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AN EMPIRICAL MODEL OF SPECIES COEXISTENCE IN A SPATIALLY STRUCTURED ENVIRONMENT

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Abstract. Ecological theory has long supported the idea that species coexistence in a homogeneous habitat is promoted by spatial structure, but empirical evidence for this hypothesis has lagged behind theory. Here we describe a Neotropical ant–plant symbiosis that is ideally suited for testing spatial models of coexistence. Two genera of ants, *Allomerus* cf. *demerarae* and three species of *Azteca* are specialized to live on a single species of ant-plant, *Cordia nodosa,* in a Western Amazonian tropical rain forest. Empirically, using census data from widely separated localities, we show that the relative colonization abilities of the two ant genera are a function of plant density. A parameterized model shows that this pattern alone is sufficiently robust to explain coexistence in the system. Census and experimental data suggest that *Azteca* queens are better long-distance flyers, but that *Allomerus* colonies are more fecund. Thus, *Azteca* can dominate in areas where host-plant densities are low (and parent colony–sapling distances are long), and *Allomerus* can dominate in areas where host-plant densities are high. Existing spatial heterogeneity in host-plant densities therefore can allow regional coexistence, and intersite dispersal can produce local mixing. In conclusion, a dispersal–fecundity trade-off appears to allow the two genera to treat spatial heterogeneity in patch density as a niche axis. This study further suggests that a spatially structured approach is essential in understanding the persistence of some mutualisms in the presence of parasites.

Key words: Allomerus; *ant–plant symbiosis;* Azteca; *competition–colonization trade-off;* Cordia nodosa; *dispersal–fecundity trade-off; habitat destruction and selection hypotheses; lottery model; metapopulation; parasite; source–sink dynamics; storage effect.*

Introduction

Hundreds of tropical plant species engage in symbioses with ants, having evolved structures to house and feed resident ants, which in turn provide benefits such as protection from herbivory (Davidson and McKey 1993). We have focused this study on an understory treelet, the ant-plant *Cordia nodosa* Lam. (Boraginaceae), which occurs abundantly in the tropical forests of Madre de Dios, Peru, and more widely across South America. Work at the Estación Biológica de Cocha Cashu (EBCC) in Manu National Park, Madre de Dios province, Peru (Yu and Pierce 1998) has revealed that the ant *Allomerus* cf. *demerarae* (Myrmicinae) occupies 79.8% of the *C. nodosa* plants, and that four ant species of *Azteca* (Dolichoderinae) inhabit a total of only 10.7% of the plants. Three of the *Azteca* species are currently undescribed, and the fourth has been identified as *Azteca ulei* var. *cordiae* Forel. The remaining plants, which are saplings, fall into one of the following three categories: do not have ant colonies, are partially inhabited by a variety of opportunistic ants with small colonies (not considered further), or are inhabited by the rare ant *Myrmelachista* sp. (<2% of plants, not considered further). Both *Azteca* and *Allomerus* ants vigorously patrol new shoots and attack and eat insect prey (Yu and Pierce 1998).

Two lines of evidence, including a synoptic collection of ant species at one location in Madre de Dios, and an expert inspection of all the ants in our field collections (S. Cover and J. Longino, *personal communication*) support the conclusion that the five focal ant species are specialized and obligate symbionts of *C. nodosa,* in the sense that queens of both genera colonize the same host-plant saplings and are entirely dependent on *C. nodosa* for colony establishment and survival. Thus, the two ant genera do not coexist by using different ant-plant species. Nor does the habitat niche partitioning between riverside and forest interior environments (i.e., habitat selection) that promotes ant species coexistence in the sympatric *Cecropia*–ant system (Yu and Davidson 1997) play a role in the *C. nodosa* system, because viable *C. nodosa* saplings exist only in the forest interior (those few on riverbanks are regularly flooded).

How, then, do *Azteca* and *Allomerus* coexist? In fact, the very survival of the *C. nodosa* system appears to depend on the persistence of the minority taxon *Azteca. Allomerus* is known to be a castration parasite of its

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host plants, preventing all fruit production in 70% of the host plants that it inhabits and drastically reducing fecundity in the remaining 30% (Yu and Pierce 1998). Thus, the answer to the species coexistence problem is also an answer to the question of how a mutualism can persist in the face of parasites of that mutualism (Yu, *in press*).

Authors have long suggested that species can coexist by partitioning space into multiple resources or niches (Skellam 1951, Levin 1974, Abrams 1988, Shorrocks 1990). One of the most commonly modeled forms of such ''spatial niche partitioning'' is the competition–colonization trade-off (Levins and Culver 1971, Horn and MacArthur 1972, Hastings 1980, Tilman 1994), which states that competing species can coexist in a homogeneous habitat via a trade-off in colonization vs. competitive abilities (such as those seen in the empirical systems described by Paine [1979], Marino [1988], Westoby et al. [1996]).

However, positive, empirical tests of competitive coexistence stabilized by competition–colonization trade-offs are rare, in large part because of logistical obstacles (Harrison et al. 1995, Steinberg and Kareiva 1997). In nature, equivalent and suitable habitat patches are difficult to define a priori. Also, species rarely consume the same set of entities, which is a simplifying and underlying assumption of competition–colonization models, and the sample sizes needed to parameterize models can be prohibitively large. Moreover, relative colonization abilities are best measured in the transient interval after arrival and before propagules begin to exclude each other competitively. Thus, most empirical tests of coexistence stabilized by such trade-offs have been limited to cage experiments (Armstrong 1976, Hanski 1990), have been confounded with other forms of niche differentiation (Werner and Platt 1976, Platt and Weis 1977, Zwolfer 1979), or have produced ambiguous results (Shorrocks 1990, Bengtsson 1991, Harrison et al. 1995; but see Gross and Werner 1982, Sevenster and Van Alphen 1993, Tilman 1997, Turnbull et al. 1999).

In contrast, the ant plant life history is ideally suited to testing models of spatial niche partitioning. As in other ant–plant symbioses (Yu and Davidson 1997), the species of the resident ant colony is determined when dispersing queens arrive at saplings (foundresses) and initiate colonies in specialized stem swellings, known as domatia (Yu and Pierce 1998) (Fig. 1). Each domatium usually houses only one foundress. The winning foundress is the first to survive and produce workers, because these attack and kill any other live foundresses on the same sapling. Adult ant colonies prevent subsequent colonization of the same plant (Yu and Pierce 1998), precluding displacement and succession.

