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Amazonian ant–plant interactions and the nesting space limitation hypothesis

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ABSTRACT: Throughout the tropics there are a few hundred ant species that nest exclusively inside myrmecophytes (i.e. ant-domatia bearing plants). For these ants, nesting space is an essential resource that must be shared among them, therefore opening the possibility for strong intraspecific and interspecific competition. Several ant–myrmecophyte systems from Central Amazonia were investigated to test the relevance and generality of the nesting space limitation hypothesis for plant-ants. Empirical patterns were drawn at four organizational levels: (a) individual level—ant species with small-bodied queens were the most frequent partners of myrmecophyte species offering small-sized domatia, while ants with large-bodied queens dominated host species with large-sized domatia, suggesting that host choice by inseminated queens and interspecific conflicts over host dominance seem to be influenced by space limitation; (b) colony level—in eight independent ant–myrmecophyte systems, ant colony size was positively correlated to the number of domatia provided by the host, and the mean occupancy level of the domatia by ants was 92%, suggesting that space can be limiting to colony growth; (c) population level—ant colony number and distribution was determined by the local availability and distribution of its plant partners; and (d) community level—across ant-myrmecophyte systems, the commonness of ant species were largely determined by the commonness of their specialized host partners. Within ant-myrmecophyte systems, rarity of ants seems to be defined by interspecific conflicts over host dominance. The ecological and evolutionary consequences of those patterns are discussed.

RESUMO. Nos trópicos existem algumas poucas centenas de espécies de formigas que nidificam exclusivamente dentro de mirmecófitas (i.e. plantas possuidoras de domácias). Para estas formigas, o espaço de nidificação é um recurso essencial que precisa ser dividido entre elas, abrindo assim a possibilidade de competição intraespecífica e interespecífica forte. Diversos sistemas formiga-plantas da Amazônia Central foram investigados para se testar a relevância e generalidade

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da hipótese da limitação de sítios de nidificação para formigas associadas às mirmecófitas. Padrões empíricos foram gerados a quatro níveis organizacionais: (a) nível individual—espécies de formigas com rainhas de tamanho corpóreo reduzido foram os parceiros mais frequentes de espécies de mirmecófitas que oferecem domácias pequenas, enquanto que espécies de rainhas grandes dominam espécies de hospedeiros que oferecem domácias grandes, sugerindo que a escolha de hospedeiros por rainhas inseminadas e conflitos interespecíficos pela dominância do hospedeiro parecem ser influenciados por limitações de espaço; (b) nível da colônia—em oito sistemas formiga-plantas independentes, o tamanho da colônia das formigas foi positivamente correlacionado ao número de domácias oferecido pelo hospedeiro, e o nível médio de ocupação das domácias por formigas foi 92%, sugerindo que espaço pode estar limitando o crescimento das colônias; (c) nível da população—o número e a distribuição das colônias de formigas foi determinado pela disponibilidade local e distribuição dos parceiros vegetais; e (d) nível da comunidade—entre os sistemas formiga-plantas, formigas comuns e raras correspondem a aquelas especializadas respectivamente em espécies de mirmecófitas comuns e raras. Dentro de cada sistema formiga-planta, a raridade das formigas parece ser definida por conflitos interespecíficos sobre a dominância dos hospedeiros. As conseqüências ecológicas e evolutivas destes padrões são discutidas.

KEY WORDS: body size, colony size, competition, community structure, insect–plant interaction, limiting factor, mutualism, myrmecophyte, nesting site, population size

INTRODUCTION

In the tropics around the world, myrmecophytes (i.e. ant-domatia bearing plants) occur in at least 141 plant genera from 47 plant families (Davidson & McKey 1993). The number of ant species nesting exclusively inside myrmecophytes is unknown, but representatives occur in 29 genera from five subfamilies (Davidson & McKey 1993). In some environments, myrmecophytes and their ant partners are conspicuous elements. In Central Amazon, for instance, 1 ha of rain forest can hold *c*. 380 myrmecophytic plants, with the local ant-myrmecophyte community comprising at least 16 plant species and 25 ant species (Fonseca & Ganade 1996). As a general rule, each established plant is occupied by a single mature ant colony and each ant colony inhabits a single host plant (but see Janzen 1973). Despite a vigorous historical debate, most ant-myrmecophyte interactions have proved to be mutualistic (Fiala *et al.* 1989, Fonseca 1994, Janzen 1967, Schupp 1986, Vasconcelos 1991, but see Janzen 1975).

Since plant-ants nest exclusively inside myrmecophytes, one expects nesting space to be an essential resource for them, influencing many aspects of the ant's life history (Benson 1985, Davidson *et al*. 1989, Davidson & McKey 1993, Fiala & Maschwitz 1992b, Fonseca 1993, Vasconcelos 1993). The nesting space limitation hypothesis, as framed here, brings forth predictions at four organisational levels. At the individual level, inseminated queens are expected to search for an adequate, enemy-free, nesting site that will enable her to survive

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and bring her colony to maturity. At the colony level, colony size is expected to grow to an upper limit that is determined by nest space limitations (Fonseca 1993). At the population level, ant colony density and distribution are expected to be controlled by the availability of nesting sites, as well as by interspecific competition for nesting space. Similarly, at the community level much of the species abundance distribution is expected to be controlled by the availability of nesting sites as well as by interspecific competition for nesting space.

Nesting space has been shown to be relevant for ants with other nesting habits (Carroll 1979, Herbers 1986, Hölldobler & Wilson 1990; Wilson 1959, 1971). Many ant species are known to nest exclusively in small hollow twigs scattered within the litter. In New Guinea tropical rain forests, Wilson (1959) observed that this strategy was restricted to small sized ant species with relatively small colony sizes. A widespread nesting strategy, also known to bees and wasps, is the use of hollows or tunnels made by stem and trunk mining organisms (e.g. beetle larvae). In this kind of system, the availability of nesting sites is dependent on the abundance and behaviour of other species. There are, also, a great number of twig-dwelling ants that are able to nest inside living tissue (Byrne 1994, Carroll 1979). Although they are able to excavate the nest for themselves, it is conceivable that nesting opportunities are restricted to plant species with adequate wood characteristics (e.g. softness, thickness).

