Asymmetries, compartments and null interactions in an Amazonian ant-plant community

CARLOS ROBERTO FONSECA* and GISLENE GANADE†

Animal Behaviour Research Group, Department of Zoology, South Parks Road, Oxford, OX1 3PS, UK; and, †NERC Centre for Population Biology and Department of Biology, Imperial College at Silwood Park, Ascot, Berks SL5 7PY, UK

Summary

1. In the tropics, many plants offer housing and food for their specialized ant partners which, in return, offer benefit in the form of defence and/or nutrients, thus forming mutualistic bonds. Such ant-plants, also called myrmecophytes, occur together at a local scale, generating community patterns of mutualistic ant-plant associations. Here, we present the first fully quantitative description of an ant–myrmecophyte community.

2. The study site in Central Amazonian tropical rainforest had a high myrmecophyte density of about 380 ind. ha^{-1}. Sixteen myrmecophyte and 25 ant species were recorded, the species abundance rank curves being highly uneven.

3. The ant–myrmecophyte matrix was highly compartmentalized, and a Monte Carlo simulation showed that the observed pattern was not a product of chance and sample size ($P < 0.0001$). Cluster analyses indicated that compartments were partially explained by occurrence of the ants in phylogenetically related host plants, but not by habitat specificity.

4. The connectance of the ant-plant community was 12%. This value seems quite low when compared with published results from other mutualistic systems (pollinator and seed-dispersor), after controlling for the total number of interacting species. The high frequency of null interactions in the ant–myrmecophyte system could not be explained by the 'phenological non-coincidence hypothesis', since both ant and plant partners occur together throughout the year.

5. Ant-plant interactions were highly asymmetrical: ant species had fewer partners than plant species and ants were more dependent on the plants than the reverse. These asymmetries are in the opposite direction to those recorded for plant-pollinators and plant-dispersors; however, they seem to be the product of the same underlying process: differential fitness benefits between mutualistic partners.

6. The low number of ant and plant partners per compartment, coupled with an apparently high temporal and spatial stability of ant–myrmecophyte interactions, suggests that compartments are the appropriate scale at which to investigate coevolution in ant–myrmecophyte systems.

Key-words: ant-plants, coevolution, community, mutualism, pollination.

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Introduction

Mutualistic interactions between plants and ants are widespread in tropical biota (Hölldobler & Wilson 1991). This kind of interaction reaches a high degree of sophistication in myrmecophytes, also called ant-plants, which offer housing and food for their specialized ant partners. Housing is provided by ant-domatia that vary between plant species from slight modifications of stems or trunks to well developed leaf-pouches. Food varies from amino acids and sugar-based solutions produced by extrafloral nectaries, to protein or glycogen-based food bodies (Hölldobler & Wilson 1991; Davidson & McKey 1993). In general, each myrmecophytic plant provides shelter for a single ant colony (Davidson, Snelling & Longino 1989). Experimental studies in phylogenetically independent ant-plant systems have demonstrated the existence of mutualism between partners (Janzen 1966, 1967; Schupp 1986; Fiala *et al.* 1989; Fiala &

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Maschwitz 1990; Vasconcelos 1991; Fonseca 1993, 1994).

In the Neotropics, more than 200 plant species have ant-domatia used as nesting sites by specialized ant species (Benson 1985). When several myrmecophytes and their ants occur sympatrically on a local scale, community patterns emerge. Despite the solid base that the field of ant–plant interaction has at the population level, community studies remain basically unexplored (Bentley 1977; Beattie 1985; Hölldobler & Wilson 1991; Huxley & Cutler 1991; Davidson & McKey 1993). Community analysis of mutualists provides information about historical, evolutionary and ecological processes that are not available from analyses at the population level (Jordano 1987; Putman 1994). A broad review of the mutualistic association between plants and their pollinators and seed-dispersors showed strong interaction asymmetries between partners (e.g. animals have more plant partners than the reverse), and a high number of null interactions (Jordano 1987). Ant-plant community studies can help assess these generalizations and shed light on the ecology and evolution of mutualism.

The community of myrmecophytes and their ant partners in a pristine Central Amazonian rainforest was quantitatively studied. Our main objectives are (i) to describe quantitatively the ant–myrmecophyte matrix, (ii) to search for patterns of compartmentalization, (iii) to compare the results from the ant-plant system with those from other mutualistic systems.

