

Development of ant gardens in secondary forests in the Colombian Amazon

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Abstract

Ant gardens are mutualistic associations between ants and epiphytic plants. We studied these ant nests in secondary forests of the Colombian Amazon. Our study had three components covering their initiation, development and epiphytic vegetation. First, a recolonization experiment was set up, to observe the reoccupation of epiphytes by ants. Second, the structure of the nests was determined by disassembling 39 nests. Of these nests all ants found were identified. Third and last, the spatial distribution of ant garden epiphytes was analyzed using permutation tests. A total of 153 nests were found in two 20 m x 20 m plots in secondary forests near Araracuara and Monochoa (Caquetá, Colombia). Nest density was similar between both forests (63 versus 90). Eight species of epiphytes were identified on the nests. In the sampled plots only three epiphyte individuals were found without an association with ants. The recolonization experiment showed that ants were drawn to the individual epiphytes but not to the original locations where nests had been removed in trees. Within days ants were defending individual plants and adding carton. All closely examined nests were inhabited by *Camponotus femoratus* and *Crematogaster limata*. We observed that these species lived in segregated parts of the nests. There was no neighbourhood effect of the epiphytes on the nests and no there was no consistent sequence of epiphytes related to the size of the nests. The latter finding suggests that there was no successional gradient of epiphytes on the gardens. We found an indication of habitat differentiation between *Codonanthe crassifolia* and *Philodendron megalophyllum* along the vertical gradient in the forests. This was the first description of ant gardens in the Colombian Amazon.

Resumen

Jardines de hormigas son una asociación mutualística entre hormigas y plantas epífitas. Estudiamos estas en un estudio con tres componentes cubriendo su iniciación, desarrollo y vegetación epífita. Primero, iniciamos un experimento de colonización, para observar la re-ocupación de las epífitas por hormigas. Segundo, describimos la estructura de los nidos, separando en componentes 43 nidos. De estos nidos las hormigas encontradas fueron determinadas hasta especie. Tercero y último la distribución espacial de epífitas en jardines de hormigas fue analizado. Un total de 153 nidos fueron encontrados en dos parcelas de 20 m x 20 m en bosques

secundario de Araracuara y Monochoa (Caquetá, Colombia). La densidad de nidos fue similar entre los dos bosques (63 contra 90). Ocho especies de epifitas fueron identificados sobre los nidos. En las parcelas monitoreadas solamente tres individuos fueron encontrados fuera de asociación con hormigas. El experimento de recolonización mostró que las hormigas son atraídas a los individuos de epifitas pero no a las posiciones en los árboles de donde se removieron los nidos. Dentro de un par de días hormigas estaban defendiendo plantas individuales y añadiendo cartón. Todos los nidos que fueron estudiados en detalle estaban habitadas por *Camponotus femoratus* y *Crematogaster limata* y observamos que estas especies habitan diferentes partes del nido. No encontramos un efecto de vecindad en las epiphytas sobre los nidos ni una secuencia consistente de especies relacionado con el tamaño de los nidos. Lo último sugiere que no hay una gradiente successional sobre los jardines. Encontramos un indicio de segregación de habitat entre *Codonanthe crassifolia* y *Philodendron megalophyllum*. Este fue la primera descripción de jardines de hormigas en la Amazonia Colombiana.

Introduction

Ant gardens are arboreal ant nests which have plants rooted in them and where ants actively plant or tend to these plants (Ule 1901). In these gardens, ants sow seeds in the interior walls and as these germinate, the plants reinforce the structure with their roots and regulate nest humidity (Yu 1994). Also, most of the plants associated with ant gardens have extrafloral nectaries, or fruits with high concentrations of sugar (Davidson 1988). The origin and characteristics of this relationship have been debated for a century, ever since it was first described, and the arguments range from coevolved mutualism (Ule 1901, Madison 1979) to an opportunistic relationship wherein both plants and ants can prosper without such an association (Wheeler 1921). Longino's (1986) hypothesis that epiphytes have adapted to an already present and stable biotic component - arboreal ant nests - is a reasonable compromise between the two aforementioned viewpoints.

Another subject of debate is the initiation of ant gardens. Nests can be formed by the accumulation of carton to which seeds are subsequently added by the ants (Kleinfieldt 1978). The other pathway to the development of ant gardens is the occupation of an epiphyte by ants around which a nest is constructed (Belin-Depoux 1991). Ant gardens tend to occur in agglomerated archipelagos of nests inhabited by polydomous colonies (Davidson 1988). This makes it likely that most of the satellite nests were initiated by ants and do not depend on the chance occurrence of ant garden epiphytes.

