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ECOLOGICAL STUDIES OF NEOTROPICAL ANT GARDENS[1]

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Abstract. In a census taken in Peru's Manu National Park, 10 epiphytic angiosperms from seven plant families established principally on arboreal carton-ant nests. These "ant gardens" (AGs) were most often inhabited by parabiotic ants, *Camponotus femoratus* and *Crematogaster* cf. *limata parabiotica,* whose polygynous and polydomous colonies fissioned to form extensive AG aggregations. AGs tended by polydomous but probably monogynous *Azteca* cf. *traili* occurred on average in smaller isolates. All three ant species enriched nest gardens with vertebrate feces, but frequencies of occurrence of most AG epiphytes were lower on the less organic carton of *Azteca* AGs. Interspecific differences in epiphyte abundance and distribution were related to light requirements of plants and to colonizing abilities, as influenced by differences in allocational preferenda and life history.

AG aggregations occupied 16–39% of five forest habitat types present and were especially common in frequently flooded habitats and areas of high light intensity. Patchy distribution was explained partly by overrepresentation on resource trees, such as *Inga* and *Calyptranthes* (parabiotic ants) and *Cordia nodosa* (*Azteca*). Habitat associations did not result from reduction of the terrestrial ant fauna in flooded forests. Other arboreal ants, but not terrestrial ants, were markedly lower in AG aggregations than in areas that lacked AGs, perhaps due to competition from aggressive and dominant AG ants.

AGs formed principally by directed dispersal of epiphyte seeds to ant nests, where larvae fed on seed attachments without damaging seeds. AG ants also recognized and retrieved seeds of at least one AG epiphyte from feces of vertebrate fruit dispersers. The preference ranking of epiphyte seeds by *Ca. femoratus* was not correlated with either obvious differences in quality of seed appendages or long-term resource potential of plants. Seeds of AG epiphytes were rejected by three ants that do not tend AGs but were collected by a fourth such species. Seed attractiveness may depend in part on nonnutritional cues.

Preadaptations of plants and ants appear to have been very important to the origin of AGs. Evidence for evolutionary specialization and coadaptation is circumstantial but suggestive.

Key words: ant competition; ant garden; ant–plant interaction; coadaptation; epiphyte; mutualism; parabiosis; preadaptation; Peru; seed dispersal; tropical rainforest.

INTRODUCTION

In lowland Amazonian rainforests, a taxonomically diverse group of epiphytic angiosperms grows principally on arboreal carton-ant nests. These "ant gardens" (AGs) were first described and named by Ule (1901, 1905, 1906). Subsequent studies of ants (Wheeler 1921, Weber 1943*a, b*) or plants (Prance 1973, Madison 1979) added substantively to our descriptive knowledge of AG species. Kleinfeldt's (1978) more detailed investigation in a Costa Rican palm plantation included only one species each of ant and plant. As yet, no comprehensive ecological studies of multispecies AGs have been carried out in a natural environmental setting.

The principal objective of this study was to investigate processes responsible for formation and maintenance of AGs and determinants of their species composition. Secondary goals were to assess the interdependence of associated ants and plants and the significance of the association for other forest species.

HABITAT AND METHODS

Study site and plant censuses

The principal study site was Cocha Cashu Biological Station in the Manu National Park of Madre de Dios, Peru (11°52′ S, 71°22′ W, elevation ≈400 m). Much of the study area consisted of seasonally inundated tropical moist forest (Holdridge 1967) with a mosaic of habitats, most seral stages in riverine succession. Mean canopy height averaged 30–35 m, but emergents could reach >60 m. Pronounced wet seasons (October through April) and dry seasons (May through September) drive cycles of flowering, fruiting, and foliage production (Terborgh 1983). Studies reported here took place from late August through early November in the years 1983–1986. These months were unusually dry in 1983 (an El Niño year) and unusually wet in 1984. (For

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further details of habitat and climate, see Terborgh 1983.)

AGs were censused in 1983 and 1984 within ≈10 m on each side of ≈12 km of the established Cocha Cashu trail system. Trails were chosen at random near the field station and included most major habitat types (Terborgh 1983). For each AG sighted, I recorded vertical height class (1–5, 5–10, 10–20, or >20 m), measured with the aid of a 210-mm Canon zoom lens. Also recorded were identities of each plant species growing from the garden and rank abundances of these species by volume, estimated visually through binoculars. Garden sizes (nest plus foliage) were estimated as small (less than ≈2500 cm^3), medium (≈2500 cm^3–0.5 m^3), and large (greater than ≈0.5 m^3). Also scored were associated ants, first categorized by number and later determined to species from collections. By following foraging columns with binoculars to low vegetation, I could identify ants from even high canopy gardens. I rated individual gardens as occurring in isolates (≤5 gardens) or large aggregations, and as growing from well or poorly maintained substrate. Deteriorating gardens typically had loose strands of nest material trailing beneath them and/or little remaining substrate.

For some exceptional gardens, not all categories of data were recorded. Vertical height was not scored when AGs had obviously fallen. Dominance by particular epiphytes was not analyzed when two to several species were approximately equally dominant, or when nests lacked epiphytes altogether. Finally, no data were taken on size class for the first 35 gardens censused.

Three additional kinds of data were taken along the census route. First, during all censuses, I searched for evidence that any of the AG epiphytes grew outside gardens. Second, brief notations were made on the presence of vine tangles and of understory species indicative of seasonal flooding. Third, I returned to each isolate and AG aggregation in 1984 to identify "prominent host trees" containing the greatest estimated biomass of AG epiphytes. Comparison of the generic representation of these hosts with that in an independent 1-ha plot census (A. Gentry, *personal communication*) helped to identify possible "preferred" AG hosts.

Focal studies were conducted on representatives of *Calyptranthes* and *Inga,* the two most abundant genera of trees apparently overrepresented as AG hosts. *Calyptranthes* cf. *lanceolata* occurs regularly on old river beaches along edges of oxbow lakes. For 1.2 km along the west bank of Cocha Totora (within the Cocha Cashu trail system), I censused AGs on trees >3 m high of *C.* cf. *lanceolata* and control trees matched for size and proximity. *Inga* trees occur throughout the forest in groves comprising *I. marginata, I. ruiziana,* and, occasionally, *I. edulis.* I recorded the numbers and sizes of AGs as well as estimated tree heights for all *Inga* trees and "other" trees >3 m in height within the boundaries of each of two *Inga* groves. Total AG volume per tree was estimated as the product of AG size rank (small = 1; medium = 2; large = 3) times the number of AGs of that size rank, summed over the three ranks.

Ant censuses

Ants were censused at baits in six AG aggregations and four nearby areas that were in the same habitat type but lacked AGs. Each census took place on a different warm, sunny day between 0700 and 1100, as discovery rates of newly established baits dropped off later in the day. At each census station, I placed baits successively (at ≈15-min intervals) at each of eight bait stations separated from each other by ≈6 m. Positioned on ≈4-cm^2 paper squares, baits consisted either of cotton soaked in saturated sugar solution or of small cheese fragments. One sugar and one cheese bait were placed on the leaf litter at each station and on leaf surfaces or small branches 1–2 m above the ground. Arboreal baits were positioned at random with respect to plant species, and all baits were a minimum of 1 m apart.

I observed the baits at a single station constantly for a 10-min period and recorded the number of minutes before discovery by AG and other ant species. After the period of constant monitoring, I moved to a new bait station but returned to each previous station to record identities and numbers of ants at 20-, 30-, and 60-min intervals after stations were established.

Interactions of ants and plants

A variety of AG ants at different localities have been reported to carry the seeds of AG plants back to their nest sites (Ule 1905 and 1906, Kleinfeldt 1978, Madison 1979). To verify these observations for the suite of AG ants and epiphytes present at Cocha Cashu, I collected seeds from all AG epiphyte species for which I could secure newly mature fruits. In independent trials for each epiphyte, six seeds were placed on a broad leaf surface or tree trunk where activity of AG ants was high, and the seeds were observed until they had been carried back to nests. In the same manner, six seeds from each of three AG epiphytes were offered to workers of four common ant species that did not nest in association with epiphytes, and responses of these species were noted. Within each test, all seeds of a given species were from the same mature plant, but seeds of different parents were used in different trials. Whenever possible, I noted the behavior of AG ants toward naturally available fruits and seeds of AG epiphytes. I also opened several AG nests (see Interactions of Parabiotic Ants, below) to determine treatment of seeds by ants inside the nest.

Seeds of the various AG epiphytes differed conspicuously in the average amount of attached fruit pulp or exocarp. Cafeteria experiments were undertaken to test for interspecific differences in the attractiveness of seeds to AG ants. Equal numbers of seeds of various AG epiphytes were placed in a shallow plastic bait tray

TABLE 1. Distribution of ant-garden (AG) aggregations (groups of >5 AGs) in relation to habitat.*

Habitat type	Trail length censused (m)	% trail with AGs
High-ground forest	5975	16
Midsuccessional forest	2175	24
Ficus–Cedrela association	1350	31
Cedrela odorata	700	29
Flooded/disturbed forest	1800	39

* Habitats defined by Terborgh (1983).