Thus, the *C. nodosa* system possesses the following logistical advantages: (1) each plant can be treated as a single patch, and saplings are unambiguously identified as empty patches; (2) the five ant species specialize entirely on *Cordia nodosa*, which fulfills a simplifying assumption of many spatial models of species coexistence that patches be equivalent in quality; (3) colonization abilities, as estimated by the abundances and mortalities of foundresses, can be measured over multiple spatial scales and at different host-plant densities. This last advantage is particularly important, as it is normally very difficult to follow offspring dispersal and measure resultant establishment success (Wennergren et al. 1995).

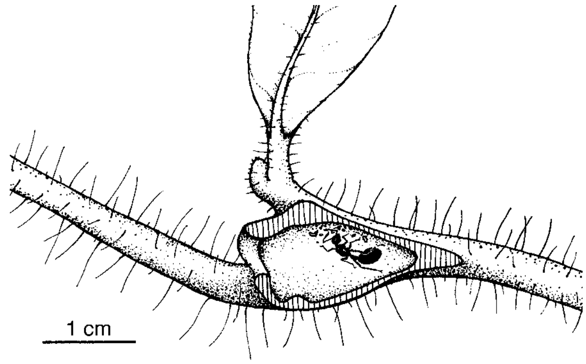

FIG. 1. A colonizing *Allomerus* cf. *demerarae* queen with brood in a domatium. The domatium is formed by the growth of an axillary bud back into the stem (Bailey 1924).

We hypothesize that *Azteca* and *Allomerus* coexist via a spatial niche partitioning mechanism. Both census and experimental data were used to estimate (for both genera) per capita colonization and mortality rates across a variety of habitats. These data were then used to parameterize a new model of species coexistence that combines elements of lottery, metapopulation, and landscape approaches to modeling species coexistence (Hanski 1998, Yu and Wilson, *in press*).

METHODS

Host-plant density and identity of ant inhabitant

Foundresses in saplings were censused at 10 locations, and adult colonies were censused at 12 locations in Madre de Dios province, which is characterized by extensive, mesic to seasonal lowland tropical rain forest (~2100 mm rain/yr) (Fig. 2). We define a location as an area of forest covering from several to tens of square kilometers, over which the density of *C. nodosa* plants varies within some bounds. For example, the Estación Biológica de Cocha Cashu (EBCC) trail system (within location 7) covers ~10 km^2, is located in floristically homogeneous high-ground, lowland forest (Terborgh et al. 1996), and supports densities of *C. nodosa* ranging 44–110 plants/ha. Obviously, different locations blend into one another, but only at location 1 did host-plant densities jump so dramatically during a line transect (from ~10 to ~100 plants/ha after crossing a stream) that a transect was ended. Because host-plant density is used here throughout as the independent variable, there is no circularity.

