

## **ANT-PLANT ASSOCIATIONS IN DIFFERENT FORESTS IN VENEZUELA**

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**Key words:** Ant, ant-plant association, Myrmecophilous plants, Myrmecophytes

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## **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.

## RESUMO

Nós avaliamos a hipótese que a distribuição da abundância e número de espécies de dois tipos diferentes de plantas myrmecophilas são influenciadas diferentemente pela diversidade e pela abundância da formiga. Em oito florestas naturais diferentes em Venezuela nós estimamos a riqueza de espécies e a abundância de plantas, de formigas no solo e no dossel, dos danos da folha das plantas e de nutrientes do solo. Os resultados principais do estudo mostram que as plantas com domatios para alojar formigas e plantas com nectários extrafloral (PEFN) têm relacionamentos diferentes com formigas e sofrem confinamentos ecológicos diferentes. O plantas com domatios atrai um grupo mais específico das formigas do que as PEFN. Nossos resultados são consistentes com a hipótese que o domatios são adaptações que ajudam a planta aumentar o acesso a nutrientes escassos mas que para a defesa do herbívoros. Nós encontramos que PEFN atraem uma variedade maior de espécies de formigas do que as plantas com domatios, e a abundância da formiga parece limitar a escala ecológica de PEFN. A atração das formigas como um mecanismo para reduzir herbivoria, como feito por PEFN, não parece ser superior aos mecanismos alternativos de prevenção da herbivoria usados por outras plantas. Contrário a muitos estudos anteriores, nós encontramos que as formigas são geralmente mais diversas no solo comparado a o dossel.

## INTRODUCTION

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). 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; Cabrera & Jaffe, 1994). 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* (3 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. Experimental studies showed that the presence of ants enhances the growth of PEFN (Bentley, 1976, 1977a, 1977b) 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 0 to 80% in neotropical habitats (Bentley, 1976, 1977a, 1977b; Keeler 1979; Oliveira & Leitão, 1987; Ibarra-Manríquez & Dirzo, 1990; Morellato & Oliveira, 1991) to 0 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 (Morellato & Oliveira, 1991). 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.

## **MATERIALS AND METHODS**

### **Study sites:**

The study sites had little human intervention, as assessed 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<sup>2</sup>, was marked with colored tape. On this transects, at 10 m intervals, we marked eighteen 10 m<sup>2</sup> areas. The plants and ants samples on this marked transect 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, each 10 m<sup>2</sup> 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.

**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 each 10 m a pitfall trap in the soil and one in the tree canopy (Fig. 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<sup>2</sup> to avoid feeding by rodents and other animals, and with a plastic roof to avoid rain filling the traps.

Along the transect, each 10 m, a pitfall trap was placed on the largest tree available in a radius 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, so as 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 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 5 minutes collecting ants in the morning (8-11 am) and 5 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 10 hours at each site distributed with 5 hours collecting on the soil and 5 hours 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 minutes. Thus, total sampling time in the canopy by direct sampling, on each site was 5 hours (in Cata and Cúpira, no or very few tall trees could be found and thus, the total number of tall trees climbed was 0 and 3 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 Entomología 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 4 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 area damaged. 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 or plant abundance was estimated using our frequency index for the transect  $FI = \sum f_i / k$ , where  $f_i$  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  $f_i$  of each ant species found. Sample units  $k$  for ants corresponded to 36 traps, and for plants  $k$  corresponded to eighteen 10 m<sup>2</sup> 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  $D_{Mg} = S - 1 / \ln N$ , where  $S$  = number of species,  $N$  = total number of individuals (frequency in our case). The Berger – Parker index was calculated as  $d = N_{max} / N$ , where  $N_{max}$  is the number of individuals of the most abundant species (frequency in our case). The similarity coefficient of Sorensen was calculated as  $I_S = 2c / a + b$ , where “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 were 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 assessed by Zouyucó's method, phosphorus 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

As can be observed in Table 1 and 2, all sites explored had MP (myrmecophilous plants). 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: 7 species from 5 families) were true myrmecophytes possessing domatia. The PEFN species most frequently encountered were from the families Leguminosae, Passifloraceae, and the PD species most frequently encountered were from the family Cecropiaceae.

