Geographic Variation and Community Structure in an Ant-Plant Mutualism: Azteca and Cecropia in Costa Rica

John T. Longino

Geographic Variation and Community Structure in an Ant–Plant Mutualism: *Azteca* and *Cecropia* in Costa Rica[1]

John T. Longino

Department of Biological Sciences, University of California, Santa Barbara, California 93106, U.S.A.

ABSTRACT

The association between *Azteca* ants and *Cecropia* trees is the most conspicuous ant–plant mutualism in the neotropics, yet little is known about the identities or community ecology of the species involved. A survey of ant communities found in Costa Rican *Cecropia* trees revealed a community of *Azteca* species obligately associated with *Cecropia,* and a diverse assemblage of non-obligate ants in a variety of genera. High occupation rates of *Cecropia* saplings and trees, and presence of many incipient colonies in saplings vs single colonies in trees, suggest that *Cecropia* are a limiting resource for which ants compete. Obligate *Azteca* appeared competitively superior to non-obligate ants, since non-obligate ants were never found dominating mature trees. Competitive relationships between obligate *Azteca* were not clear; local communities contained three to four *Azteca* species using the same host tree species resource. Two *Azteca* species had a parapatric distribution, the zone of parapatry co-occurring with a similar zone of parapatry between two *Cecropia* species. At the boundary, the *Azteca* species were not host specific.

Possible factors influencing the outcome of competition between ants for *Cecropia* trees include queen and worker behavior, priority effects, partial hostplant specialization, and habitat specialization. Explanation of current distributions may require knowledge of historical factors and stochastic effects.

SPECIALIZED MUTUALISMS BETWEEN ANTS AND MYRMECOPHYTES are not isolated pairs of interacting species. They usually involve communities of many species. Myrmecophytes, as used here, are plants that produce cavities (domatia) within which specialized ants nest. Myrmecophytic *Acacia* trees in Central America are occupied by several *Pseudomyrmex* species (Janzen 1967, 1973a), at least one of which is a parasite rather than a mutualist (Janzen 1975). *Leonardoxa africana* in Cameroon is occupied by the mutualist *Petalomyrmex phylax* and the parasite *Cataulacus mckeyi* (McKey 1984). New World *Triplaris* are inhabited by sympatric species of *Pseudomyrmex,* and Old World *Barteria* by sympatric species of *Tetraponera* (P. S. Ward, pers. comm.). *Cordia alliodora* in Costa Rica is occupied by sympatric populations of *Azteca longiceps* and *Zacryptocerus setulifer* (pers. obs.). Examining the structure and spatial variation of these communities may provide insight into how specialized mutualisms evolve and are maintained.

Wilson (1987) reported a very rich arboreal fauna occupying single rain forest tree canopies in Peru, and raised questions regarding the mechanisms promoting such high local species richness. Communities of myrmecophytes and their ants provide a microcosm within which to examine the community ecology of arboreal ants. By examining a specialized ant–plant interaction at the community level one can address the following questions. What is the spatial variation in community composition? Do ants exhibit hostplant specificity? Are plants a limiting resource for ants? What factors influence the outcome of competition between ants for plants? Results from a study of an ant–plant community in Peru suggest that a variety of ants do compete for plants, and that specialized inhabitants are competitively superior (Davidson *et al.,* in press).

A prominent ant–plant mutualism whose community ecology has received little attention is the *Cecropia–Azteca* interaction. *Cecropia* trees occur throughout the neotropics. They are a common element of forest clearings, second growth forest, and roadside vegetation. Most species in the genus form associations with *Azteca* ants (Bequaert 1922; Wheeler 1910, 1942; Janzen 1969, 1973b; Harada 1982; Benson 1985). Numerous morphological traits and some experimental evidence suggest that the relationship is a specialized mutualism (Janzen 1969, Schupp 1986).

In Costa Rica, there is a community of *Azteca* species that are obligately associated with three species of *Cecropia.* Reported here are the results of a survey of these *Cecropia*-inhabiting ants. Each species' distribution is examined at four scales: 1) total species range, 2) distribution within Costa Rica, 3) fine-scale distribution along transects, and 4) distribution with respect to *Cecropia* hostplant species. Results are also presented on the occupation rates of young versus mature *Cecropia* plants by both the obligate *Azteca* species and non-obligate ants.

Factors influencing competition for trees by ants—host tree species, climate, priority effects, queen and worker behavior, social parasitism, and stochastic effects—are discussed with regard to their ability to explain distributions of ants in *Cecropia* trees.

