Competition Among Ants for Myrmecophytes and the Significance of Plant Trichomes[1]

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ABSTRACT

Data on founding queens and established ant colonies of eight Peruvian rain forest myrmecophytes suggest that ants compete interspecifically for host plants. Plant-ants show negative interspecific associations on plants with actively foraging colonies, but not on plants housing only founding queens or incipient colonies. In several ant-plants, small and large individuals regularly have different ants. Experimental evidence indicates that one ant species may deterministically replace another over time on *Clidemia heterophylla,* but the pattern may have different explanations in other myrmecophytes.

Among five myrmecophytes with long, dense stem trichomes, sizes of the most frequent ant associates are positively correlated with trichome spacing. Ants larger than a threshold body size cannot move readily through the trichomes without first cutting trail networks. Many obligate plant-ants appear to be species requiring special forms of protection from competing and predatory ants. Preferential nesting by such ants on plants with protective trichomes may explain the frequent co-occurrence of inhibitory trichomes and domatia in a number of ant-plant genera.

MANY PLANT SPECIES provide food and/or nest sites for ants in exchange for known or presumed protection from herbivores or for nutrient advantages (Buckley 1982, Beattie 1985). The majority of these ant-plant associations tend to be opportunistic and unspecialized (Schemske 1982, 1983; Beattie 1985). Evidence for evolutionary specialization is strongest where plants provide major resources such as nest sites and relatively complete ant diets (*e.g.,* Janzen 1966, 1967a, b, 1969, 1972) and the correlated diversity of ant associates is low (Schemske 1983). However local and geographic variation in ant associates is well documented for many obligate ant-plants that supply major ant resources (Bequaert 1922, Wheeler & Bequaert 1929, Wheeler 1942, Janzen 1983, Schemske 1983, Benson 1985). A better understanding of this variation may enable us to assess whether specificity and obligation result from "diffuse coevolution" (Futuyma & Slatkin 1983) or from ecological processes leading to "species sorting" (Jordano 1987).

Ant biology has been largely ignored in studies of ant-plant interactions, and adding the "ant's perspective" may help to account for variability in species composition. Comparatively generalized food and nest requirements frequently set the stage for competition among ants (Wilson 1971, Jeanne & Davidson 1984), and plant-ants may compete for domination of host resources. If so, the outcome of these interactions may have influenced the likelihood and nature of evolutionary specialization by both ants and plants (Law & Koptur 1986). This idea has precedent in pollination systems, where competition among floral visitors has apparently affected the evolution of floral morphology (Heinrich & Raven 1972).

Our investigations address ant-ant competition as a determinant of variation among the ant inhabitants of tropical myrmecophytes. We surveyed variation in the ant associates of eight myrmecophytes in tropical moist forests of western Amazonia and tested four hypotheses. (1) Plant species are colonized by more than one species of ants that compete for dominance of their hosts. (2) For particular myrmecophytes, the species composition of ant associates in larger plants differs from that in smaller plants, favoring one or a subset of the colonizing species. (3) In myrmecophytes with long, dense stem trichomes, ants predominating on larger individuals of a host species are those whose small body size enables them to move readily among trichomes. Moreover, across several plant species with different ant associates and trichome densities, worker sizes of the common ant associates are correlated positively with trichome spacing. (4) Host-restricted foraging is more characteristic of the primary ant associates of myrmecophytes than of rare and occasional associates.

Finally, we use the results of our ecological studies to propose a scenario for the history of these ant-plant associations and to interpret the relative contributions of coevolution versus preadaptation and ecological processes leading to species sorting.

METHODS

Our investigations were conducted from September through November (end of the dry season through the beginning of the wet season) in 1985 and 1986. The ant faunas of eight woody myrmecophytes were surveyed at the Estación Biológica de Cocha Cashu, in the remote and pristine Parque Nacional Manu, Madre de Dios, Perú (elev. ~400 m, latitude 11°52'S, longitude 71°22'W). Included within the station's primary trail system is a mosaic of habitat types representing different seral stages of succession after disturbance by the meanderings of the Río Manu (see Terborgh 1983). As much as 80 percent of this forest can be inundated at least briefly during a distinct wet season (October through April). In addition to the lowland trail system, a second system of trails spans *terra firma* forest across the Río Manu. In comparison with soils of lowland habitats, *terra firma* soils are poorly drained and dissected by steep, stream-cut ravines. With the exception of a few widely scattered tall canopy trees, the forest here is lower in stature than frequently flooded forests, and treefalls appear to be far more frequent. Ant abundance is notably much higher in *terra firma* than in low-lying habitats.