(12 × 12 cm) and offered simultaneously to AG ants by taping the bait tray to a branch or vine used as a major thoroughfare. Simultaneous availability of mature epiphyte fruits determined the numbers of plant species (3–6) and the numbers of seeds per species (6–10, and equal for all species in each test) included in each test. I recorded the species of epiphyte seeds in the order that they were taken from the tray and summed the ranks independently for seeds of each species. Between 1984 and 1986, eight different trials were carried out, each in a different AG aggregation or isolate.

Fruit morphology of AG epiphytes suggested the possibility that birds, monkeys, and bats might also disperse fruits and seeds. I assessed responses of the most common AG ants to seeds passed through the digestive tracts of two captive frugivorous bats. A single individual of each of two frugivorous species was placed alone in a large aluminum can covered with wire mesh. Separate feedings of the same bats with figs of AG epiphyte *Ficus paraensis* and those of an unidentified congener permitted safe separation of the two kinds of seeds from fecal samples passed at different times. Seeds passed by the bats were offered to AG ants in the same manner as reported above, with six seeds of each of the two fig species offered simultaneously.

Interactions of parabiotic ants

The majority of AGs at Cocha Cashu were occupied by both *Camponotus femoratus* Fab. and *Crematogaster* cf. *limata parabiotica* (Forel), which not only shared foraging trails and territories but also nested in different chambers of the same garden. The exact nature of this relationship, termed "parabiosis" (Forel 1898), is poorly understood. To assess whether the two common parabiotic ants can occur independently of one another, I looked for these ants throughout the forest. Although *Ca. femoratus* was readily identified in the field on the basis of morphology, behavior, and the odor of formic acid, it was necessary to identify collections of *Cr.* cf. *l. parabiotica* microscopically. Voucher specimens are in collections of J. Longino (University of California, Santa Barbara). Whenever possible, I also noted the contributions of the two species to nest construction.

A more than twofold difference in body size (length) of the parabiotic ants suggested that the two species might on average use resources of different energetic quality. To test this hypothesis, I established bait stations consisting of three small cotton balls (≈1.5 cm in diameter) soaked in honey solutions that gave readings of 5, 10, and 20% sucrose equivalents, respectively, on a hand refractometer (American Optical temperature compensated model number 10430). Numbers of workers of each species using each of the baits were recorded at 10-min intervals over a 190-min period. Cotton balls were replenished with the respective honey solutions at 40, 80, 120, and 160 min. Four such tests were carried out in October of 1983, each on a different day and in a different AG aggregation.

To assess the distribution of ant species among chambers and the probable resources of larvae, I dismantled a number of AG nests on host trees destined to be lost through riverbank erosion. Ants were collected on a white plastic ground cloth after spraying nests with Resmithrin insecticide. I searched among ants that had fallen and ants that remained in the nests to determine the number of species present and the number of queens per species.

RESULTS

Censuses of AGs and ants

AG censuses of ≈12 km of trail revealed 879 gardens, or an average of one garden every 14 m. As AG ants commonly foraged over distances as great as 10 m, aggregations were classified as continuous if gardens were encountered at least every 20 m along the trail. So defined, aggregations occurred over ≈16–39% of the study area, depending on habitat type (Table 1). Least well-represented in more mature forests on relatively high ground, gardens reached their greatest abundance in the most frequently flooded habitats, *Ficus–Cedrela* forest, *Cedrela* forest, and flooded/disturbed forest. Midsuccessional forest, a mosaic of seasonally inundated and high-ground patches, was intermediate with respect to disturbance by flooding (Terborgh 1983) and to representation of AGs. Within high-ground forest and midsuccessional forest, AGs occurred almost exclusively in disturbed patches such as treefall zones and along borders of the river, an oxbow lake, and a seasonally and deeply inundated *Ficus trigona* swamp. *Heliconia metallica,* an understory plant characteristic of flooded forests, was present in most AG areas and used as a resource plant by AG ants tending homoptera.

Ants showed much interspecific variation in attraction to sugar baits, but all foraged avidly for cheese baits, to which the following analyses are restricted. Ants other than parabiotic species discovered a significantly smaller fraction of arboreal baits per unit time in AG areas than in areas without AGs (Fig. 1A). This relationship held even during continuous moni-

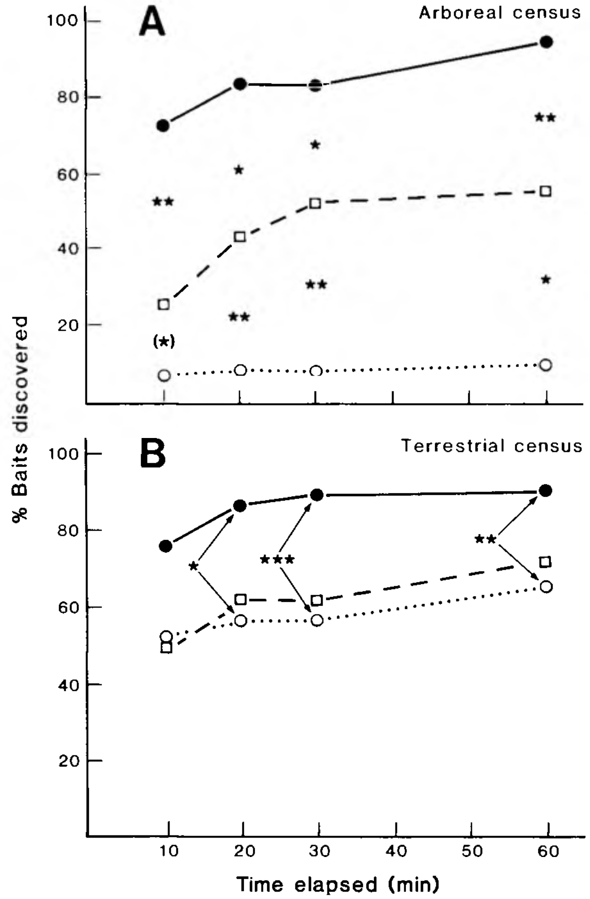

FIG. 1. (A) Percentages of arboreal cheese baits discovered after various time intervals by parabiotic AG ants (*Camponotus femoratus*) and/or *Crematogaster* cf. *limata parabiotica*, ●——●) and by all other ants combined within (○· · · ·○) and outside of (□- - - - -□) AG areas. Two-tailed probabilities in Mann-Whitney U tests are: $^{*}.02 < P \leq .05$; $^{**}.01 < P \leq .02$; $^{***}P \leq .01$. (B) Same data as in Fig. 1A, but for terrestrial cheese baits. For all time periods, percentages of baits discovered by AG ants exceed percentages for other ants inside AG areas at $P < .01$.

toring of baits over the first 10-min period, suggesting that these ants were less numerous or less active in AG areas than in areas without AGs. Rates of discovery of terrestrial baits by other than parabiotic ants were statistically indistinguishable between AG areas and paired areas lacking AGs (Fig. 1B). Together, parabiotic AG ants discovered both arboreal and terrestrial baits at a faster rate than did all other ant species combined (Fig. 1A and B). This relationship was significant over the initial 10-min observation period and may indicate that AG ants were more numerous or more active than ants of all other species combined. Finally, ants as a whole discovered a greater percentage of baits per unit time in AG areas than did ants in areas without AGs.

Ants in four different subfamilies and seven species nested in Cocha Cashu AGs but differed markedly in their abundance and distribution (Table 2). Together, *Camponotus femoratus* and *Crematogaster* cf. *limata parabiotica* occupied large aggregations of gardens scattered throughout the forest. Jointly or independently, these species inhabited 94.5% of 758 ant-occupied gardens at Cocha Cashu, and 98.2% of these gardens appeared (without dismantling nests, but see below) to contain both parabiotic species. Although a species of *Solenopsis* (subgenus *Diploroptrum*) nested with undetermined frequency in gardens occupied by *Ca. femoratus* and *Cr.* cf. *l. parabiotica,* the term "parabiotic" is reserved here for the relationship between *Ca. femoratus* and *Cr.* cf. *l. parabiotica.*

Azteca cf. *traili* occurred on all but three of the inhabited AGs lacking parabiotic ants. Of these 39 gardens, 84.6% occurred in large AG aggregations, and 15.4% were in isolates. This distribution differed significantly from that of parabiotic ants, for which 94.4% of 716 gardens occurred in aggregations and only 5.6% in isolates ($P = .026$ in a two-tailed Fisher Exact Test).

Scored as deteriorating were 5.1% of *Azteca* AGs, 6.1% of those inhabited by either or both parabiotic species (including 25.0% of those with *Cr.* cf. *l. parabiotica* alone), and all three gardens with *Odontomachus* and *Pheidole* ants. Two of these three gardens had fallen to the ground and possibly had been abandoned by previous inhabitants. *Odontomachus* and *Pheidole* ants were relatively inconspicuous, and their presence may have been overlooked in a small fraction of the 118 AGs scored as lacking ants.

Epiphytes

Ten "AG-restricted" epiphytes, representing seven plant families, appeared to become established exclusively or almost exclusively on AGs (Table 3). *Peperomia macrostachya* was by far the most frequent resident and dominant of AGs. Only *P. macrostachya* (5 of 674 sightings), *Ficus paraensis* (1 of 202 sightings),

TABLE 2. Ant-garden ants at Cocha Cashu (Madre de Dios, Peru). Worker head widths (mm) in parentheses. ND = no data.