The most common MP was *Cecropia peltata* (Cecropiaceae), found in 4 out of 8 localities. No PD, but only PEFN were found in Cata and Uracoa. In Cupira we found *Triplaris caracasana* which was associated with *Pseudomyrmex symbioticus* and *Cecropia peltata* with *Azteca ovaticeps*, 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* sp1. and *Cecropia* spp. with *Azteca xanthrochroa*. In Sartenejas *Cecropia* spp. - *Azteca ovaticeps* associations were common in addition to *Tillandsia pruinosa* associated with *Strumigenys usbense* and *Crematogaster* spp. In Rancho Grande, *Cecropia* spp. were associated with *Azteca australis* and *Azteca coeruleipennis*.

Analyzing the field data for plants with diversity and frequency indices (Table 2), reveals 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 Cupira 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 8 biotopes explored we found a total of 352 ant species. These are 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, we collected 208 ant species (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* (7), *Camponotus abdominalis* (7), *Ectatomma tuberculatum* (6), *Wasmannia auropunctata* (6), *Pseudomyrmex boopis* (6), *Crematogaster* sp. 18 (6), *Pseudomyrmex gracilis* (5), *Ectatomma ruidum* (5).

When comparing species richness and FI of ants among strata in different sites (Table 4), we found that only in the sites with the lowest altitude (Cata and Cupira) 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 shows 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 ( $r= 0.92$ ,  $p= 0.0013$ ). 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 (Table 6 and 7), we found that 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* 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 *Camponotus crassus* in Uracoa and *Solenopsis* 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

We found by direct sampling of MP and their ants on and outside the transect (Table 4) that PEFN were visited by ants more than non-MP ( $p < 0.05$ , binomial test). Although MP are 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 *Camponotus crassus* (23); in Cúpira: *Azteca foreli* (21); in Uraoa: *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: *Wasmannia 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, we found some interesting relations. 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 phosphorus in the soil. That is, high phosphorus containing soils favored ants on MP. Phosphorus (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 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.

## **DISCUSSION**

The number of families represented in our 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, our study seems to cover a representative fraction of the MP of the neotropics. The large number of variables assessed in our study allows for a very large number of comparisons and correlations. Yet, we studied only eight different sites. Although 8 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, as 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<sup>+</sup> 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 and 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 scarce nutrients.

### **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 shows 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 (Blüthgen *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 and 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 4 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 % the four sites. We found much higher percentages of exclusive ant species than that reported by the authors 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 (Rico-Gray, 1993; Rico-Gray *et al.*, 1998; Blüthgen *et al.*, 2000), myrmecophilic lepidopteran larvae (Lycaenidae & Riodinidae) (DeVries, 1992; Rico-Gray, 1993; Rico-Gray *et al.*, 1998), floral nectar or fruits (Rico-Gray, 1993; Rico-Gray *et al.*, 1998). The ants most frequently found on PEFN were from the genera *Crematogaster*, *Camponotus*, *Azteca*, *Solenopsis*, *Brachymyrmex* and *Wasmannia*. These genera have also been reported in canopies in México (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; Coley, 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 allelopathic effect on neighboring plants (Janzen, 1969; Downhower, 1975; Schupp, 1986; Davidson *et al.*, 1988; Davidson and 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 we 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 of 0 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. Our results showed that 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.

## **CONCLUSION**

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<sup>+</sup> 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.

**Acknowledgements:** We thank Lourdes Cardenas, Rafael Cardoso and Aurimar Blanco, for help in the identification of plants. Solange Issa, Manfred Verhaagh and Anne Zillikens and anonymous referees for helpful comments on the manuscript.