The entire 4800 m upland trail system and *ca* 8500 m of the higher elevation sections of the lowland trail system (designated "high ground forest" in Terborgh 1983) were surveyed for woody myrmecophytes growing near the trails. Some of these ant-plants produce modular ant domatia consisting of swollen stem nodes or foliar pouches, and others house ant colonies in hollow stems or in stems hollowed by the ants themselves. For plants in the former category, we recorded the number of domatia on live branches of each plant and the ants associated with each of these structures. Identities of ants were confirmed on the basis of workers entering and leaving domatia, or by opening domatia when no external activity of ants could be elicited. Similarly, for plants housing ant colonies in hollow stems, we noted the identities of ants entering and leaving all nest entrances and dissected the stems of plants with no external ant activity. (For large *Triplaris* trees, we censused the majority of nest entrances at higher portions of trees with binoculars, but could not verify that we had checked every entrance to the hollow stems.)

Representative collections of each ant species (all castes when possible) were made into vials of 70 percent ETOH. Worker body lengths, indicative of turning radii in movements among trichomes, were measured with the aid of a PEAK pocket microscope ($\times 60$) and ocular micrometer.

For most ant species, we measured five workers from each of five colonies or from as many colonies as possible when colony samples sizes were less than five. For ants exhibiting strong worker size polymorphisms, we measured 25 ants per colony.

To assess the possibility of negative associations among ants of a given host species, we computed the 2×2 Fisher Exact Probability that individual plants with and without a given ant species or genus were equally likely to be inhabited by representatives of another species or group of species. We analyzed plants with obvious external ant activity independently of those with no evidence of such activity. Plants in the latter group typically contained only founding queens or incipient colonies whose callow workers were not yet foraging externally. Statistical tests were one-tailed for plants with external ant activity and two-tailed for those lacking such activity, in accord with our prediction of competitive interactions among ants on the former category of hosts, and no prediction for plants in the latter category.

For myrmecophyte species whose stems were covered with long and dense trichomes, we collected one section of stem from each of five individual plants. To standardize our samples for fully expanded stems, we chose stem sections from the middle of the stem segments separating the second and third domatia, as counted from the terminal ends of branches. Using a $\times 10$ pocket magnifier and transparent plastic ruler graduated in millimeters, we measured the distances between five randomly chosen pairs of neighboring trichomes on each stem sample. Measurements were made to the nearest 0.25 mm.

In the field, three kinds of observations were recorded for each ant species whose workers foraged actively on stems and leaves. First, for ants occurring on myrmecophytes with trichomes, we noted whether or not ants cut and used "trails" through these trichomes. Second, we observed whether or not workers readily left their host plants to forage on the ground or on neighboring plants. When foraging off the host plant was not observed under natural conditions, we attempted to induce such behavior by tying branches of myrmecophytes to neighboring vegetation and/or by placing food baits near the tree base. Finally, we observed ant responses to baits of tuna fish, cheese, and peanut butter to determine whether or not these foreign substances were recognized as food.

On 20 October 1986, we initiated studies to test directly for the nature of interactions between one pair of hypothesized competitors. *Pheidole minutula* and *Crematogaster* cf. *victima* often occur on neighboring plants of *Clidemia heterophylla* whose branches extend in parallel over small stream courses. We located six such pairs of neighbors inhabited by the two different ant species and left three of the pairs unmanipulated, except for marking single branches on each of the six control plants for further

TABLE 1. *Ant inhabitants of eight myrmecophytes.*

Ants[c]	Plants[a]							
	C.n. 45[b] (11)	T. sp. 8 (12)	M.g. 11 (4)	C.h. 15 (11)	T.p. 14 (1)	T.a. 31 (1)	C. sp. 24 (27)	P. sp. 14 (0)
A.d.	35 (8)	—	—	—	—	—	—	—
Az–1	4 (7)	2 (4)	—	—	—	—	—	—
Az–2	—	—	—	—	12 (1)	—	—	—
Az–3	—	5 (6)	—	—	—	—	—	—
Az–4	—	1 (0)	—	—	—	—	—	—
Az–7	—	—	—	—	2 (0)	—	—	—
Az–8	—	—	—	—	—	—	—	4 (0)
Az–9	1 (0)	—	—	—	—	—	—	—
C.p.	2 (0)	—	—	—	—	—	—	—
C.v.	—	0 (7)	6 (3)	7 (7)	—	—	—	—
P.m.	—	—	5 (1)	8 (8)	—	—	—	—
C.b.	—	—	—	—	—	—	5 (0)	—
P.l.	—	—	—	—	—	—	19 (27)	—
M. sp.	—	—	—	—	—	—	—	10 (0)
P.d.	—	—	—	—	—	30 (1)	—	—
S. sp.	—	0 (1)	—	—	—	—	—	—
B.g.	0 (2)	—	—	—	—	—	—	—
G.p.	1 (0)	—	—	—	—	—	—	—
None	2 (0)	—	—	—	—	0 (1)	—	—

[a] Plant species are: *C.n.* = *Cordia nodosa* Lam; *T.* sp. = *Tococa* sp.; *M.g.* = *Maieta guianensis* Aubl.; *C.h.* = *Clidemia heterophylla* (Desr.) Gleason; *T.p.* = *Triplaris poeppigiana*; *T.a.* = *Triplaris americana* L.; *C.* sp. = *Cecropia* sp. nov.; *P.* sp. = *Pleurothyrium* sp. Host plants in the Melastomataceae often grew as groves of shrubs or small trees, dominated by the same ant species. To insure independence of observations in this and subsequent analyses, we used only one randomly chosen tree per grove.