NATURAL HISTORY

Early accounts of the relationship between *Azteca* ants and *Cecropia* trees include those of Belt (1874), Müller (1876, 1880), and von Ihering (1891, 1907). The candelabra-shaped trunk and branches of *Cecropia* trees consist of hollow bamboo-like internodes in which the ants live. At the base of each leaf petiole is the trichilium, a velvety pad which produces glycogen-rich food bodies (Mullerian bodies) that are harvested by worker ants (Rickson 1971, Janzen 1973b).

Founding queens begin to occupy *Cecropia* saplings when they are less than 1 m tall. On the side of each internode is a thin spot called the prostoma (Janzen 1973b). A newly fertilized *Azteca* queen locates a juvenile *Cecropia* tree and chews a hole in a prostoma, through which it enters. The queen seals the entrance hole with a temporary plug of particulate matter (D. Perlman, pers. comm.) and subsequently plant callous tissue grows to form a pro-stomal scar where the entrance hole used to be (Müller 1880). Individual juvenile trees are usually multiply colonized: separate founding colonies of one or more *Azteca* species are found simultaneously in different internodes (von Ihering 1907). Both single and mixed species as-sociations of queens can be found in the same sealed internode (Skwarra 1934), suggesting multiple coloniza-tion of internodes before the prostoma is sealed. The queen or queens rear a first brood of workers without leaving to forage. The first workers reemerge through the prostoma and begin harvesting food bodies from the tree. As the worker force grows, they enter other internodes and per-forate the internal septa between internodes.

By the time a sapling reaches 3–4 m in height, it usually houses a dominant colony with a large worker force. A mature colony contains many thousands of work-ers, and individual trees contain a single colony (pers. obs.). Workers emerging from different parts of the same tree are always conspecific. Even if a tree has two or more major trunks emerging from a common base near ground level (a common occurrence along roadsides due to cutting and subsequent stump sprouting) the different parts are still occupied by what appears to be the same colony. In contrast, separately rooted trees each appear to contain an independent colony, even when the trees are closely spaced with contiguous crowns. On three occasions clumps of mature trees were observed with overlapping crowns that contained *Azteca* colonies of different species.

In mainland Costa Rica, there are four *Cecropia* species, three of which routinely harbor ants (Burger 1977). Species are distinguished primarily on the basis of reproductive structures and leaf shape. *C. peltata* is common throughout the Pacific slopes and lowlands, and occurs very rarely on the Atlantic side of Costa Rica. *C. obtusifolia* is the reverse, being very abundant on the Atlantic side, and present on the Pacific side only at high elevations and in wet areas.

These two species are by far the most abundant in Costa Rica. They are early successional species, often dominating large forest gaps and common along road edges. *C. insignis* is a forest species, and can become a 30 m tall rain forest tree. It is found on both Atlantic and Pacific sides of Costa Rica, but is most common in what forests remain on mid-elevation Atlantic slopes (pers. obs.). *C. polyphlebia* is strictly a high elevation species, typically occurring above 1400 m. It has long hairs covering the trichilium, low Mullerian body production, partly occluded internodes, and is not known to harbor *Azteca* ants (Janzen 1973b).

Azteca is a large neotropical genus, the species of which exhibit a variety of arboreal nesting behaviors (Emery 1893, 1912; Forel 1929). In Central America, four species are considered to be obligate *Cecropia* inhabitants: *A. alfari, A. constructor, A. coeruleipennis,* and *A. xanthochroa* (Emery 1896, Wheeler 1942). My current investigations suggest the following distributions and taxonomies of these species. *A. alfari* is by far the most widespread of the obligate *Cecropia* ants, occurring wherever ant-inhabited *Cecropia* occur (Kempf 1972). It is actually a group of closely related species, all of which share similar queen head shape and a lack of erect hairs on the tibiae. At least two species occur in Costa Rica, the queens differing much more than workers. In this study, most of the results were based on worker identifications in the field where species in this group were not distinguished (referred to as the *A. alfari* group in these cases). *A. constructor* occurs from Guatemala to northern South America, *A. coeruleipennis* occurs from Mexico to Costa Rica, and *A. xanthochroa* occurs from Mexico to northern South America. *A. xan-thochroa* may also be a group of closely related species, but a single species occurs within Costa Rica. Queens of these three species differ greatly in head shape, pilosity, and color; worker differences are less pronounced but iden-tifications can be made on the basis of head and thoracic shape. Thus, there are four major species or species groups that are broadly sympatric in Central America.