In this study, I show some correlative results which suggest that nesting space is an important limiting resource for ants living in Amazonian myrmecophytes. In particular, I looked for generalities that could apply to other ant–plant systems elsewhere in the world. The results were drawn from taxa representative of different phylogenetic backgrounds and life histories and were gathered to test the nesting space limitation hypothesis at four organizational levels. The specific questions were: (a) Does nesting space affect individual host choice? (b) Does nesting space limit ant colony size? (c) Does nesting site availability control ant population size and distribution? (d) Do nesting site availability and interspecific competition for nesting sites determine community structure?

METHODS

This work was carried out in the reserve 'Km 41' of the Biological Dynamics of Forest Fragments Project, located about 100 km north of Manaus, Central Amazon. The reserve comprises 1000 ha of undisturbed tropical rain forest (30–40 m in height) inserted in a much larger area of continuous forest. The landscape is formed by plateaux at an altitude of 80–140 m, with a clay-sandy soil which is characteristically deep, acid and well drained. The regional climate is classified as Wet Tropical in Holdridge's (1967) life zone scheme. The floral diversity is very high, with about 1000 canopy tree species, and an understorey dominated by palms. A complete description of the area is given by Lovejoy & Bierregaard (1991).

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In the study area, the ant–myrmecophyte community is constituted of at least 25 ant species and 16 plant species (Fonseca & Ganade 1996). However, for the questions at the individual and colony level, only a subset of eight ant–plant systems was considered. This subset was chosen to maximize the diversity of phylogenetic groups (Table 1). The eight plant species represent all but one myrmecophyte genus in the community (*Amaioua* was not included due to its rarity). The ants included in this study were simply the most frequent ant partners (in terms of colony number) in the selected myrmecophytes. At the colony level, the second most frequent ant species in *Tachigali* was investigated, since the most frequent has already been considered in detail in Fonseca (1993). Among the six ant genera in the community, only *Solenopsis* (Myrmicinae) was not included since it was uncommon. The myrmecophyte genera included *Tachigali* (Caesalpinaceae), *Maieta* and *Tococa* (Melastomataceae), *Hirtella* (Chrysobalanaceae), *Cordia* (Boraginaceae), *Cecropia, Pourouma* (Cecropiaceae), and *Duroia* (Rubiaceae). The selected plant-ant genera included *Pseudomyrmex* (Pseudomyrmecinae), *Azteca* (Dolichoderinae), *Allomerus, Crematogaster, Pheidole* (Myrmicinae) and *Camponotus* (Formicinae). Therefore, the myrmecophyte species represent six angiosperm families while the ant species represent four different sub-families of ants.

Besides reflecting phylogenetic diversity, the chosen species reflected ecological diversity. The myrmecophyte species represent an array of life forms, domatia structures and trophic relationships, occurring in a diversity of microhabitats (Table 1). In regard to life-form, myrmecophytes vary from small shrubs (e.g. *Maieta*), understorey trees (e.g. *Duroia*), to large canopy and emergent trees (e.g. *Tachigali*). In relation to the domatia structure, myrmecophytes can have hollow trunks (e.g. *Cecropia*), leaf pouches (e.g. *Hirtella*, *Maieta* and *Tococa*), swollen and hollow stems (e.g. *Cordia*), hollow rachis and petiole (e.g. *Tachigali*) or external modifications to the petiole base (e.g. *Pourouma*). Furthermore, some myrmecophytes offer food resources directly to the ants through food bodies (e.g. *Cecropia, Pourouma*), while other ant-plants do not. In relation to topography *Maieta* occurs in lowland and stream ravines, for example, while *Hirtella* occurs mainly on terra firme. In terms of light regime, *Cecropia* is a light-demanding species, while *Cordia*, and many other myrmecophytes, are shade-tolerant species. The ants include species with different social structures, caste differentiation and body sizes (Table 1). Some ants are monogynous (e.g. *Pseudomyrmex nigrescens*) while others are polygynous (e.g. *Pheidole minutula*). Ant species may have monomorphic (e.g. *Pseudomyrmex nigrescens*), dimorphic (e.g. *Pheidole minutula*) or polymorphic workers (e.g. *Azteca* and *Camponotus*).

From May to September 1993, a number of plants (<10 m high) representing each ant–myrmecophyte system were haphazardly located inside a 100-ha grid. No *a priori* information about the size or activity of the colony was used in selecting these plants. Each plant was checked for the ant partner

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Table 1. The eight ant–myrmecophyte systems used to investigate the nest space limitation hypothesis at the individual and colony level. The plant species represent all but one myrmecophyte genera in the study site. Note the diversity of growth forms, domatia type, plant habitat and food reward among myrmecophyte species. The ant species are the most frequent ant partners in their respective hosts (except for *Tachigali*, in which the second most frequent ant partner was used, see text). Note the diversity of phylogenetic backgrounds, queen number and worker polymorphism among ant species.

Plant species (Family)	Growth form	Domatia type	Preferred habitat	Food body	Ant species (Sub-family)	Queen number	Worker polymorphism
Hirtella physophora (Chrysobalanaceae)	Shrub	Leaf	Plateau	Absent	*Allomerus octoarticulata* A* (Myrmicinae)	1	Monomorphic
Duroia saccifera (Rubiaceae)	Tree	Leaf	Plateau	Absent	*Allomerus octoarticulata* B* (Myrmicinae)	1–4	Monomorphic
Pourouma heterophylla (Cecropiaceae)	Tree	Petiole	Small gaps	Present	*Allomerus* D (Myrmicinae)	1–2	Monomorphic
Cordia aff. *nodosa* (Boraginaceae)	Shrub	Stem	Plateau	Absent	*Azteca* G (Dolichoderinae)	1	Polymorphic
Tococa bullifera (Melastomataceae)	Shrub	Leaf	Plateau	Absent	*Azteca* G (Dolichoderinae)	1	Polymorphic
Cecropia purpuracens (Cecropiaceae)	Tree	Trunk	Large gaps	Present	*Camponotus balzanii* (Formicinae)	1	Polymorphic
Maieta guianensis (Melastomataceae)	Shrub	Leaf	Ravines	Absent	*Pheidole minutula* (Myrmicinae)	1–13	Dimorphic
Tachigali myrmecophila (Caesalpinaceae)	Tree	Petiole	Plateau	Absent	*Pseudomyrmex nigrescens* (Pseudomyrmecinae)	1	Monomorphic

* Ants from the *Allomerus octoarticulata* complex occur in *Hirtella* and *Duroia*. Some behavioural observations suggest that they are indeed two cryptic species, therefore, when possible they will be treated as such.

identity and only the plants with the most frequent ant species were considered. Each plant was then classified into five classes of domatia number. From each size class, one plant was randomly selected, totalling five plants per ant–myrmecophyte system. For most myrmecophytes, domatia number was used as the estimate of nesting space availability. For *Cecropia*, however, trunk height was used as a more sensible estimate of nesting space availability since in this genus domatia size is quite variable.