[b] Numbers without parentheses indicate externally obvious ant activity; entries in parentheses indicate incipient colonies and no externally visible ant activity. Each queen and each occurrence of a species' workers in the absence of a queen is defined as a colonization event.

[c] Ant species are *A.d.* = *Allomerus demararae* Wheeler; *Az* spp. 1–4, 7, 8, and 9 = unknown but different species of *Azteca*; *C.p.* = *Crematogaster limata parabiotica* (Forel); *C.v.* = *Crematogaster* cf. *victima*; *P.m.* = *Pheidole minutula* (Mayr); *C.b.* = *Camponotus balzani* Emery; *P.l.* = *Pachychondyla luteola* Roger; *M.* sp. = *Myrmelachista* sp.; *P.d.* = *Pseudomyrmex dendroicus* Forel; *S.* sp. = *Solenopsis*, unknown species; *B.g.* = *Brachymyrmex goeldii* Forel; *G.p.* = *Gnamptogenys pleurodon* (Emery).

censusing. Nylon cord was used to tie together single branches of members of each of the other three plant pairs. Branches were tied to connect their distal ends, where leaves were comparatively new and foliar pouches currently inhabited by ants. In the ensuing combat on each of the experimental plant pairs, we noted the identities of the first five workers killed. After 3 days, and again after 16 days, we returned to census the stems and domatia of marked branches on control and experimental plants. On day 16, all domatia on all 12 branches were opened to reveal their contents.

RESULTS

ANT-PLANT ASSOCIATIONS.—Our survey included eight species of woody myrmecophytes (Table 1): *Triplaris americana* and *T. poeppigiana* (Polygonaceae); *Cordia nodosa* (Boraginaceae); *Tococa* sp., *Maieta guianensis,* and *C. heterophylla* (Melastomataceae); *Pleurothyrium* sp. (Lauraceae); and *Cecropia* sp. nov. (Moraceae), probably an undescribed species (C. Berg, pers. comm.). Of these species, the three melastomes produce foliar pouches, *C. nodosa* has domatia comprised of swellings along its stems, and the remaining myrmecophytes house ants in hollow stems. *C. nodosa* occurs at both *terra firma* and lowland sites, but data on this species were taken only in the lowlands, where it was more common. The three melastomes were confined to *terra firma* forests, and the remaining species were encountered only in the lowlands. In *terra firma, Tococa* sp. occurred on the shoulders of steep ravines, and *C. heterophylla* was largely restricted to the borders of streams that dissect this habitat. *M. guianensis* occurred on both stream banks and the steep slopes of ravines.

Two very general observations are consistent with the possibility that ants compete for possession of myrmecophytes. First, only three of all 229 plants sampled completely lacked ant associates. Second, seven of the eight plant species were colonized by more than one ant species with demonstrated success at developing colonies on these

TABLE 2. *Fisher Exact Probabilities for hypotheses of no association among ant species.*[a]

Myrmecophyte	Comparison of ants	N	P value[b]
Cordia nodosa	*Allomerus demararae* versus all other	45	0.001
		8	(0.286)
Tococa sp.	*Azteca* spp. versus *Crematogaster* cf. *victima*	8	0.018
		12	(0.273)
Maieta guianensis	*Pheidole minutula* versus *Crematogaster* cf. *victima*	11	0.002
		4	(0.250)
Clidemia heterophylla	*Pheidole minutula* versus *Crematogaster* cf. *victima*	15	0.001
		11	(0.530)
Triplaris poeppigiana	*Azteca*-2 versus *Azteca*-7	14	0.011
Pleurothyrium sp.	*Myrmelachista* sp. versus *Azteca*-8	14	0.001
Cecropia sp. nov.	*Pachychondyla luteola* versus *Camponotus balzani*	24	0.001

[a] See text for justification of choices for comparisons.
[b] *P* values are one-tailed for trees with ants active externally (no parentheses) and two-tailed for trees with no external ant activity (parentheses).

hosts (Table 1). The exception was *T. americana,* whose association with *Pseudomyrmex dendroicus* Forel appears to be highly specific at this site (Davidson *et al.,* 1988; and see Discussion). It is also noteworthy that some ant species colonized more than one species of myrmecophyte. For example, *Azteca* sp. 1 colonized domatia of both *C. nodosa* and *Tococa* sp., and *C.* cf. *victima* and *P. minutula* colonized domatia of both *C. heterophylla* and *M. guianensis.*

Table 2 presents the results of Fisher Exact tests for negative associations among ants. For host plants occupied only by founding queens and/or incipient colonies not yet active on plant surfaces, none of the exact probabilities is statistically significant. This is true even if we take advantage of the procedure for combining probabilities from four independent tests of significance ($\chi^2 = 4.57$ with 8 df, $P > 0.5$, see Sokal & Rohlf 1969, pp. 621–624). In contrast, where ant activity is visible on the host plant, probabilities are uniformly and highly significant.