There are a number of studies which deal with the spatial distribution of arboreal ants (Hölldobler 1979, Hölldobler and Lumsden 1980), but not of arboreal ant nests. Ant gardens offer a special kind of habitat for epiphytes in many respects.

in the canopy or whether the availability of ant garden epiphyte individuals was more important. Second, we described the internal structure of nests of different sizes to describe the development in their internal structure. Finally, we mapped the ant gardens and constituent epiphytes to determine their spatial distribution. We expected this spatial distribution to depend on the seed dispersal by ants, with little influence of the ecological requirements of individual species. This study is the first description of ant nests in the Colombian Amazon.

Materials and methods

Study area

Field work was carried out between May and August 1998 in the north-eastern part of the Amazon basin, in the department of Caquetá, Colombia (72° 23' W, 00° 47' S). The area had a yearly precipitation of 3060 mm, and the wettest months are April to July, while the driest period lasts from December to February. The monthly average of relative humidity is always high, varying between 82% and 92% (Duivenvoorden and Lips 1993).

We found two aggregations of ant gardens along a 9 kilometer dirt road, which runs through secondary vegetation from Araracuara (Araracuara, 72° 22' W; 00° 38' S) to Puerto Arturo (Monochoa, 72° 30' W; 00° 25' S), with approximately 5 km between them (Figure 1). We refer to these as Araracuara and Monochoa. Both these plots had tree heights up to 15 m and an approximate age of 30 years. Additionally, an experimental plot was laid out across the road from the Araracuara plot. This experimental plot was a young stand (less than 8 years) with tree heights up to 9 m and was surrounded by chagras (indigenous cultivation fields) and houses.

Colonization experiment

In the 15 m x 15 m experimental plot 7 small nests were taken apart and the constituent epiphytes were separated carefully without damaging shoots or roots.

Table 1. Epiphyte species associated with ant nests in Araracuara (ARA and EXP) and Monochoa (MON)

| Species | Family | MON | ARA | EXP |
|---|--------------|-----|-----|-----|
| <i>Philodendron megalophyllum</i> Scholt. | Araceae | + | + | + |
| <i>Anthurium gracile</i> (Rudge.) Scholt. | Araceae | + | + | + |
| <i>Streptocalyx angustifolius</i> Beer. | Bromeliaceae | + | + | + |
| <i>Aechmea brevicollis</i> L.B. Smith | Bromeliaceae | + | + | + |
| <i>Clusia androphora</i> Cuatr. | Clusiaceae | + | + | |
| <i>Codonanthe crassifolia</i> (Foche) Morton | Gesneriaceae | + | + | + |
| <i>Peperomia macrostachya</i> (Vahl) Dietrich | Piperaceae | + | | |
| <i>Markea ulei</i> (Dammer) Cuatr. | Solanaceae | | | + |

Loose organic material, debris and ants were removed from these plants by submerging them for 24 hours in water. Thirty clean, undamaged, epiphytes were subsequently placed in trees in the same plot from where the nests were taken. We attached them to trees with small pieces of wire and purposefully did not place them on the same location from which we took the nests. The plants were distributed more or less regularly across the plot. The relocated plants were young individuals of *Anthurium gracile*, *Aechmea sp.*, *Codonanthe crassifolia*, *Markea ulei* and *Streptocalyx angustifolius* (see Table 1 for authors and family names). These plants and the original locations of the nests were mapped and monitored regularly during four months.

Description of nest structure

We collected nests in both Monochoa and Araracuara for disassembly. Of each nest we measured the size and made a sketch of their exterior shape. A preliminary collection of ants was made while the nests before collecting them in plastic bags. Each nest was opened and the position of the brood, and the position and shape of the epiphyte roots was sketched and described in field notes. Also the presence or absence of dealate queens, alate queens and males was recorded. In each plot we also collected ants with no apparent relationship to the gardens (mostly on the forest floor). We did so to identify species which could potentially form or take over ant gardens.

A series of different castes were collected from each nest. This entomological material was identified and deposited at the Von Humboldt Institute (Villa de Leyva, Colombia). The plant collections were deposited at the Herbarium of the University of Antioquia (HUA, Medellín, Colombia).