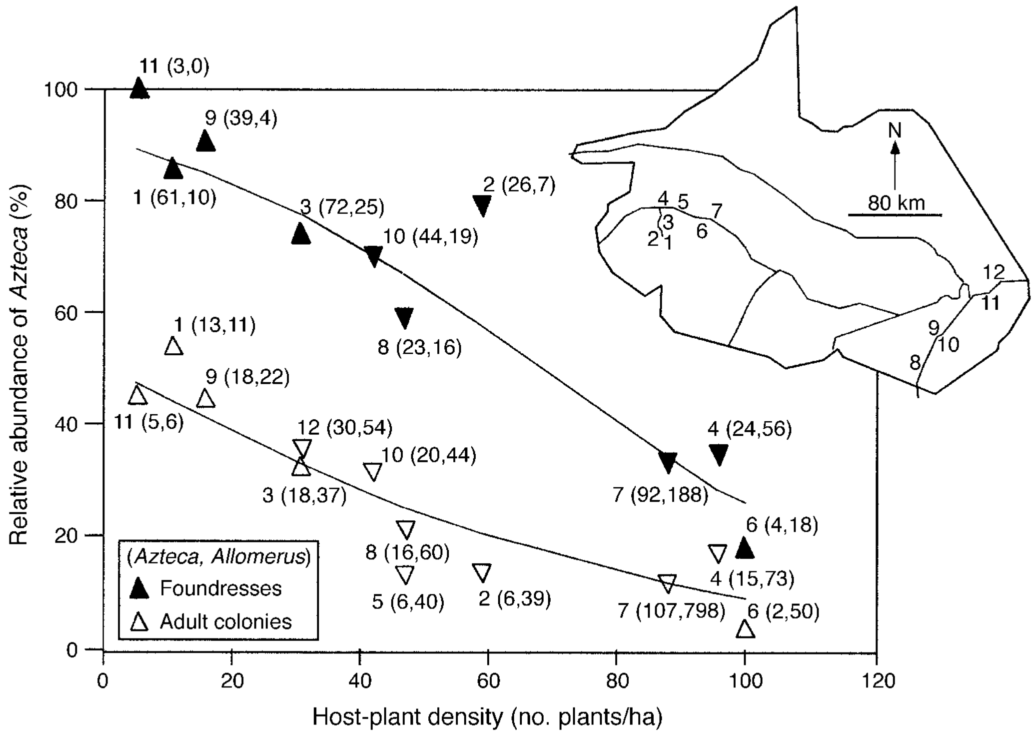

FIG. 2. The effect of host-plant density on the relative abundances of *Azteca* colonies and of *Azteca* foundresses. Relative abundances of colonies (adults) are calculated as the number of host plants occupied by *Azteca* colonies, divided by the total number of host plants occupied by colonies of both genera. Relative abundances of *Azteca* foundresses are calculated as the number of *Azteca* foundresses divided by the total number of foundresses. Colonies are defined to be those with patrolling worker ants (which preclude subsequent colonization), whereas saplings are those with foundresses only, and have no patrolling workers. The lines represent fitted logistic regressions (foundresses, variance explained = 92.8%, $\chi^2 = 158.5$, df = 1, $P < 0.001$; colonies, variance explained = 85.1%, $\chi^2 = 85.94$, df = 1, $P < 0.001$). The slope of the foundress regression line (-0.03308 ± 0.003596 SE) is significantly steeper than that of the colony regression line (-0.02316 ± 0.003041 SE) ($t = 7.016$, df = 20, two-tailed, $P < 0.001$, after rescaling for moderate overdispersion), indicating that the dispersal advantage of *Azteca* foundresses rises as mean patch density falls. Sample sizes of *Azteca* and *Allomerus* foundresses (both live and dead), and of *Azteca* and *Allomerus* colonies, are given in parentheses. Upland vs. lowland forest type (Terborgh et al. 1996) is indicated by an upward or downward pointing triangle. Note that although host-plant densities are generally lower in upland forests, in upland forest location 6, host-plant density was high (as is also true in several other upland locations; D. Yu, *personal observation*), and the relative abundances of *Azteca* foundresses and colonies were low; in lowland forest locations 10 and 12, host-plant density was moderately low, and *Azteca* foundresses and colonies were moderately abundant, as expected. Inset: Map of the census locations in Madre de Dios, Peru, labeled by number: (1) Yomybato uplands, (2) Yomybato lowlands, (3) Tayakome uplands, (4) Tayakome lowlands, (5) Zacarias' Trail lowlands, (6) Estación Biológica de Cocha Cashu (EBCC) uplands, (7) EBCC lowlands, (8) Collpa Tambopata lowlands, (9) Tambopata Jungle Lodge uplands, (10) Tambopata Jungle Lodge lowlands (11) Lago Sandoval uplands, (12) Cuzco-Amazonico Lodge lowlands.

Foundresses were collected from planted saplings at locations 9 and 10 in August 1993 and again in November 1993, from the planted and naturally volunteering saplings used in the colonization experiment (see *Methods: Colonization experiment*) at location 7 in September 1995 and again in November 1998 (natural saplings only), as well as from natural saplings at locations 1, 2, 3, and 6 in July/August 1996, and at locations 4, 8, and 11 in September/October 1999. Foundresses were scored for species and mortality. The sampling periods spanned both dry (May to mid-October) and wet seasons. In four locations (3, 7, 9, and 10), collections were made in both seasons (Table 1). Relative abundances of *Azteca* foundresses dropped in the rainy season in three of the four locations, but the

TABLE 1. Dry (May–October) vs. rainy season foundress collections in Madre de Dios Province, Peru.

Location	Collection date	*Allomerus*	*Azteca*	*P*†
3	August 1996	13	51	0.092‡
3	November 1998	12	21	
7	September 1995	151	72	0.690‡
7	November 1998	37	20	
9	August 1993	2	26	0.602
9	November 1993	2	13	(0.002)§
10	August 1993	10	34	0.076‡
10	November 1993	9	11	

† *P* values pertain to data on a site-by-site basis.
‡ Log-likelihood contingency table *G* test.
§ Mean (1 SE), Monte Carlo contingency table test (Engels 1988).

drops were not statistically significant. Foundress data were therefore pooled within location.

Host plants with adult colonies (which persist for years) were scored for ant inhabitant at locations 10 and 12 in 1992, location 7 in 1994, locations 1, 2, 3, 5, 6, and 9 in 1996, location 9 again in 1998, and locations 4, 8, and 11 in 1999.

Host-plant densities were estimated using a combination of line transects and quadrats. We used preexisting quadrats (tree plots) only when there was more than one and they were widely separated, so as to average over micro-variation (10–100 m scale) in host-plant density. Thus, for example, in location 1, we estimated host-plant densities using both three 0.25-ha quadrats and line transects (to supplement the sample size). In location 12, we used two 1.0-ha quadrats; and in location 7, we used the five 1.0-ha quadrats from the colonization experiment. Densities in the other locations were estimated with line transects. Only plants hosting either *Allomerus* or *Azteca* colonies were used to calculate relative abundances, but all *C. nodosa*, regardless of inhabitant, were used in the density estimate.

Colonization experiment

On 23–25 June 1995, 25 *C. nodosa* saplings grown from seed were planted in randomly selected spots within the central 2500 m^2 of each of five 1.0-ha quadrats located within the >1000-ha trail system at EBCC (location 7; Fig. 2). Naturally established *C. nodosa* plants were mapped. All colonizing queens were collected on 6–13 September from both the planted saplings ($N_{tot} = 125$) and from the naturally volunteering saplings within the central 2500 m^2 of each plot ($N_{tot} = 84$). Foundresses were scored for species and mortality. Relative abundances of adult colonies were estimated from the 905 *C. nodosa* plants used in a phenology census during 1994–1995 and hosting either *Allomerus* or *Azteca* colonies (see Yu and Pierce [1998] for details). The plots are located within the trail system along which the phenology census was conducted.

RESULTS

Host-plant density and identity of ant inhabitant

The relative abundance of *Azteca* colonies decreases as host-plant density increases (Fig. 2). As the question at hand concerns the coexistence of the two genera, we have pooled the four *Azteca* species, and we are looking at the alternative problem of species coexistence within the *Azteca* genus separately. Note that coexistence models are largely agnostic as to the nature of the competing entities; they may be species (most commonly), plant life histories (e.g., perennials vs. annuals; Crawley and May 1987), or even genotypes (Geritz 1995, Haig 1996).

Also shown in Fig. 2 are the relative abundances of *Azteca* foundresses in saplings, which also decrease as plant density increases. It should be noted that these two sets of data were collected independently and that one does not necessarily imply the other. The key result is that the foundress line has a significantly steeper slope than does the adult colony line ($P < 0.001$; Fig. 2), indicating that even after the higher *Azteca* colony density has been taken into account, there still remains an unexplained increase in the arrival rate of *Azteca* foundresses at saplings with decreasing plant density. This unexplained increase is the key to coexistence of the two genera. We should emphasize that this is a result based on the data analysis and not due to any later model fitting.

We confirmed the robustness of the difference in slopes by sequentially and individually removing entire locations. The foundress slope remained significantly steeper than the colony slope (at the $P < 0.005$ level) no matter which location was removed. A jackknifed version (Sokal and Rohlf 1995) of the analysis also upheld the same result at the $P < 0.001$ level (results not shown). In summary, the significant difference in slopes does not depend on any individual location (and in fact is robust to removal of multiple combinations of locations at once).