Plant harvesting was performed during rainy periods, when most workers are normally inside the domatia. The plants were collected in plastic bags and preserved in 70% alcohol. Workers that eventually dropped on the ground, or attacked the author during the harvesting, were counted and added to the final estimates of colony size. In the laboratory, each individual domatium was dissected, their contents recorded, and the ants transferred to glass containers. Each individual ant was classed by caste, and the number of individuals in each caste was determined by direct counting.

Body sizes of queens and workers were measured under a binocular microscope (Zeiss, Germany, 40×). Body size is defined as the linear measure of head plus alitrunk. For each ant species, 50 randomly chosen workers were measured (five colonies; ten workers per colony) and five queens (one per colony). Interspecific differences in domatium volume were characterized by measurements of five domatia per plant species (one randomly selected domatium per plant). The domatia were completely filled with modelling clay that was subsequently weighed on a digital scale (Mettler AE163, 0.0001 g). Since the specific weight of the clay is 1.23 ± 0.004 g ml^{-1}, the domatia volume could be estimated.

For the estimation of myrmecophyte and ant densities, a square grid of 100 ha was chosen and ten transects of 1000 m^2 each, 200-m × 5-m, were randomly located. For each transect, the number of plants of each myrmecophyte species and the number of colonies of each ant species were recorded. These censuses were used to uncover patterns at the population and community levels (see details in Fonseca & Ganade 1996).

RESULTS

Domatium volume and ant body size

Central Amazon myrmecophyte species bear distinct domatia structures that vary in form and size, exhibiting a range of 250 times difference in domatium volume. *Cecropia purpuracens* domatia are cylindrical hollow nodes of the trunk which offer a very large internal volume as nesting site, while the leaf-domatia of *Hirtella* consist of two spherical rollings of the leaf blade which provide a very restricted nesting space. Ant species nesting in Central Amazon myrmecophytes have a marked interspecific variation in body size (head plus alitrunk). Among the studied species, the mean body size of queens ranged from 2.27 mm (± 0.02 SE) in *Pheidole minutula* to 6.51 mm (± 0.07 SE) in *Camponotus balzani*, a difference of almost 3-fold in linear dimensions. The body size of workers also showed a large interspecific variation, ranging from 1.09 mm (± 0.01 SE) in

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Allomerus octoarticulata to 4.48 mm (± 0.07 SE) in *Camponotus balzani*. There was a positive interspecific correlation between queen body size and worker body size ($r^2 = 0.866$, n = 8, $P < 0.01$).

Since both domatium volume and ant body size varied significantly among species, I investigated a possible interspecific relationship between the space provided by individual domatium of a given myrmecophyte species and the body size of its most frequent ant partner. The mean domatium volume (log-transformed) of a given myrmecophyte species was found to provide a very good predictor of the mean body size (log-transformed) of its main ant partner (Figure 1a, b). This relationship was highly significant for both queen body size ($y = 0.179x + 1.353$, $r^2 = 0.801$, n = 8, $P < 0.02$) and worker body size ($y = 0.284x + 0.613$, $r^2 = 0.877$, n = 8, $P < 0.001$).

Number of domatia and colony size

At the colony level, evaluation of the nesting space limitation hypothesis requires two empirical tests. First, since each host plant is normally occupied by a single ant colony, if nesting space is a limiting factor for colony growth,

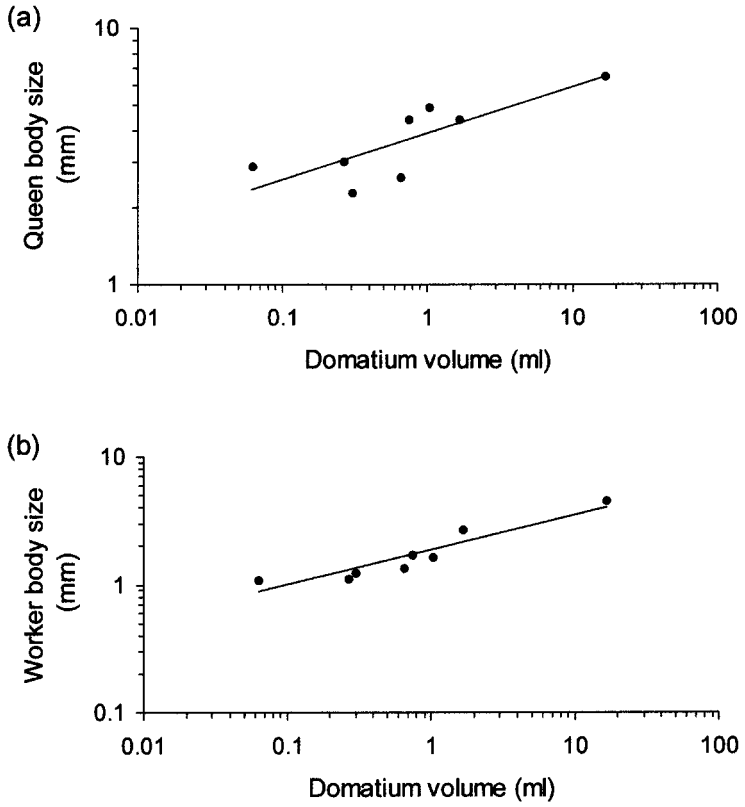


Figure 1. Relationship between ant body size and domatium volume for eight Central Amazon ant-myrmecophyte systems. (a) Queens' body size ($y = 0.179x + 1.353$, $r^2 = 0.801$, F = 10.7, df = 1,6; $P < 0.02$). (b) Workers' body size ($y = 0.284x + 0.613$, $r^2 = 0.877$, F = 42.8, df = 1,6; $P < 0.001$). Graphs and regressions use log-transformed data.