Table 2. Species present in the colonization experiment and the number of these individuals that died or lived and were colonized. The last column shows the percentage of occupation by ants of the surviving individuals. See Table 1 for taxonomical authorities.

| Species | n | Dead | Colonized | % |
|-----------------------------------|----|------|-----------|-----|
| <i>Anthurium gracile</i> | 10 | 0 | 8 | 80 |
| <i>Aechmea brevicollis</i> | 8 | 1 | 2 | 29 |
| <i>Codonanthe crassifolia</i> | 8 | 3 | 3 | 60 |
| <i>Markea ulei</i> | 1 | 0 | 1 | 100 |
| <i>Streptocalyx angustifolius</i> | 3 | 0 | 2 | 67 |
| Total | 30 | 4 | 16 | 62 |

Mapping of nests and epiphytes

The Monochoa and Araracuara plots were subdivided into 5 m x 5 m quadrants to facilitate the measurement of the nests' coordinates. The height of the nests was measured using a clinometer (Suunto pm-5). We also recorded the position of the host tree, as well as the percentage of the nest area covered by epiphytes. We were not able to gain access to all the nests and only collected ant specimens from nests within arm's reach. The identity and abundance of epiphytes on higher nests were recorded with the aid of binoculars. Given the low height, and the relatively simple architecture of these young secondary forests this was feasible. Nevertheless, we could not count the number of epiphyte individuals present because some of the species had (clonal) ramets which were impossible to distinguish from individual genets at a distance.

Statistical analysis

To test the spatial pattern of the epiphytes on the nests, a method was sought that could test against a random assignment of individuals on the nests found in the study plots. The epiphytes under study only occurred on ant gardens, so that all other locations in the forest volume were unavailable to them. This meant that most measures of spatial aggregation were not applicable because the plants were constrained to the location of the nests. The null model against which a spatial pattern could be tested was not complete spatial randomness, but a pattern whereby all individual plants were distributed randomly over the nests.

The most appropriate statistical method we found was a permutation (or randomization) test (Manly 1991). These tests consist of the repeated calculation of a chosen test statistic on random permutations of the original data. The outcome of these calculations is subsequently ordered so that the position of the test statistic calculated for the original (non-randomized) data can be determined. In other words,

Table 3. Phases of occupation of the epiphyte individuals in the colonization experiment.

| Order | Colonization phase | Description |
|-------|----------------------------|--|
| 1 | Not colonized | Occasional presence of ants |
| 2 | Start of colonization | First accumulation of nest material, aggressive response to perturbation, presence of <i>Camponotus</i> workers. |
| 3 | Colonized | Larger quantity of nest material, vigilance of the shoot. <i>Crematogaster</i> workers. |
| 4 | Fine grained nest material | Accumulation of organic material (fine grain). Vigilance and aggressive response. |
| 5 | Course nest material | Addition of course nests material (woody). Vigilance and aggressive response. |

Table 4. Ant species found in the sampled plots which were not directly associated with ant nests.

| Species | Sub family | ARA | MON | EXP |
|--|------------|-----|-----|-----|
| <i>Odontomachus haematodus</i> Lin. | Ponerinae | + | + | |
| <i>Pachycondyla apicalis</i> Latreille | Ponerinae | | | + |
| <i>Pachycondyla villosa</i> Fabricius | Ponerinae | + | + | |
| <i>Paraponera clavata</i> Fabricius | Ponerinae | | + | |
| <i>Ectatomma quadridens</i> Fabricius | Ponerinae | | | + |
| <i>Megalomyrmex leoninus</i> Forel | Myrmecinae | + | | |
| <i>Nomamyrmex esenbreckii</i> Westwood | Ecitoninae | + | | |
| <i>Cephalotes atratus</i> Lin. | Myrmecinae | + | | |

based on 9999 permutations, the 250 largest and 250 smallest values of the calculated test statistic mark the limits of a 5% significance level (two sided). By comparing the value of the original data to these limits a decision about the significance of the pattern can be made. The test statistics we chose for the permutation tests in this study were average height and sum of distances to the nearest neighbour (Besag and Diggle 1977). Permutations were carried out using a Fisher-Yates shuffle (Christiansen and Torkington 1998) on the array of presence-absence values of each species, and were implemented in MacPerl (version 5.06, www.CPAN.com).

The attractiveness of species in the colonization experiment was tested using the chi square statistic of a contingency table. Mantel correlation coefficients (Legendre and Legendre 1998) were calculated and tested with Le Progciciel R (version 4.1b13, Philippe Casgrain, Université de Montreal). For the data from the mapping of nests and epiphytes, non parametric tests (Kruskal-Wallis) were performed because size was estimated in four discrete classes (JMP, version 3.2.2. SAS Institute Inc.).