Methods

The research was carried out in the reserve 'Km 41' (2°24′S, 59°43′W) of the Biological Dynamics of Forest Fragments Project, about 80 km north of Manaus, Amazonas, Brazil. The 1000 ha reserve is continuous within an area of *c*. 500 000 ha of relatively undisturbed upland rainforest on sandy or clay yellow latosols (xanthic ferralsols). The climate in the Manaus area is wet tropical with an average annual temperature of 26·7 °C and an annual rainfall of 2186 mm. The area is fully described in Lovejoy & Bierregaard (1991).

From June to August 1990, 10 transects of 1000 m² (200 × 5 m) were randomly located within a previously defined square area of 100 ha. All myrmecophytes were recorded, tagged and identified. To determine whether rare species had been missed in the quantitative sampling, we made a complementary sample, from May to July 1991, looking for rarer myrmecophytes with no selection for host size or ant species. Plant taxonomy follows the botanical collections of the Instituto Nacional de Pesquisas do Amazonas (Brazil) and Kew Royal Botanic Gardens (UK), and voucher specimens were deposited in the herbarium of the Universidade Estadual de Campinas (Brazil). For each host plant, voucher specimens from

each ant colony were collected for identification and deposited in the INPA entomological collection. The ant fauna of the region is poorly described, so several ant species were identified to generic level and are presented as morphotypes.

The ant–myrmecophyte community was arranged as a matrix of occurrence of $m \times n$-values, *m* being the total number of plant species and *n* the total number of ant species. The matrix element a_{ij} is the number of records for a given pairwise interaction between plant species *i* and ant species *j*. When no mutual interaction occurs then $a_{ij} = 0$. Whether the observed matrix either has a particular arrangement emerging for ecological reasons (e.g. mutualism), or is simply a product of random association and sampling effort, was tested by a Monte Carlo simulation. The simulation measures the deviation of a given matrix from the expected frequencies through the test statistics *T*, equivalent to the log-likelihood ratio. The test statistics *T* is defined as $T = \text{const} - \Sigma_{ij} [a_{ij} \ln (a_{ij})]$ (Monte Carlo, R × C Contingency Table module, Engels 1988). The program generates random matrices assuming the same marginal values for rows and columns as for the observed data, and consequently the same sampling effort. Host plants without ants were excluded from the randomization procedure. The number of trials in which the *T* from randomly generated matrices was greater or equal to the observed *T* in relation to the total number of trials ($n = 10\ 000$ trials) gives the *P* value ($\pm$ SE, binomial standard error).

Ant and myrmecophyte species differ in the relative frequency with which they are associated with different partners. Therefore, the structure of the association between ants and myrmecophytes can be visualized as a series of clusters of similarity in relation to partner sharedness. The ant analysis takes each plant species as a variable and its relative frequency per ant species as the score. An analogous procedure was followed for the plants. Cluster analyses were performed using the average linkage method on gamma distances (Systat 1992). Similar results were reached by other methods and are not presented here.

The connectance of a mutualistic system is the proportion of the possible interactions that are actually taking place, or in other words, it is the proportion of non-null interactions in a community (Yodzis 1980). The connectance (*C*) is calculated as $C = x/mn$, *x*-being the number of observed interactions, and *m* and *n* being the number of plant and ant species, respectively. Note that this definition follows Jordano (1987) and it differs from that of food web studies (Warren 1994).

As the three components required for the calculation of connectance are sensitive to sample size, we performed a simulation to test if our sample effort was enough to stabilize the estimate for connectance of this ant-plant community. The simulation is based on the frequencies in the cells of the actual ant-plant matrix. The program starts by calculating the con-

nectance for the $m \times n$ matrix (i.e. 16×25), based on the total number of records (i.e. 417). Then, it subtracts one record from a randomly chosen cell, decreasing the sample size. The random selection is weighted: cells with larger numbers of records were more likely to be chosen. When the total number of records of either a given plant species or a given ant species reaches zero, the matrix size is reduced accordingly. Finally, a new connectance index is calculated based on the remaining number of observed interactions and the remaining number of ant and plant species. The program continues until the sample size is equal to one. The expected connectance for a given sample size was estimated as the mean ($\pm$ SD) of 100 runs.

