values for the frequency index and species richness obtained for canopy ants are difficult to compare with data from the literature. Many former works studying ants in canopies used insecticide spray to collect ants (eg. Wilson 1987, Majer 1990, Basset & Kitching 1991, Stork 1991, Tobin 1995, Brühl *et al* 1998), due to difficulties in accessing the canopy (Basset & Kitching 1991). A search for a more comparable sampling method for ants in different strata has been going on for some time (Erwin 1995). Here we used pitfall traps, which are a very simple method to collect ants in the canopy, which do not affect natural ant communities significantly, allowing for long term studies requiring repeated sampling. Pitfall traps are much less efficient in collecting arboreal ants, but if used together with direct collection, are more comparable to pitfall trap collections plus direct sampling of soil ants than tree fogging samples. Thus, results using only pitfall traps might be biased, underestimating ant diversity in the canopy relative to the soil, whereas fogging will overestimate ant diversity in the canopy.

Our data for ant species richness on the soil is consistent with reports in the literature for the neotropics (Majer & Queiroz 1990, Levings 1983, for example). We used frequency of capture as an indicator for ant abundance instead of number of workers captured because it is a better indicator for inter-species comparison than total number of ants captured (Romero & Jaffé 1989). This is because ants live in colonies and thus, the presence of a single worker signals the existence of the colony. Our method attempts to compare the frequency of capture and species richness of ants on the soil with that in tree canopies. The data show that ants are more numerous on the soil, except in the Dry Forest of Cata and the Humid Premontane Forest at Sartenejas. Direct sampling, with a similar effort in both, canopy and soil, suggest that trapping efficiency in both strata was equivalent. That is, direct sampling complements trapping with pitfall traps, as many species do not fall in pitfalls but can be collected by direct sampling (Blöthgen *et al* 2000). This is true for both strata. Thus, we propose for the exploration of canopy ant diversity, the use of pitfall traps as a simple method for robust relative comparisons of ant diversity in canopies. Stork (1991), among others, suggested that ants are more common in the canopy than on the soil. We found this to be true only in sites at very low and very high altitudes. In sites with the highest ant diversity, more ant species were found on the soil than in the canopy. Thus, relative ant abundance between soil and canopy is variable and can not be assumed to be a constant (see also Longino & Nadkarni 1990, Brühl *et al* 1998).

Strong partition between both strata, as found here, was also reported by Longino and Nadkarni (1990) for Costa Rica. The specificity of ant species to certain habitats has been investigated in Brazil by Adis *et al* (cited in Tobin 1995) who found that in three different forests, 78% of 69 ant species were found in only one of the forests, and only 4% of the species were found in all three forests. Wilson (1978) studied ants in four different sites in the Peruvian Amazon. He reported that 53.5% of 99 species were found only in one of the sites, 16.2% in two sites, 17.2% in three sites and 13.1% in four sites. We found much higher percentages of exclusive ant species than that just mentioned. This might reflect a greater diversity among the sites studied by us. The most similar localities regarding ant species were the sites closest to each other and with the same biotope (morichal). Thus, our results confirm Tobin's (1995) hypothesis that ant species show a high specialization to their habitat.

Ants on MP. A few ant species, which were frequent on canopies, were also frequently found on MP. It seems that PD attracted a specific guild of ants which is not the case for PEFN. Most of the ants found on PEFN have also been reported to visit Homoptera, myrmecophilic lepidopteran larvae (Lycaenidae & Riodinidae) and floral nectar or fruits (DeVries 1992, Rico-Gray 1993, Rico-Gray *et al* 1998, Blüthgen *et al* 2000). The ants most frequently found on PEFN were from the genera *Crematogaster*, *Camponotus*, *Azteca*, *Solenopsis*, *Brachymyrmex* and *Wasmannia*. These genera were also reported in canopies in Mexico (Rico-Gray 1993, Rico-Gray *et al* 1998) and in the Peruvian Amazon (Wilson 1987).

Foliar damage. The larger foliar damage found on mature leaves, compared to younger ones, probably only reflect the fact that older leaves have been exposed for more time to herbivores. Yet, it is surprising that in general, levels of foliar damage did not differ between MP and non-MP. This fact suggests that plants use a variety of anti-herbivore mechanisms, among which, attracting predatory ants is only one of them. A similar phenomenon was found in a canopy in the Venezuelan Amazon explored with the help of a crane (Blüthgen *et al* 2000), where trees with Homoptera were found to attract many ants. Other strategies to attract ants are known, they include, besides harboring Homoptera and Lepidoptera mirmecophiles chemical and physical defenses (Rehr *et al* 1973), and the translocation of essential nutrients and/or lower photosynthetic activity, characteristic of plants with perennial leaves (Coley 1980, 1983, Coley *et al* 1985). But ants certainly diminish herbivory through depredation of herbivorous arthropods (Barton 1986, Smiley 1986, Oliveira 1997), which diminishes defoliation (Keeler 1977, Schupp 1986) and seed loss (Bentley 1977, Barton 1986). Ants might even have alelopatic effect on neighboring plants (Janzen 1969, Downhower 1975, Schupp 1986, Davidson *et al* 1988, Davidson & McKey 1993). Yet our study found no robust ecological advantage, regarding leaf-damage, for plants making special efforts in attracting ants vs. other plants. The advantage of EFN for example was evidenced only in habitats with rich ant faunas. Our results suggest that PEFN abundance increases in sites with more ant species .Thus, PEFN seemed not only to be able to attract ants which confer them a better protection against herbivores than non-MP (see also Barton 1986, Smiley 1986, Oliveira, 1997, Blüthgen *et al* 2000); but seemed to prosper more in sites with higher ant species richness. In contrast, PD seemed to attract more specific guilds of ants than PEFN which have a different effect on herbivory (see also Schupp 1986). These results mirror very closely the ecological relationships between ants and plants reported for the paleotropics (Fiala *et al* 1994, for example).