That these *Azteca* taxa are obligate *Cecropia* inhab-itants seems certain. They are all commonly found in *Cecropia* trees, and so are generally abundant in the en-vironment. Yet there is no literature record, no known museum specimens, and no record from my collection of these taxa nesting anywhere except in *Cecropia* trees (see also Skwarra 1934).

METHODS

Distribution data were obtained from museum specimens verified by me (Los Angeles County Museum of Natural History, United States National Museum of Natural His-tory), my collection, and field identifications. Collections and field identifications were made from 1979 to 1987. *Cecropia* plants were usually identified to species in the field, but saplings of *C. peltata* and *C. obtusifolia* could
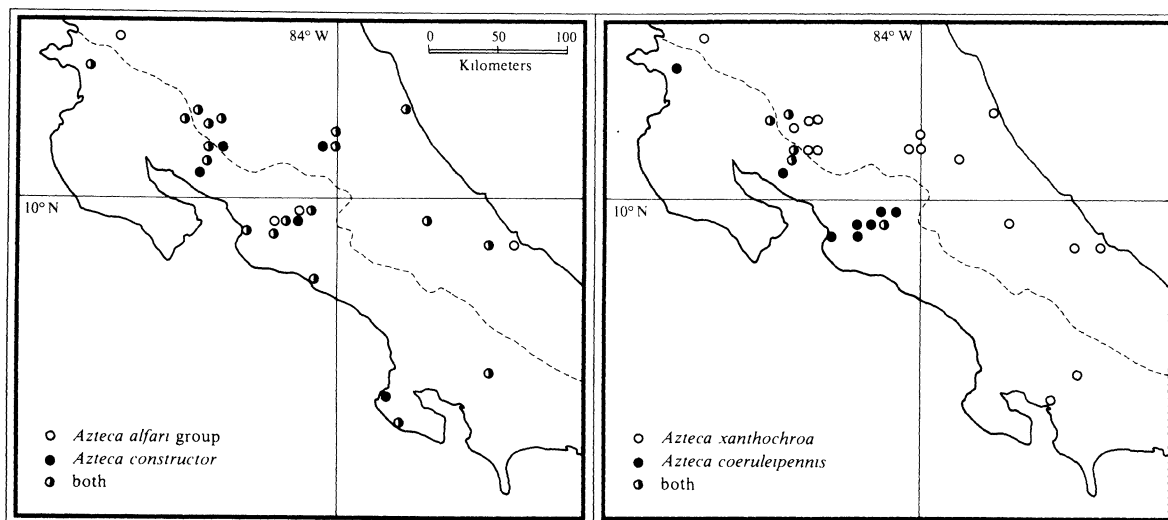
FIGURE 1. Distributions of *Cecropia*-inhabiting *Azteca* species in Costa Rica. The dotted line is the continental divide.

not be distinguished. *Azteca* workers could be identified in the field with a 20× handlens.

Two transects were surveyed intensively. Roadside and trailside *Cecropia* plants were sampled haphazardly as they were encountered. The Monteverde transect, surveyed in 1985, was along roads in Monteverde (10°18'N, 84°49'W) and nearby Santa Elena and the San Luis Valley. It ranged in elevation from 700 to 1500 m, over a distance of 9 km from lowest point to highest. Using the terminology of Gómez (1986, vegetation maps), the transect began in lowland semideciduous forest at its lower end, entered submontane evergreen rain forest near 1000 m, and abutted montane rain forest at its upper end. Little of the transect was actually forested, most of the surrounding land having been converted to pastures.

The Arenal transect, surveyed in 1987, was along the road from Tilarán (10°29'N, 84°58'W), around the north side of Laguna Arenal and Volcán Arenal, to Fortuna. It was approximately 35 km long in an east–west direction and ranged in elevation from 400 to 700 m. The western portion of the transect was in lowland semideciduous forest, the eastern portion in submontane evergreen rainforest (*sensu* Gómez). Again, little forest remained, having been replaced by urban development, pastures, and scrub vegetation.

All 97 *Cecropia* plants along the Monteverde transect were mature trees identified to species and sampled by cutting branches. Branches were cut or pulled from mature trees, and workers were either identified in the field or collected and identified later. Along the Arenal transect, 83 plants sampled were mature trees identified to species, 44 were trees large enough to contain active ant colonies but too young to identify, and 60 were small plants 1–

2 m high, with no dominant ant colony. The former two groups were sampled by prodding. Branches were prodded with an 8 m tall telescoping range pole, which elicited attacks by resident ants. The pole was lowered and the clinging ants identified. The 60 small plants were destructively sampled. Plants were cut at the base and examined internally by splitting internodes sequentially from the top and recording the contents.