A given ant species can be associated with one or more plant partners; likewise, a given plant species can be associated with one or more ant partners; therefore, the frequency distributions of the number of partners for ant and plant species are shown. Furthermore, for a given pair of mutualistic partners it is possible to estimate the level of mutual dependence (*sensu* Jordano 1987). Here, the dependence of a plant species i on ant species j was calculated as the percentage of the realized interactions (a_{ij}) in relation to all records of that plant species. Note that according to this definition, dependence is not an estimate of the quality of the mutualistic services; that can only be evaluated through comparative and experimental studies (as Fonseca 1993, 1994). Similarly, the dependence of the ant species on that plant species is calculated in relation to the total number of records for that ant species. The frequency distributions of dependence of the ants on plants and of the plants on ants are shown. Only species with sample size $\geqslant 5$ were considered.

Results

The local richness and abundance of myrmecophytes and ant partners in the study area were very high. Sixteen myrmecophyte species were recorded from 487 myrmecophyte plant records with a mean ($\pm$ SE) density of 377 ± 55 ind. ha^{-1}; while 25 ant species were recorded from 417 ant colony records, with a mean ($\pm$ SE) colony density of 307 ± 46 colonies ha^{-1}. The species abundance rank distribution of both myrmecophytes and ants was highly uneven (Fig. 1). The four most abundant plant species (*Maieta guianensis* Aubl., *Hirtella physophora* Martius & Zuccarini, *Cordia* aff. *nodosa*, and *Tachigali myrmecophila* Ducke) represent more than 75% of the plant records. Not surprisingly the dominant ants in those hosts (*Pheidole minutula* Mayr, *Allomerus* aff. *octoarticulata*, *Azteca* G and *Pseudomyrmex concolor* F. Smith) are the four most abundant ant species, representing about 80% of the colony records. Of the myrmecophyte species known around the study site, only *Myrcia* sp. (Myrtaceae), normally associated
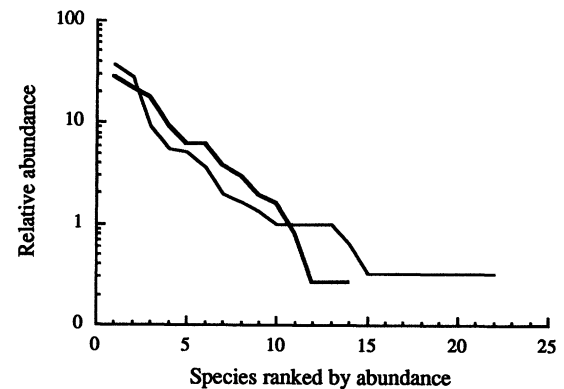

Fig. 1. Rank abundance curves of ant species (thin line) and myrmecophyte species (thick line) in a total area of 1 ha of tropical rainforest in Central Amazon. Abundance expressed as log-transformed relative frequency.

with *Myrcidris epicharis* Ward (Pseudomyrmecinae), was absent from this sample, perhaps due to its rarity and patchy distribution. Moreover, some rare ant species probably would appear with further sampling effort.

The ant–myrmecophyte matrix shows a highly structured community (Table 1). Indeed, the test statistics for the 10 000 randomly generated matrices in the Monte Carlo simulation ranged from 80 to 160, far below the observed value of 680 (Fig. 2), producing a P value < 0.0001 (± 0.0 SE). Therefore, the arrangement of the observed ant–myrmecophyte matrix is not a product of chance, indicating that ants and myrmecophytes do show strong preference for certain partners.

The cluster analysis of the myrmecophytes in relation to the relative frequency of the colonies of ant partners produced seven distinct groups with evident phylogenetic affinity (Fig. 3, right). The two *Tachigali*
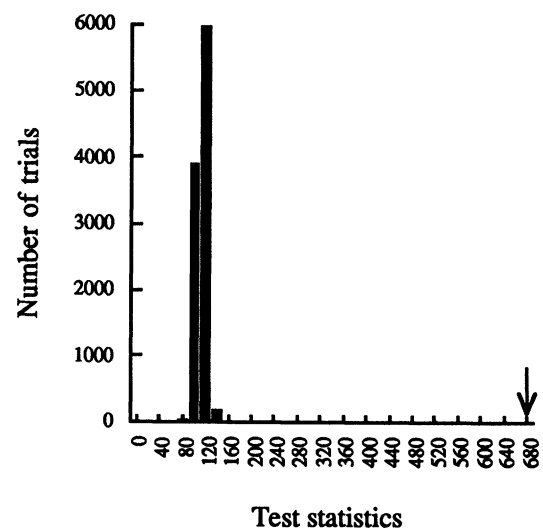

Test statistics

Fig. 2. Comparison of the frequency distribution of the test statistics T of randomly generated matrices of a Monte Carlo simulation ($n = 10000$ trials) in relation to the real value (arrow) calculated from the observed ant–myrmecophyte matrix.