Results

Colonization experiment

Of the 30 plants used in the colonization experiment, 16 were colonized by ants. The first defensive behaviour on these plants was observed as soon as two days after starting the experiment. No significant preference for one of the included plants species could be found ($\chi^2 = 5.83$, $P=0.21$; Table 2). Visual inspection of the data did not suggest any effect of the vicinity of other nests on the occupation of the plants, but this was not subjected to any further statistical analysis.

The observations were divided into the categories shown in Table 3, based on field notes. The nest initiation on *A. gracile* consisted mainly of wood (observed as yellowish particles) while on *C. crassifolia* a darker material was found which

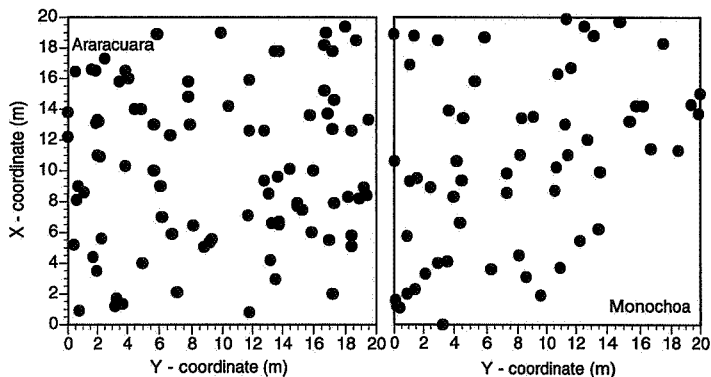


Figure 2. Horizontal distribution maps of the nests found in Araracuara and Monochoa.

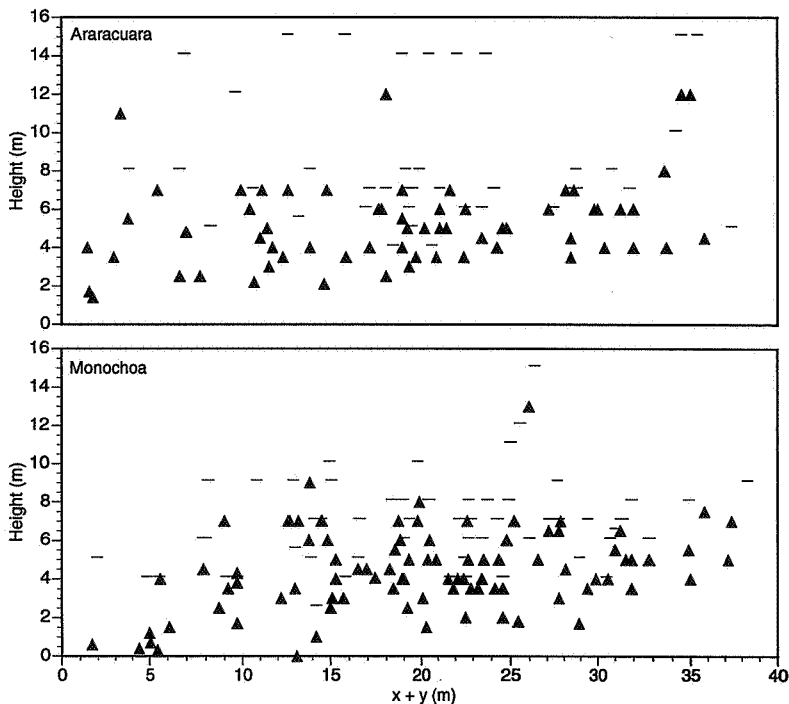


Figure 3. Distribution of nests along height gradient in Araracuara and Monochoa. The black triangles show the position of a nests, the horizontal bars show the heights of the host trees. On the the horizontal axis the values of the (x, y) coordinates were added so that nests do not overlap in the graph. Factual horizontal position is shown in Figure 2.