The Monteverde transect rose 800 m in 9 km, while the Arenal transect changed less than 300 m over 35 km. Thus, distributions of *Cecropia* and *Azteca* were examined with respect to elevation in the former, east–west position in the latter.

RESULTS

DISTRIBUTION IN COSTA RICA.—*Azteca alfari* group and *A. constructor* were found throughout Costa Rica (Fig. 1). Based on identifications of queens in saplings, two species in the *A. alfari* group were also broadly sympatric. *A. coeruleipennis* was found only in the dry Pacific lowlands, while *A. xanthochroa* was found nearly everywhere except there (Fig. 1).

DISTRIBUTION ALONG TRANSECTS.—Both transects exhibited sharp transitions in hostplant communities. Relative abundance of *C. peltata* sharply decreased with elevation in the Monteverde transect, while *C. obtusifolia* increased (Fig. 2). *C. obtusifolia* was restricted to isolated wet ravines on the dry Pacific slopes, but above 900 m it was widespread and abundant (pers. obs.). *C. peltata*, much more abundant and widespread than *C. obtusifolia* at lower elevation, was rare above 1100 m. Not shown in Figure 2 are seven
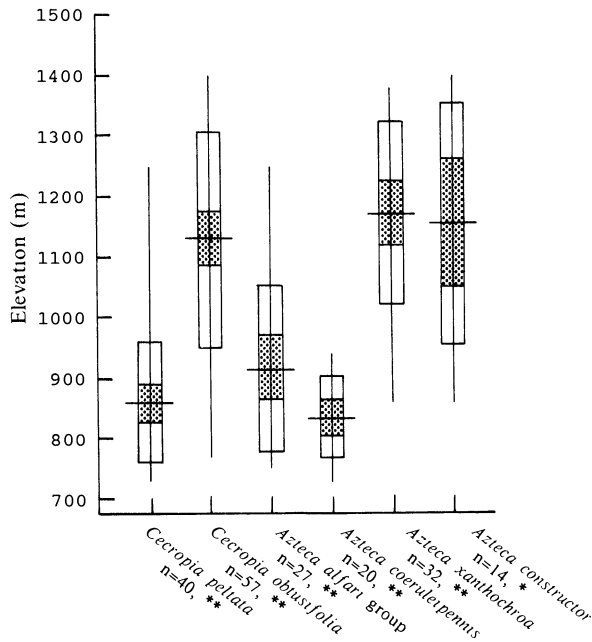
FIGURE 2. Elevational distributions of *Cecropia* and *Azteca* at Monteverde. Hubbs-Miller diagrams show mean, range, ± one standard deviation (open bar), and 95% confidence interval (stippled bar). Elevations of trees in a category (tree species or species of ant occupant) were compared with elevations of all other trees in the sample using *t*-tests (*: $P < .005$, **: $P < .001$).

C. polyphlebia trees that were sampled, all of which were above 1400 m. Above 1500 m, only *C. polyphlebia* was found.

In the western portion of the Arenal transect almost all mature trees sampled were *C. peltata* (Fig. 3). These represented nearly every reachable *Cecropia* tree along the road in an area where *Cecropia* trees were sparse. In the eastern portion, *C. obtusifolia* and *C. insignis* were much more abundant, and *C. peltata* vanished. Hundreds of *C. obtusifolia* could be seen from the road, but no *C. peltata*. Within the sample of mature trees, the three *Cecropia* species were significantly different in east–west position (Kruskal-Wallis test, $P < .001$).