Subfamily	Species	% of AGs†
Dolichoderinae	*Azteca* cf. *traili** (0.70–1.30)	4.5
Formicinae	*Camponotus femoratus**‡ (1.20–1.50)	80.4
Myrmicinae	*Crematogaster* cf. *limata parabiotica**‡ (0.55)	81.6
	Solenopsis‡ (0.20)	ND
	Pheidole sp. 1§ (0.70)	0.1
	Pheidole sp. 2 (ND)	0.1
Ponerinae	*Odontomachus haematodus*§ (2.15)	0.2

* Ants incorporate vertebrate feces into nest carton. Data consist of 37 independent recorded observations for parabiotic ants and experimental tests on two colonies of *A.* cf. *traili.* Data are not available for other species.

† Percent of 876 AGs (with or without ants).

‡§ Same symbol indicates capacity for the indicated species to nest in different chambers of same AG.

TABLE 3. AG epiphytes at Cocha Cashu. Epiphyte classes are defined in Results: Epiphytes.

Family	Species	% of AGs* Occupied	 Dominated
	AG-restricted epiphytes		
Araceae	*Anthurium gracile*	29.0	8.2
	Anthurium sp. nov.†	2.6	2.1
	Philodendron megalophyllum	15.0	9.6
Bromeliaceae	*Neoregelia* sp.	1.8	1.4
	Streptocalyx longifolius	3.2	1.3
Cactaceae	*Epiphyllum phyllanthus*	12.6	3.6
Gesneriaceae	*Codonanthe uleana*	15.8	2.9
Moraceae	*Ficus paraensis*	22.9	12.1
Piperaceae	*Peperomia macrostachya*	76.1	51.3
Solanaceae	*Markea ulei*	6.6	1.9
	Rare AG epiphytes		
Gesneriaceae	*Codonanthe* (*Codonanthopsis*) sp. 2	0.2	0.4
Orchidaceae	*Vanilla planifolia*	0.7	0.5
	Epiphytes not AG-restricted		
Araceae	*Anthurium clavigerum*	3.1	2.1
	Monstera adansonii	1.2	1.0
	Syngonium spp.	0.9	0.1
	Philodendron sp.	0.3	0.5
Orchidaceae	*Epidendron* sp.	0.1	0.0
Piperaceae	*Peperomia* sp. 2	0.1	0.0
Pteridophyta	Various species	3.2	1.0

* Percents of AGs occupied or dominated by epiphyte species. Percents based, respectively, on all censused gardens (including those lacking plants and/or ants) or all censused AGs for which dominance was scored.

† Species probably undescribed. Voucher material sent to T. Croat, Missouri Botanical Garden.

and *Anthurium gracile* (6 of 261 sightings) grew where there was no evidence of previous assocation with AGs (remains of AG substrate and/or presence of other AG epiphytes). Relatively small, isolated individuals of the former two species grew from tree crevices containing carton similar to that constructed by *Cr.* cf. *I. parabiotica.* Isolated individuals of *A. gracile,* an epiphyte with velamentous roots, occasionally grew independently of ant carton.

Two additional epiphytes were found only on AGs but were too rare for me to determine the extent of their restriction to ant nests (Table 3). In each case, these plants resided in well-maintained and actively tended AGs. *Vanilla planifolia* grew luxuriantly from three AGs on a single host tree inhabited by no other epiphytes. By the following year, ants were absent, substrate had deteriorated, and all epiphytes had died. *Codonanthe* (*Codonanthopsis*) sp. grew on gardens of only two host trees, both of which were occupied by the rare *Azteca* cf. *traili.*

Eight occasional epiphytes were rare AG residents usually growing elsewhere (Table 3). This heterogeneous species group included hemiepiphytic aroids that could have grown into AG associations from germination sites elsewhere. Among these species, *Anthurium clavigerum* was exceptionally abundant in AGs. Three small individuals had obviously germinated in gardens, but five others may have grown into gardens secondarily. Various unidentified ferns were occasional residents only of AGs with deteriorating substrate, and only one of their 29 occurrences was on a garden actively tended by both parabiotic ants.

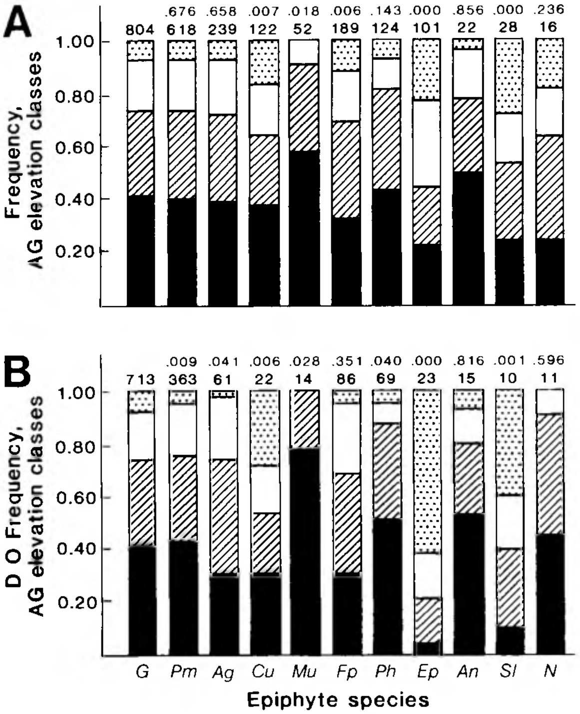

FIG. 2. (A) Frequency distributions of all AGs (*G*) or AGs with specific epiphytes (*Pm* through *N*) at 0–4 m (■), 5–10 m (▨), 10–20 m (□), or >20 m (⬚) canopy elevation. Epiphyte species are: *Pm, Peperomia macrostachya*; *Ag, Anthurium gracile*; *Cu, Codonanthe uleana*; *Mu, Markea ulei*; *Fp, Ficus paraensis*; *Ph, Philodendron megalophyllum*; *Ep, Epiphyllum phyllanthus*; *An, Anthurium* sp. nov.; *Sl, Streptocalyx longifolius*; and *N, Neoregelia* sp. Distributions of AGs with focal epiphytes were compared with distributions of AGs without these epiphytes in chi square tests (corrected where necessary for small sample sizes) or by Fisher Exact Tests when dictated by small sample sizes. (B) Frequencies of dominance occurrences (DO) on AGs in relation to AG elevation, for epiphytes *Pm* through *N*. *G* is the frequency distribution of elevations of all AGs for which both elevation and dominance were scored. Significance levels (above) and sample sizes (below) are shown above bars in both A and B.

Distributions of AG-restricted epiphytes differed interspecifically in relation to canopy height, vine tangles, AG size, and epiphyte diversity (Figs. 2, 3, 4, and 5). Six species were overrepresented in occurrence, dominance, or both in relatively light-intense environments of higher canopy strata (Fig. 2A and B). These included *Anthurium gracile, Codonanthe uleana, Ficus paraensis, Epiphyllum phyllanthus, Streptocalyx longifolius,* and *Neoregelia* sp., although the trend was not significant at low sample sizes for *Neoregelia.* This same suite of species also exhibited negative associations

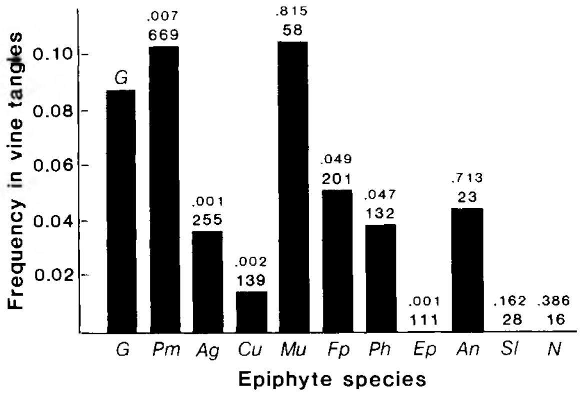

FIG. 3. Frequency of all AGs (*G*) or AGs with specific epiphytes (*Pm* through *N*) growing in vine tangles. Species identifications, sample sizes, and probability levels are shown as in Fig. 2. Distributions of AGs with focal epiphytes were compared in chi square tests or Fisher Exact Tests with distributions of AGs lacking these epiphytes.

with darker vine tangles, again excepting species with low sample sizes (*S. longifolius* and *Neoregelia*; Fig. 3). Of these light-demanding species, four were significantly overrepresented in occurrence or in both occurrence and dominance on large AGs, *A. gracile* was overrepresented on small gardens, and sizes of AGs with and without *C. uleana* were statistically indistinguishable (Fig. 4A and B). Significantly associated with AGs of high epiphyte diversity were all of the species in this group except *Neoregelia*, which was significantly overrepresented on low-diversity AGs (Fig. 5).

