

# Experimental demonstration of species coexistence enabled by dispersal limitation

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## Summary

1. Dispersal limitation is widely invoked to explain species coexistence and cooperation in the face of competition and cheating. However, empirical evidence from natural ecosystems for the stabilizing effect of space is sparse.
2. We use a Neotropical ant–plant and its ant symbionts to show how mutual dispersal limitation brings about the stable persistence of coexistence and mutualism.
3. We demonstrate that two ant genera exhibit hierarchies in competitive ability, fecundity and dispersal ability, which suggests that a competition–colonization trade-off could be producing coexistence. However, we also show that this trade-off is not a sufficient explanation for coexistence.
4. Instead, we provide evidence that a dispersal–fecundity trade-off stabilizes the system by making each genus more dispersal-limited in a different portion of the environment. In this way, dispersal limitation can be seen as a form of environmental niche partitioning.
5. We also find that regeneration niche partitioning and a competition–colonization trade-off may help to bring about local mixing.
6. This study shows that care needs to be taken in identifying the critical mechanisms producing coexistence. Trade-offs between different stages of colonization may be more important for explaining coexistence than any trade-offs between competitive ability and colonization rate.

*Key-words:* habitat destruction hypothesis, metacommunity, mutualism, myrmecophyte, recruitment limitation, spatial ecology.

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## Introduction

A major innovation in population biology over the previous decade has been the incorporation of space into models of competition, predation and cooperation (Tilman & Kareiva 1997; Dieckmann, Law & Metz 2000). The most influential model has been the competition–colonization trade-off (Levins & Culver 1971; Tilman 1994; Rees *et al.* 2001). However, the model's ability to explain coexistence in real systems

remains empirically unestablished (Harrison, Thomas & Lewinsohn 1995; Wennergren, Ruckelshaus & Kareiva 1995; Adler & Mosquera 2000; Yu & Wilson 2001; Levine & Rees 2002), due to the logistical challenges of defining spatial structure, measuring dispersal, and assembling the requisite large sample sizes.

In addition, one must also consider alternative explanations, such as resource niche partitioning (Comins & Noble 1985; Tilman & Pacala 1993; Pacala & Tilman 1994; Chesson 2000; Rees *et al.* 2001; Yu & Wilson 2001), recruitment limitation (Hurtt & Pacala 1995; Bolker & Pacala 1999), and negative density dependence caused by natural enemies (Connell, Tracey & Webb 1984). Thus, the challenge these days is identifying which mechanisms most contribute to

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coexistence in a given community of species (Yu & Wilson 2001; Chave, Muller-Landau & Levin 2002; Wright 2002), and the answer matters in part because it helps to predict the extinction trajectories we expect upon habitat alteration and loss (Tilman *et al.* 1994; Yu & Wilson 2001; Higgins & Cain 2002).

For example, in tropical forests all the above mechanisms have been implicated (Chave *et al.* 2002; Wright 2002). Seeds of tropical tree species vary in size (Foster & Janson 1985), suggesting that competition–colonization trade-offs are acting (Chave *et al.* 2002). Tree seedlings suffer increased mortality as conspecific density increases (Connell *et al.* 1984; Hammond & Brown 1998; Webb & Peart 1999; Harms *et al.* 2000). Distributions of tree seedlings are dispersal limited (Hurt & Pacala 1995; Hubbell *et al.* 1999; Dalling *et al.* 2002; Wright 2002), and resource niche partitioning is suggested by topographic patterning of tree distributions (Whitmore 1989; Sollins 1998; Shepard *et al.* 2001; Wright 2002; Tuomisto, Ruokolainen & Markku 2003).

However, ascertaining the relative contributions of these mechanisms is more difficult. Ideally, one would remove individual coexistence mechanisms, such as using seed addition experiments to examine the coexistence role of dispersal limitation (Rees 1995; Turnbull, Rees & Crawley 1999; Rees *et al.* 2001). Often, however, experiment is not feasible, and instead an alternative approach has been to try to use community-level patterns, such as relative species abundances, to discern key coexistence mechanisms (Hubbell 2001). However, Chave *et al.* (2002) have found that very different coexistence mechanisms can bring about similar community-level patterns, which would seem to limit this pattern-to-process approach.

Thus, a growing trend is to combine large-scale observations with model fitting, taking advantage of natural experiments that result in spatial or temporal variation in relative species densities (Freckleton & Watkinson 2001; Condit *et al.* 2002; Dalling *et al.* 2002; Plotkin *et al.* 2002). One can also take advantage

of not-so-natural experiments. Because communities coexisting via different sets of mechanisms will respond differently to habitat loss, one can in principle reverse the order and use observed extinction trajectories in perturbed habitats to identify the key coexistence mechanisms.