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Table 1: Myrmecophiles and their associated ants in different sites

Families and species of myrmecophilous plants	Plant trait	Ants*	Sites
APOCYNACEAE			
<i>Plumeria alba</i>	EFN	5** <i>Camponotus crassus</i> 5 <i>Crematogaster</i> sp. 9	C
BIGNONACEAE			
Bignoniaceae 1	EFN	2 <i>Azteca foreli</i> 3 <i>Cephalotes atratus</i> 2 <i>Cephalotes pusillus</i> 2 <i>Leptothorax</i> sp. 3 2 <i>Pseudomyrmex</i> sp. 5	Cu
BORAGINACEAE			
<i>Cordia nodosa</i>	Domatia	0; 8 <i>Azteca</i> sp. 2 0; 2 <i>Crematogaster</i> sp. 18 8; 0 <i>Myrmelachysta</i> sp. 1 3; 0 <i>Solenopsis</i> sp. 7 2; 0 <i>Wasmannia auropunctata</i>	SI, SF
BROMELIACEAE			
<i>Tillandsia pruinosa</i>	Domatia	2 <i>Crematogaster</i> sp. 7 2 <i>Crematogaster</i> sp. 18 5 <i>Strumigenys usbense</i>	S
CACTACEAE			
<i>Hylocereus venezuelensis</i>	EFN	4 <i>Crematogaster</i> sp. 9 2 <i>Dolichoderus debilis</i>	C
<i>Opuntia caracasana</i>	EFN	2 <i>Camponotus</i> sp. 7 3 <i>Crematogaster</i> sp.9	C
CAPPARIDACEAE			
<i>Capparis hastata</i>	EFN	5 <i>Camponotus crassus</i> 7 <i>Camponotus</i> sp. 7 3 <i>Dolichoderus debilis</i>	C
<i>Capparis</i> sp.	EFN	6 <i>Camponotus crassus</i> 3 <i>Cephalotes atratus</i> 4 <i>Solenopsis</i> sp. 5	Cu
CONVOLVULACEAE			
<i>Ipomoea batatoides</i>	EFN	3 <i>Camponotus</i> sp. 7 2 <i>Crematogaster</i> sp. 3 8 <i>Crematogaster</i> sp. 9	C
EUPHORBIACEAE			
<i>Croton xanthochloros</i>	EFN	3 <i>Crematogaster</i> sp. 7 6 <i>Pseudomyrmex pallens</i>	S
<i>Croton</i> sp.	EFN	1 <i>Solenopsis</i> sp. 1	RG
FABACEAE			
<i>Acacia glomerosa</i>	EFN	8 <i>Azteca foreli</i> 8 <i>Cephalotes atratus</i> 4 <i>Ectatomma ruidum</i>	Cu
<i>Acacia</i> sp.	EFN	7 <i>Azteca foreli</i> 4 <i>Cephalotes minutus</i> 4 <i>Leptothorax</i> sp. 3 3 <i>Pseudomyrmex gracilis</i>	Cu
<i>Crotalaria incana</i>	EFN	1 <i>Pseudomyrmex oculatus</i>	C