Distributions of the remaining four AG-restricted epiphytes suggest greater shade tolerance. *Peperomia macrostachya, Markea ulei,* and *Philodendron megalophyllum* were overrepresented in occurrence and/or dominance on gardens in the lower strata (Fig. 2A and B). (The commonness of *P. macrostachya* makes visual comparisons difficult in these figures.) Parallel trends in *A.* sp. nov. lacked significance at low sample sizes. Alone among these four species, *P. macrostachya* showed a significant association with vine tangles (Fig. 3). In both occurrence and dominance, *P. macrostachya* was significantly overrepresented on small AGs, while the other three species were statistically associated with larger gardens (bordering on significance for low sample sizes in *A.* sp. nov.). Correlated with this, *P. macrostachya* was statistically overrepresented on gardens with low epiphyte diversity and the other three species, on high-diversity gardens (trend significant only for *M. ulei*). On gardens easily observed in the low forest strata, *P. macrostachya* was almost always the first plant to colonize newly established gardens. Thus, despite its tendency to occur in the understory, dominance by this species typically increased with elevation in the canopies of host trees with gardens in more than one elevational class (76.5% of 17 cases in which dominance changed with height class).

Depressed abundances characterized most AG epiphytes on AGs with deteriorating substrate (Fig. 6). At low sample sizes, this trend was not significant for the two bromeliads. *Anthurium* sp. nov. was exceptional in its significant overrepresentation on poor substrate.

Finally, distributions of at least some AG epiphytes may be influenced by the identities of their ant associates. All but two plant species occurred at lower frequencies on *Azteca* gardens than on those tended by parabiotic ants, but this trend was significant in Fisher Exact Tests only for *P. macrostachya* ($P \ll .001$), *F. paraensis* ($P = .008$), *Ph. megalophyllum* ($P = .032$), and *E. phyllanthus* ($P = .032$). Reversal of this trend was not significant for *M. ulei*. The rare *C.* (*Codonanthopsis*) sp. grew only on *Azteca* AGs, but its occurrences on two host trees in the same aggregation were probably not independent events.

AG hosts

Calyptranthes cf. *lanceolata* hosted AGs of parabiotic ants at a higher frequency than did neighboring trees of similar size but different species. Along 1.2 km of trail, I encountered 35 treelets of *C.* cf. *lanceolata*

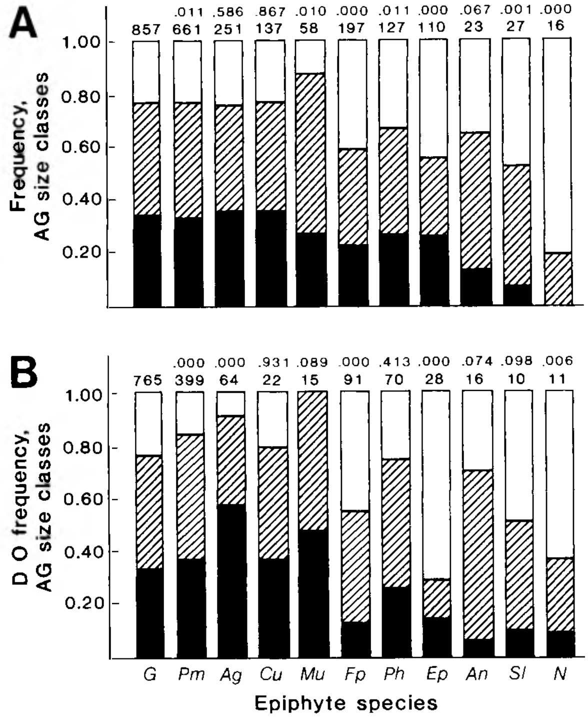

FIG. 4. (A) Frequency distributions of all AGs (*G*) or AGs with specific epiphytes (*Pm* through *N*) in small (■), medium (▨), and large (□) size classes of AGs. (B) Frequencies of dominance occurrences (DO) on AGs in relation to AG size class, for epiphytes *Pm* through *N*. *G* is the frequency distribution of size classes for all AGs for which both size class and dominance were scored. In both A and B, species designations, sample sizes, and significance levels are shown as in Fig. 2. Distributions of AGs with focal epiphytes were compared in chi square tests or Fisher Exact Tests with distributions of AGs lacking these epiphytes.

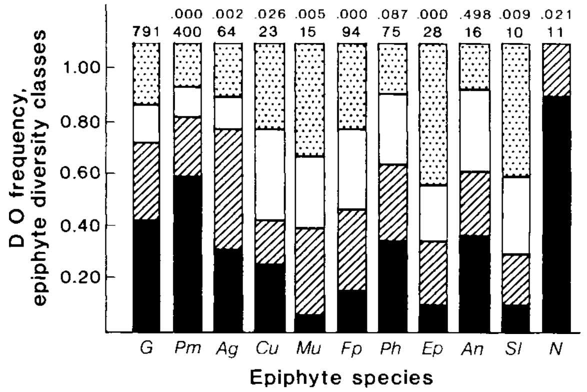

FIG. 5. For epiphytes *Pm* through *N*, frequencies of dominance occurrences (DO) on AGs in relation to epiphyte diversity on AGs. Diversity classes are one species (■), two species (□), three species (□), and four or more species (⊡). Sample sizes and probability levels are shown as in Fig. 2. *G* is the frequency distribution of epiphyte diversity on AGs for all AGs for which both diversity and dominance were scored. Distributions of AGs with focal epiphytes were compared in chi square tests or Fisher Exact Tests with distributions of AGs lacking these epiphytes.

>3 m in stature, 19 of which contained AGs. In contrast, only one of 35 control trees contained AGs. This difference was highly significant (one-tailed Fisher Exact Test, $P < .001$). Many of the *Calyptranthes* that lacked fully developed AGs with epiphytes contained what may have been incipient AGs, or carton shelters built over homoptera on leaves, stems, and, especially, fruit pedicels. Each of the six fruiting *Calyptranthes* contained AGs.

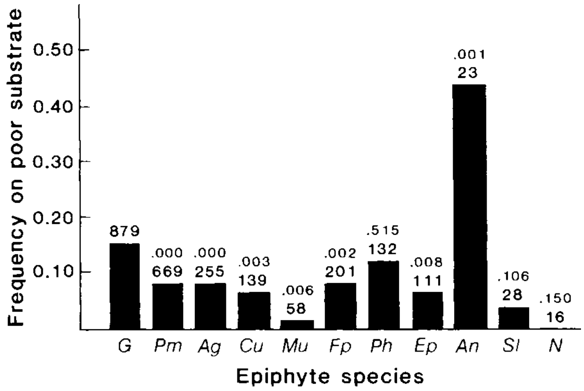

FIG. 6. Frequency of all AGs (*G*) or AGs with specific epiphytes (*Pm* through *N*) composed of deteriorating or poor substrate (see Habitat and Methods: Study Site and Plant Censuses). Species identifications, sample sizes, and probability levels are shown as in Fig. 2. *G* is the frequency of gardens on poor substrate for all gardens censused. 36.1% of these gardens contained no epiphytes. In contrast, only 5.4% of gardens with well-maintained substrate contained no epiphytes. This difference is significant at $P < .001$ in a chi square test. Distributions of AGs with focal epiphytes were compared in chi square tests or Fisher Exact Tests with distributions of AGs lacking these epiphytes.

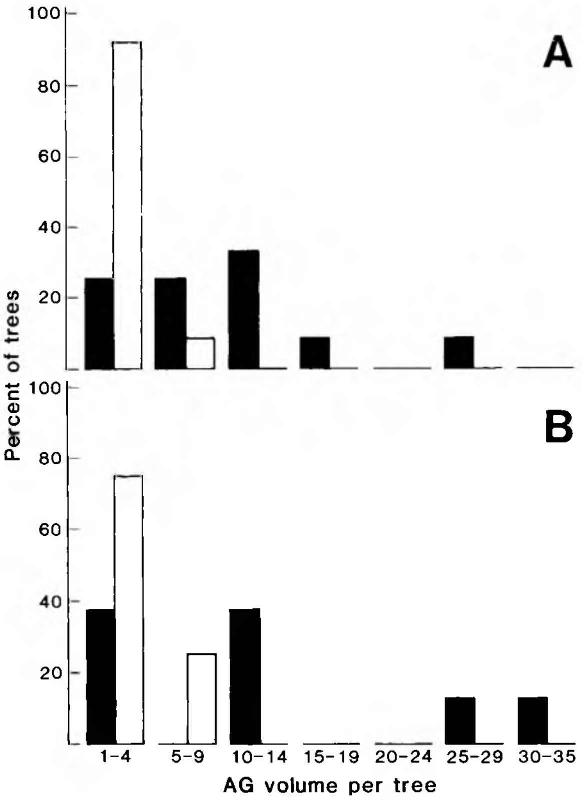

FIG. 7. For two different AG aggregations (A and B), frequency distributions of AG volume on *Inga* (■) and other (□) host trees. For each tree, volume was estimated as the summed product of garden size rank (small = 1; medium = 2; large = 3) and number of AGs per size class. The greater AG volume on *Inga* is significant for A ($P < .001$) and borders on significance for B ($P = .065$).