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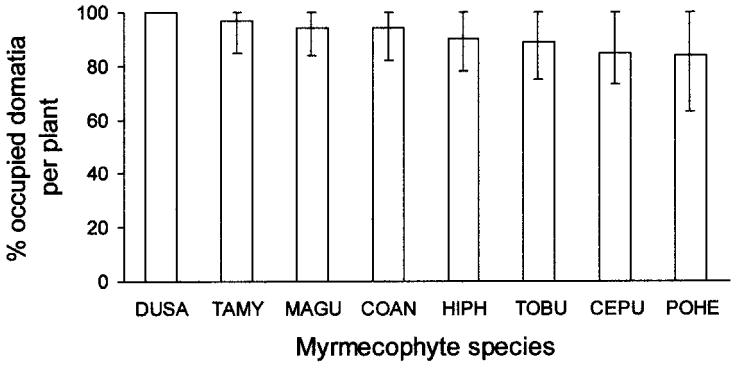


Figure 2. Domatia occupancy per plant for eight Central Amazon ant–myrmecophyte systems. The bars show the mean percentage occupancy per myrmecophyte species while the vertical line represents the maximum and minimum occupancy values (n = 5 plants per myrmecophyte species). DUSA, *Duroia saccifera* (Rubiaceae); TAMY, *Tachigali myrmecophila* (Caesalpinaceae); MAGU, *Maieta guianensis* (Melastomataceae); COAN, *Cordia* aff. *nodosa* (Boraginaceae); HIPH, *Hirtella physophora* (Chrysobalanaceae); TOBU, *Tococa bullifera* (Melastomataceae); CEPU, *Cecropia purpuracens* (Cecropiaceae); POHE, *Pourouma heterophylla* (Cecropiaceae).

one would expect the colony to expand to most, or even all, domatia being offered by the host plant. Indeed, across the eight ant–myrmecophyte systems the mean occupancy level was 92%, varying from 84% in *Pourouma heterophylla* to 100% in *Duroia saccifera* (Figure 2). It is worth mentioning that these occupancy values are underestimates since some domatia recorded as unoccupied at the harvest could have been occupied at other times.

Second, if space sets limits for colony growth, one would expect a positive relationship between the total space offered by a plant for nesting ants and the number of individuals of its associated ant colony. Indeed, for the eight ant–myrmecophyte systems considered, there was a positive relationship between the number of domatia on a plant and the size of its associated ant colony (Figures 3a–h). Furthermore, this simple relationship explained more than 75% of the variation in ant colony size in all but one system (Table 2), despite the large range of phylogenetic lineages, morphological variations and ecological conditions.

The local density of ants and plants

At the population level, evaluation of the nesting space limitation hypothesis required two further empirical tests. First, if the number of plants in a myrmecophyte population is limiting the number of colonies in an ant population, at any given time one could expect most or all plants to be occupied by colonies of their ant partners. Indeed, all but two myrmecophyte populations in the community presented colonization levels higher than 80%, while in half of the species all plants were colonized (Figure 4). However, it should be borne in mind that most unoccupied plants were young saplings, so there could be a certain time lag between the production of the first domatium and the colonization event.

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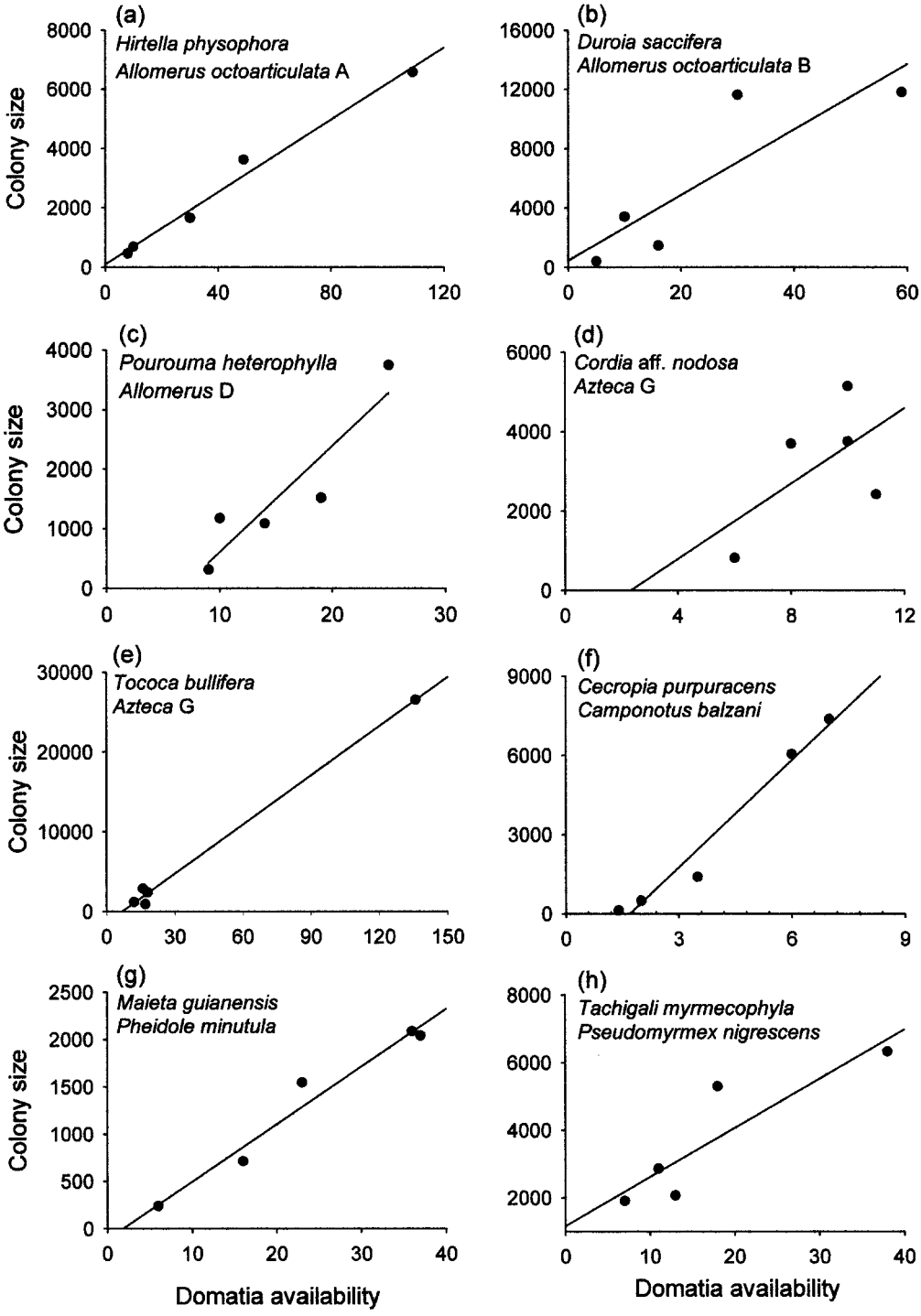


Figure 3. Ant colony size in relation to domatia availability for eight Central Amazon ant–myrmecophyte systems. The graph title shows the plant species above and the ant species below. Domatia availability was estimated by the total number of domatia for all systems, except for *Cecropia purpuracens* in which trunk height was used as a better estimator (see text). Statistics are given in Table 2.