Table 1. Community matrix of ant–myrmecophyte associations in a Central Amazon tropical rainforest, organized according to partner similarity (see main text)

MYRMECOPHYTES & ANTS	*Cecropia purpuracens*	*Cecropia concolor*	*Cecropia distachya*	*Cecropia ficifolia*	*Pouruma heterophylla*	*Hirtella myrmecophila*	*Hirtella physophora*	*Duroia saccifera*	*Cordia nodosa*	*Cordia aff. nodosa*	*Tococa bullifera*	*Maieta guianensis*	*Maieta poeppiggi*	*Tachigali polyphylla*	*Tachigali myrmecophila*	*Amaioua aff. guianensis*
Camponotus balzanii	1	1														
Azteca alfari	1															
Azteca isthmica	1	1	1	1												
Azteca aff. isthmica	1			2												
Allomerus D					23											
Allomerus prancei						5										
Allomerus aff. octoarticulata						3	70	27								
Solenops A							3	1								
Allomerus auripunctata								2		2						
Crematogaster B								1	1	1						
Azteca HC										3						
Azteca G										24	11	2				
Crematogaster D										3	2					
Azteca CO										1						
Pheidole minutula											1	93	28			
Crematogaster A							1				7	7	1			
Azteca TO											1					
Crematogaster C											3		3			
Azteca schummani														2	1	
Pseudomyrmex nigrescens														7	16	
Pseudomyrmex concolor														16	18	
Azteca D															1	
Azteca polymorpha															2	
Crematogaster E													1		1	
Azteca Q																3
Unoccupied plants	14	0	0	0	0	0	3	8	0	31	0	5	5	6	5	0

species, the four *Cecropia* species, the two *Cordia* species and the three Melastomes, formed distinct groups. *Pouruma heterophylla* Mart. and *Amaioua* aff. *guianensis* were completely isolated from the rest because both had only one specific partner that was never shared with other plants of the community. The two *Hirtella* (Chrysobalanaceae) species were grouped together with *Duroia saccifera* Benth. (Rubiaceae), being the single exception to the general pattern that plants with phylogenetic affinity tend to share similar ant fauna.
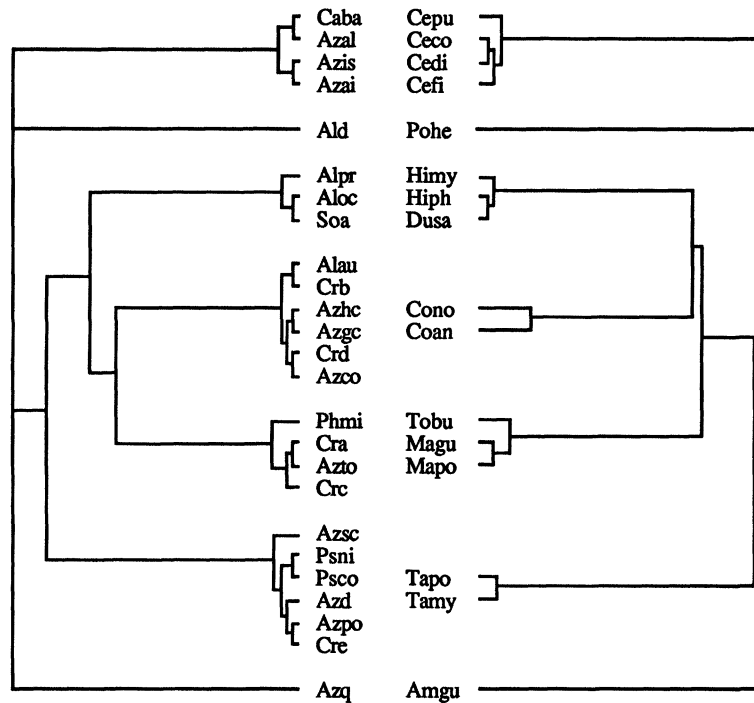
The cluster analysis of the ant species in relation to the relative abundance of the plant partners also produced seven large groups, corresponding to the ant partners of the seven major plant groups described above, but of no striking phylogenetic affinity (Fig. 3, left). Five of the seven ant groups contained ant species from two or three genera. Furthermore, ant species of the genera *Azteca*, *Allomerus* and *Crematogaster* occurred in five, three and three groups of the dendrogram, respectively. As phylogenies of these taxa are not available we cannot yet discern whether ant species of a given genus within a group are more closely related to each other than to species in other