Parabiotic AG ants also nested disproportionately in *Inga* trees. In the first AG aggregation, 12 of 14 *Inga* trees and 37 of 66 control trees hosted AGs (one-tailed Fisher Exact Test, $P = .027$). Seven of eight *Inga* in the second *Inga* grove and only eight of 17 control trees contained AGs ($P = .012$). Among hosts of AGs, estimated total AG volume (number × size ranking) was greater on average on *Inga* than on control trees (Fig. 7). This difference was significant for the first census (Mann-Whitney $U_{[12,36]} = 67.5$, one-tailed $P < .001$), but only bordered on significance in the second census ($U_{[8,8]} = 17.0$, one-tailed $P = .065$). In neither census did estimated tree size differ between *Inga* and control trees ($U_{[12,36]} = 189$, two-tailed $P = .520$ and $U_{[8,8]} = 21.5$, $P = .270$).

Of 12 prominent hosts of *Azteca* AGs (four identified in 1986 from outside the previously censused area), fully eight were *Cordia nodosa*. This understory treelet occurs at low densities throughout much of the Cocha Cashu trail system, but accounted for only 2 of 359 stems identified in the Gentry tree plots (see Habitat and Methods: Study Site and Plant Censuses).

TABLE 4. Some traits of AG epiphytes.[*]

Plant species[†]	Fruits[‡]	Seed attachments	Ant response to seeds[§]		Exudates or pearl bodies
			Collect	Reject	
AG-restricted species					
Anthurium gracile^{Y}	Red berries	Sticky, gelatinous matrix	1, 2	···	Not conspicuous
Anthurium sp.^{N}	Lavender-pink berries on threads	Pulp	1, 2	···	Not conspicuous
Philodendron megalophyllum^{N}	White berries; strong, sweet smell	Sticky, gelatinous matrix	1, 2	···	Petiole at leaf base; nectaries
Neoregelia sp.^{Y}	Blue berries	Sticky, gelatinous matrix; long white funicular strand	1	···	Not conspicuous
Streptocalyx longifolius^{Y}	Blue berries	White aril; sticky gelatinous matrix	1, 2, 3	4, 5, 6	Not conspicuous
Epiphyllum phyllanthus^{Y}	Large, fleshy, ripening pink	Sticky pulp	1, 2	···	Developing fruits; nectaries
Codonanthe uleana^{N}	Fleshy blue capsule	Fading yellow aril; sticky gelatinous matrix	1, 2, 3	4, 5, 6	New leaves; nectaries Developing fruits; nectaries
Ficus paraensis^{N}	Green fig, purple stripes	Sticky pulp	1, 2	···	Adaxial leaves; pearl bodies
Peperomia macrostachya^{N}	Pendent spike, crowded, exserted one-seeded drupes	Flesh-colored arils	1, 2, 3	4, 5, 6	Developing fruits (oil?);[‡‡] glands
Markea ulei^{N}	White berries	Pulp	1, 2	···	Persistent sepals; nectaries
Other species					
Codonanthopsis sp.ND	Capsule, drying open	Wing; tiny aril	1, 2	···	Abaxial leaves; nectaries
Anthurium clavigerumND	Pink berries	Pulp	1	1	Not conspicuous

[*] Data also summarized in Kleinfeldt (1986) with some differences.

[†] Greenhouse plants known to be capable of selfing? Superscript Y = yes; N = no; ND = no data.

[‡] Fruit dispersal by vertebrates: *A. g.* and *Ph. m.*: monkeys *Cebus apella* and *Saimiri sciureus* (D. W. Davidson, *personal observation* and C. Mitchell, *personal communication*); *E. p.*: *Cebus albifrons* (Terborgh 1983) and *Cebus apella* (C. Mitchell, *personal communication*); *C. u.*: avian frugivores *Paroaria gularis* and *Ramphocelus carbo* (S. Robinson, *personal communication*); *F. p.*: *Saimiri sciureus* (C. Mitchell, *personal communication*) and bats (L. Emmons, *personal communication* and this study); *P. m.*: seeds in droppings beneath bat roosts (D. W. Davidson, *personal observations*).

[§] Tests of single colonies of ant species: 1 = *Ca. femoratus*; 2 = *Azteca* cf. *traili*; 3 = *Hypoclinea bidens*; 4 = *Camponotus sericeiventris*; 5 = *Dolichoderus imbecillus*; 6 = *Zacryptocerus spinosa*. Entries are lacking for ant species not tested for particular seed species. Except for *A. clavigerum*, entries signify unanimous treatment of each of six seeds offered.

[††] Moore 1973.

[‡‡] Madison 1979.

Ant–plant interactions

Workers of *Ca. femoratus, A.* cf. *traili*, and *Hypoclinea bidens* consistently retrieved seeds of all AG epiphytes whose seeds were available for tests (Table 4). However, only two of six *Anthurium clavigerum* seeds were taken to the nest by *Ca. femoratus*; the remainder were investigated and consistently rejected. Workers of *Cr.* cf. *limata parabiotica* demonstrated great interest in the seeds and foraged on fruit pulp, but were too small to carry seeds farther than 1–2 cm. Seeds of three AG epiphytes were consistently rejected by three species that do not tend AGs.

Workers of *Ca. femoratus* and *A.* cf. *traili* frequently carried naturally available seeds of AG-restricted epiphytes back to their nests. *Camponotus* regularly patrolled infructescences and removed seeds as fruits ripened. In addition to harvesting exposed seeds of *P. macrostachya*, ants broke open the pericarp of ripe fruits of *M. ulei, A. gracile*, and *C. uleana* to remove seeds. Fruit pulp and sticky, gelatinous material coating epiphyte seeds were collected independently of the seeds themselves.

Disparities in the numbers and species of seeds available for inclusion in cafeteria experiments led to small sample sizes for pairwise comparisons. Nevertheless, the concordance of rankings from different cafeteria trials (Appendix and Table 5, with few nonzero entries below the diagonal) demonstrates that some transitive property of seeds determines a consistent ranking of attractiveness to ants.

Occasional sightings confirmed that a variety of vertebrates collects fruits of AG epiphytes (Table 4). Experiments with caged bats verified that *Ca. femoratus* could discriminate seeds of *Ficus paraensis* from those

Table 5. Results of cafeteria trials to determine preferences of *Camponotus femoratus* workers for seeds of various AG epiphytes.*

		Species with higher preference ranking							
		Pm	*Fp*	*Ph*	*Sl*	*Mu*	*Ag*	*An*	*Cu*
Species with lower preference ranking	*Pm*	—	2	0	4	3	7	1	4
	Fp	1	—	1	2	3	3	1	1
	Ph	1	0	—	—	1	1	1	—
	Sl	0	0	—	—	2	5	—	3
	Mu	0	0	0	1	—	4	1	1
	Ag	0	0	0	0	0	—	1	5
	An	0	0	0	—	0	0	—	—
	Cu	0	0	—	0	0	0	—	—

* Entries are numbers of trials (out of 8) with the preference indicated. Dashes indicate that no comparisons were made. Epiphyte species designations as in Fig. 2. Concordance and transitivity of rankings from separate trials are highly significant (analysis in Appendix).

of an unidentified congener after seeds of both species had passed completely through the digestive tracts of bats. In independent trials with single caged individuals of *Vampyrops helleri* and *Uroderma bilobatum*, all six seeds of *F. paraensis* were carried into the nest within a 20-min period after the seeds were offered. Twelve hours later, seeds of the unknown fig still had not been removed. In each case, these differences were statistically significant in Fisher Exact Tests (one-tailed, $P < .001$). Although seeds of the two figs may have differed slightly in size and mass, both were well within the size range of seeds regularly carried by *Ca. femoratus*, and workers typically backed away from seeds of the unknown fig without handling them.

Inside dissected nests, epiphyte seeds lay in the separate brood chambers of both *Ca. femoratus* and *Cr.* cf. *limata parabiotica* with developing larvae. Intact seeds remained appended to walls of even deserted brood chambers, and numbered in the hundreds to thousands, even in very small AGs ($\approx$18–200 cm^3). I found no evidence of seed destruction or partial consumption by ants.

Finally, ants may influence growth environments of epiphytes by carrying vertebrate feces into their nests (Table 2). Although small ant fecal pellets were apparent in disassembled nests, it was difficult to determine with certainty whether the ants characteristically leave fecal pellets inside their nests, rather than discarding them.

Queen number and parabiosis

As many as three ant species maintained separate brood chambers in a single AG. In order of increasing nest volume ($\approx$18, 58, 180, and 576 cm^3, and 0.65 m^3), disassembled AGs contained two, one, one, four, and 31 dealate queens of *Ca. femoratus*. Although *Cr.* cf. *limata parabiotica* maintained brood chambers in three of the five nests, dealate, physogastric queens (two) were found only in the 180-cm^3 AG. A queenright colony of *Solenopsis* (*Diploroptrum*) sp. occurred in the 576-cm^3 AG, and some *Solenopsis* workers were found in brood chambers of *Ca. femoratus*. Dissection of four small- to medium-sized *Azteca* AGs in one AG isolate and two small gardens in a second isolate revealed no members of the reproductive castes.