Azteca species also varied in their distributions along the transects (Figs. 2, 3). *A. alfari* group was found significantly more often at lower elevations on the Monteverde transect and in the western portion of the Arenal transect. *A. constructor* was found more often at higher elevations at Monteverde and in the western portion of the Arenal transect. *A. coeruleipennis* was found only at low elevations near Monteverde and in the western portion of the Arenal transect. The mean positions for *A. coeruleipennis* were strongly biased, and the range of values did not extend very high or very far east. *A. xanthochroa* showed a complementary distribution to *A. coeruleipennis*, being found at high elevations near Monteverde and in the eastern portion of the Arenal transect. However, the range of values was greater than the range of *A. coeruleipennis*.
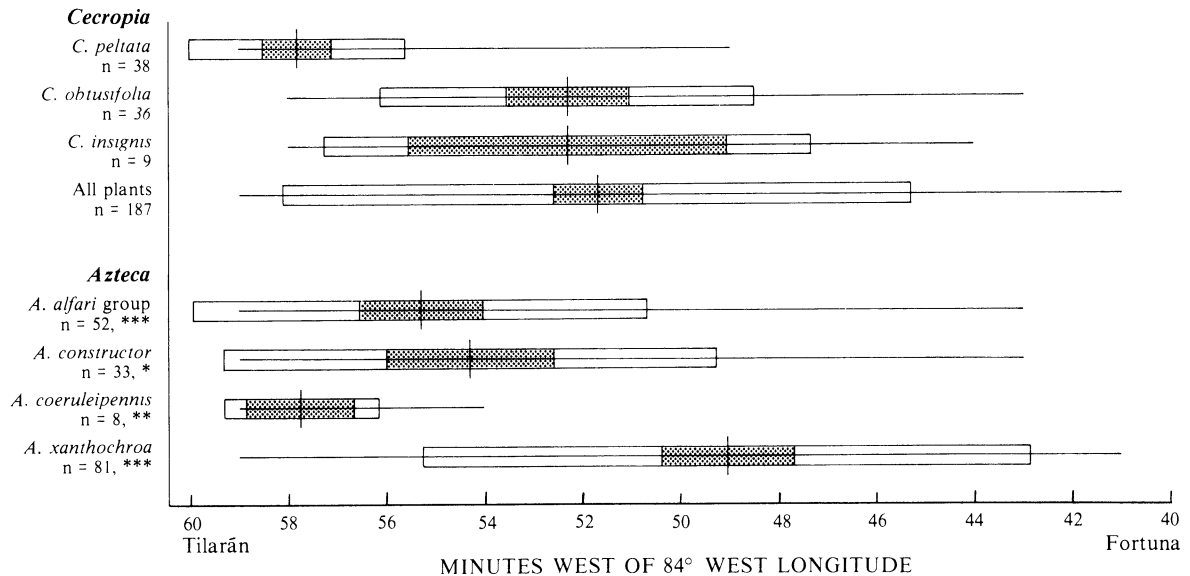

FIGURE 3. East–west distributions of *Cecropia* and *Azteca* on the Arenal transect. Positions were measured to the nearest minute of longitude. Hubbs-Miller diagrams are as in Figure 2. The top three bars are for mature trees only; the lower bars are for all plants sampled. For each *Azteca* species, east–west positions of plants with and without that species were compared with a Mann-Whitney *U* test (*: $P < .05$, **: $P < .005$, ***: $P < .001$).

TABLE 1. *Distribution of* Azteca *species in* Cecropia *species.*

	Azteca species*				
	alf	con	coe	xan	Other
Monteverde transect					
C. peltata	20	0	16	9	3
C. obtusifolia	7	13	4	29	1
Arenal transect					
C. peltata	17	3	4	8	6
C. obtusifolia	6	8	0	19	3
C. insignis	6	0	0	0	2
Cecropia saplings**	17	20	3	36	10
C. insignis saplings	6	2	1	18	10

* alf = *A. alfari* group, con = *A. constructor,* coe = *A. coeruleipennis,* xan = *A. xanthochroa,* other = not containing one of the obligate *Azteca* species.
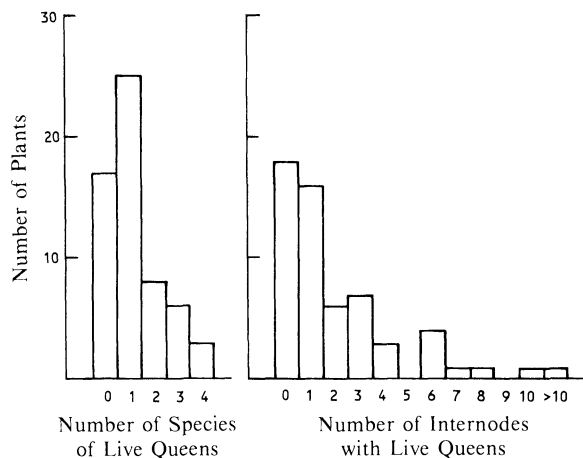** Either *C. peltata* or *C. obtusifolia.*

FIGURE 4. Occupation rates of collected *Cecropia* saplings on the Arenal transect. For these collected saplings, queens in the *A. alfari* group were identified to species, of which there were two. A total of five species was encountered along the transect.