groups. However, at least some cases suggest this is so. *Pseudomyrmex concolor* and *P. nigrescens* Forel are sister species, both occurring in *Tachigali* (Ward 1991; P.S. Ward, personal communication); while *Azteca isthmica* Wheeler and *A.* aff. *isthmica*, both occurring in *Cecropia*, can also be considered sister species (A. Y. Harada, personal communication).

The connectance of this ant–myrmecophyte community, based on 417 records, is 12%. The simulation shows that connectance is strongly affected by sampling size (Fig. 4). Considering the 100 simulation runs, the expected connectance drops dramatically from its maximal value ($C_{max} = 1$) when sample size is one, to less than 20% for $n > 12$, to finally stabilize at less than 13% for $n > 53$, reaching 12% when $n = 417$. The standard deviation of the expected connectance was extremely low and it decreases with increasing sample size (for $n > 5$, SD < 0·005; for $n > 15$, SD < 0·001), showing a high degree of confidence. Therefore, 12% seems to be a robust estimate of the connectance of this mutualistic ant-plant community
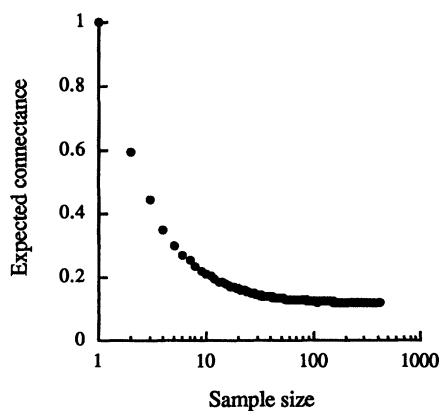
Plants were associated with up to seven ant species while ants only colonized up to four plant species
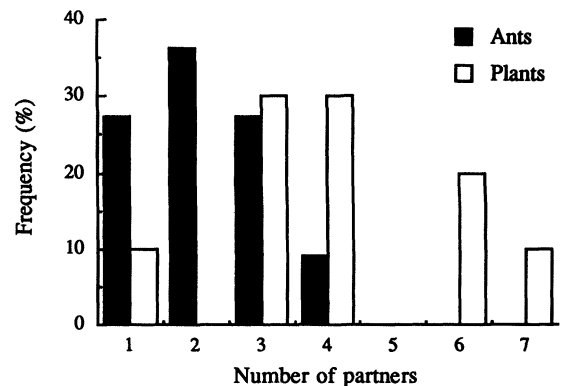
Fig. 3. Cluster analysis of ant (left) and myrmecophyte (right) species in relation to their similarity of partners. Methods are in the main text. Abbreviations for plant species are: Cepu, *Cecropia purpuracens*; Ceco, *Cecropia concolor*; Cedi, *Cecropia distachya*; Cefi, *Cecropia ficifolia*; Pohe, *Pouruma heterophylla* (Cecropiaceae); Himy, *Hirtella myrmecophila*; Hiph, *Hirtella physophora* (Chrysobalanaceae); Dusa, *Duroia saccifera*; Amgu, *Amaioua* aff. *guianensis* (Rubiaceae); Cono, *Cordia nodosa*; Coan, *Cordia af. nodosa* (Boraginaceae); Tobu, *Tococa bullifera*; Magu, *Maieta guianensis*; Mapo, *Maieta poeppigii* (Melastomataceae); Tapo, *Tachigali polyphylla*; Tamy, *Tachigali myrmecophila* (Caesalpiniaceae). Symbols for ant species are: Caba, *Camponotus balzanii* (Formicinae); Psni, *Pseudomyrmex nigrescens*; Psco, *Pseudomyrmex concolor* (Pseudomyrmecinae); Azal, *Azteca alfari*; Azis, *Azteca isthmica*; Azsc, *Azteca schummani*; Azpo, *Azteca polymorpha*; Azai, *Azteca* aff. *isthmica*; Azd, *Azteca* D; Azhc, *Azteca* HC; Azgc, *Azteca* G; Azto, *Azteca* TO; Azq, *Azteca* Q; Azco, *Azteca* CO (Dolichoderinae); Phmi, *Pheidole minutula*; Alpr, *Allomerus prancei*; Aloc, *Allomerus* aff.*octoarticulata*; Alau, *Allomerus auropunctata*; Ald, *Allomerus* D; Soa, *Solenops* A; Crb, *Crematogaster* B; Crd, *Crematogaster* D; Cra, *Crematogaster* A; Crc, *Crematogaster* C; Cre, *Crematogaster* E (Myrmicinae).