Surveys of forest trails revealed no *Ca. femoratus* colonies living independently of *Cr.* cf. *limata parabiotica*. Although AGs may have lacked queens and even workers of the latter species, *Cr.* cf. *limata parabiotica* always occurred in large numbers on the surfaces and/or in the immediate vicinities of these gardens. Twenty collections of *Crematogaster* from forest areas lacking *Ca. femoratus* were identified by J. Longino as *Cr.* cf. *l. parabiotica*. Although capable of building carton runways along tree crevices and carton shelters over scale insect resources, *Cr.* cf. *l. parabiotica* never nested in large carton nests in the absence of *Ca. femoratus*. Nests were located in hollow stems of various plants and were not associated with epiphytes.

At both artificial and naturally available food sources, *Ca. femoratus* aggressively usurped higher quality resources from *Cr.* cf. *l. parabiotica* but did not exclude

Table 6. Numbers of workers of each of the two common parabiotic AG ants visiting honey solutions of three concentrations.*

Experiment number	Species	Honey concentration			
		20%	10%	5%	$P<$†
1	*Camponotus femoratus*	75	8	13	
	Crematogaster parabiotica	162	119	200	.000
2	*Ca. f.*	20	8	5	
	Cr. p.	83	85	50	.049
3	*Ca. f.*	10	10	2	
	Cr. p.	105	64	42	.254
4	*Ca. f.*	42	28	10	
	Cr. p.	75	99	83	.001

* Within an experiment, data are lumped for 10 evenly spaced observation periods over a 190-min interval.

† Probability (Pearson χ^2) that worker distributions of the two species over baits of different quality differ due to chance alone. Combining probabilities from each of the four tests (see Sokal and Rohlf 1969: 621–624) gives $\chi^2 = 63.49$ and $P < .001$.

the smaller species from poorer quality resources. In experiments with three concentrations of honey solutions, *Ca. femoratus* fed disproportionately from highly concentrated solutions in each of four experiments (Table 6). Although in no case were numbers of the smaller ants negatively correlated with those of larger ants feeding from more concentrated solutions, *Ca. femoratus* workers frequently interfered with feeding by smaller ants by actively chasing them away. *Ca. femoratus* also fed at the large foliar nectaries of host trees *Inga marginata* and *I. ruiziana*, and defended these against intrusions by the smaller species (D. W. Davidson, *personal observations*). However, the larger ants ignored much smaller nectaries of *Hasseltia floribunda* (Flacourtiaceae), *Sapium ixamasense* (Euphorbiaceae), and *Citharexylum poeppigii* (Verbenaceae). Table 7 documents the considerably higher nectar production rates and slightly higher nectar concentrations of the two *Inga* species compared with *H. floribunda.*

TABLE 7. Quality and quantity of extrafloral nectar produced by three resource plants of parabiotic ants.*

Plant species	Plant no.	Plant nectar per 12 h			Nectar concentration (% sucrose equivalents)
		N	$\bar{X}$	*s*	
Inga ruiziana^{c}	1^{bc}	10	1.9	0.8	12.5
					12.5
					10.5
	2^{bc}	5	5.6	3.6	10.5
					13.0
					14.0
					12.5
					12.5
I. marginata^{de}	1	7	5.9	2.9	15.5
					17.0
	2	11	6.1	3.4	18.5
					18.5
					16.5
Hasseltia floribunda^{de}	1^{b}	2	0.2	0.1	9.0
	2^{c}	3	0.2	0.1	8.0

* Nectar was measured in 1 μL microcapillary pipettes to the nearest ½ or ⅓ μL. *N* = number of measurements of nectar per nectary (*Inga* species) or nectaries per microlitre (*H. floribunda*, which has very low nectar production rates). For plants or species marked with the same superscript letter, differences in plant (b,c) or species (d) nectar volumes or species nectar concentrations (e) are significant in Mann-Whitney *U* tests at probability levels ranging from .05 to .001.

DISCUSSION

AG epiphytes

The natural history of AG epiphytes at Cocha Cashu resembles that described in studies for other regions of northern and western Amazonia. Representatives of several families of both monocots and dicots share the AG habitat and often grow in the same gardens (Ule 1901, 1905, 1906, Prance 1973, Madison 1979). Establishment of the commonest AG epiphytes appears to be principally or exclusively restricted to AGs (Ule 1901, Madison 1979, but see Kleinfeldt 1986). Seeds of these same epiphytes are attractive to AG ants, which consistently carry propagules back to their carton nests (Ule 1905, 1906, Kleinfeldt 1978, Madison 1979). Plants supply ant resources in the form of seed attachments, pearl bodies, and sweet exudates of extrafloral nectaries and/or homoptera (reviewed in Kleinfeldt 1986). Moreover, fibrous roots of some AG epiphytes ramify through ant carton, lending it greater structural integrity (Ule 1905, 1906, Madison 1979, Kleinfeldt 1986).

The AG flora at Cocha Cashu consists of six light-demanding and four shade-tolerant epiphytes. All are from families rich in epiphytes (Kress 1986), and most have light requirements typical of congeners (Richards 1952). Within each group, species with lower investment in support structures and earlier maturity (*Peperomia macrostachya, Anthurium gracile*, and *Codonanthe uleana*) tend to occur in smaller and less diverse AG communities than do species investing heavily in woody stems (*Ficus paraensis* and *Markea ulei*) or maturing relatively late. Thus, reproductive individuals of late-maturing *Anthurium* sp. nov. and *Philodendron megalophyllum* typically grew in abandoned gardens on tree trunks ≈10 m below crowns with active AGs in their foliage. *Neoregelia* sp., a "tank bromeliad" (e.g., Benzing 1970), is exceptional in occurring on large gardens of low diversity. Mineral nutrition derived from decaying debris among tank leaves may allow this species to outlast and/or overgrow other epiphytes on crowded or deserted AGs. Altogether, these observations suggest that the assembly of epiphyte communities on AGs is governed by processes similar to those governing species composition and succession in other plant communities (Huston and Smith 1987).

Interspecific differences in growth rate, age at maturity, and other traits may affect the interactions of these epiphytes with ant associates. Pioneer and early-maturing species tend to be particularly abundant and widespread across their constantly renewing habitats (see also Prance 1973 and Madison 1979) and may contribute disproportionately to ant nutrition and/or to the structural support of ant carton. Epiphytes producing extrafloral nectar, homopteran honeydew, or pearl bodies may partially subsidize ant activities in relation to plants that produce no food rewards. *Anthurium* sp. nov. is a particularly likely candidate as a parasite of mutualistic associations between AG ants and other epiphytes (see Janzen 1974 for a similar parasitism in Asian epiphytes). It produces no obvious food substance on vegetative tissues, often reproduces after ants have moved their nests, and has dense and invasive velamentous roots that gradually exclude both other epiphytes and *Ca. femoratus* nest chambers.

Consistent interspecific differences in seed attractiveness to *Ca. femoratus* (Table 5) cannot account for differences in epiphyte distributions. The most abundant epiphyte, *P. macrostachya*, has the least preferred seed. Moreover, although the rank order of attractiveness appears to be based on some transitive property, it is not obviously correlated with the plant's probable contribution to ant nutrition. For example, arillate seeds of *P. macrostachya* rank below seeds bearing no apparent nutritional supplements other than occasionally adhering fruit pulp (*F. paraensis, M. ulei*, and *Anthurium* sp. nov.). Preferences are also uncorrelated with long-term expectation of food supplements, as seeds of important resource species such as *F. paraensis* and early-maturing *P. macrostachya* rank lower than seeds of late-maturing species that produce no extrafloral nectar or pearl bodies (*Anthurium* sp. nov. and *Streptocalyx longifolius*).

Two final observations also suggest that seed attractiveness does not depend purely on nutritional criteria. Arillate seeds of three AG epiphytes were consistently rejected by three ant species that do not tend AGs (Table 4). Although *Ca. sericeiventris* and *Dolichoderus imbecillus* are generalized foragers like *Ca. femoratus* (D. W. Davidson, *personal observation*), their workers often responded to epiphyte seeds by alarming and/or fleeing. Second, the capacity of *Ca. femoratus* to identify *F. paraensis* seeds that had passed through the digestive tracts of bats also suggests the importance of nonnutritional cues in seed recognition. This finding is also important in refuting Wheeler's (1921) assertion that dispersal of epiphyte seeds by ants cannot play a role in epiphyte colonization of widely separated AGs.

Ants

Ants associated with AGs at Cocha Cashu are generally representative of AG ants in other parts of Amazonia (Ule 1906, Wheeler 1921, Weber 1943*a, b*, Prance 1973). Parabiotic *Ca. femoratus* and *Cr.* cf. *l. parabiotica* dominate numerically. *Solenopsis* sp., occurring at unknown frequency in gardens of parabiotic ants, belongs to subgenus *Diploroptrum*, whose members parasitize broods of other ants (Hölldobler 1928). The rarity of foraging by these ants outside the nests and the presence of workers in brood chambers of *Ca. femoratus* suggest they may parasitize broods here as well. Contrary to previous interpretations (Wheeler 1921, Kleinfeldt 1986), *Azteca* ants cultivate AGs successfully. Like parabiotic species, these ants gather seeds of AG epiphytes and incorporate vertebrate feces into nest carton. However, their nest carton is noticeably more brittle and less rich in organic matter than that of parabiotic ants, and most epiphytes fare relatively poorly here.