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Table 2. Linear regression of ant colony size against domatia availability for eight ant–plant systems (n = 5 plants per system). r^2 is the coefficient of determination, F tests the significance of the regression, P is the probability.

Plants	Ants	Slope	Intercept	r^2	$F_{[1,3]}$	P
Hirtella physophora	*Allomerus octoarticulata* A	61	94	0.984	188.7	0.001
Duroia saccifera	*Allomerus octoarticulata* B	221	448	0.744	8.7	0.060
Pourouma heterophylla	*Allomerus* D	178	−1175	0.838	15.5	0.029
Cordia aff. *nodosa*	*Azteca* G	478	−1132	0.341	1.6	0.301
Tococa bullifera	*Azteca* G	205	−1367	0.995	621.2	0.000
Cecropia purpuracens	*Camponotus balzani*	1353	−2293	0.968	90.4	0.002
Maieta guianensis	*Pheidole minutula*	61	−109	0.963	78.6	0.003
Tachigali myrmecophila	*Pseudomyrmex nigrescens*	146	1164	0.782	10.8	0.046

Second, it is necessary to test how natural spatial variation in the abundance of plants on the landscape affects the local abundance of colonies of its main ant partner. For this purpose, local abundance was defined by the number of plants or colonies within an individual transect. Therefore, this test was carried out by considering differences in abundance of both partners among transects. As expected, due to the high host specificity of the ant species, the number of colonies of the ant species in a given transect was mostly determined by the local availability of its major host species. This pattern was true for all main ant partners but, due to the very low abundance of some of the ant–plant systems, this could be demonstrated quantitatively only for the four most abundant ones. The number of colonies of *Pheidole minutula* in a given transect was well explained by the number of *Maieta guianensis* ($r^2 = 0.956$, $F = 174$, $df = 1,8$; $P < 0.001$). However, as *P. minutula* was also the major partner of *Maieta poeppigii*, when both host species were considered together as explanatory variables, the model was improved significantly ($r^2 = 0.992$, $F = 444$, $df = 2,7$; $P < 0.001$). The local abundance of *Allomerus octoarticulata* colonies was driven mainly by the local presence of *Hirtella physophora* ($r^2 = 0.951$, $F = 156$, $df = 1,8$; $P < 0.001$). The local colony abundance of *Azteca* G was explained by the abundance of *Cordia* aff. *nodosa* plants, although the unexplained occurrence of unoccupied plants produced a relatively poor fit ($r^2 = 0.583$, $F = 11.2$, $df = 1,8$; $P < 0.01$). Finally, the local abundance of *Pseudomyrmex nigrescens* colonies was greatly determined by the abundance of *Tachigali myrmecophila* ($r^2 = 0.855$, $F = 47.3$, $df = 1,8$; $P < 0.001$). Therefore, the local abundance and spatial distribution of the myrmecophyte species seem to set the local abundance (as measured by the number of colonies) and the spatial distribution of the ant populations.

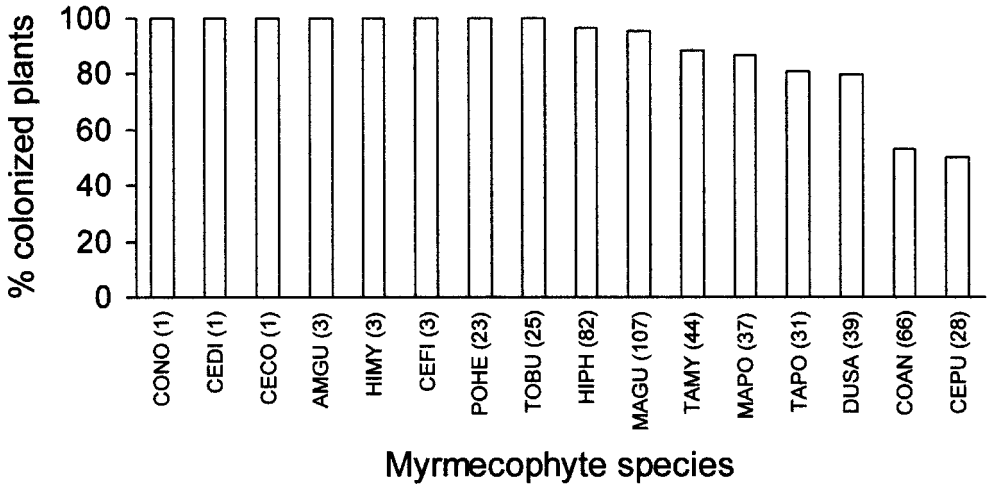


Figure 4. Percentage of plants with established ant colonies, in a given time, for 16 Central Amazon myrmecophytes. Unoccupied plants generally correspond to young saplings. Sample size are between brackets. The key for the abbreviations of the myrmecophyte species names is shown in Figure 5.

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The abundance distribution of ants and plants

At the community level, the nesting space limitation hypothesis predicts that the interspecific abundance distribution of ant colonies should be determined by host availability as well as by interspecific competition for nesting space. In this section, data from all ten transects were pooled together to generate the abundance distributions of both partners, this being considered the community scale.

The abundance distribution of ant colonies in the community was highly skewed; a few species were highly abundant while the remnant species were represented by only a few ant colonies (Figure 5a). As predicted, two main mechanisms seem to be important in generating such a pattern: nesting site availability and interspecific competition for nesting site.

Across ant–myrmecophyte systems, the abundance distribution of the host plants seems to define the rank of the main ant partners (Figure 5b). Indeed, the rank of the four most common ant species matched the rank on the availability of their main plant partners. For instance, *Pheidole minutula* was the most abundant species in the area because it is the most frequent partner nesting in *Maieta guianensis*, the most common myrmecophyte. Ants from the *Allomerus octoarticulata* complex were very abundant, since they occurred in *Hirtella myrmecophila*, the second most abundant myrmecophyte. *Azteca* G, the third most abundant ant species, was a major partner of *Cordia* aff. *nodosa*, the third most common myrmecophyte. *Pseudomyrmex concolor* and *P. nigrescens*, the fourth and fifth most abundant ants, shared the dominance of *Tachigali myrmecophila*, the fourth most abundant myrmecophyte. Furthermore, a few main ant partners appeared in the tail of the abundance distribution since they relied on relatively rare plant partners. This is, for example, the case of *Allomerus* D and *Azteca Q*, which nest respectively in *Pourouma heterophylla* and *Amaioua guianensis*.