HOSTPLANT SPECIFICITY.—No *Azteca* species was a strict host tree specialist (Table 1). Mature colonies of *A. alfari* group, *A. constructor,* and *A. xanthochroa* were found in all three species of ant-inhabited *Cecropia. A. coeruleipennis* was found in mature trees of both *C. peltata* and *C. obtusifolia,* and a queen was found in one sapling of *C. insignis.* In Monteverde, queens of *A. constructor* were occasionally found in saplings of *C. polyphlebia,* even though mature trees never contained *Azteca* colonies. Chi-square tests show non-random distributions of *Azteca* species in *Cecropia* species, but this is an expected result given the correlated spatial distributions of *Azteca* and *Cecropia* species shown in Figures 2 and 3.

CECROPIA OCCUPATION RATES.—Of the 284 *Cecropia* plants sampled on the Monteverde and Arenal transects, 39 (14%) lacked obligate *Azteca* species. Of these plants lacking *Azteca,* 23 were saplings, generally the smallest with only a few narrow internodes. Sixteen were mature trees. These trees either 1) elicited no response upon prodding, 2) were empty when branches were cut, or 3) contained scattered colonies of carpenter ants (*Camponotus*). When empty trees were investigated, they showed signs of former *Azteca* occupation. Causes of mature tree abandonment were unknown, but insecticide poisoning is always a possibility in agricultural areas.

Sixty small saplings that did not contain dominant colonies (few or no internodes with emerging workers) were collected along the Arenal transect and examined quantitatively for number of species of live *Azteca,* number of internodes occupied by live queens, total number of live queens, and presence of other ant species (Fig. 4). Saplings were found with up to four species of *Azteca,* routinely had queens in more than one internode, and some internodes contained multiple queens. These results

were not peculiar to the Arenal transect; saplings were observed to be similarly occupied throughout Costa Rica.

OCCUPATION BY NON-OBLIGATE ANTS.—*Cecropia* saplings frequently contained nests of other ants from a wide range of ant genera: *Heteroponera, Gnamptogenys, Pachycondyla, Pseudomyrmex, Crematogaster, Pheidole, Solenopsis, Wasmannia, Zacryptocerus,* and *Camponotus.* In the full data set of Costa Rican *Cecropia,* 30 percent of 202 collected saplings contained nests of other species. Many of these were common arboreal species that were frequently seen nesting in other situations. Others were unique collections or otherwise poorly known taxonomically. Most of these ants co-occurred in the saplings with founding *Azteca* queens. In contrast, co-occurrence of species in mature trees was never found, and non-obligate ants (the carpenter ants mentioned above) were found in mature trees only rarely.

DISCUSSION

In Costa Rica, at least five species of *Azteca* are obligate inhabitants of *Cecropia* trees. Although all the species are broadly sympatric throughout Central America, two species are parapatric at a smaller scale. Their zone of parapatry corresponds to a sharp transition in host tree species. The remaining species are found throughout Costa Rica. A local community of *Cecropia* trees typically contains at least four species of *Azteca,* each of them well represented in terms of relative abundance.

Given the high occupation rates of saplings and mature trees, *Cecropia* plants must be a limiting resource for ants.

Young saplings are colonized by a variety of ants, *Azteca* and non-*Azteca* alike. One of several obligate *Azteca* species then proceeds to dominate the *Cecropia* saplings as they grow. Competition between obligate and non-obligate ants is thus deterministic, favoring obligate species. Competition between obligate species appears to be non-deterministic, with a variety of possible outcomes. What factors might influence the outcome of competition between colonies for the ownership of a *Cecropia* tree?

There is certainly a priority effect, in the form of a race to produce the first workers. These workers can then monopolize food sources and perhaps aggressively exclude other incipient colonies. *Azteca* queens are clearly adapted for occupying *Cecropia* saplings. Queens must have a strong chemical sense for locating *Cecropia* plants, because they are routinely found in small plants buried in vegetation, with no mature *Cecropia* trees in sight. They also always enter through the prostoma, while non-specialist ants may try to enter elsewhere. Making an entrance hole elsewhere causes copious sap to flow and the internode to fill with water (Benson 1985). However, non-obligate ants do find their way into young *Cecropia*, and locating a sapling first does not insure success for a colony-founding queen.