Table 5. Results of the randomization tests of the sum of distances to the nearest neighbour (sum NN). The rank number shows the position of the test statistic of the original data set. These are all two sided tests, tested at the 5% level so that to be significant a value has to be in the 250 highest or the 250 lowest values generated by the permutation.

| Species | Sum NN | Rank nr. | P value |
|-------------------------|--------|----------|---------|
| Monochoa | | | |
| <i>S. angustifolius</i> | 18.6 | 4085 | 0.409 |
| <i>P. macrostachya</i> | 108.8 | 942 | 0.094 |
| <i>P. megalophyllum</i> | 106.5 | 2740 | 0.274 |
| <i>C. crassifolia</i> | 38.9 | 3142 | 0.314 |
| <i>C. androphora</i> | 23.9 | 2950 | 0.295 |
| <i>A. gracile</i> | 97.1 | 9316 | 0.068 |
| <i>A. brevicollis</i> | 48.6 | 5586 | 0.441 |
| Araracuara | | | |
| <i>S. angustifolius</i> | 51.7 | 6562 | 0.344 |
| <i>P. megalophyllum</i> | 101.9 | 2899 | 0.290 |
| <i>C. crassifolia</i> | 126.6 | 5173 | 0.483 |
| <i>C. androphora</i> | 74.0 | 6003 | 0.400 |
| <i>A. gracile</i> | 117.2 | 2637 | 0.264 |
| <i>A. brevicollis</i> | 62.5 | 859 | 0.086 |

Table 6. Results of the randomization tests of the average nest height. The rank number shows the position of the test statistic of the original data set. These are all two sided tests, tested at the 5% level so that to be significant a value has to be in the 250 highest or the 250 lowest values generated by the permutation. Significant results ($P < 0.025$) are marked in bold

| Species | Average height | Rank nr. | P value |
|-------------------------|----------------|----------|--------------|
| Monochoa | | | |
| <i>S. angustifolius</i> | 2.7 | 233 | 0.023 |
| <i>P. macrostachya</i> | 5.5 | 9747 | 0.025 |
| <i>P. megalophyllum</i> | 5.4 | 9016 | 0.098 |
| <i>C. crassifolia</i> | 3.8 | 141 | 0.014 |
| <i>C. androphora</i> | 4.3 | 2111 | 0.211 |
| <i>A. gracile</i> | 5.4 | 7040 | 0.296 |
| <i>A. brevicollis</i> | 4.7 | 2393 | 0.239 |
| Araracuara | | | |
| <i>S. angustifolius</i> | 3.8 | 856 | 0.086 |
| <i>P. megalophyllum</i> | 4.1 | 158 | 0.016 |
| <i>C. crassifolia</i> | 5.0 | 9999 | 0.000 |
| <i>C. androphora</i> | 4.4 | 3538 | 0.354 |
| <i>A. gracile</i> | 4.6 | 7843 | 0.216 |
| <i>A. brevicollis</i> | 4.4 | 3780 | 0.378 |

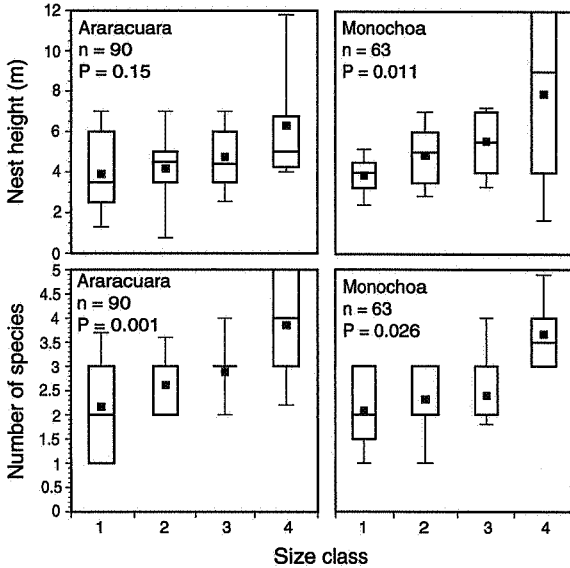


Figure 4. Box plots of the number of species and the height of the nests in Araracuara and Monochoa. The results of a Kruskal-Wallis non parametric ANOVA are shown inside the plot boundaries.

looked like humus. There was a direct relationship between the amount of material deposited and the aggressive response of the ants to touching the plant, but this was not quantified. Ten plants did not accumulate any nest material, but had occasional presence of ants. Four plants died, three *C. crassifolia* and one *A. brevicollis*, probably as a result of the treatment before placement on a tree (Table 2).

The ants that colonized these nests were either *Camponotus femoratus* Fabricius or *Crematogaster limata* s.l. F. Smith. A rough estimate of the proportion is 20 individuals of *Cr. limata* s.l. for each *Ca. femoratus*.