In contrast to arrival rates, post-arrival foundress mortalities did not vary with host-plant density and were higher for *Azteca* than for *Allomerus* (Fig. 3). Mortalities are due to the intrinsic stress of colony production and also to the predation of *Azteca* foundresses (but not queens with colonies) by the parasitoid wasp, *Compsobraconoides* sp. (Braconidae) (Yu and Quicke 1997) and (to a lesser extent) to the attack of *Allomerus* foundresses by an entomophagous fungus (*Hirsutella* cf. *formicarum*, Fungi Imperfecti). Across locations, 12–39% of dead *Azteca* foundresses were collected with evidence of wasp parasitism, which accounts for nearly all the difference in mortality between the two genera. The probability of survival of *Azteca* and *Allomerus* foundresses over the course of colony founding is calculated to be only 14% and 28%, respectively (see Appendix A).

Parameterization of a species coexistence model

The results of the location censuses (Fig. 2) suggest that *Azteca* and *Allomerus* coexist by using host-plant density as a resource niche axis. We investigate this possibility by parameterizing a model of species coexistence. Consider the following simple model:

$$\frac{dp_{1,j}}{dt} = c_1(h_j)[(1 - r_1)p_{1,j} + r_1\bar{p}_1](h_j - p_{1,j} - p_{2,j}) - m_1 p_{1,j} \quad (1a)$$

$$\frac{dp_{2,j}}{dt} = c_2(h_j)[(1 - r_2)p_{2,j} + r_2\bar{p}_2](h_j - p_{1,j} - p_{2,j}) - m_2 p_{2,j} \quad (1b)$$

where $p_{i,j}$ is the fraction of host plants occupied by

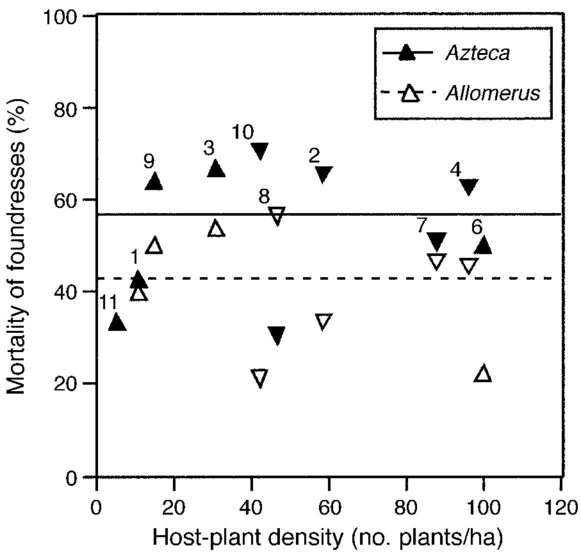

FIG. 3. Nonsignificant (NS) effect of host-plant density on the percentage mortalities of *Azteca* and *Allomerus* queens (solid line is *Azteca*; dashed line is *Allomerus*; logistic ANCOVA, variance explained by host-plant density <0.05%, $\chi^2 = 0.017$, df = 1, NS). However, a significantly higher fraction of *Azteca* queens were found dead than *Allomerus* queens (*Azteca*, 56.8%; *Allomerus*, 43.1%; variance explained by genus, 26.8%, $\chi^2 = 11.7$, df = 1, $P = 0.017$). Sample sizes of foundresses are as in Fig. 2.

adults of species i (where $i = 1$ or 2) in a site j, h_j is the fraction of the total habitat in site j that is colonizable (and is therefore an index of host-plant density), $c_i(h)$ is the per capita colonization rate and depends on host-plant density (as indicated by the data), m_i is the per capita adult colony mortality, r_i is the fraction of foundresses that disperse to other sites rather than attempt to colonize saplings within the same site, and $\bar{p_i}$ is the mean p_i over all sites j. For all analyses, *Azteca* is species 1, and *Allomerus* is species 2.

A site is defined as an area small enough such that host-plant density (h) is uniform and total mixing occurs within it. Plot maps at the hectare scale from the colonization experiment (data not shown) indicate that there is very little intraspecific clumping in the system, and results from the colonization experiment (see *Results: Evidence for a dispersal–fecundity trade-off*) suggest that foundresses can fly >100 m. Thus, we consider a site to be on the order of one to several hectares, and a metapopulation model with within-site mixing is justified. A location consists of several sites with densities varying within some range. For example, host-plant densities in location 7, where the colonization experiment was conducted, had a mean value of 88 plants/ha and ranged 44–110 plants/ha.

This model differs from the traditional Levins and Culver (1971) formulation in that adults of both species are impervious to displacement, whereas the Levins and Culver model allows propagules of one species to displace adult colonies of the inferior species. In our model, the population of each species retains, in the form of adults, the effects of successful recruitment events (the storage effect; Chesson and Warner 1981) and thus applies to a large class of sessile organisms where adults cannot be displaced by juveniles (such as trees or the ant–plant system here). Instead, juveniles compete to replace adults that die at a density-independent rate and is therefore a model of replacement competition. Within a site, this model is analogous to lottery models (Chesson and Warner 1981, Shmida and Ellner 1984, Comins and Noble 1985, Hubbell and Foster 1986, Pacala and Tilman 1994, Yu et al. 1998), but it also introduces metapopulation structure, as there is migration between sites (producing source–sink dynamics [Pulliam 1996]). A fuller treatment of replacement competition models is found elsewhere (Yu and Wilson, *in press*).

When there is no migration between sites ($r_i = 0$), the parameterized replacement competition model (Eq. 1) predicts that coexistence within a site is not possible. The species with the highest value of $c_i(h)/m_i$ competitively excludes the other species (i.e., species 1 wins if $c_1(h)/c_2(h) > m_1/m_2$, otherwise species 2 wins). Annual adult colony mortality rates m_i were calculated from a November 1998 recensus of the plots used in the colonization plots and from a one-year phenology census (Yu and Pierce 1998) (12.0% vs. 8.0% for *Azteca* and *Allomerus*, respectively). We thus need to estimate the ratio $c_1(h)/c_2(h)$ in order to understand which species wins in which environment.