<i>Inga laurina</i>	EFN	1 <i>Myrmelachysta</i> sp. 3	RG
<i>Inga oerstediana</i>	EFN	2 <i>Pseudomyrmex pallens</i>	S
<i>Inga panaensis</i>	EFN	1 <i>Solenopsis</i> sp. 7	SI
		1 <i>Wasmannia auropunctata</i>	
<i>Inga tribaudina</i>	EFN	5 <i>Brachymyrmex</i> sp. 3	SI
		3 <i>Solenopsis</i> sp. 7	
		3 <i>Wasmannia auropunctata</i>	
<i>Inga vera</i>	EFN	0,2 <i>Crematogaster</i> sp. 1	SI,U
		2,0 <i>Ectatomma tuberculatum</i>	
		3,0 <i>Solenopsis</i> sp. 7	
<i>Inga villosissima</i>	EFN	1 <i>Camponotus crassus</i>	RG
		1 <i>Myrmelachysta</i> sp. 3	
<i>Inga</i> sp.1	EFN	2 <i>Azteca</i> sp. 2	SF
<i>Inga</i> sp.2	EFN	3 <i>Azteca foreli</i>	Cp
		3 <i>Brachymyrmex</i> sp. 2	
		4 <i>Crematogaster</i> sp. 2	
		2 <i>Ectatomma tuberculatum</i>	
		2 <i>Wasmannia auropunctata</i>	
<i>Inga</i> sp.3	EFN	3 <i>Azteca foreli</i>	Cp
		4 <i>Brachymyrmex</i> sp. 2	
		2 <i>Pseudomyrmex boopis</i>	
		2 <i>Wasmannia auropunctata</i>	
<i>Inga</i> sp. 4	EFN	2 <i>Azteca foreli</i>	Cp
		2 <i>Brachymyrmex</i> sp. 2	
		2 <i>Ectatomma tuberculatum</i>	
		2 <i>Wasmannia auropuctata</i>	
<i>Piptadenia flava</i>	EFN	5 <i>Camponotus crassus</i>	C
		6 <i>Crematogaster</i> sp. 9	
<i>Pithecellobium lingustrinum</i>	EFN	4 <i>Azteca foreli</i>	Cu
		2 <i>Camponotus crassus</i>	
		2 <i>Cephalotes minutus</i>	
		3 <i>Ectatomma ruidum</i>	
		2 <i>Pseudomyrmex</i> sp. 4	
		5 <i>Solenopsis</i> sp. 5	
<i>Pithecellobium unguis-cati</i>	EFN	8 <i>Camponotus crassus</i>	C
		8 <i>Crematogaster</i> sp. 9	
<i>Pithecellobium</i> sp. 1	EFN	3 <i>Azteca</i> sp. 3	U
		4 <i>Camponotus crassus</i>	
		3 <i>Paratrechina</i> sp. 1	
<i>Pithecellobium</i> sp. 2	EFN	1 <i>Azteca foreli</i>	Cp
Papilionoideae 1	EFN	2 <i>Camponotus</i> sp. 22	C
		5 <i>Crematogaster</i> sp. 9	
Papilionoideae 2	EFN	2 <i>Camponotus</i> sp. 7	C
		5 <i>Crematogaster</i> sp. 9	
Papilionoideae 3	EFN	2 <i>Azteca foreli</i>	Cu
		2 <i>Camponotus crassus</i>	
Papilionoideae 4	EFN	7 <i>Brachymyrmex</i> sp. 3	SI
		2 <i>Solenopsis</i> sp. 7	
Papilionoideae 5	EFN	1 <i>Azteca</i> sp. 2	SF
		1 <i>Pheidole</i> sp. 5	
Papilionoideae 6	EFN	4 <i>Azteca</i> sp. 3	U
		3 <i>Camponotus crassus</i>	
		2 <i>Wasmannia auropunctata</i>	
Mimosoideae	EFN	5 <i>Azteca foreli</i>	Cp
		3 <i>Brachymyrmex</i> sp. 2	
		2 <i>Crematogaster</i> sp. 2	

			2 <i>Wasmannia auropunctata</i>	
Fabaceae 1	EFN		1 <i>Crematogaster</i> sp. 2	Cp
MALVACEAE				
<i>Gossypium hirsutum</i>	EFN		3 <i>Azteca</i> sp. 2	C
			4 <i>Camponotus crassus</i>	
			2 <i>Camponotus</i> sp. 7	
			5 <i>Camponotus</i> sp. 22	
			3 <i>Crematogaster</i> sp. 9	
MORACEAE				
<i>Cecropia palmatisecta</i>	Domatia		2 <i>Azteca australianus</i>	RG
			3 <i>Azteca coeruleipennis</i>	
<i>Cecropia peltata</i>	Domatia		3,1,0 <i>Azteca ovaticeps</i>	S, Cu, Cp, SF
			0,0,3 <i>Azteca</i> sp. 2	
<i>Cecropia</i> sp.	Domatia		1 <i>Azteca xanthochroa</i>	SI
MELASTOMATAACEAE				
<i>Tococa guianensis</i>	Domatia		0,3 <i>Azteca</i> sp. 2	SI, SF
			0,2 <i>Azteca</i> sp. 8	
			0,3 <i>Crematogaster</i> sp. 12	
PASSIFLORACEAE				
<i>Passiflora serrulata</i>	EFN		4 <i>Camponotus crassus</i>	C
			7 <i>Crematogaster</i> sp. 9	
<i>Passiflora</i> sp.1	EFN		3 <i>Azteca</i> sp. 2	SF
			3 <i>Azteca</i> sp. 8	
			2 <i>Camponotus</i> sp. 4	
			9 <i>Crematogaster</i> sp. 18	
			4 <i>Ectatomma tuberculatum</i>	
Passifloraceae 1	EFN		3 <i>Camponotus crassus</i>	U
			2 <i>Daceton armigerum</i>	
			2 <i>Pseudomyrmex</i> sp. 1	
			3 <i>Wasmannia auropunctata</i>	
Passifloraceae 2	EFN		1 <i>Azteca</i> sp. 3	U
			1 <i>Wasmannia auropunctata</i>	
Passifloraceae 3	EFN		2 <i>Camponotus crassus</i>	SF
			2 <i>Cephalotes minutus</i>	
			2 <i>Ectatomma tuberculatum</i>	
			2 <i>Pheidole</i> sp. 5	
			3 <i>Wasmannia auropunctata</i>	
POLYGONACEAE				
<i>Triplaris caracasana</i>	Domatia		3 <i>Azteca foreli</i>	Cu
			9 <i>Pseudomyrmex symbioticus</i>	
ROSACEAE				
<i>Licania pittieri</i>	EFN		1 <i>Camponotus</i> sp. 7	RG
			1 <i>Myrmelachysta</i> sp. 3	
			1 <i>Solenopsis</i> sp. 1	
VERBENACEAE				
<i>Aegiphila fendleri</i>	EFN		2 <i>Solenopsis</i> sp. 10	RG
ZINGIBERACEAE				
<i>Costus</i> sp.(C)	EFN		1 <i>Azteca</i> sp. 8	SF
			1 <i>Camponotus crassus</i>	
Non identified families				
A	EFN		7 <i>Camponotus</i> sp. 7	C
			4 <i>Lepthorax asper</i>	
B	EFN		1 <i>Crematogaster</i> sp. 9	C
C	EFN		4 <i>Azteca</i> sp. 4	U
			3 <i>Camponotus crassus</i>	
			2 <i>Crematogaster</i> sp. 1	