Description of nest structure

A total of 39 nests were collected for detailed observations of their structure, divided over the different size classes found in the plots. In addition to the 7 disassembled nests in the experimental plot, we collected 18 in Araracuara and 14 in Monochoa. Eight epiphytic plant species were found (Table 1) and two species of ants (*Ca. femoratus* and *Cr. limata* s.l.) Another eight ant species were found on the forest floor of the plots (Table 4).

The brood of *Cr. limata* s.l. was present in superficial cavities less than 2.0 cm deep, and sometimes between the folds of leaves on the nests. . In contrast, the

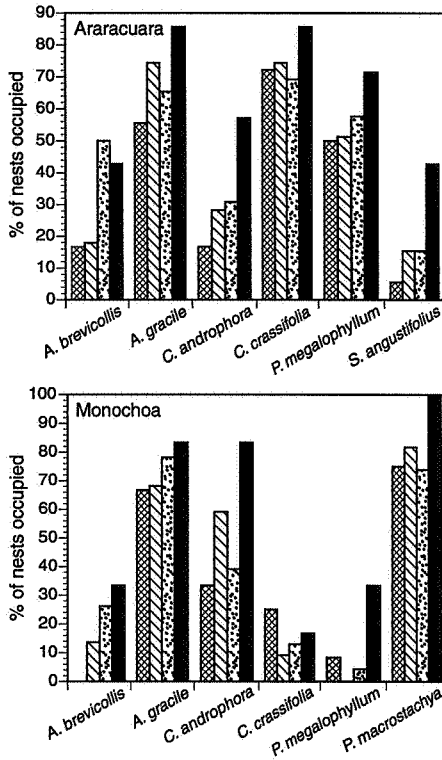


Figure 5. Relative importance of the epiphyte species on the nests in Araracuara and Monochocha. The pattern of the bars represent the size classes of the nests: $x \leq 15$ cm diameter (cross hatched bars), $15 \text{ cm} < x \leq 30$ cm diameter (hatched bars), $30 \text{ cm} < x \leq 50$ cm diameter (dotted bars) and $x > 50$ cm diameter (black bars).

brood of *Ca. femoratus* was found in deeper, often more spacious, cavities which were protected by thick walls often reinforced by *A. gracile* or *C. crassifolia*. Males of *Ca. femoratus* were also found in separate cavities and these were cared for by conspecific workers. We found no dealate or alate queens inside the nests.

The nests had various shapes, which generally ranged from a sphere to a cone. There were two distinct factors which accentuated these irregularities. First, the presence of a fallen leaf which was surrounded by organic material and incorporated in the nest (depending on its initial position) which gave rise to irregularities and outcrops. Second, especially in the case of younger nests, the point at which the roots of *A. gracile* ended tended to elongate the nest. The two bromeliads (Table 1) had the smallest contribution to the structure of the nests, with very shallow roots.

The material which formed these nests was of organic origin, a mixture of humus, entire leaves and triturated leaves (mostly either of the host tree or one of the epiphytes present on the nest). In most cases the material was soft, especially in the inner parts of the nest, humid but never soaked nor compacted, firm and porous.

The roots of *C. crassifolia* are deep and delimit interior cavities of the nest. In contrast, the root system of *P. macrostachya* is superficial and does not delimit cavities. Also, the roots of the latter are more fragile than the roots of *C. crassifolia*. *A. gracile* was characterized for having a large number of thick roots which intertwine to form a net. The position of these roots in the nest is mostly on the exterior, and appears to function as the columns of the nests holding the main part of the structure. *C. crassifolia* had an intricate root system which forms a fine net on the inside of the nests defining the cavities and tunnels. There are many fleshy leaves of this plant with abundant extrafloral nectaries and its fruits have many seeds. The two bromeliads, with shallow roots were not an intricate part of the nest wall.

Spatial distribution of nests and epiphytes

We recorded 153 nests, 90 in the Araracuara plot, 63 in the Monochoa plot. A total of 27 host tree species were found. In Monochoa, the two most common occupied trees were *Aparisthmium cordatum* (Juss.) Baillon (Euphorbiaceae) and *Pentagonia sp.* (Rubiaceae). Neither of these two trees were found in Araracuara, where *Lacistema aggregatum* (Berg.) Rusby (Lacistemataceae) and *Vismia lauriformis* (Lam.) Choisy (Guttifereae) were the most common hosts.