Within ant-myrmecophyte systems, the abundance of a given ant species seems to be a function of its position in the dominant hierarchy among ant competitors (Figure 6). For each myrmecophyte species, there is one or rarely two ant species that will dominate the possession of most available plants; any other species that may be present will live a subordinate or opportunistic existence in the system. For dominant species, any increase in the density of its host plants had a strong impact on the density of their colonies ($y = 0.779x - 3.287$, $r^2 = 0.882$, $F = 97.2$, $df = 1,13$; $P < 0.001$, Figure 6). For the secondary ant partners, although ant and host density were significantly linked, great increases in host density generated a marginal effect in density of ant colonies ($y = 0.031x - 0.256$, $r^2 = 0.406$, $F = 13.6$, $df = 1,20$; $P < 0.001$, Figure 6).

DISCUSSION

The individual level: large rooms, large guests

Large ant species dominate myrmecophyte species bearing spacious domatia while small ants nest successfully in hosts offering small-sized domatia. This

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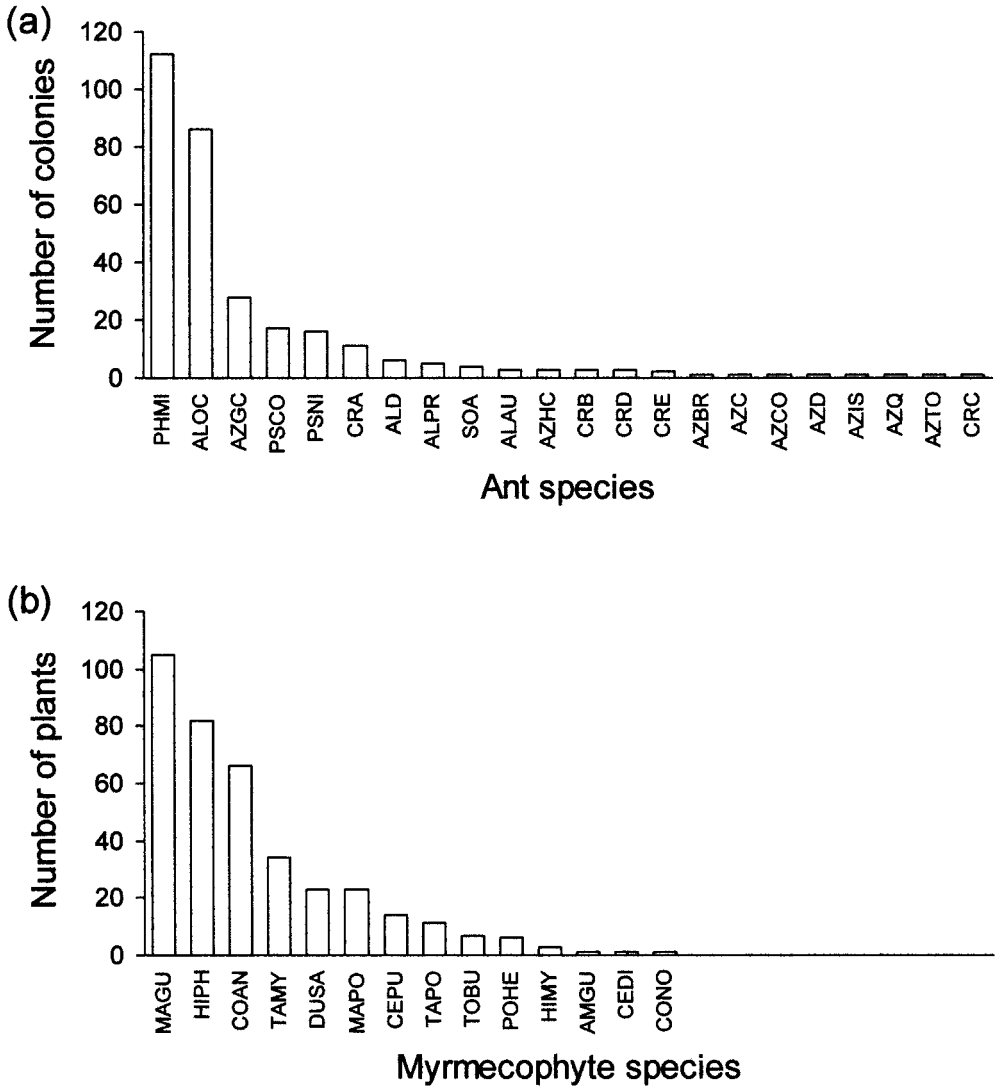


Figure 5. Relative abundance of ants (top graph) and plants (bottom graph) in a Central Amazon ant–myrmecophyte community. Note the correspondence between the number of colonies of a given ant species and the number of individuals of its specific hosts. Abbreviations for ant species are: PSCO, *Pseudomyrmex concolor*; PSNI, *Pseudomyrmex nigrescens* (Pseudomyrmecinae); AZIS, *Azteca isthmica*; AZBR, *Azteca* BR; AZC, *Azteca* C; AZCO, *Azteca* CO; AZD, *Azteca* D; AZGC, *Azteca* GC; AZHC, *Azteca* HC; AZTO, *Azteca* TO; AZQ, *Azteca* Q; (Dolichoderinae); PHMI, *Pheidole minutula*; ALPR, *Allomerus prancei*; ALOC, *Allomerus octoarticulata* complex; ALAU, *Allomerus auropunctata*; ALD, *Allomerus* D; SOA, *Solenops* A; CRA, *Crematogaster* A; CRB, *Crematogaster* B; CRC, *Crematogaster* C; CRD, *Crematogaster* D; CRE, *Crematogaster* E (Myrmicinae). Abbreviations for plant species are: CEPU, *Cecropia purpuracens*; CEDI, *Cecropia distachya*; POHE, *Pourouma heterophylla* (Cecropiaceae); HIMY, *Hirtella myrmecophila*; HIPH, *Hirtella physophora* (Chrysobalanaceae); DUSA, *Duroia saccifera*; AMGU, *Amaioua cf. guianensis* (Rubiaceae); CONO, *Cordia nodosa*; COAN, *Cordia aff. nodosa* (Boraginaceae); TOBU, *Tococa bullifera*; MAGU, *Maieta guianensis*; MAPO, *Maieta poeppigii* (Melastomataceae); TAPO, *Tachigali polyphylla*; TAMY, *Tachigali myrmecophila* (Caesalpinaceae).