The colonization of saplings can be divided into three stages: arrival rate at a new patch (which combines adult colony fecundity and mortality during dispersal), survival after arrival, and growth to reproductive maturity. Hence $c_1(h)/c_2(h)$ = (relative arrival rate) × (relative survival after arrival) × (relative growth rate to fecund adults). By definition, the relative arrival rate is the relative number of foundresses divided by the relative number of adults (Fig. 2). *Azteca* has approximately two-times higher foundress mortality across all host-plant densities (Fig. 3, Appendix A). Finally, *Allomerus* has a two-fold growth advantage, due to its castration behavior (see Yu and Pierce 1998). In the forest understory, the net growth rate of *Azteca*-occupied plants has been measured to be only half as fast as *Allomerus*-occupied plants (Yu and Pierce 1998). This is because *Allomerus* is a castration parasite of *C. nodosa*, preventing most fruiting by destroying flowers, and thereby decreasing the rate of branch senescence (Yu and Pierce 1998). The higher growth rate in *Allomerus*-occupied plants gives it an advantage over *Azteca* by allowing the former to reach reproductive size (≥25 domatia; Yu and Pierce 1998) more quickly. The castration behavior of *Allomerus* also reveals why *Allomerus*-occupied plants have a lower overall mortality rate, as prevention of fruiting delays senescence. Thus, at any given h,

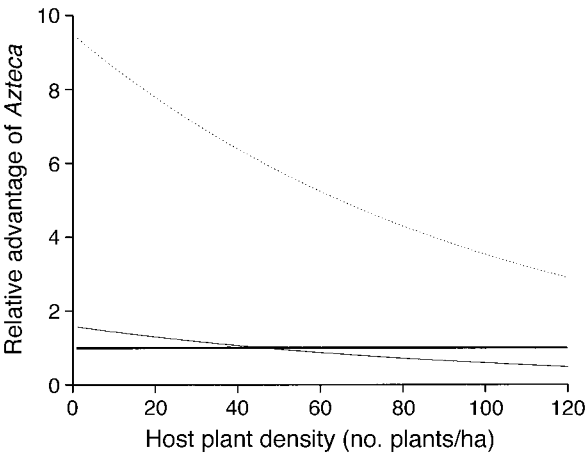

FIG. 4. The relative advantage of *Azteca* over *Allomerus* $[c_1(h)/m_1)/(c_2(h)/m_2]$ vs. host-plant density (Eq. 2). The dotted line is *Azteca*'s relative dispersal advantage uncorrected for post-arrival foundress mortality, growth, or adult mortality (see *Results: Host-plant density and identity of ant inhabitant*). The thick horizontal line indicates equal colonization rates.

$$\frac{c_1}{c_2} = \left(\frac{\dfrac{q_1}{q_2}}{\dfrac{p_1}{p_2}}\right) \times \left(\frac{0.14}{0.28}\right) \times (0.49) \qquad (2)$$

The ln(odds ratios) of the number of foundresses, $\ln(q_1/q_2)$, and adults, $\ln(p_1/p_2)$, are the response variables of the logistic regressions from Fig. 2. Thus, the relative arrival rates over all censused h's can be found by exponentiating the equations for the regression lines and dividing the former by the latter. As expected from the different slopes, *Azteca*'s relative arrival rate increases at lower host-plant densities (h) (Fig. 4).

The relative arrival rate can also be directly estimated by fitting a line directly to the ratio of foundresses to colonies. If the same assumptions about binomial error distributions are made, then almost precisely the same quantitative result is achieved. However, the confidence intervals are much larger using this technique. This is because the direct use of ratios as the response variable is very sensitive to noise in the denominator of the ratio (reviewed by Jasienski and Bazzaz [1999]). We thus adopt the more statistically rigorous methodology of first calculating $\ln(q_1/q_2)$ and $\ln(p_1/p_2)$ separately and then calculating the ratio.

The parameterized model predicts *Azteca* to exclude *Allomerus* when host-plant density <46 plants/ha, and *Allomerus* to exclude *Azteca* when host-plant density >46 plants/ha. Thus, in an environment characterized by spatial variation in host-plant density and zero intersite migration, host-plant density is used as a niche axis, and regional (but not local) coexistence is possible.

However, when intersite migration occurs ($r_{Allomerus} > 0$, and $r_{Azteca} > 0$), declining populations of *Allomerus* in low-density sites (i.e., sinks) may be rescued by immigration from high-density sites (i.e., sources), and vice versa for *Azteca*, thereby maintaining mixed local populations. Although our data do not allow us to calculate absolute colonization rates at each plant density (but we can calculate the absolute values at the location where the colonization experiment was performed; see Appendix B), we are able to calculate the relative rates (Fig. 4) and, consequently, the relative abundance of each species.

Thus, despite its simplicity, the empirically parameterized model with intersite migration can produce a qualitative fit to a complex, large-scale, and natural system (Fig. 5). We do not claim that the fit of the model to data is quantitatively accurate. There are a number of important biological details that have been omitted from the model that influence relative abundances (for example the presence of forest gaps), and we return to these in the *Discussion.* However, colonization rates, foundress mortality, adult mortality, and migration rates (r_i) have all been varied extensively in numerical integrations, which show that this phenom-