D	EFN	3 <i>Pseudomyrmex</i> sp. 1	U
		4 <i>Azteca</i> sp. 4	
		2 <i>Brachymyrmex</i> sp. 1	
		2 <i>Camponotus crassus</i>	
		3 <i>Crematogaster</i> sp. 1	
		3 <i>Daceton armigerum</i>	
		2 <i>Pseudomyrmex</i> sp. 1	
		3 <i>Wasmannia auropunctata</i>	
E	EFN	2 <i>Crematogaster</i> sp. 1	U
		1 <i>Lepthorax</i> sp. 2	
F	EFN	1 <i>Azteca</i> sp. 5	U
		1 <i>Camponotus</i> sp. 9	
G	EFN	4 <i>Brachymyrmex</i> sp. 3	SI
		3 <i>Solenopsis</i> sp. 7	
H	EFN	1 <i>Azteca</i> sp. 8	SF
I	EFN	3 <i>Wasmannia auropunctata</i>	SF
J	EFN	4 <i>Camponotus crassus</i>	SF
K	EFN	2 <i>Crematogaster</i> sp. 18	S
		5 <i>Pseudomyrmex pallens</i>	
L	EFN	1 <i>Camponotus crassus</i>	RG
M	EFN	1 <i>Solenopsis</i> sp. 1	RG

\*=Only ant species found on more than one plant per site are given.

\*\* = Number of plants on which the ant species was collected

EFN = Extra floral nectaries

Domatia = Adaptations of plants on leaves or inside trunk or branches to house ants, including hollow trunks and other structures housing ants.

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

Table 2: Frequency index (FI: plant number per 10m<sup>2</sup>) 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	<b>17.7</b>	<b>15.6</b>	0.00	0	0.0	0.0	0.63	14	0.00	0
Cupira	1.3	71	0.11	2	8.5	2.8	0.05	2	<b>3.8</b>	<b>1.4</b>	0.31	6	0.07	2
Uracoa	1.2	73	0.14	7	<b>11.6</b>	<b>9.6</b>	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	<b>5.5</b>	<b>1.2</b>	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

Table 3: Frequency of capture of ant species in pitfall trap; on MP (number after & sign); and species collected by hand (\*) in 8 different forest sites