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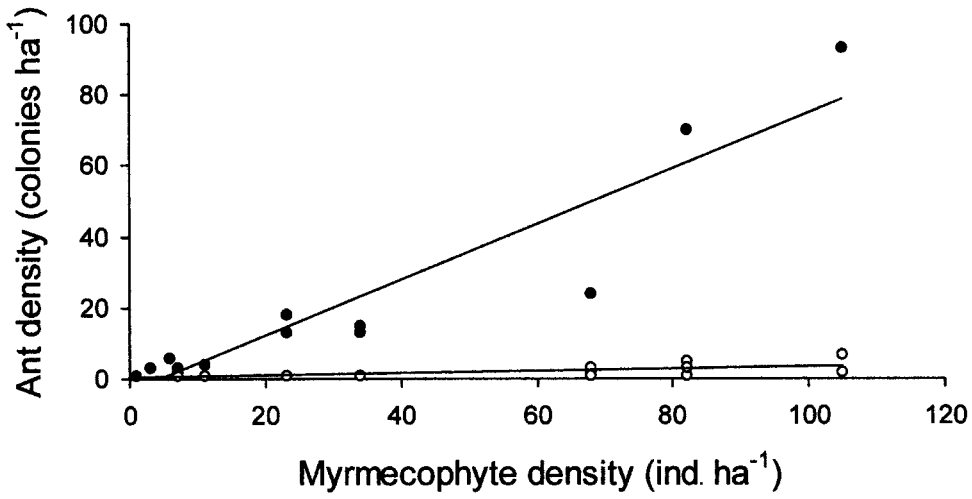


Figure 6. Ant colony density in relation to host density in a Central Amazon ant–myrmecophyte community. Closed circles represent the main ant partner in each system ($y = 0.779x - 3.287$, $r^2 = 0.882$, $F = 97.2$, df = 1,13; $P < 0.001$) while the open circles represent the less frequent ones ($y = 0.031x + 0.256$, $r^2 = 0.406$, $F = 13.6$, df = 1,20; $P < 0.001$). Each point corresponds to one ant–plant interaction.

pattern, recognized here for the first time, is partly explained by an obvious, but fundamental, constraint: large-bodied queens are simply physically unable to fit inside small-sized domatia. This does not, however, explain why small-bodied ant species do not become main partners of myrmecophytes offering large domatia. A possible explanation is that in the establishment phase agonistic interactions tend to occur at the individual level, with aggression incidents occurring between two queens or a few workers (Davidson *et al.* 1989, Vasconcelos 1993). In this situation, it is likely that species with large-bodied individuals would tend to dominate and exclude small-bodied ones. Additionally, it is possible that small-bodied ant species are inefficient in defending large domatia from invaders.

Once the queen finds an adequate host and starts reproducing, physical impediment could be less of a problem for individual workers as they generally have smaller bodies than their respective queens. If this is the case, the correlation between domatium volume and worker's body size could be a spurious correlation resulting from the fact that body size of queens and workers are correlated. However, it also possible that if the domatium has enough space for only a few individuals, space limitation may jeopardize the performance of social tasks. For instance, some activities inside the domatia, such as offspring care and nurture, could not be satisfactorily executed. Also, by being forced to a highly fragmented (polydomous) colony structure, workers could spend much time travelling between domatia, spending more energy in colony integration (e.g. communication, food sharing and defence) and increasing their exposure to predators, parasites and pathogens. This will tend to mitigate against oversized ants occupying smaller domatia.

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If domatia quality can drive the outcome of ant–ant competition, and domatia size and shape are genetically determined, myrmecophyte populations could be expected to possess domatia with characteristics that would facilitate the presence of their most efficient local partners (see Thompson 1994 for the geographic mosaic theory of coevolution). Although no data are available to test this proposition, it is worth mentioning that geographic variation in domatia size is well known to occur across myrmecophyte populations (e.g. Cameroon and Gabon populations of *Leonardoxa africana*, McKey 1984) and across closely related species (Fiala & Maschwitz 1992b). Similarly, if ant body size and shape are heritable characters, and genetic variants possessing a better match with domatia size and form can obtain fitness advantages, differential selective responses among ant populations along geographical gradients are expected. These predictions are certainly worth following.

The colony level: larger house, larger family

Ant colony size varies over eight orders of magnitude among species, reflecting very different life-history strategies (Hölldobler & Wilson 1990, Kaspari & Vargo 1995). Within species, colony size is a very important trait that can influence the colony's reproductive success. For ants living in myrmecophytes, nesting space rather than food or territory was suggested as the main limiting factor for ant colony size (Fonseca 1993). However, this proposition was based on a comparative study made within a single ant–plant system (*Pseudomyrmex concolor* nesting in two *Tachigali* species).

In the present study, eight other ant–myrmecophyte systems showed high levels of space occupancy, as recorded in other ant–plant systems (Janzen 1967, McKey 1984, but see Alonso 1998 for geographic variation in occupancy levels), and presented positive relationships between ant colony size and the total number of domatia offered by the host. For all but one system, more than 75% of the variation in colony size was explained by space availability. Therefore, the generality of the nesting space limitation hypothesis was supported by other Central Amazon ant–myrmecophyte systems with very different phylogenetic backgrounds and life histories that broadly represent not only the local community but also the taxonomic composition of Amazonian myrmecophytes.

In principle, plants control the production of domatia to be used by ant colonies as nesting space. By managing nesting space, myrmecophytes can keep the colony to a size that better reflects their interest in terms of defence allocation (Fonseca 1993). From the plants' perspective, the number of ants per unit of photosynthetic area to be defended is an important allocation parameter. Yet, the plant's optimum is not necessarily the ants' optimum and ant–plant conflicts can arise. However, by efficiently defending the plant's photosynthetic tissues (e.g. Fonseca 1994) or by making limiting nutrients available to the plants (Huxley 1978), mutualistic ants are able to foster the growth of their partners and consequently stimulate further supply of nesting space. Therefore, under nesting space limitation, domatia space is expected to be the main

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currency offered by the myrmecophyte to the ants in exchange for efficient mutualistic services. Indeed, in a comparative work in the *Macaranga–Crematogaster* system that contrasted trees with facultative to obligatory ant associations, the emergence of domatia rather than extrafloral nectaries or food bodies was pointed out as the most important step towards the evolution of myrmecophytism (Fiala & Maschwitz 1991, 1992a,b).