Even within AG aggregations of parabiotic species, *Azteca* AGs typically occurred as small enclaves in one or a few host trees. Differences in the reproductive biology of ants may explain the relatively high proportion of *Azteca* AGs classed as isolates (see also Ule 1906). Six disassembled *Azteca* nests lacked queens, suggesting that, as reported for *Azteca traili* elsewhere (Gomez 1974, 1977), this polydomous species is monogynous. In contrast, colonies of *Ca. femoratus* are regularly polygynous and probably fission to form new AG nests. Workers occasionally commute between AGs, sometimes with brood, and show little or no hostility to ants from neighboring gardens. Seeds of AG epiphytes must be transported from one garden to another, as they appear in nest carton at the earliest stages of nest construction. Polygyny (confirmed independently by J. Longino, *personal communication*) and colony fissioning may also be typical of *Cr.* cf. *l. parabiotica*. On three occasions, workers dragged dealate females into their AG nests. This behavior is characteristic of species with secondary polygyny (Hölldobler and Wilson 1977).

Among more casual associates of AG epiphytes, ants in the genera *Odontomachus* and *Pheidole* probably nest opportunistically in abandoned AGs and do not appear to maintain the substrate (see also Kleinfeldt 1986). Congeners of these species also nest in loose accumulations of organic debris (Davidson and Epstein, *in press*). At least two ant species carry seeds of AG epiphytes back to nest sites that are inadequate for plant growth. *Hypoclinea bidens*, a congener of casual AG associates in other parts of Amazonia (Forel 1912, Mann 1912; *Dolichoderus* spp. now classified as *Hypoclinea*), lives in temporary, rolled-leaf nests bound together by a thin line of carton. Seeds incorporated into this carton do not appear to germinate. On terra firma soils across the Rio Manu, AG epiphytes grow from poorly developed carton structures of a second *Azteca* ant nesting regularly on *Tococa* sp., but apparently few or no plants become reproductively mature on this inadequate substrate.

Parabiosis

Parabiosis is not unique to AG ants and occurs both in other neotropical species (Swain 1977) and in Asian *Camponotus* and *Crematogaster* that do not associate with epiphytes (D. W. Davidson, *personal observation* and U. Maschwitz, *personal communication*). Forel's (1898) epithet is still useful, because the reciprocal fitness consequences to associated species remain unclear. Several observations suggest that *Cr.* cf. *l. parabiotica* might be a persistent parasite of *Ca. femoratus*. *Camponotus* workers resist (though mildly) movement of *Crematogaster* queens into their nests. Workers of *Cr.* cf. *l. parabiotica* cannot carry epiphyte seeds over long distances to their nests, yet their brood chambers contain these seeds. A relatively high fraction of nests occupied by this species alone was scored as deteriorating. Although both parabiotic ants carry feces into nests, most of the organic material incorporated appears to be due to activities of *Ca. femoratus*, whose workers occasionally carry strips of bark, leaf mulch, or portions of abandoned AGs into their nests. Ants similar or identical to *Cr.* cf. *l. parabiotica* nest in stems and cavities outside AGs at Cocha Cashu. Carton built by these ants over homoptera is typical of that of congeners not living in AGs. Poor in organic content, it does not support epiphyte growth. Within AG areas, some of these carton structures are eventually elaborated as AGs, as activities of *Ca. femoratus* increase in the areas. This sequence of nest-building steps may explain why at Cocha Cashu, nest chambers of *Cr.* cf. *l. parabiotica* typically occurred at the centers of AGs (contra Wheeler 1921).

Cr. cf. *l. parabiotica* may benefit from protection by *Ca. femoratus* against vertebrates that would open and destroy nests, as *Ca. femoratus* is among the most aggressive of all ants (Wheeler 1921, Wilson 1987). Excited workers regularly either fall or leap onto observers from 1–2 m distance (see also Madison 1979). The ants bite fiercely and release formic acid into wounds. Monkeys often open stems of forest plants to eat ant brood but are visibly uncomfortable when collecting epiphyte fruits on *Inga* trees with large *Ca. femoratus* populations. They leave these host trees to eat the fruits and do not open nests to eat ant brood. In contrast, *Ca. femoratus* probably confers little protection against at least some army ants, except if it is preferred over the smaller species as prey. During an invasion of *Eciton burchelli,* workers lined up side by side and immobile beneath epiphyte leaves. Army ants carried off large numbers of workers and soldiers with apparent disregard for the formic acid they released.

Indirect evidence suggests that, despite the observations above, the net effect of *Cr.* cf. *l. parabiotica* on *Ca. femoratus* may be only weakly negative or even beneficial. First, the latter species regularly builds nests around scale insects tended by the smaller ants. Second, the larger ants relinquish poor-quality resources to the smaller species (Table 6 and Swain 1977). High levels of activity and aggression may demand correspondingly high rates of resource supply and explain why small homopteran nymphs are commonly ignored by *Ca. femoratus* but are eventually taken over as they grow. For example, scale insects tended by these ants on a leaf of *F. paraensis* were significantly larger than those tended by *Cr.* cf. *l. parabiotica* on the same leaf (Mann-Whitney *U* test: $U_{[57,40]} = 0.00$, $P < .001$). Similarly, membracid nymphs tended by *Ca. femoratus* on an inflorescence of *Heliconia metallica* were significantly larger than those tended by the smaller ants on the same inflorescence ($U_{[10,22]} = 10$, $P < .001$). If *Ca. femoratus* cannot forage profitably on poor-quality resources, this species may benefit from care provided to nymphs by *Cr.* cf. *l. parabiotica* during the early developmental stages of these homoptera. Swain (1977) has suggested that *Ca. femoratus* follows recruitment trails of *Cr.* cf. *l. parabiotica* and usurps the more valuable resources. In experimental trials (D. W. Davidson, *personal observation*), I have been unable to confirm interspecific use of recruitment trails. This is not surprising if trails of the smaller ants lead as often to poor-quality as to high-quality resources. Neither did I observe the reported feeding of *Cr.* cf. *l. parabiotica* by *Ca. femoratus* (Wheeler 1921).

AGs in rainforest communities

AG distributions within Cocha Cashu forests accord well with naturalists' observations in other parts of Amazonia. Concentrated in lower forest strata, gardens are most common in areas of relatively high light intensity, along borders of rivers, lakes and swamps, as well as in treefall zones and flooded, disturbed forests (Wheeler 1921, Weber 1943*a,* Prance 1973, Madison 1979). Patchiness in AG distributions is not adequately explained as a response to reduction of the terrestrial ant fauna in flooded forests (Fig. 1A and B). Although activities of other arboreal ants at baits are markedly lower in AG areas than in nearby areas lacking AGs, those of terrestrially foraging ants are statistically indistinguishable in the two types of sites. Moreover, both parabiotic species dominated baits to the exclusion of all other species contesting baits in the Cocha Cashu censuses, except where baits had been placed by chance at the nest entrances of other ants (D. W. Davidson, *personal observation*). Behavioral dominance may allow parabiotic species to monopolize arboreal resources to the exclusion of competing ants. In terrestrial habitats, *Ca. femoratus* may forage primarily for nest materials and feces and thus interfere less with activities of other ants.

Both strikingly high abundance of ants in AG areas and disproportionate representation of particular resource trees as prominent AG hosts suggest that AGs may be locally abundant in areas where productivity of ant resources is especially high. *Inga* and many other common AG host genera (e.g., *Pithecellobium, Senna, Guazuma, Sapium,* and *Hasseltia*) have extrafloral nectaries, and ants regularly maintain large populations of phloem-feeding homoptera (membracids and coccids) on some of these species as well as on hosts that lack such nectaries (*Calyptranthes, Rheedia,* and *Guatteria*). Plants with extrafloral nectaries tend to occur at higher frequencies in relatively disturbed habitats where incident light is most intense (Bentley 1977 and this study). Rates of supply of resources through homoptera may also be greatest in these areas.

Although both *Cordia nodosa* and *Tococa* sp. typically host ants that do not build carton nests (Davidson et al., *in press* for Cocha Cashu), associations of *Azteca* AGs with these hosts occur in other parts of Amazonia (Forel 1904, Wheeler 1942) and may also have their basis in ant nutrition. Ants feed on pearl bodies on the lower leaf surfaces of *C. nodosa,* and on coccids inside the domatia of *Tococa* sp. in upland terraces across the river from Cocha Cashu. Long, dense stem trichomes characterize both of these myrmecophytic hosts and may provide some protection for nests against larger competing and predatory ants (Davidson et al. 1988).

Lower resource demands may enable *Azteca* ants to exploit shaded habitats that are unavailable to parabiotic species; their regular hosts characteristically grow in shaded understory rather than light gaps and edge habitats.