(Fig. 5). The plant species were associated with a mean ($\pm$ SE) of $4\cdot10 \pm 0\cdot57$ ($n = 10$) ant species, about 16% of the total ant richness. The ant species interacted with a mean ($\pm$ SE) of $2\cdot18 \pm 0\cdot30$ ($n = 11$) plant species, about 14% of the total plant richness. Thus, the plants formed 1·9 times more partners than the ants. The mean dependence value ($\pm$ SE) for the plants on the ants is $24\cdot39\% \pm 4\cdot96$ ($n = 41$), almost two times lower than the dependence of the ants on the plants ($45\cdot83\% \pm 6\cdot25$, $n = 24$) (Fig. 6). Sample size was not significantly associated with the number of partners of either the plants ($\beta = -0\cdot005$,

Fig. 4. Expected connectance in relation to sample size. The expected connectance, for a given sample size, was calculated as the mean connectance of 100 trials in a simulation where some records were randomly eliminated from the total number of records (i.e. 417). The standard deviations were extremely low and are not shown (see details in the text). Note that the sample size axis is logarithmic.

Fig. 5. Frequency distribution of the number of partners associated with ants (closed bars, $n = 11$ species), and with myrmecophyte species (open bars, $n = 10$ species).
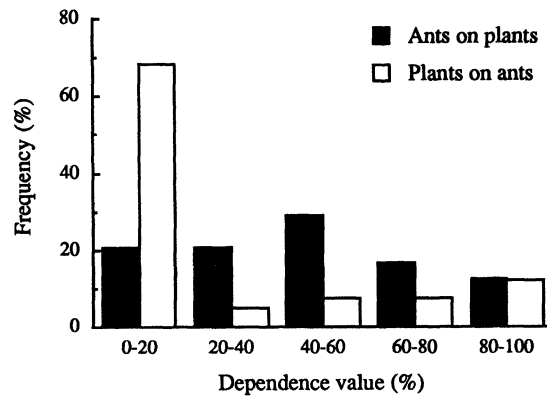
Fig. 6. Frequency distributions of dependence values of ants on plants (closed bars, $n = 24$ interactions) and of plants on ants (open bars, $n = 41$ interactions) in the ant–myrmecophyte community.

$F_{[1,8]} = 0.056$, $P > 0.05$, $r^2 = 0.007$) or the ants ($\beta = 0.012$, $F_{[1,9]} = 2.668$, $P > 0.05$, $r^2 = 0.229$). Also, sample size was not significantly associated with the dependence values of either the plants ($\beta = 0.037$, $F_{[1,39]} = 0.031$, $P > 0.05$, $r^2 = 0.001$), or the ants ($\beta = -0.204$, $F_{[1,22]} = 1.894$, $P > 0.05$, $r^2 = 0.079$).

Discussion

COMUNITY STRUCTURE AND NULL INTERACTIONS

Neotropical rainforests possess a much greater richness of myrmecophytic trees than the old world tropics (Benson 1985; Huxley 1986; Hölldobler & Wilson 1991; Davidson & McKey 1993), and our study site in Central Amazonia has twice as many myrmecophyte species as were recorded in Western Amazonia (Davidson *et al.* 1989). However, even these simple comparisons cannot easily be made as this is the first fully quantitative description of an ant–myrmecophyte community. Around the Manaus area, more than 600 ant species have been collected on ground and canopy samples (Benson & Harada 1988; Bandeira & Harada 1991); plant-ants representing a small subset of the whole ant biota.