There is a great deal of mortality in internodes. Lower internodes in young *Cecropia* plants often contain the remains of dead queens lying in moldering piles. Causes of queen death are mostly obscure. A parasitic wasp, *Conoaxima* (*Eurytomidae*), is an occasional cause of queen death (Wheeler 1942, and pers. obs.) but is not abundant enough to explain the routine presence of failed colonies in the lower internodes. Internodes in very young plants must be somehow unsuitable for queen survival. During colony establishment queens may feed from callous tissue produced by the prostoma (Müller 1876), and food produced by very young plants is possibly inadequate. Alternatively, the lower trunk position of early internodes may be shaded by surrounding vegetation, slowing colony growth and favoring the growth of pathogens. Because of the irregularity of queen death in lower internodes, there is no clear relationship between internode position and colony success. The first queen to find a plant is not necessarily the most successful. Given the common presence of non-obligate ant colonies in saplings, and the uncertainty of success of a particular internode, why do non-obligate ants never become dominant in *Cecropia* trees?

The difference in competitive ability may lie in the nesting behavior of non-obligate ants. Most of these are arboreal ants that either have small colonies, or have large colonies spread in many small nests (polydomous colonies). One or a few internodes may be a typical nest size for these species, so they do not expand their nest area, even if they are initially the most successful colony. Once a nest site is full, resources may be diverted to the production of sexuals, or to the development of additional nest sites off the plant. For the obligate *Azteca*, in contrast, the entire tree forms the potential nest boundary, and they continually expand.

Obligate *Azteca* species compete not only with non-obligate ants, but among themselves. What is the ecological basis of their coexistence? Possibilities include hostplant specialization, habitat specialization, social parasitism, and historical effects.

There is no absolute hostplant specificity. Each *Azteca* species can be found in a variety of *Cecropia* species. However, the range of *A. xanthochroa* closely matches that of *C. obtusifolia* both across Costa Rica and at a finer scale, and the range of *A. coeruleipennis* similarly matches *C. peltata*. These ant species could have special adaptations to particular plant species, beyond the range of which they are competitively excluded.

Alternatively, *Azteca* species and *Cecropia* species may be adapted to particular habitats. Distribution shifts from *C. peltata* to *C. obtusifolia* corresponded to habitat shifts from dry to wet conditions in both the Monteverde and Arenal transects. Sharp environmental changes from dry to wet habitats could result in spatially correlated changes in *Azteca* and *Cecropia* communities, as occurs between *A. coeruleipennis* and *A. xanthochroa*. *A. constructor* and the *A. alfari* group, however, not only lack any hostplant specificity, but their ranges do not reflect that of any particular *Cecropia* species. One is still left with local communities of three or more *Azteca* species using *Cecropia* communities of no more than two species, and exhibiting no hostplant specificity.

Social parasitism could explain coexistence. Numerous ant species, particularly in the temperate zone, are known to be social parasites (Wilson 1971). Queens of social parasites invade colonies of their usually congeneric hosts, killing the host queen and using the heterospecific worker force to rear their offspring. *Azteca* species could be coexisting as the result of a host–parasite interaction that results in a stable equilibrium. However, there was no evidence of social parasitism among *Azteca* species. There were no obvious positive associations between species of *Azteca* queens, which one would expect if one were a parasite of the other. Also, mixed-species colonies would be expected if the parasitic species used host workers to rear parasite workers.

Competitive differences between species are likely, and historical effects and current non-equilibrium conditions may explain the coexistence of *Azteca* species. Numerous factors may contribute to a large stochastic component in colony establishment, resulting in slow resolution of competitive differences. Such factors could include 1) the timing of gap or disturbance formation where *Cecropia* plants become established, 2) the proximity of source trees releasing new queens, 3) the timing of queen production by source trees, 4) lack of competitive interactions after colony establishment, and 5) the long life-time of mature colonies in *Cecropia* trees.

The discrete nature of *Cecropia* plants and internodes, and the well-defined hostplant use of the obligate *Azteca* species, make the *Cecropia–Azteca* association an ideal system for experimentation. Common garden experiments with different species of *Cecropia* saplings could isolate components of queen searching behavior, such as microhabitat vs plant species effects on hostplant selection. Long-term monitoring of experimental plants could reveal factors that influence subsequent colony success: microhabitat, plant species, *Azteca* species, and internode position. However, spatial variation in the *Cecropia–Azteca* community may affect the conclusions drawn from site-specific experimental measurement of ecological interactions. These experiments need to be imbedded in a greater knowledge of the biogeography and systematics of the species involved.