Figure 1 compares the ant associates of small and large myrmecophytes with foliar or nodal domatia. In three of the four species, species composition differs significantly on large plants from that on small plants with fewer domatia. The particular comparisons made in Figure 1 reflect our need to lump ant species whose sample sizes are small. *C. nodosa* is colonized by several ant species, but *Allomerus demararae* dominates larger plants. On *Tococa* sp., ants other than *Azteca* species comprise 45 percent of colonists of plants with ≤ 10 domatia, but are totally absent from larger plants. The identical two species, *P. minutula* and *C.* cf. *victima,* occupy both *M. guianensis* and *C. heterophylla.* On the former host plant, there is no significant difference between the ant associates of small and large plants. In contrast, the smaller *P. minutula* is numerically dominant on large *C. heterophylla* plants, despite its relative rarity on smaller plants.

Our experimental studies of ants on *C. heterophylla*

enable us to test the hypothesis that *P. minutula* can competitively displace *C.* cf. *victima* on this host plant. Combat between these species was observed on all three experimental plant pairs. In each case, both workers and soldiers of *P. minutula* moved onto branches initially occupied by *C.* cf. *victima* and attacked the latter species. Soldiers of *P. minutula* killed their opponents by grasping them between the head and thorax with mandibles and crushing them or clipping off their heads. The first five deaths on each plant pair were those of *C.* cf. *victima.* Workers of the latter species did not move onto branches occupied by *P. minutula* but retreated into their leaf domatia.

Table 3 presents the data on occupancy of domatia. After three days, some of the domatia initially inhabited by *C.* cf. *victima* had been taken over by *P. minutula,* while no takeovers in the reverse direction were observed. Workers of *P. minutula* were active on the stems and leaves of all experimental branches, while those of *C.* cf. *victima* were not active externally on any experimental branch. Their occupancy of domatia on some of these branches was ascertained by drawing the workers out with fine forceps. Leaves were missing from two of the three experimental plants. After 16 days, all domatia on all experimental branches were occupied by *P. minutula,* and no workers of *C.* cf. *victima* were found on any of these branches. All of the domatia on marked branches of six control plants were inhabited by the same ant species before the experiments and 16 days after their initiation. On plants initially occupied by *C.* cf. *victima,* significantly more experimental branches than control branches were taken over by *P. minutula* ($P = 0.05$ in a one-tailed Fisher Exact test).

ROLE OF PLANT TRICHOMES.—Although trichomes of some description occur on six of the eight host plants, these structures are likely to interfere with the movements of
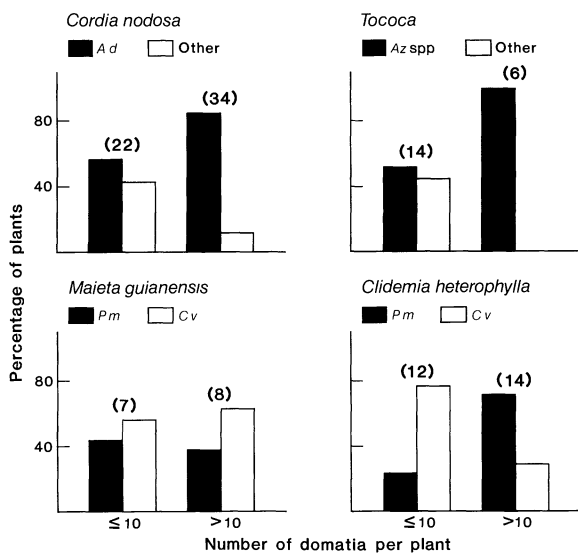
FIGURE 1. For four species of myrmecophytes with foliar or nodal domatia, the percentage of plants occupied by various species or genera of ants in relation to plant size is shown. Small plants have ≤10 domatia. Sample sizes are in parentheses. See Table 1 for species identifications and text for justification of categories of ants. One-tailed Fisher Exact Probabilities are: *Cordia nodosa*, 0.017; *Tococa*, 0.054; *Maieta guianensis*, 0.622; *Clidemia heterophylla*, 0.016 for hypothesis that small and large plants have the same proportions of their two categories of ant associates.

TABLE 3. Inhabitants of foliar domatia on control and experimental plants (branches) of Clidemia heterophylla.