The connectance of this Central Amazon ant–myrmecophyte community was 12%, indicating that both ant and plant species are quite specialized. Data from an ant–myrmecophyte community from Peruvian Amazon, with eight myrmecophytes and 18 ant species (from 242 records), suggests a connectance level of 15% (Davidson *et al.* 1989). Based on 242 records, the expected connectance for the present study would be about 12%, given a consistent low figure for ant-plant mutualistic communities. Comparisons with other mutualistic systems generate an interesting counterpoint. Jordano (1987) reviewed 36 plant-pollinator systems and 19 plant-dispersor systems, and found that connectance (*C*) decreases exponentially

with the total number of species (*S*) in those mutualistic systems. The pollination ($C = 0.4994e^{-0.017S}$) and the seed-dispersal ($C = 0.04745e^{-0.009S}$) curves predict, for a community with 41 species, connectance levels of 25% and 33%, respectively. Therefore, this comparison suggests that ant–myrmecophyte systems have lower connectance than the other two systems.

Comparisons between different studies should be undertaken with care. Differences in sampling procedures, sampling effort, definition of an association event, matrix shape, taxon definition and aggregation, and richness of both partners can potentially affect the estimate of connectance (Auerbach 1984; Paine 1988; Cohen & Newman 1988; Hall & Raffaelli 1993; Warren 1994). For example, the comparison between Western and Central Amazon ant-plant communities was made more accurate by the expected connectance simulation which standardizes the sampling effort, although not the sampling procedure. The comparison among mutualistic systems was made more accurate by standardizing the total richness of the partners; however, other variables such as matrix shape and the definition of an association event have not been controlled for. Of particular concern is the fact that the connectance index presents minimum and maximum values which are dependent on the topology of the community matrix (Auerbach 1984). Although such criticisms are of real concern in comparative studies, some are not exclusive to connectance as they apply equally to other community ecology indices such as diversity and dominance. The fact remains that the behaviour of the connectance index in different analytical contexts, especially when applied to mutualistic systems, is poorly known, and more adequate comparative techniques are required.

Regardless of these constraints, a major pattern that arises is that null interactions are dominant in all mutualistic systems. Jordano (1987) wrote 'I expect the largest fraction of null interactions in pollination and seed dispersal to be explained by phenological non-coincidences. Conversely, the degree of temporal matching between the flowering and fruiting seasons and the foraging lives of the animals will set limits on the evolution of mutual dependence'. In the ant–myrmecophyte system, the 'phenological non-coincidence hypothesis' does not apply, as both ant colonies and domatia-bearing plants are perennial entities, co-occurring spatially and temporally throughout the year. The absence of a given pairwise interaction must therefore be explained by the ecological and evolutionary differences that moulded the preference and performance of ant and plant species in relation to the possible partners.

COMPARTMENTS: PHYLOGENY OR HABITAT SPECIALIZATION

The 25 ant species and the 16 myrmecophyte species of this community are not associating at random.

Although this is a very general and simple finding, it enables us to look further for organizational patterns. As far as we know, two methods have been proposed for the detection of compartmentalization in biological communities, both for food web systems (Pimm & Lawton 1980; Raffaelli & Hall 1992). Both methods are only for binary associations (presence or absence of links), disregarding the strength of the associations and, as pointed out by Raffaelli and Hall, both methods are unlikely to detect compartmentalization if only a small proportion of the web species comprise a compartment. Since ant-plant systems show a high degree of specificity, we felt that the use of these methods in the present study was inappropriate. Instead, we have used a cluster analysis which considers the quantitative nature of our dataset. However, this approach is a description of the organization of the community rather than a statistical test for the existence of compartments.

The cluster analysis showed that the ant–myrmecophyte community is organized into seven well-defined compartments. As a rule, phylogenetically related myrmecophytes shared a set of ant species from different phylogenetic lineages. These community compartments correspond to the major ant–myrmecophyte systems that are repeatedly recognizable throughout South and Central America. Although local variations are known, the candelabriform *Cecropia* trees normally host *Azteca* ants (Harada & Benson 1988; Longino 1989; Davidson & Fisher 1991), *Tachigali* trees are well known everywhere for their ferocious *Pseudomyrmex* (Ward 1991; Fonseca 1994), *Hirtella* by its tiny *Allomerus* (Benson 1985), and *Maieta* by its timid but efficient *Pheidole* (Davidson *et al.* 1989; Vasconcelos 1991).