Ant gardens were conspicuously aggregated in these secondary forests. However, on the scale of our plots, there seemed to be no horizontal aggregation of the nests (Figure 2). The tree density was high, and trees were spaced regularly, and no effect of tree placement was observed. The position of the nests on their host trees is shown in Figure 3. As on the horizontal plane, there is no obvious pattern of the nests along the tree heights. Using the three dimensional coordinates of the nests, we tested the aggregation of the individuals from each plant species and found no aggregation (Table 5). This lack of spatial pattern was confirmed by Mantel tests on the distance matrices of the three dimensional coordinates and the similarity (Jaccard's index) of the nests (Monochoa: $M_r = -0.02$, $P = 0.255$, Araracuara: $M_r = -0.024$, $P = 0.225$).

We did, however, find spatial structuring of the individual epiphytes along the height axis. The average height at which *C. crassifolia*, *P. megalophyllum* and *Streptocalyx angustifolius* were found was significantly different from the average that would result from random placement of the individuals of these species on the nests (Table 6). On average, *Codonanthe crassifolia* is positioned higher than expected in the forest in Araracuara, but lower in Monochoa, *Philodendron*

megalophyllum (Araracuara) and *Streptocalyx angustifolius* (Monochoa) are at a lower height than expected (Table 6). There was a significant effect of nest size on the number of species present in Araracuara and on the height of nests in Monochoa (Figure 4). Nest height in Araracuara and the number of species in Monochoa had an upwards trend, but no significant effect against nest size (Figure 4). Across the range of nest sizes, *Anthurium gracile* and *C. crassifolia* are present in almost all nests in Araracuara, while *A. gracile* and *P. macrostachya* are present in almost all nests in Monochoa (Figure 5). The two bromeliads and *C. androphora* were present more often on larger nests than smaller nests (Figure 5).

In the Araracuara plot, three individual plants were found with no apparent association with ants, namely *A. gracile* (2 ind.) and *P. megalophyllum* (1 ind.). All three were young individuals. On the forest floor, *P. megalophyllum* was common with 9 and 16 individuals in Araracuara and Monochoa respectively. *Clusia androphora* (1 individual in ARA) and *Aechmea brevicollis* (two individuals in MON) were also found on the forest floor. We had the distinct impression that these plants were remnants from fallen nests.

Discussion

Colonization experiment

The active reoccupation of the relocated plants was in striking contrast to the unpublished results of Davidson reported by Hölldobler & Wilson (1990:547). She also performed an experiment offering ant garden epiphytes but did not observe any occupation by ants. Possibly the colonization we observed was a result of scent traces left on the plants in our study. It is also possible that the ants which were left in the plot without a nests were more eager to establish a new one than they would have been had their nests still been in place. There was no new nest building activity on any of the positions in the trees where the nests had been removed. Although this does not close the argument on whether the gardens start with a plant, or with a nest, it does suggest that there is less preference for specific locations on trees than for plants available for occupation. The higher number of *Cr. limata* ants on the newly occupied epiphytes was surprising. A differential role of these species in nest initiation has not been reported before.

For a full experiment a control is needed consisting of greenhouse-raised plants. What kind of founder event triggers the establishment of these nests remains enigmatic, given that suitable epiphytes need to be available for the growth and development of these interconnected mazes of nests. The three epiphytes found without ant association in the Araracuara plot are likely to be colonized at some point in time, given that these plants are seldom observed without ant association (Davidson 1988). The fact that these three had not been colonized while the plants in the experiment received almost immediate attention is another indication that

scent or the need for housing activated the ants to colonize the plants.

Nest structure

The two species of ant we have found to inhabit the nests have been reported as common species on trunks and in tree crowns (Wilson 1987). The association between two species - called parabiosis - has been defined as a special kind of symbiosis only known from a few tropical ant species, where two or more species occupy a single nest, foraging together but maintaining their brood in separate cavities (Swain 1980, Orivel *et al.* 1997). All nests that were opened showed this characteristic. There are few descriptions of the internal structure of ant gardens. The drawings provided by Belin-Depoux (1991) also show separate interconnected chambers for each species. We can confirm this but also found that the ants prefer different locations in the nests. *Cr. limata* dwells close to the nest surface and *Ca. femoratus* deeper in the nests. We did not find earlier reports of this distinction.