Altitudinal distribution of ants and plants. Brown (1973) reported optimal altitudes for ant diversity in the tropics at around 800 masl. Our data confirm this report. Altitude affected ant and plant diversity similarly. At higher altitude we found a higher percentage of ants captured exclusively in the canopy. This result could be explained by the fact that forests at higher altitude had taller trees which helped in separating the ant faunas from the soil and the canopy as suggested by Brühl *et al* (1998). The biotope with the richest ant fauna were San Ignacio and Morichal San Francisco at 975 and 980 masl. At higher altitudes, the ant fauna diminished. A similar pattern was reported by Janzen *et al* (1976), who collected ants using sweeping nets in an altitudinal gradient in the Venezuelan Andes. They found 13 species of ants at 200 and 1600 m and none at 3550 and 3600 m. Olson (1994) reports maximum ant diversity in Costa Rica at 800 masl.

In Jamaica, Keeler (1979) found that ants were more abundant at lower altitudes, the same was found in the present study. Altitude, of course, affects various ecological relevant parameters, such as temperature. At higher altitudes (1.000 to 2.000 masl), humid forests tend to have a more closed canopy, maintaining low light conditions on the soil thus affecting the rate of growth of small plants (Kursar & Coley 1992a,b). Climatic conditions at higher altitudes seem to reduce populations of several ant species (Brown 1973, Janzen 1973b, Olson 1994, Fisher 1999).

Ecological factors favoring MP. Few works reporting the geographic distribution of MP exist, especially for South America (but see Morellato & Oliveira 1991). Fewer still relate MP distribution with that of ants. Keeler (1979) observed that ant abundance correlated positively with ant diversity on the soil, but she did not study arboreal ants. Bentley (1977b) found a similar correlation studying only diurnal ants.

MP in the tropics have a relative abundance from zero to 80% respect to the total plant species (Bentley 1976, 1977a, Keeler 1979, Ibarra-Manríquez & Dirzo 1990, Morellato & Oliveira 1991). Our values fall in the lower part of this large range (PEFN: 1.4 - 18% ; PD: 0 - 5.1%).

It is known that MP (Bentley 1976, Morellato & Oliveira 1991) and ants (Bentley 1976) are more abundant in successional forests and shrubland. Non-ecological causes such as taxonomic affinity or history would make plants with EFN to have a uniform geographic distribution (Keeler 1980). But abundance of plants with EFN varies predictably between habitats according to ant abundance, suggesting that both are strongly correlated. This does not mean that EFN may provide other benefits to the plants as was shown with *Inga* (Koptur 1985). In general, ant species richness on MP was greatest in habitats with soils rich in phosphor. Our results show that PD and PEFN are affected by different ecological factors. MP are a diverse group of species, and different factors may affect their distribution. Such factors may relate to soil fertility, the carrying capacity of the habitat, alternative nesting sites and availability of food for ants (Keeler 1980), and to competition for light (Janzen 1973a), nutrients, or space. PD were relatively more common in higher altitudes in contrast to PEFN which diminished their diversity with altitude. It seems thus, that at lower altitudes, where ant diversity is high, PEFN are favored as a large variety of ants may be attracted to EFN. At higher altitudes, plants seem to require more specialized features, such as domatia, in order to attract ants, and ants, at least in some PD species, have a role in providing specific nutrients rather than in protection against herbivores as was reported for *Tococa* spp. (Cabrera & Jaffe 1994), whereas on PEFN ants reduced foliar damage in locations where ants are more diverse and abundant.

The main conclusion we can draw from our results is that the ant-plant relationship differs for PEFN and PD. PD attract a more specific group of ants, because they need them to nest in the domatia. We propose that domatia are specialized in attracting ant wastes from a reduced range of ant species as an adaptation for nitrogen and/or K^+ poor habitats. In contrast, PEFN establish generalist associations with ants, as extra-floral nectaries attract a larger variety of ant species, and ant abundance seems to limit their ecological range of PEFN. The attraction of ants as a mechanism to reduce herbivory, as done by PEFN, does not seem to be superior to alternative anti-herbivore mechanisms used by plants.

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