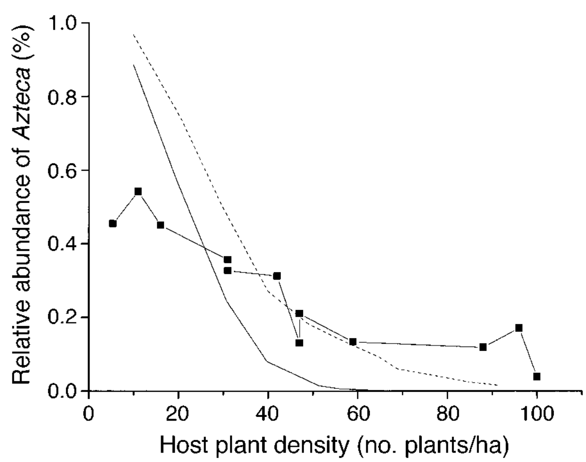

FIG. 5. The relationship between host-plant density and the relative abundance of *Azteca*-inhabited plants. The line with squares is the observed colony data from Fig. 2; the solid line is the model output after 1000 yr (although longer simulations show no differences), and the dashed line is model output including the effect of gaps. The figure was constructed by running a separate numerical integration at each mean plant density, where at each density there are 1000 sites (so that $j = 1, \ldots, 1000$ in Eq. 1). Each plant density therefore represents a separate location (on the order of tens of square kilometers) with 1000 sites (each site being a few hectares in extent). At each location the density varies across sites as an exponential distribution with the appropriate mean plant density, as observations indicate considerable variance of plant density across sites at one location. Other parameters are $r_1 = r_2 = 0.1$. The simulations were started with equal amounts of both genera and $p_{i,j} = 0.02h_j$. The model with gaps assumes that 18% of the plants are either in or bordering a canopy gap (using the definition of gaps in Brokaw [1996]). Mortality of *Allomerus* in gaps is 0.203 conlonies/yr and 0.053 colonies/yr in the understory (calculated from data in Yu and Pierce [1998]), and growth rates in the gaps are equal (see Yu and Pierce 1998). All other parameters are the same.

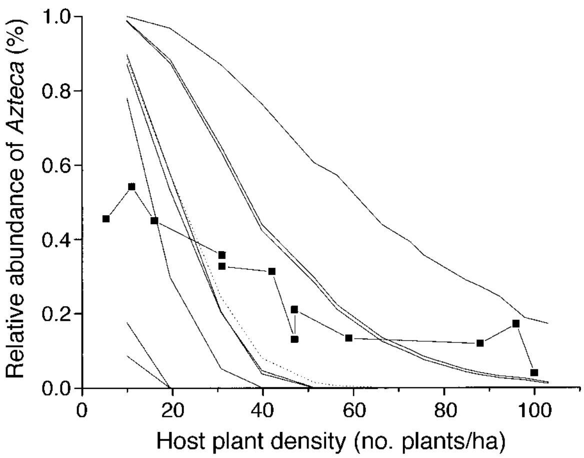

FIG. 6. Sensitivity of the model to variation in each of the parameters. The line with squares is the observed colony data from Fig. 2, and the dashed line is the model output from Fig. 5. Other lines are created by individually increasing each parameter in turn by 30%. Starting from the uppermost line, the lines represent the following: constant in the arrival rate function (i.e., increases in the overall arrival rate advantage of *Azteca*); probability of *Azteca* surviving the colony founding stage; *Allomerus* adult mortality m_2; amount of dispersal between sites r_1, r_2; effect of plant density on the arrival rate function (makes the decrease in *Azteca*'s arrival rate drop more sharply with plant density); probability of *Allomerus* surviving the colony founding stage; and *Azteca* adult mortality m_1. Obviously, increasing *Azteca*'s advantage (by increasing *Allomerus* adult mortality or foundress mortality or increasing *Azteca*'s dispersal advantage) increases the relative abundance of *Azteca* and vice versa. The two lines closest to the original line indicate changes to the level of dispersal between sites, r_i.

enological model is a robust predictor of both coexistence and the inverse relationship between host-plant density and *Azteca* relative abundances (Fig. 6). In particular, the model fit is robust to variations in r_i, which is the one parameter not estimated from data (varied within 0.01–0.5).

Only intersite migration ($r_i > 0$) and differential foundress arrival rates with host-plant density are needed to produce local coexistence in the replacement competition model. No further assumptions about factors varying with plant density are necessarily needed, or are known (although some may exist). Given that the foundress arrival rates appear to be so important, what is the mechanism causing arrival rates to differ with host-plant density and across ant genera?

Evidence for a dispersal–fecundity trade-off

Available evidence, on three counts, suggests that *Azteca* and *Allomerus* exhibit a dispersal–fecundity trade-off, such that *Azteca* foundresses are able to disperse over longer distances than can *Allomerus* foundresses, but that *Allomerus* colonies have a higher per capita fecundity: (1) Collections of alates from multiple adult colonies at locations 9 and 7 reveal that *Azteca* colonies contain significantly fewer alates than do *Allomerus* colonies (Mann–Whitney $U = 624\,212$, df = 1, $P < 0.001$). (2) *Azteca* foundresses are larger than *Allomerus* foundresses, which should allow *Azteca* foundresses to fly longer distances, as is seen in other insect species (e.g., Shirai 1993, Vasconcelos 1993; see also *Discussion*). (3) Spatially explicit data from the colonization experiment suggest that *Allomerus* foundresses are drawn from a smaller neighborhood of adult plants than are *Azteca* foundresses, indicating that *Azteca* foundresses are able to find saplings at longer distances from the adult plant (D. Yu and H. Wilson, *unpublished data*). While these data are suggestive, the small-scale nature of our experiments (1 ha) did not allow this result to be resolved at a statistically significant level, and we are currently pursuing this avenue with a larger scale experiment.

Hence, our results suggest that in areas of high host-plant density, *Allomerus*' per capita colonization rate is higher, due to its higher fecundity; but, as host-plant density decreases and the distances between adult plants and saplings increase, *Azteca*'s dispersal advantage grows, leading to increases in the relative abundance of *Azteca* foundresses attempting to found new colonies. Accordingly, at the locations with the lowest recorded host-plant densities, 90–100% of the foundresses collected were *Azteca* (Fig. 2).

DISCUSSION

The simple model presented here explains both coexistence and the general patterns in the data. However, in sites characterized by high host-plant density, our simulations indicate a lower abundance of *Azteca* than that observed, despite immigration from *Azteca* source habitats (i.e., sites of low host-plant densities), and in the lowest-density habitat *Azteca* is more common than indicated in the data. An exact quantitative fit to data will need a more complex model that incorporates known aspects of the biology of this system not included in the simple model presented here.