Identity of plant[a]		Number of Domatia with *Pheidole minutula* (Mayr) (or *Crematogaster* cf. *victima*)		Number domatia missing
		Day 3	Day 16	
Experimentals				
EP1	(5)	5 (0)	5 (0)	0
EP2	(6)	6 (0)	6 (0)	0
EP3	(5)	5 (0)	5 (0)	0
EC1	(4)	2 (0)	2 (0)	2
EC2	(6)	0 (6)	6 (0)	0
EC3	(7)	0 (7)	6 (0)	1
Controls				
CP1	(5)	5 (0)	5 (0)	0
CP2	(5)	5 (0)	5 (0)	0
CP3	(9)	9 (0)	9 (0)	0
CC1	(7)	0 (7)	0 (7)	0
CC2	(7)	0 (7)	0 (7)	0
CC3	(8)	0 (8)	0 (8)	0

[a] First letter of identity code refers to treatment: E = Experimental; C = Control. Second letter refers to initial ownership of plant (branch) by *P. minutula* (P) or *C.* cf. *victima* (C). Number designates plant (branch). Numbers in parentheses refer to number of domatia on branch.

ants only in *C. nodosa, M. guianensis, C. heterophylla,* and *T. poeppigiana,* four species in which trichomes are long, dense, and distributed continuously over stems. Bristles on the stems *Cecropia* sp. nov. are very short (<0.25 mm), and branches and domatia of *Tococa* sp. develop with trichomes on the upper and lower surfaces only. The relatively large *Azteca* workers using this latter host plant travel rapidly up and down stems on the flattened and trichome-free sides of branches.

Figure 2 depicts the significant positive correlation between trichome spacing and worker body size for the four myrmecophytes with long, dense, and continuously distributed stem trichomes (points 1–4; $r = 1.00$, $P = 0.05$ in a one-tailed Spearman Rank test). Point 5 on this graph shows worker body size in relation to the width of trichome-free areas on the sides of branches in *Tococa* sp. With this data point included, the positive correlation in Figure 2 is even more highly significant ($P < 0.001$).

ATTRIBUTES OF ANTS.—The numerically dominant ant species of our myrmecophytes differ from rarer species in at least three noteworthy ways. On plants with stem trichomes (Table 4a), common species tend not to prune

trails through the trichomes, whereas rarer ants do. *C.* cf. *victima* is exceptional in pruning facultatively. It cuts trails on most *C. heterophylla* (where it is numerically subordinate to *P. minutula*), but apparently not on *M. guianensis,* whose trichomes are spaced slightly farther apart than those of *C. heterophylla.* Open circles in Figure 2 depict the relationships between worker body sizes and widths of pruned trails for two of the pruning species. Here sample sizes for path widths are 25 measurements made at random points along stem trail systems of a single plant.

Second, host-restricted foraging is typical of six of the eight ants occurring as numerical dominants on at least one of the eight myrmecophytes. In contrast, only one of the remaining eight ants in Table 4, *Camponotus balzani,* is so restricted. This difference is statistically significant at $P < 0.05$ in a two-tailed Fisher Exact test. Since *C. balzani* is the typical inhabitant of *Cecropia ficifolia* (Davidson, Foster, & Snelling, unpublished), a rare ant-plant at our site, the test is a conservative estimate of the tendency for numerically dominant plant-ants to show host-restricted foraging. By implication, host-restricted ants depend directly or indirectly on the host plant for all of the colony's food resources. Third and related to this, three of seven host-restricted ants and none of the nine species regularly foraging off their hosts failed to take baits of tuna fish, cheese, and peanut butter ($P < 0.06$ in two-tailed Fisher

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TABLE 4. *Some attributes of the residents of myrmecophytes.*[a]

Plant	Ant[a]	Prunes trichomes	Forages on host[b]	Forages at baits[c]
Myrmecophytes with long, dense, and continuous stem trichomes:				
Cordia nodosa	A. demararae[S]	0 (10)[d]	0 (10)	3 (3)
	Azteca sp. 1[C]	4 (4)	4 (4)	2 (2)
	C.l. parabiotica[C]	2 (2)	2 (2)	2 (2)
	Azteca sp. 9[C]	1 (1)	1 (1)	1 (1)
Triplaris poeppigiana	Azteca sp. 2[C]	0 (10)	0 (10)	0 (3)
	Azteca sp. 7[C]	2 (2)	2 (2)	2 (2)
Clidemia heterophylla	P. minutula[S]	0 (8)	0 (8)	2 (2)
	C. cf. victima[C]	0 (7)	2 (2)	2 (2)
Maieta guianensis	C. cf. victima[C]	0 (6)	1 (1)	2 (2)
	P. minutula[S]	0 (5)	0 (5)	2 (2)
Other myrmecophytes:				
Tococa sp.	Azteca sp. 3[C]	NA	4 (5)[e]	2 (2)
	Azteca sp. 4[C]	NA	1 (1)	1 (1)
Triplaris americana	P. dendroicus[S]	NA	0 (10)	0 (3)
Cecropia sp. nov.	P. luteola[S]	NA	0 (10)	0 (2)
	C. balzani[C]	NA	1 (5)[e]	2 (2)
Pleurothyrium sp.	Myrmelachista sp.[C]	NA	0 (10)	2 (2)
	Azteca sp. 8[C] ·	NA	4 (4)	2 (2)

[a] For each myrmecophyte, ant species are listed in order of decreasing frequency of encounters in our survey. Ant superscripts: C = genus or subfamily with chemical defenses, but lacking functional stings, and S = genus or subfamily with sting defenses (Blum & Hermann 1978).
[b] Nocturnal checks of all ants with host-restricted foraging confirmed host plant restriction during noctural activity as well. Only two colonies of *C.* cf. *victima* on *C. heterophylla* and one colony on *M. guianensis* exhibited diurnal foraging activity.
[c] Baits were comprised of tuna fish, cheese, and peanut butter, and ant species tended to recognize either all or none of these as food resources.
[d] Entries are numbers of colonies demonstrating a particular behavior, and sample sizes are in parentheses. NA = not applicable.
[e] Variation in host fidelity likely attributable to colony age.