The documented abundance of parabiotic AG ants and the specificity of their associations with habitats and host plants suggest a previously unappreciated potential for members of these symbioses to affect other forest species. By building their own nests and cultivating certain of their food resources, AG ants are, to some extent, liberated from food and nest-site limitations that often restrict populations of other ants (Wilson 1971, Jeanne and Davidson 1984). Pyrethrin "knock-down" samples of canopy insects at nearby Tambopata Nature Reserve reveal that parabiotic AG ants are the most abundant ant species in these forests (Wilson 1987, Davidson et al. 1988, for *Cr.* cf. *l. parabiotica*). Studies at Cocha Cashu demonstrate a likely effect of these ants on other ants in the community. In view of their high frequency and abundance on particular host trees and resource species (e.g., *Heliconia metallica*), it would be surprising if AG ants had no effect (positive or negative) on host-plant fitnesses. Reciprocally, even resource plants that do not host AGs may influence the abundance and distribution of AG ants and epiphytes.

Origin of the AG symbiosis

The natural history of AG species can, perhaps, shed light on the origins of the remarkably diverse AG symbiosis. A parsimonious hypothesis is that the phenomenon originated as the "capture" of unrelated epiphyte taxa by "frugivorous" arboreal ants that built carton around homoptera or nectaries on fruits or their pedicels. Kleinfeldt (1978) observed that *Crematogaster longispina* builds carton nests around sugar-secreting fruits of *Codonanthe crassifolia*, and parabiotic ants in this study exhibited the same behavior with respect to membracids at the base of *F. paraensis* fruits. As on fruiting *Calyptranthes* host trees, where many extraordinarily sweet fruits regularly remain on branches to rot, large numbers of aggressive and chemically defended ants may deter vertebrate dispersers. (The high frequency of autogamy in Table 4 supports Madison's [1979] suggestion that pollinators are deterred as well.) If seeds germinated in situ in ant-tended fruits, tree seedlings would not fare well, but epiphyte seedlings might establish successfully in the nutrient-rich carton. If these epiphytes had small (but not microscopic) seeds, worker ants might even use seeds to transport fruit pulp or sweet, gelatinous seed coatings to larval nest chambers. Sticky seeds could become fastened to walls of nest chambers and become difficult to remove or even useful in nest construction.

In this way, the AG symbiosis could have arisen without special adaptation on the part of plants or ants. Extrafloral nectaries, pearl bodies, and nutritional attachments to seeds are not unique to AG epiphytes and may not be special adaptations to AG life. Similarly, many arboreal ants tend nectaries and homoptera and construct carton over these relatively long-lived sources of liquid food. Enlargement of carton nests could have occurred without evolution as an automatic response to added structural support of nests by epiphyte roots. *Camponotus*, *Crematogaster*, and *Azteca* ants are specialized to use liquid resources and are unlikely to have destroyed seeds while feeding. The extreme aggression of *Ca. femoratus* might also have preceded the origin of AGs, though it possibly intensified in an environment rich in resources. Thus, closely related *Ca. abdominalis* (Wheeler 1921) is also markedly aggressive.

Moreover, transport of feces to nest sites is not unique to AG ants. Many ants specializing on plant exudates collect feces, blood, perspiration, and other sources of salts not supplied in the diet (D. W. Davidson, *personal observation*). The frequency of this behavior and its consequent contribution to epiphyte nutrition will almost certainly vary with environmental productivity and animal biomass. On the relatively rich Cocha Cashu soils, vertebrate biomass is especially high (Emmons 1984), and it is commonplace to observe ants enriching their gardens in this manner. *Iridomyrmex myrmecodia*, an associate of myrmecophytic epiphytes in Asia, exhibits a similar behavior (D. W. Davidson, *personal observation*), but the behavior may not be expressed frequently in relatively unproductive forests where these plants often grow (Janzen 1974).

Some arboreal ants that do not tend AGs also place AG seeds in their nest carton. Depending on the permanence of carton and its suitability as a plant growth medium, success of these plant propagules varies from germination failure (*Hypoclinea bidens* nests), through seedling failure (*Azteca* nests on *Tococa*, and *Cr.* cf. *l. parabiotica* carton), to successful establishment and growth to reproductive maturity (nests of *A.* cf. *traili* and *Ca. femoratus*). Polydomy can help to produce sizeable local populations of ant-associated epiphytes. Together with polygyny, it may lead automatically to the extensive and apparently long-lived AG aggregations associated with parabiotic ants. (The many sites named *tracua* or *taracua* ["the ant that eats flowering stalks"] in Brasilian Amazonia attest to the long lives of these aggregations: W. L. Brown, *personal communication*.) Polydomy (though not polygyny) is comparatively common among tropical arboreal ants and could have preceded associations of ants with epiphytes.

At least at the population level, AG residents *Ca. femoratus* and *A.* cf. *traili* seem not to occur without their epiphytes, nor vice versa (but see Gomez 1974 and 1977 for *Azteca traili* elsewhere). Rare *Ca. femoratus* nests lack epiphytes on their surfaces (Wheeler 1921, Madison 1979, and this study), but these are typically neighbors of epiphyte-covered gardens, contain epiphyte seeds, and grow in deep shade that may limit plant growth. At Cocha Cashu, isolated AG epiphytes appear either to have germinated on AGs and survived desertion by their ants, or to have germinated independently but not reached reproductive maturity. Correlated occurrences and high local abundances of AG ants and epiphytes are most likely the outcome of mutualism. However, the apparent obligacy of these associations is not necessarily indirect evidence of special adaptation by AG ants and plants. Alternatively, it may arise only from the population dynamics of strong mutualism, coupled with efficient seed gathering by ants.

Although many ant and plant traits most obviously related to the AG symbiosis can be interpreted as preadaptation, evidence of coadaptation between ants and plants might still be sought in more subtle traits. Like some other ant-defended plants (reviewed in Beattie 1985), AG epiphytes may have relatively poor chemical defenses and rely principally on ants for protection from insect herbivores (Davidson and Epstein, *in press*). Moreover, these epiphytes might have evolved or amplified production of specialized seed attractants that influence their associations with different ant species and enable ants to recognize seeds after passage through vertebrate dispersers. Seeds of most AG epiphytes produce a noticeable aroma of sweet vanilla. Recently, Seidel (1988) has confirmed the widespread occurrence of an identical volatile oil on seeds of 9 of the 10 AG epiphytes from Cocha Cashu, and a second, unrelated compound is common to seeds of at least six of these species. As compounds structurally similar to these two substances retard growth of fungi and bacteria (Greathouse and Rigler 1940), seed compounds may have originated as protection against microbial pathogens of epiphyte seeds and later assumed importance in protecting ants from their own nest pathogens. Parallels exist in bees, where nests of some species are lined with plant resins releasing fungistatic volatile oils (Messer 1985). At present, it is unclear whether seed compounds originated prior to ant–epiphyte associations or afterwards, and whether their origins in unrelated taxa were independent or related (Davidson and Epstein, *in press*).

Finally, in response to relatively rapidly expanding, nutrient-rich habitat, available almost exclusively to AG epiphytes, these plants may have evolved physiological traits or allocational preferenda more typical of opportunistic colonizing species. Similarly, secondary polygyny and reproduction by colony budding in large unicolonial populations of each of the parabiotic AG species may be a response to the patchy but rich and long-lived resource base available to competitively dominant ants cultivating many of their own resources (Hölldobler and Wilson 1977). Polygyny is the derived condition of *Pseudomyrmex* ants on *Acacia* and apparently favors rapid occupation of expanding local populations of this myrmecophytic tree (Janzen 1973). Although conversion from monogyny to polygyny can apparently occur with or without reproductive isolation leading to evolutionary divergence and speciation (Ross et al. 1987), behavioral and other correlates of polygyny in *Acacia* ants provide strong indirect support for evolutionary specialization (Janzen 1973).

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APPENDIX

Statistical analysis of transitivity in seed preference rankings by *Camponotus femoratus* (by Thomas Philippi)

Two problems prevented the application in our study of Petraitis's (1979) analysis of transitivity. First, there were empty cells, where pairs of seeds were never available simultaneously for comparison. Second, each pairwise comparison was not a separate experiment, but a tournament where 3–6 seed species were presented together. Within each tournament, there could be no intransitivities, so possible intransitivities were far fewer than the total number of pairwise comparisons would indicate. Therefore, following Gilpin et al. (1986), the number of results beneath the diagonal of the sorted matrix of pairwise results (Table 5) was used as a measure of intransitivity.

For the set of cafeteria trials conducted, there were 5.16×10^{12} possible outcomes. Of these, 8! or 40 320 would result in a perfectly transitive matrix of pairwise preferences (equivalent to renaming the seed species). The numbers of cafeteria trials that would have produced preference matrices with exactly 1, 2, and 3 pairwise preferences below the diagonal were calculated similarly. These outcomes were summed and then divided by the total number of possible outcomes to give a tail probability of random rankings within each cafeteria trial producing ≤ 3 pairwise preferences below the diagonal in a sorted pairwise preference matrix. This corresponds to a test of the null hypothesis that the observed concordance of rankings from the different cafeteria trials was due to chance. Values are as follows:

Denominator: 5.16×10^{12}
Zero pairwise preferences: 40 320
One pairwise preference: 1 088 640
Two pairwise preferences: 28 304 640
Three pairwise preferences: 709 269 120

$P \simeq .00014.$

Note added in proof: L. B. Smith has identified *Neoregelia* sp. as *Neoregelia eleutheroptala*.