ANTS	Canopy								Soil							
	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg	Ca	Cu	Ur	Cp	Si	Sf	Sa	Rg
MYRMICINAE																
<i>Acromyrmex octospinosus</i>				3						*	3	1				
<i>Acromyrmex coronatus</i>																1
<i>Apterostigma urichi</i>											3	4	4			
<i>Apterostigma</i> sp.2																1
<i>Basiceros militaris</i>																1
<i>Cephalotes atratus</i>		9&10		2&1	*						1					
<i>Cephalotes clypeatus</i>	1&2		3				1	1								
<i>Cephalotes minutus</i>		5&10			1&1	&3										
<i>Cephalotes spinosus</i>					4&1	2										
<i>Cephalotes umbraculatus</i>					1	3&1										
<i>Cephalotes</i> sp. 2			2&1													
<i>Cephalotes</i> sp. 3				*												
<i>Cephalotes</i> sp. 4			1&2													
<i>Cephalotes</i> sp. 5				*												
<i>Cephalotes</i> sp. 6	3															
<i>Cephalotes</i> sp. 7		&2														
<i>Cephalotes</i> sp. 8							&1									
<i>Cephalotes</i> sp. 9		2&5														
<i>Cephalotes</i> sp. 10					1											
<i>Crematogaster</i> sp.1			10&9													
<i>Crematogaster</i> sp.2				5&8												
<i>Crematogaster</i> sp.3	&4															
<i>Crematogaster</i> sp.4		1&2														
<i>Crematogaster</i> sp.5					5&1											
<i>Crematogaster</i> sp.6						&1										
<i>Crematogaster</i> sp.7							6&6									
<i>Crematogaster</i> sp.8	11							3	1							
<i>Crematogaster</i> sp.9	12&59															
<i>Crematogaster</i> sp.10		&1														
<i>Crematogaster</i> sp.11					3&2											
<i>Crematogaster</i> sp.12						3&3										
<i>Crematogaster</i> sp.13			1													
<i>Crematogaster</i> sp.14												2				
<i>Crematogaster</i> sp.15	9															
<i>Crematogaster</i> sp.16					4									5		
<i>Crematogaster</i> sp.17						1&1										
<i>Crematogaster</i> sp.18		4	5	&2		8&12	6&4				5	2	4		8	
<i>Crematogaster</i> sp.19					1								1			
<i>Crematogaster</i> sp.20																
<i>Crematogaster</i> sp.21		1														
<i>Crematogaster</i> sp.22															1	
<i>Crematogaster</i> sp.23													1			
<i>Crematogaster</i> sp.24													1	10		
<i>Crematogaster</i> sp.25													1			
<i>Cyphomyrmex</i> sp.1												1				
<i>Cyphomyrmex</i> sp.2									1		5					
<i>Cyphomyrmex</i> sp.3										1					3	
<i>Cyphomyrmex</i> sp.4																



<i>Pheidole</i> sp. 41				7					
<i>Pheidole</i> sp. 42		1				5		6	
<i>Pheidole</i> sp. 43									
<i>Pheidole</i> sp. 44								2	
<i>Pheidole</i> sp. 45				2					
<i>Pheidole</i> sp. 46							2		
<i>Pheidole</i> sp. 47							5		
<i>Pheidole</i> sp. 48									1
<i>Pheidole</i> sp. 49									1
<i>Pheidole</i> sp. 50								1	
<i>Pheidole</i> sp. 51						2			
<i>Pheidole</i> sp. 52							5		
<i>Pheidole</i> sp. 53				7					
<i>Pheidole</i> sp. 54							1		
<i>Pheidole</i> sp. 55				13					
<i>Pheidole</i> sp. 56							2		
<i>Pheidole</i> sp. 57								1	
<i>Pheidole</i> sp. 58				4					
<i>Pheidole</i> sp. 59				1					
<i>Pheidole</i> sp. 60				5					
<i>Pheidole</i> sp. 61							6	4	
<i>Pheidole</i> sp. 62								2	
<i>Pheidole</i> sp. 63									
<i>Pheidole</i> sp. 64							1		
<i>Pheidole</i> sp. 65							1		
<i>Pheidole</i> sp. 66							6		
<i>Pheidole</i> sp. 67								2	
<i>Pheidole</i> sp. 68								5	
<i>Pheidole</i> sp. 69								2	
<i>Pheidole</i> sp. 70							13		
<i>Pheidole</i> sp. 71							2		
<i>Pheidole</i> sp. 72							3		
<i>Pheidole</i> sp. 73							2		
<i>Pheidole</i> sp. 74							1		
<i>Pheidole</i> sp. 75							3		
<i>Pheidole</i> sp. 76							13		
<i>Pheidole</i> sp. 77						6			
<i>Pheidole</i> sp. 78						17			
<i>Pheidole</i> sp. 79						1			
<i>Pheidole</i> sp. 80									
<i>Procryptocerus</i> sp. 1			*						
<i>Procryptocerus</i> sp. 2									
<i>Rogeria</i> sp. 1									1
<i>Solenopsis</i> sp. 1								4&7	17
<i>Solenopsis</i> sp. 2					11				1
<i>Solenopsis</i> sp. 3				2					
<i>Solenopsis</i> sp. 4					5			13	9
<i>Solenopsis</i> sp. 5				5&9					
<i>Solenopsis</i> sp. 6									2
<i>Solenopsis</i> sp. 7		1			16&19			10	
<i>Solenopsis</i> sp. 8		13&2					6		
<i>Solenopsis</i> sp. 9			1&1					1	
<i>Solenopsis</i> sp. 10								1	