Corbara and Dejean (1996) have studied the initiation of nests by ants of the family Ponerinae, and found that members of this family build arboreal carton nests, which are turned into gardens. This may mean that some of the ants found on the forest floor (Table 4) have at least the potential of either building their own nests in the area, given the availability of epiphyte seeds, or to occupy the *Crematogaster-Camponotus* nests. We do not have reason to assume that the nests included in our census were occupied by species other than *Ca. femoratus* or *Cr. limata*. The nests in our plots were likely satellites from the same polydomous colony given the absence of queens in the disassembled nests. This was in line with the description of ant garden aggregations by Davidson (1988).

The relationship between *C. longispina* and *C. crassifolia* was studied by Kleinfeldt (1978) who, besides the showing the trading of structural support for dispersion, also showed the effect of nutrients of the nests on the plants. In her study, *C. crassifolia* had higher growth rates when it was associated with an ants nest than when it was not. It might be possible that a trade-off exists between the structural role of the root system and the nutrient supply of the shoot, since *P. macrostachya*, while it does not substantially influence the structure of the nest, is rich in nectaries and fleshy fruits.

Spatial distribution of nests and epiphytes

Conspecific epiphytes did not have an aggregated distribution on the nests. We were interested in this spatial pattern because it might reflect the foraging and seed collecting behaviour of the ants. Apparently fruits and seeds are available across the colony and no preference is given to foraging on the nearest neighbouring garden. Random spatial distributions of ant dispersed plants have been reported before (Horvitz and Le Corf 1993) but these results are discussed by the authors in relation

to the scale of their sampling, and do not point at specific strategies or mechanisms that may underlie these observations. Terrestrial ant nests on the other hand, usually show both intraspecific and interspecific overdispersion, possibly as a result of competition for resources (Levings and Franks 1982). The patterns shown by arboreal ant communities are also largely unpredictable (Floren and Linsenmair 2000).

The height preference of *C. crassifolia* and *P. megalophyllum* was a surprising result, because we expected the seed dispersal of all nest inhabiting epiphytes to be structured exclusively by the transport by the ants. The preference for a position along the height axis suggests the possibility that epiphytes respond to the environment gradient along the height of the forest. However, the pattern was not consistent, and in the absence of relevant measurements of local micro climate no definitive conclusion could be drawn.

No nests were found with only one species of plant, and this agrees with the idea of Yu (1994) that the success of the nests lies in the combined effect of structural and nutritional elements offered by various plants at the same time. In neither Monochoa nor Araracuara did a nest occur which harbored all species present in the plot. In both plots there was a maximum number of five species on a single nest. Catling (1995) suggests that nest substrate is partitioned in time, in other words that there is some form of succession of the plant community associated with ant gardens. He attributes this to differences in colonizing and competitive abilities of the epiphytes. Davidson (1988) carefully suggests a similar process. We have found no evidence to support these claims. We did find that the number of species increases with nest size, but there seems to be no particular order in the settlement of plant species nor did we find evidence of competitive exclusion. The ubiquitousness of the species which we identified above as most important to the structure of the nests, suggests preferential harvesting and transport of these species to newly formed nests. We also had the impression that once *P. megalophyllum* reaches a certain size, the integrity of the nest is compromised and they fall to the ground, were *P. megalophyllum* can continue to grow, while most other species die.

Only few species are consistently dominant on the nests across all size classes and are apparently preferred by the ants (Figure 5). These species (*A. gracile*, *C. crassifolia*, *P. macrostachya*) have a large contribution to the nest, with deep roots. The overall composition of the nests, on the other hand, appears to be limited by the available species pool in the area. The provenance of the seeds remains unclear but possibly they could have been brought to the area from a large distance by birds. The observation that almost no epiphytes were present outside of the ant nests, confirms the conclusion by Catling (1997) that ant gardens have a significant contribution to epiphyte diversity in forests. Apparently ants play an important role in facilitating the colonization of secondary forests by epiphytes, as evidenced by the lack of

epiphytes in the forest surrounding the sampled plots.

Concluding remarks

We found that colonization of individual epiphytes can be a fast process wherein *Cr. limata* is the most active participant. Within nests there is a separation between *Cr. limata* and *Ca. femoratus* where the former reside closer to the nest surface and the latter deeper in the nest. There was some indication of habitat partitioning among the epiphyte species but the results were not consistent between plots. No evidence for a sequential succession of epiphytes on the gardens was found.

Ant gardens are a striking and fascinating phenomenon in tropical forests. More work is needed to fully understand their ecology and evolutionary biology. The intricate nature of this plant - animal relationship are likely to make such studies a worthwhile endeavour.

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