Exact test). *Azteca* sp. 2 simply ignored the baits, but *P.* cf. *triplarinus* discarded them from the leaves, and workers of *Pachychondyla luteola* stung the tuna fish and cheese before discarding it.

DISCUSSION

COMPETITION FOR HOST PLANTS.—Although negative interspecific associations are not always assignable to competition, interspecific competition among ants for host plants is a compelling explanation for the patterns observed here. In the four myrmecophyte species whose individuals have multiple domatia that allow independent colonizations by queens in different domatia, no negative interspecific associations are apparent among colonizing queens or incipient colonies (Table 2). Thus, although different ant species colonize myrmecophytes independently of one anothers' presence, and although most colonizing species can successfully produce active colonies on these host plants (Table 1), the development or persistence of colonies beyond the incipient stage apparently is not independent of the presence of other species.

Second, direct observations and experimental evidence are consistent with the hypothesis that aggression occurs during interspecific encounters. On *Cecropia* sp. nov., workers of *C. balzani* pursue and attack älate females of *P. luteola* (DWD, two observations). Interspecific aggression among worker populations can lead to the displacement of one ant species by another (Table 3). In dense populations of *C. heterophylla* along stream borders, branches of plants with different ant species may frequently come into contact, leading to competitive replacement of *C.* cf. *victima* by *P. minutula*. Moreover, if the latter species is able to colonize and persist beyond the incipient colony stage in individual domatia on plants with established colonies of *C.* cf. *victima*, *P. minutula* may even be capable of usurping host plants from numerically superior colonies of *Crematogaster*. When contact between the two ant species was imposed experimentally, workers of *C.* cf. *victima* did not join together to engage invading *P. minutula*. Thus, interspecific interactions tended to occur between individuals of the two ant species and were resolved in each case in favor of *P. minutula*.

Differences in the ant inhabitants of small and large

myrmecophytes are intriguing and probably not fully explained as the deterministic replacement of one species by another through time. We cannot rule out differential effects of various ant inhabitants on plant growth rates, nor that plant growth rates affect the outcome of ant competition. Our survey of *M. guianensis* revealed a trend (not statistically significant at small sample sizes) for habitat separation between ants. Thus, *C*. cf. *victima* tended to dominate plants on the steep slopes of ravines, and *P. minutula* was more common along stream banks. Riparian habitats may be more favorable environments for nutrients and light, and the aggressive and dominant *P. minutula* may be favored by conditions of rapid plant growth and ready supply of resources. The host plant it dominates most consistently is *C. heterophylla*, which grows only along stream banks.

STEM TRICHOMES.—Indirect evidence also suggests that plant morphology can influence the identities of ant associates, perhaps by affecting the outcome of competition among ants. Worker body sizes of the numerically predominant ants of five myrmecophytes with long and dense stem trichomes are correlated positively and significantly with the mean distances between stem trichomes (Fig. 2). The species composition of ant associates differs significantly on small and large individuals of three of four myrmecophytes with foliar or nodal pouches and stem trichomes. In two of these three plant species, *C. nodosa* and *C. heterophylla*, and in *T. poeppigiana*, a myrmecophyte with hollow stems, trichomes occur over the full perimeters of plant stems, forming a continuous impediment to ants with relatively large worker body sizes. Without exception, these larger ants construct networks of trails through the host plant's stem trichomes (Table 4a). When workers of these species are transferred to hosts lacking such trail systems, these ants cannot travel between the trichomes and have obvious difficulties traversing stems over the tops of these hairs. In *C. nodosa*, *C. heterophylla*, and *T. poeppigiana*, larger individuals are dominated numerically by the colonizing ant species with the smallest worker body sizes (Figs. 1 and 2).

Long, dense, and inhibitory epidermal trichomes characterize many Neotropical and paleotropical myrmecophytes. In addition to the five genera represented in this study, they include species of *Conostegia* and *Ossaea* (Melastomataceae), *Canthium* and *Duroia* (Rubiaceae), *Hirtella* (Chrysobalanaceae), and *Cola* (Sterculiaceae) (Bequaert 1922, Wheeler & Bequaert 1929). Within at least some of these genera, the disproportionate occurrence of domatia in species with inhibitory stem trichomes (Davidson, unpublished) may have had a single origin within a clade of myrmecophytes (*e.g.*, Prance 1972 for *Hirtella*). However, associations between domatia and restrictive trichomes almost surely had independent origins in the dif-
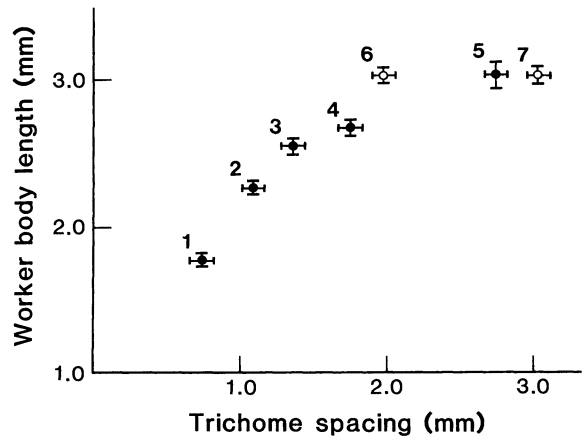