<i>Camponotus</i> sp.26				2					
<i>Camponotus</i> sp.27	6			1	1		2	5	11
<i>Camponotus</i> sp.28	2								
<i>Camponotus</i> sp.29									1
<i>Camponotus</i> sp.30									
<i>Camponotus</i> sp.31						6			
<i>Camponotus</i> sp.32			&1						
<i>Camponotus</i> sp.33							1		
<i>Gigantiops destructor</i>									*
<i>Myrmelachista</i> sp.1				&8			3&3		
<i>Myrmelachista</i> sp.2	1								
<i>Myrmelachista</i> sp.3									
<i>Myrmelachista</i> sp.4				1					
<i>Myrmelachista</i> sp.5				2					
<i>Myrmelachista</i> sp.6						&1			
<i>Paratrechina</i> sp.1				&1					
<i>Paratrechina</i> sp.2			1&4			3&3		16	
<i>Paratrechina</i> sp.3									8
<i>Paratrechina</i> sp.4									
<i>Paratrechina</i> sp.5				1					
<i>Paratrechina</i> sp.6			2						
<i>Paratrechina</i> sp.7									2
<i>Paratrechina</i> sp.8									10
<i>Paratrechina</i> sp.9									
<i>Paratrechina</i> sp.10							1&2		
<b>DOLICHODERINAE</b>									
<i>Azteca alfari</i>							&2		
<i>Azteca australianus</i>								&2	
<i>Azteca coeruleipennis</i>								&3	
<i>Azteca foreli</i>		14&27		27&16			8&1		3
<i>Azteca ovaticeps</i>		&4		&2					
<i>Azteca xanthochroa</i>					&1				
<i>Azteca</i> sp. 1					5&1				
<i>Azteca</i> sp. 2	4&4								
<i>Azteca</i> sp. 3			7&20						
<i>Azteca</i> sp. 4						6&18			
<i>Azteca</i> sp. 5			3&1						
<i>Azteca</i> sp. 6	2&1								
<i>Azteca</i> sp. 7					2				
<i>Azteca</i> sp. 8						4&14			
<i>Azteca</i> sp. 9							3		
<i>Azteca</i> sp. 10			*						
<i>Azteca</i> sp. 11							1		
<i>Azteca</i> sp. 12								2	
<i>Azteca</i> sp. 13						2			
<i>Azteca</i> sp. 14						1			
<i>Azteca</i> sp. 15									2
<i>Azteca</i> sp. 16							1		
<i>Dolichoderus bispinosa</i>	1&1		2					1	1
<i>Dolichoderus debilis</i>	4&12	&3							
<i>Dolichoderus lobicornis</i>					8			10	
<i>Dolichoderus lutosus</i>			2						
<i>Dolichoderus</i> sp. 1			1						
<i>Dolichoderus</i> sp. 2									