It has been suggested that ant species have a higher specificity to habitat than to host identity, and that this specificity could determine species sorting (Davidson *et al.* 1989; Davidson & McKey 1993). However, this hypothesis emerged mainly from observational studies of plant genus-based taxocenoses (Benson 1985; Harada & Benson 1988; Longino 1989). The question is how much of the community level ant–myrmecophyte associations can be explained by habitat specificity? The presence of two or more phylogenetically related plant species in this community sharing a similar ant fauna suggests that, at the community level, host identity and not habitat specificity is structuring the system. It could be that plants within a compartment share specific habitats that are not occupied by plants in other compartments, but no evidence supports this view. The high density of myrmecophytes in this undisturbed forest results in different plant species, most of them shade-tolerant, occurring closely together in the same environment but each one hosting its characteristic ant. *Maieta* occurs preferentially in stream-side areas and *Hirtella* on flat plateau areas; however, when these plants are found in their less preferred habitats they still are inhabited by their characteristic ants. In gaps, fast-growing *Cecropia* and *Tachigali* trees sometimes occur side-by-side, nevertheless hosting distinct ant faunas.

ASYMMETRIES IN MUTUALISTIC SYSTEMS

In the ant–myrmecophyte system, three correlated asymmetries were found: (i) the matrix contains more ant than plant species, (ii) ants have fewer partners than plants do, and (iii) ants depend more on the plants than vice versa. Opposite asymmetries were recorded by Jordano (1987): both pollination and seed dispersal systems tend to have more plant than animal species; plant species are associated with fewer partners than animal species; and the plants are more dependent on the animals than the reverse. We propose that although the asymmetries were in the opposite direction, they are in fact produced by the same underlying process. The differential increase in the fitness of the two partners, generated by intrinsic differences in the mutualistic services exchanged, would cause greater specialization by the partner that receives the greater benefit from the relationship.

The services exchanged during pollination and seed-dispersal seem to have differential effects on the fitness of the partners (Feinsinger 1983), thus failure of pollination represents loss of a meal for the pollinator but reproductive failure for the plant (for other asymmetries, see Dawkins & Krebs 1979). Plant reproduction is frequently pollen limited (Bierzychudek 1981) which can generate intense intra- and inter-specific competition among plants for pollinators (Heinrich 1975). Under these circumstances, plants are expected to be more specialized than their pollinators, the pattern observed by Jordano (1987). Indeed, plant populations within species present different behavioural and morphological characters that match the potentially most effective visitor at each locality (Grant & Grant 1965), but no evidence has suggested that pollinators' traits match local partners (Howe & Westley 1988).

In the ant-plant system, failure of ant colonization results in the plant having to survive temporarily without ant-defence, but it represents death for the unsuccessful queen and partial failure to reproduce for her colony of origin. Several lines of evidence suggest that ant populations are directly limited by their host plant populations, generating strong intra- and inter-specific competition among ants for nesting sites (Benson 1985; Davidson *et al.* 1989; Longino 1989; Fonseca 1993). If nest site limitation is a fact, ant–ant competition could drive ant specialization toward fewer plant partners that provide most of their requirements, but with the plants in turn not relying on any one specific ant partner. Therefore, we predict that ant behaviour, physiology, morphology and colony structure should exhibit modifications among populations to match their local hosts, while the myr-

mecophytes will exhibit less pronounced local adaptations.

The role of coevolution (Janzen 1980) vs. coadaptation (i.e. fortuitous match of characters of independent origins) in determining ant-plant associations is controversial (Janzen 1966, 1967; Koptur 1979; Benson 1985; Davidson *et al.* 1989; Davidson & McKey 1993). Both are certainly relevant and it is the relative strength of the processes that is in question. Ward (1991) showed that the evolution of the plant–ant associations is complex, with independent origins and host switching, depending on coadaptation, but also phylogenetic radiation within the host genus (e.g. the monophyletic complex *Pseudomyrmex concolor* is specialized on *Tachigali* species) showing the potential for coevolution. High interaction diffuseness and high spatiotemporal variation are major constraints for coevolutionary processes (Howe 1984). The high compartmentalization of the ant-plant community indicates low interaction diffuseness, and the fact that major ant–myrmecophyte systems can be recognized throughout the Neotropics indicates high spatial and temporal stability. Therefore, compartments seem to represent an appropriate scale at which to investigate coevolution in ant–myrmecophyte systems.

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