FIGURE 2. Worker body lengths of ant species as a function of trichome spacing, either unmanipulated (closed circles) or manipulated (open circles) by ants. Bars are one standard error. Ants and plants are (1) *Pheidole minutula* on host *Clidemia heterophylla*; (2) *Allomerus demararae* on *Cordia nodosa*; (3) *Crematogaster* cf. *victima* on *Maieta guianensis*; (4) *Azteca*-2 on *Triplaris poeppigiana*; (5) *Azteca*-3 on natural paths through the trichomes of *Tococa* sp.; (6) trails pruned by *Azteca*-1 on *Cordia nodosa*; and (7) trails cut by *Azteca*-7 on *Triplaris poeppigiana*.

ferent genera and families. Nonrestrictive trichomes (short, sparse, and/or discontinuous) commonly occur in non-myrmecophytic members of these same genera. Together, these observations suggest that inhibitory stem trichomes may have preceded domatia in plant evolution and pre-adapted species for associations with ants (see below). Relationships with ants apparently have evolved independently in other types of ant-plants whose progenitors had traits exposing them to strong and consistent selection pressures imposed by regular ant occupancy (Jebb 1985).

HOST-RESTRICTED FORAGING.—What is the significance of the host-restricted foraging that characterizes the numerically predominant ants of myrmecophytes, but not the occasional species? Several kinds of indirect evidence suggest that the host plant represents a protected environment for ants that otherwise would be behaviorally and/or competitively subordinate. In some cases, ant behavior suggests a need for protection from other ants (Davidson *et al.*, 1988). For example, surrounding its *T. americana* host plants, *P. dendroicus* maintains clearings that reduce invasions of the host by common and dangerous *Crematogaster limata parabiotica*. *Allomerus* ants of *Cordia*, and *Pachychondyla* on *Cecropia* attack and sting encroaching vines if these vines bear *Crematogaster* workers. The results of the present study are in accord with the general pattern that pruning of vines and other encroaching vegetation is significantly more characteristic of stinging ants than of

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ants with chemical defenses (Table 4, Davidson *et al.*, 1988). The latter appear to be generally superior to the former in contests among ants.

Four host-restricted ants in our study apparently do not prune vegetation. Colonies of *P. minutula* and *Azteca* sp. 2, like those of *A. demararae* (Davidson *et al.*, 1988), may be protected by host plant trichomes from invasions by alien ants. *Myrmelachista* sp., *C. balzani*, and *Azteca* sp. 2 timidly retreated into stem nests when host plant branches were disturbed or invaded, and the last of these species deserted branches of its host when the branches were tied artificially to neighboring ant plants (Davidson, unpublished). Plant-ants of other well-studied myrmecophytes are often timid as well (Letourneau 1983, McKey 1984).

Exceptional ant species can be interpreted in the context of the generalizations above. *Tococa* sp. is inhabited primarily by *Azteca* sp. 3, which forages regularly off its host, does not prune vegetation, and is not protected by a continuous barrier of trichomes on stems and domatia. This aggressive ant, like most of its congeners, may rely on chemical defenses for protection against competitors and predators (Table 4). *C.* cf. *victima* is unusual as a common plant-ant not restricted to its host. Despite the fact that *Crematogaster* tends to be a chemically defended and behaviorally dominant genus, this species resembles other plant-ants in its timid retreat to domatia in response to disturbance or to invasion by *P. minutula*. Our classification of this species is conservative in that we have no direct evidence that the ants' activity off the host plant constitutes foraging. The relatively large queens must cut away the narrow entrance tunnels to access domatia of *M. guianensis*, and our sampling suggests that queens at least occasionally live off the host plant. Workers may leave the plant to collect newly laid eggs for placement in host domatia.

At Cocha Cashu, we have found no established colonies of ants with host-restricted foraging living independently of the host plant genera reported here. Perhaps because of their general rarity, the same is also true for most species that are not host restricted (Tables 1 and 4). However, *C. l. parabiotica*, one of the most common ants in these forests (Wilson 1987), clearly nests in hollow stems and cavities of a variety of plant hosts (Davidson, 1988), as do *Brachymyrmex goeldii* and *Gnamptogenys pleurodon*. *Azteca* spp. 4, 7, and 9 build carton nests on many different plant species in the vicinities of their myrmecophytic hosts. These species can probably also live independently of myrmecophytes, unless restricted to such hosts during colony foundation.