For example, *Azteca*-inhabited host plants are relatively more abundant in, and bordering, forest canopy gaps than are *Allomerus*-inhabited host plants (Yu and Pierce 1998). This is due to gap-centered predation of the largest individuals of the latter by the cerambycid beetle *Trachysomus* sp. (details in Yu and Pierce [1998]), causing mortality of *Allomerus* in and near gaps to be more than three times as high as in the forest understory, but leaving *Azteca* mortality unaffected (Yu and Pierce 1998). In addition, growth rates of *Cordia* occupied by either ant species are similar in gaps. This provides a temporary advantage for *Azteca,* even in areas of high host-plant density, and this effect can be represented in the model by including the higher mortality and similar growth rates for *Allomerus*-inhabited plants in gaps. Plants are randomly allocated to gaps, but remain in a gap only for a certain length of time (two years is used here), after which it is considered a normal plant again. The total abundance of *Cordia* in and bordering gaps is kept constant (at 18%, empirically measured at location 7 and consistent with the estimate of 12.2% of the forest in gaps reported by Hubbell et al. [1999] for a similar forest in Panama). Fig. 5 shows that the effect of gaps is to increase the abundance of *Azteca* over the whole range of plant densities and that this effect is most marked at high host-plant densities. Note that domination of gaps by *Azteca* is not sufficient to explain the observed pattern of decreasing *Azteca* abundance with increasing host-plant density. A thorough investigation of the effect of gaps and of the growth advantage of *Allomerus* due to its castration behavior needs a formal, size-structured modeling assessment, which is currently underway. However, it is clear that the general abundance of *Azteca* is increased when gaps are included, particularly at high densities.

Various alternative coexistence mechanisms are possible in this system; indeed, we feel it is unlikely that only one mechanism is acting. However, current evidence suggests that the alternatives either have a relatively small effect compared to the dispersal–fecundity trade-off, or do not account for the major patterns in the data.

Competition amongst foundresses.—High foundress mortalities appear to preclude the action of a competition–colonization trade-off among foundresses as a mechanism of coexistence. Only 22% of colonized saplings in the colonization experiment contained foundresses of both genera (live or dead). Therefore, in only (22% × 14% × 28% =) 0.8% of all saplings had there been even the possibility of direct competition between incipient colonies. Note that these mortality rates reflect individual sources of mortality (e.g., stress, parasitoids, and fungi), because the rates are estimated from sapling collections, before colony expansion of a winning foundress. However, it remains possible that direct foundress–foundress competition might occur, but be undetected, if winning foundresses discard the corpses of losers. This possibility is being investigated experimentally.

Competition amongst adult colonies.—There is no evidence for succession from one ant genus to another within the same host plant (suggested as a coexistence mechanism in other ant plants; Fonseca 1993, Young et al. 1997). Host-plant size structure is not significantly different between genera (location 7, Mann–Whitney $U = 12\,022.0$, df = 1, $P = 0.32$), in part because *Trachysomus* attacks the largest *Allomerus*-inhabited plants (Yu and Pierce 1998). In addition, experimental attachment by means of string and palm rachises of *Azteca*-inhabited to nearby *Allomerus*-inhabited plants failed to produce invasions in all 25 cases (Yu and Pierce 1998). Finally, we know of 12 *C. nodosa* plants with bifurcated trunks that host *Allomerus* in one trunk and *Azteca* in the other, apparently the result of simultaneous colonization in the two trunks (Yu and Pierce 1998). These "double-colony" plants have been observed to persist for years.

Temporal niche partitioning.—Obvious temporal niche partitioning (sensu Chesson and Warner 1981) does not seem to be acting, as the relative abundances of *Azteca* and *Allomerus* foundresses do not reverse over rainy and dry seasons (Table 1). Also, simultaneous collection of foundresses in neighboring locations with different host-plant densities, (i.e., locations 9 and 10 in Fig. 2, where the saplings were originally planted on the same day) reveal that foundress abundances in the two locations are clearly different and are explained by host-plant densities, whereas temporal niche partitioning would predict similar relative abundances. However, we can discern a marginally significant drop in *Azteca* relative abundances in three of the four locations, consistent with its hypothesized lower fecundity. Thus, temporal variation in colonization frequencies is also a possible mechanism aiding coexistence, particularly amongst the four *Azteca* species, and this possibility is being investigated further.

Disturbance niche partitioning.—We have suggested that forest gaps increase *Azteca*'s advantage by increasing adult mortality rates in *Allomerus*. As a result, *Azteca* might dominate forests with high gap formation rates and *Allomerus* might dominate in lower turnover forests. However, this explanation does not seem to apply. For example, location 6 is dominated by bamboo (*Guadua* sp.), which establishes in areas characterized by high rates of gap formation, but has a low relative abundance of *Azteca* colonies, in accordance with the high density of host plants. Also, locations 10 and 12 are lowland forests with typically low turnover rates (relative to location 6), and *Azteca*'s relative abundance is moderately high, in accordance with the measured host-plant densities. So, although we believe that gaps increase *Azteca*'s advantage across the board, which promotes mixing in the sites with high host-plant density and increases the robustness of coexistence, existing spatial heterogeneity in gap formation rates does not appear to be creating the pattern found in Fig. 2.

In summary, mechanisms other than the dispersal–fecundity trade-off (particularly gaps) could be acting to promote coexistence, but evidence to date suggests that they are less important (although they could be very important for promoting coexistence of the four *Azteca* species).

Precise parameterization of our model depends on the fact that we estimate the effects of host-plant density at each site by using measurements taken at the larger scale of locations (Fig. 2). This is because intersite migration (r_i) is expected to obscure measurements made at individual sites. By censusing over several to tens of square kilometers in each location, we effectively average over thousands of host plants and foundresses. This is probably why just one explanatory variable, host-plant density, can explain >90% of the variance in *Azteca* relative abundances (Fig. 2). In this way, relatively cheap measurements taken at large spatial scales stand in for the huge sample sizes normally needed to parameterize spatial models with confidence (Steinberg and Kareiva 1997), and we hope that this approach proves useful for others.

Finally, as mentioned above, *Allomerus* is known to be a castration parasite of *C. nodosa* (Yu and Pierce 1998). The dispersal–fecundity trade-off identified here suggests that the castration behavior might have evolved to increase *Allomerus*' advantage due to competition with *Azteca* (although a mutation for castration behavior should always be at an advantage in a non-castrating population). More generally, the apparent absence of mechanisms normally invoked to limit the spread of parasites (Axelrod and Hamilton 1981, Bull and Rice 1991, Yu and Pierce 1998) suggests that a spatially structured approach (e.g., spatial games; Nowak and May 1992) could explain how the *C. nodosa*–*Allomerus* interaction persists. The results shown here support that view, and we propose that spatial mechanisms of competitive coexistence may stabilize mutualistic interactions, despite the presence of parasites, in many other systems (West and Herre 1994, Pellmyr et al. 1996, Young et al. 1997, Bao and Addicott 1998, Yu, *in press*).