ACKNOWLEDGMENTS

LITERATURE CITED

BELT, T. 1874. The naturalist in Nicaragua. Bumpas, London.
BENSON, W. W. 1985. Amazon ant-plants. *In* G. T. Prance and T. E. Lovejoy (Eds.). Amazonia, pp. 239–266. Pergamon Press, Oxford, England.
BEQUAERT, J. 1922. Ants of the American Museum Congo expedition. IV. Ants in their diverse relations to the plant world. Bull. Am. Mus. Nat. Hist. 45: 333–583.
BURGER, W. 1977. Moraceae. *In* W. Burger (Ed.). Flora Costaricensis, Fieldiana, Botany 40: 94–215.
DAVIDSON, D. E., R. R. SNELLING, AND J. T. LONGIANO. Competition among ants for myrmecophytes and the significance of plant trichomes. Biotropica. In press.
EMERY, C. 1893. Studio monografico sul genere *Azteca* Forel. Mem. Accad. Sci. Ist. Bologna (5)3: 319–352, 2 pls.
———. 1896. Alcune forme nuove del genere *Azteca* For. e note biologiche. Boll. Mus. Zool. Anat. Comp. Univ. Torino 11(230): 1–7.
———. 1912. Subfam. Dolichoderinae. Genera Insectorum Fasc. 137: 1–50.
FOREL, A. 1929. The social world of the ants (C. K. Ogden, Trans.). Albert & Charles Boni, New York.
GÓMEZ, L. D. 1986. Vegetación de Costa Rica, apuntes para una biogeografía Costarricense. Vegetación y clima de Costa Rica, vol. 1. Editorial Universidad Estatal a Distancia, San José, Costa Rica.
HARADA, A. Y. 1982. Contribuição ao conhecimento do gênero *Azteca* Forel, 1878 (Hymenoptera: Formicidae) e aspectos da interação com plantas do gênero *Cecropia* Loefling, 1758. Thesis, Instituto Nacional de Pesquisas da Amazônia e Fundação Universidade do Amazonas, Manaus, Amazonas, Brasil.
IHERING, H. VON. 1891. Die Wechselbeziehungen zwischen Pflanzen und Ameisen in den Tropen. Das Ausland 24: 474–477.
———. 1907. Die Cecropien und ihre Schutzameisen. Engler's Botan. Jahrb. 39: 666–714, pls. 6–10.
JANZEN, D. H. 1967. Interaction of the Bull's-Horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Kans. Univ. Sci. Bull. 47: 315–558.
———. 1969. Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. Ecology 50: 147–153.
———. 1973a. Evolution of polygynous obligate acacia-ants in western Mexico. J. Anim. Ecol. 42: 727–750.
———. 1973b. Dissolution of mutualism between *Cecropia* and its *Azteca* ants. Biotropica 5: 15–28.
———. 1975. *Pseudomyrmex nigropilosa*: A parasite of a mutualism. Science 188: 936–937.
KEMPF, W. W. 1972. Catálago abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). Studia Ent. 15: 3–344.
McKEY, D. 1984. Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rainforest in Cameroon. Biotropica 16: 81–99.
MÜLLER, F. 1876. Ueber das Haarkissen am Blattstiel der Imbauba (Cecropia), das Gemüsebeet der Imbauba-Ameise. Jenaische Zeitschr. Naturwiss. 10: 281–286.
———. 1880–1881. Die Imbauba und ihre Beschützer. Kosmos 8: 109–116.
RICKSON, F. R. 1971. Glycogen plastids in Mullerian body cells of *Cecropia peltata*—a higher green plant. Science 173: 344–347.
SCHUPP, E. W. 1986. *Azteca* protection of *Cecropia*: ant occupation benefits juvenile trees. Oecologia 70: 379–385.
SKWARRA, E. 1934. Ökologie der Lebensgemeinschaften mexikanischer Ameisenpflanzen. Zeitschr. Morph. Ökol. Tiere 29: 306–373.
WHEELER, W. M. 1910. Ants, their structure, development and behavior. Columbia Univ. Press, New York.
———. 1942. Studies of neotropical ant-plants and their ants. Bull. Mus. Comp. Zool. Harv. Univ. 90: 1–262, 57 pls.
WILSON, E. O. 1971. The insect societies. Harvard University Press, Cambridge, Mass.
———. 1987. The arboreal ant fauna of Peruvian Amazon forests: a first assessment. Biotropica 19: 245–251.