*Neivamyrmex emersoni*  
*Neivamyrmex postcarinatus*  
*Nomamyrmex hartigi*

4 1 \*

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**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 masl	Soil ants		Canopy ants		% of PEFN with ants	% of PD with ants	% of non-MP with ants
		FI	SR	FI	SR			
Cata	15	1.8	21	3.5	32	89	*	10
Cupira	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			Canopy & Soil	Found in	
		Canopy	Soil	MP		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 (Dil), Berger-Parker's dominance index (Dol) 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	Soil				Pitfall Traps in: Canopy				Total				SR of ants on MP			Total SR A+B+DS
		FI	SR	Dil	Dol	FI	SR	Dil	Dol	FI	SR (A)	Dil	Dol	Total (B)	+ Canopy	+ Soil	
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
Cupira	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	<b>7.7</b>	0.1	2.6	28	<b>6.0</b>	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	<b>9.3</b>	0.1	2.8	39	<b>8.3</b>	0.2	9.1	<b>80</b>	13.7	0.1	18	8	4	89
S. Francisco	980	4.5	46	<b>8.9</b>	0.1	2.5	28	<b>6.0</b>	0.2	6.9	<b>70</b>	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

Table 7. Shannon'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	<i>Solenopsis sp. 8</i>
Cúpira	3.23	0.075	0.14	<i>Solenopsis sp. 12</i>
Uracoa	3.74	0.058	0.08	<i>Camponotus crassus</i>
Cupo	3.12	0.078	0.14	<i>Azteca foreli</i>
S. Ignacio	3.97	0.051	0.08	<i>Solenopsis sp. 7</i>
S. Francisco	3.79	0.057	0.093	<i>Camponotus abdominalis</i>
Sartenejas	2.85	0.084	0.25	<i>Pseudomyrmes pallens</i>
Rancho Grande	2.43	0.122	0.31	<i>Solenopsis sp. 1</i>

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
	Cupira		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
	Cupira		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
	Cupira		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

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

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

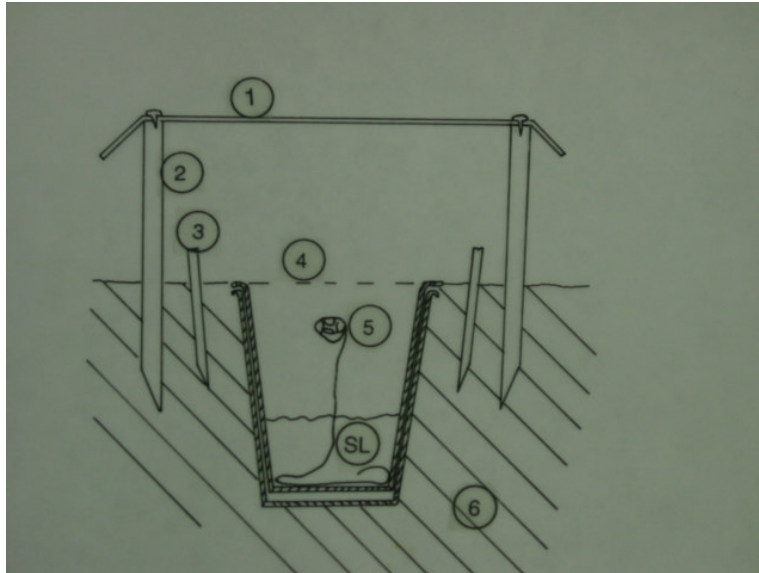
Locality	Leaves on PEFN				Leaves on PF		Leaves on non-MP		% of plants visited by ants		
	Ants + mature	Ants + young	Ants - mature	Ants - young	mature	young	mature	young	PEFN	PF	Non-MP
Cata	8.2 (27)	4.6*** (27)	17.3 (6)	11.3 (6)	&	&	10.7 (10)	12.7 (10)	89	&	10
Cupira	17.2 (44)	14.2*** (44)	24.2 (5)	8.2*** (5)	17.5 (13)	11.9*** (13)	11.2 (10)	<b>9.0*</b> <b>(10)</b>	96	100	<b>80</b>
Uracoa	13.9 (42)	8.2*** (42)	15.6 (7)	6.5*** (7)	&	&	25.8 (10)	<b>8.7***</b> <b>(10)</b>	77	&	<b>70</b>
Cupo	16.0 (29)	14.0*** (29)	13.3 (6)	11.2 (6)	&	&	14.1 (10)	<b>10.8**</b> <b>(10)</b>	89	100	<b>80</b>
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.

**Figure 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



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