The population level: more houses, more families

Under nesting site limitation, three aspects of the ant populations seem to be inexorably bonded to the population structure of their respective plant partners: (a) The colony-level carrying capacity. Due to the high host fidelity, the colony-level carrying capacity of each ant species (i.e. the maximum number of colonies in the population) is constrained by the general abundance of its host plants. Ant species nesting on locally abundant myrmecophyte species are more abundant than those specialized on rare hosts. However, it should be noted that, although the colony-level carrying capacity is controlled by the plant, the realized number of colonies will be dependent on the dominance hierarchy among ant competitors; (b) The population temporal pattern and age structure. In Central Amazon, abandoned pastures that have been burned are readily occupied by saplings of *Cecropia*. Accordingly, there is an upsurge in the number of young colonies of *Azteca* soon after the establishment of the host population. Following the cessation of burning the *Cecropia* population will suffer a progressive decline apparently due to self-thinning processes. Similarly, *Azteca* colonies become progressively less abundant, but surviving colonies are able to accommodate a greater number of individuals. *Cecropia* trees will dominate the overstorey for more than one decade, but eventually will be replaced by later successional tree species, causing their ant partner populations to reach very low levels in the closed secondary forest (*pers. obs.*); (c) The spatial distribution of the ant colonies. The spatial distribution of the colonies is dependent on the idiosyncrasies of the spatial distribution of the hosts, because colonies can be only initiated in established plants and the ants have little control over the dispersal and initial establishment of their hosts.

Effective mutualistic ants, however, can improve the reproductive output of their partners and ultimately change the relative abundance of the host plant in the community. For instance, the allelopathic effect of some *Pseudomyrmex* ants, which remove all vegetation from the neighbourhood of their host plant, may have led to the development of large stands of *Acacia* in Western Mexico (Janzen 1973). Furthermore, if the anti-herbivory services provided by the ant partners change spatially, for example due to abiotic conditions, differential survival can lead to alterations in the spatial distribution of the myrmecophytes. Furthermore, ant partners can play a decisive role in the reproduction of their plant partners (Vasconcelos 1991), potentially affecting their population dynamics. In sum, ants can indirectly affect spatial and temporal patterns

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of their host populations, and this can potentially affect the availability of nesting space for their own descendants.

On an evolutionary time-scale, nesting space limitation at the population level is expected to drive ant specialization via intraspecific competition. Since most mature colonies in the population are normally producing tens to hundreds of potential queens in a year, and just a few new saplings will be available for colonization, strong intraspecific competition for nesting site is expected to occur. Some observations support the view that earlier-arriving queens are more prone to success (pre-emption model of competition), so selection is expected to improve traits that favour the success of this founding phase. For instance, alate production can be extravagant (Janzen 1973), alate sex-ratio can be biased towards females (Hamilton 1967), alate production can be synchronized with the emergence of new domatia (Fonseca 1995), or the queen's search image can be improved by the use of chemical clues of specific host species. Although this last mechanism has not been demonstrated for alate queens, workers of *Crematogaster boreensis* were shown to have the ability to chemically recognize their usual *Macaranga* hosts (Fiala & Maschwitz 1990). In sum, intraspecific competition for nesting sites can be expected to mould efficient host-finding mechanisms by the alate queens.

The community level: interspecific household conflicts

The search for causes of species abundance distribution curves is a classical community ecology quest (Begon *et al.* 1995). In this study, the skewness of the abundance distribution of ant colonies from different species is explained by two nesting space limitation processes. First, the carrying capacity for an ant population is dictated by the availability of its myrmecophytic hosts. Second, when two or more ants share the same host species, strong interspecific competition for nesting space takes place. In this situation, differential efficiency in host acquisition and guarding among ant species makes some species dominant while others are pushed to a subordinate existence. Like any extreme specialization, nesting site specialization is a two-sided game. On one hand, nesting site specialization can enable a given ant species to have priority over competitors for nesting opportunities, thus becoming relatively abundant. On the other hand, it can drive down an ant population when hosts become locally rare or superior competitors are faced.

Fonseca & Ganade (1996) suggested that this Central Amazonian ant–myrmecophyte community was divided into a number of well-defined compartments, and that this compartmentalization was partially explained by the occurrence of ants in phylogenetically related host plants. However, the question remained about which mechanism was leading ants to choose host species of close phylogenetic affiliation. The close match between ant body size and domatium size represents one mechanism that helps us to understand the compartmentalization of this ant–myrmecophyte community. Myrmecophyte species of the same genus tend to produce domatia that are very similar in

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size, but very distinct from the sizes offered by other myrmecophyte genera. As a consequence, ants of a given size are more prone to occupy plant species that are closely related than species that are phylogenetically far apart. Davidson *et al*. (1989) suggested that the distance between trichomes was another mechanism that could influence host selection by ant species. Interestingly, in Central Amazon, small-sized domatia species are the ones with denser trichomes (e.g. *Hirtella*, *Maieta* and *Duroia*), medium-sized domatia species are the ones with medium-density trichomes (e.g. *Tococa*, *Cordia*), while large-sized domatia species have glabrous or widely spaced trichome leaves (e.g. *Cecropia*, *Tachigali*). This suggests that myrmecophytes can be using both mechanisms concomitantly to define ant species associations. However, the above mechanisms seem insufficient to explain all ant–myrmecophyte associations, since ant species of similar size do specialize in host species of different phylogenetic lineages. Therefore, other ecological attributes encapsulated by the term 'phylogeny' seem to contribute to the definition of the ant–myrmecophyte compartments.

From correlation to causation

This study has provided strong empirical support, at several organizational levels, for the hypothesis that nesting space is a relevant limiting resource for ants living in myrmecophytes. However, due to its correlative nature, the possibility cannot be discarded that some of the patterns presented here are cross-correlated with other hidden factors such as food availability. A positive point, nevertheless, is that the nesting space hypothesis holds across several organizational levels, phylogenetic backgrounds and life histories. Alternative explanations will be challenged to work across this same spectrum. Future experimental work could certainly help us to discern among alternative causal mechanisms.

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