In particular, the dispersal–fecundity trade-off model might also explain coexistence of two ant genera specialized on the ant plant *Leonardoxa africana* (Caesalpinaceae) in Cameroon (McKey 1984). The ant *Petalomyrmex phylax* (Formicinae) is a mutualist, because it invests heavily in patrolling workers; but the ant *Cataulacus mckeyi* (Myrmicinae) is a parasite that invests little in worker ants. *Leonardoxa* plants inhabited by colonies of *Petalomyrmex* have many times more workers attacking insect herbivores on new leaves than do host plants inhabited by *Cataulacus.* As a result, host plants inhabited by *Cataulacus* suffer more herbivory (McKey 1984, Gaume and McKey 1999). Saplings of the host plant *Leonardoxa* are found in small, dense stands on slopes, often around groves of adults or adjacent to inundated areas, and are also found as widely scattered individuals in forested level terrain (McKey 1984). Queens of *Cataulacus* are better colonizers of isolated and unoccupied shoots of *Leonardoxa,* but *Petalomyrmex* colonies are secondarily polygynous, suggesting higher fecundity. In one population surveyed by McKey (1984), where numbers of adult *Leonardoxa* are ''substantial,'' *Cataulacus* is rare (2%) and *Petalomyrmex* is common (98%). Where trees are less common, 10–60% of *Leonardoxa* are inhabited by *Cataulacus.*

Tantalizingly similar results to ours were found by Vasconcelos (1993) in the ant-plant *Maieta guianensis* (Melastomataceae), which is inhabited by two specialized ant species, *Pheidole minutula* and *Crematogaster* sp. (both Myrmicinae). A colonization experiment showed that relatively more *Pheidole* foundresses arrived at saplings placed near (<30 m) adult colonies, but that abundances were equal in saplings placed far (>70 m) from adults. In addition, colonizations of the same sapling by both genera were normally separated by several months, precluding direct competition between genera. There is also inferential evidence of a dispersal–fecundity trade-off. Body masses of *Crematogaster* foundresses are 10-fold greater those of *Pheidole,* suggesting that *Crematogaster* foundresses ''have a higher ability to colonize more distant seedlings.'' On the other hand, multiqueen colony founding (pleometrosis) is found only in *Pheidole*, suggesting higher adult fecundities.

In summary, we have taken a model-fitting approach (Hilborn and Mangel 1997) to a natural and large-scale system and have found that explaining coexistence in this lottery system does not require the assumption of heterogeneity in patch quality (Comins and Noble 1985), but only the assumption of heterogeneity in the spatial *arrangement* of patches (host-plant density). A trade-off between dispersal ability and adult fecundity appears to allow *Azteca* and *Allomerus* to treat spatial variation in patch density as a niche axis. These results show how local processes can be governed in part by larger scale regional processes (Ricklefs 1987, Hanski 1998), and the densely packed habitat mosaic characterizing Western Amazonia now takes on added significance (Tuomisto et al. 1995). Elsewhere (Yu and Wilson, *in press*), we explore the implications for the Habitat Destruction Hypothesis of Tilman et al. (1994).

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APPENDIX A

Calculating the Probability of Surviving the Colony Founding Stage

Let n_t be the number of foundresses alive at time t. Assuming a constant rate of foundress mortality, μ, over the colony founding stage then $dn_t/dt = -\mu n_t$ and $n_t = n_0\exp(-\mu t)$. The number dead at time t is $(n_0 - n_t)$. Sampling can take place equally at any time t over the whole range 0–T, where T is the time taken to become an adult colony from initial colonization of an empty domatium. So that the total number found alive over this period is proportional to $\int_0^T n_t\, d_t$, and the total number found dead is proportional to $\int_0^T (n_0 - n_t)\, dt$. The relative fraction found alive is therefore,

$$\int_0^T n_t\, dt \bigg/ \left(\int_0^T (n_0 - n_t)\, dt + \int_0^T n_t\, dt\right) = \frac{1 - e^{-\mu T}}{\mu T}.$$

This equals 0.569 for *Allomerus* and 0.432 for *Azteca* and so can be solved numerically for each genus for the quantity μT (the equation is transcendental and so cannot be solved analytically). The probability of surviving the colony founding stage can then be calculated as $n_T/n_0 = e^{-\mu T}$.

APPENDIX B

Calculating Absolute Arrival Rates in the Colonization Experiment

Absolute values of c_1 and c_2 can be estimated at a particular value of h, using data from the colonization experiment conducted at location 8 (host-plant density = 88 plants/ha; Fig. 2). The relative abundances of adult plants occupied by each ant genus are $p_1 = 0.107$ and $p_2 = 0.798$ (see *Introduction*). The ratios of *Azteca* to *Allomerus* foundresses collected were not significantly different across planted and natural saplings ($G = 2.44$, df = 1, $P = 0.119$) and were thus pooled. There were initially 406 empty domatia, of which 151 were colonized by *Allomerus*, 72 by *Azteca*, and 183 were still empty (after 78 d, the mean time between planting and collection date across all plots). We use the following relationships, where δt is the experimental time period (= 78/365 = 0.214 yr):

$$\frac{c_1 p_1}{c_2 p_2 + c_1 p_1} = \text{relative number of } \textit{Azteca} \text{ foundresses} = \frac{72}{151 + 72} \quad \text{(B.1a)}$$

$$\exp(-c_1 p_1 \delta t - c_2 p_2 \delta t) = \text{fraction of domatia empty} = \frac{183}{406} \quad \text{(B.1b)}$$

(where c_1 and c_2 refer only to the foundress arrival rates and are not corrected for differential mortality after arrival (see *Results: Parameterization of a species coexistence model*). The relative number of *Azteca* foundresses in saplings is a function of the relative colonization rates and relative abundances of parent colonies (Eq. 3a). Under the assumption of random dispersal, the fraction of domatia that are empty is given by the zero term of the Poisson distribution (Eq. 3b). This gives two equations in two unknowns (c_1 and c_2) and so can be solved: $c_1(88) = 11.236$; $c_2(88) = 3.160$.