Ecology, evolution, and biogeography.—Local ecological processes cannot always be extrapolated to explain patterns at greater temporal and spatial scales. Neverthe-

less, we conjecture that ecological processes leading to species sorting may have preadapted certain ants and plants for evolution of more specialized symbioses. In attributes influencing ownership of host plants (*e.g.*, body size and defense mode), regular plant-ants are not particularly distinctive from congeners lacking symbiotic associations with plants. Similarly, myrmecophytes resemble nonmyrmecophytic relatives in growth form, pith density (utility as nest cavities), and the presence of trichomes of varied sizes and densities.

Nests of social insects in the tropics are notoriously susceptible to depredation by ants (Jeanne 1975), and ants lacking elaborate chemical defenses may be especially vulnerable. Rapidly growing trees with low density pith and relatively straight, unbranched growth forms (*e.g.*, *Cecropia* and *Triplaris*) provide uniquely suitable and defensible homes for both ants and associated homoptera. Similar selection pressures may determine the frequent association of polistine wasp nests on isolated tree crowns (also sought out by casiques avoiding their own nest predators [Robinson 1985]).

Likewise, trichomes appear to provide protection from potential predators and competitors. Herre *et al.* (1986) describe associations of wasp nests with myrmecophytes in the genera *Tococa* and *Maieta*. Although a demonstrated immunity of these trees to invasion by army ants is attributed by these authors to defense by *Allomerus* and *Pheidole* ants, there was no test of the alternative hypothesis that epidermal trichomes inhibited invasions by these predators. Circumstantial evidence indicates that trichomes may also exclude competitors. At Cocha Cashu, two species of *Azteca* ants tending Neotropical ant gardens locate their carton nests preferentially on myrmecophytes *C. nodosa* and *Tococa* sp., respectively (Davidson, 1988). Trichomes of *C. nodosa* inhibit movements of invading *C. l. parabiotica* (Davidson *et al.*, 1988), which occurs on more than 80 percent of all ant gardens here (Davidson, 1988).

Persistent occupation of certain hosts by particular ants almost certainly would have affected plant fitness. Where net fitness outcome was positive (*e.g.*, protection from herbivores outweighed negative effects of resource loss through ant-tended homoptera), plants might have been strongly and consistently selected to supplement ant diets. Food supplements should not only increase worker densities on plant surfaces but reduce the need for ants to forage in more dangerous environments, to allow open avenues by which enemies might invade, and to maintain potentially costly aggressive behaviors and defenses. A possible side effect of food production may be increased attractiveness of these hosts to better-defended ants not dependent on protection by host plant morphology (the rare ants in this study). Any facultative tendency for subordinate ants to prune encroaching vegetation might then be magnified by selection. Interestingly, this behavior ap-

pears best developed in regular inhabitants of hosts lacking protective trichomes, e.g., in Pseudomyrmex on Acacia and Triplaris (Janzen 1967a, Davidson et al., 1988), Tetraponera on Barteria (Janzen 1972), Azteca on Cecropia (Janzen 1969), and Crematogaster on Macaranga (Davidson, unpublished; B. Fiala, pers. comm.).

Most plants and several ants in our study appear to exhibit evolutionary specializations to their symbiotic associations. With the possible exceptions of poorly studied Pleurothyrium and T. poeppigiana, the ant-plants studied here have evolved traits obviously related to housing and/or feeding ants (Bequaert 1922; Davidson, unpublished data, on food production by T. americana and C. nodosa). Both host-restricted foraging, and the pruning behavior and dietary specialization exhibited by a subset of host-restricted ants suggest evolutionary specialization on the part of ants as well.

If evolution between ants and plants has been reciprocal, it need not have occurred in response to pairwise species interactions (see Futuyma & Slatkin 1983). A number of myrmecophytes—e.g., Acacia (Janzen 1967a), Cecropia spp. (Benson 1985), Leonardoxa africana (McKey 1984), and M. guianensis and T. americana (Davidson, unpublished)—are inhabited by different ants in different habitats or geographic regions. The predominance of one or another representative of a "guild" of plant-ants may depend on the manner in which local physical and biotic parameters affect processes that, like ant competition, influence species sorting. Many tropical myrmecophytes grow over broad habitat and geographic ranges, and their evolution as ant-plants may have occurred in response to a variety of ant associates. Similarly, more than one ant-plant may provide suitable habitat for a given plant-ant (e.g., P. minutula and C. cf. victima in the present study) and influence its evolution. Lack of consistency in the species-specificity of ant-plant associations may be expected often to have inhibited pairwise coevolution (Beattie 1985). It may also offer a partial explanation for the paucity of symbiotic ant-plant associations at temperate latitudes and higher elevations (Bentley 1977, Keeler 1979, Koptur 1985). There, diurnal and seasonal temperature variation and the inability of ants to nest inside host plants in cold climates (Bequaert 1922) can lead to inconsistency in the resolution of ant competition and other processes affecting species sorting.

ACKNOWLEDGMENTS

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