For instance, the Habitat Destruction Hypothesis (Tilman *et al.* 1994) posits that in a community coexisting by means of competition–colonization trade-offs, habitat loss will cause superior competitors (the poorest colonizers) to go extinct first. At the other extreme, if dispersal limitation is the main contributor to coexistence, communities are not at equilibrium, and habitat loss will affect species loss idiosyncratically. And if resource niche partitioning or density dependence are the key mechanisms, then extinction trajectories will depend on how habitat loss affects patterns of resource availability and populations of natural enemies (Brokaw & Busing 2000; Yu & Wilson 2001).

Here we show how, in a simple community of ants, one can measure the relative contributions of competition–colonization trade-offs, dispersal limitation, density dependence, and resource niche partitioning. We find that the bulk of the evidence suggests that a trade-off between long-distance dispersal ability and adult fecundity brings about stable coexistence.

#### THE SYSTEM

Our model is the community of ants living symbiotically with the Neotropical ant–plant *Cordia nodosa* Lam. (Boraginaceae), which provides housing in domatia (specialized stem swellings) for the ants *Allomerus* cf. *octoarticulatus demerarae* Wheeler (Myrmicinae, named *A. demerarae* in previous papers) and four species of *Azteca* Forel (Dolichoderinae) (Fig. 1). Three of the *Azteca* species are currently undescribed, and the fourth has been identified as *Azteca ulei* var. *cordiae* Forel. Each plant hosts only one ant colony, the handful of exceptions being double-trunked plants in which

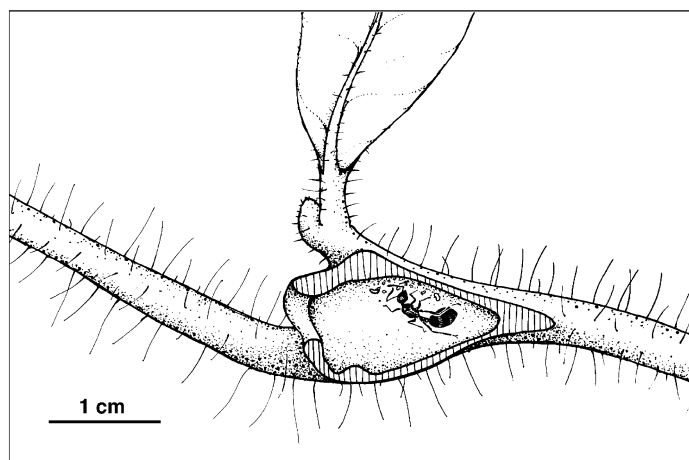


Fig. 1. An *Allomerus* foundress colonizing a domatium of a *C. nodosa* sapling. Domatia are specialized stem swellings produced by the plant to house ant colonies, and the number of domatia can be used as an index of plant and colony size (Yu & Pierce 1998).

one can sometimes find an *Azteca* colony on one trunk and an *Allomerus* colony on the other (Yu & Pierce 1998). Most of the remaining plants are saplings, which means that they do not have established ant colonies or are partially inhabited by a variety of opportunistic ants with small colonies (not considered further). Finally, some plants are inhabited by the rare ant *Myrmelachista* sp. Roger (< 2% of plants, also not considered further) (Yu, Wilson & Pierce 2001).

In return for housing, both *Azteca* and *Allomerus* protect their host-plants from herbivory, meaning that at the vegetative level this ant-plant symbiosis is mutualistic. However, *Allomerus* workers uniquely destroy flowers and prevent most fruiting in order to increase host-plant net growth rate, and thereby colony fecundity. Thus, *Allomerus* is a castration parasite of the *Azteca*-*Cordia* mutualism, and the persistence of this mutualism proximately depends on the persistence of at least one species of *Azteca* (Yu & Pierce 1998; Yu 2001).

For this reason, and to maximize statistical power, we treat the *Azteca* species as a single entity (Yu *et al.* 2001), as coexistence theory is agnostic as to taxonomic category [i.e. the same models can describe the coexistence of competing species or of competing guilds (Leigh 1982; Pacala & Rees 1988)]. All five focal ant species are specialized and obligate symbionts of *C. nodosa*, in the sense that alates (winged, dispersing ant queens) of both genera enter domatia and attempt to found colonies and are thus entirely dependent on *C. nodosa* for colony establishment and survival (Yu *et al.* 2001). 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 that promotes ant coexistence in the sympatric *Cecropia*-ant system (Yu & Davidson 1997) play

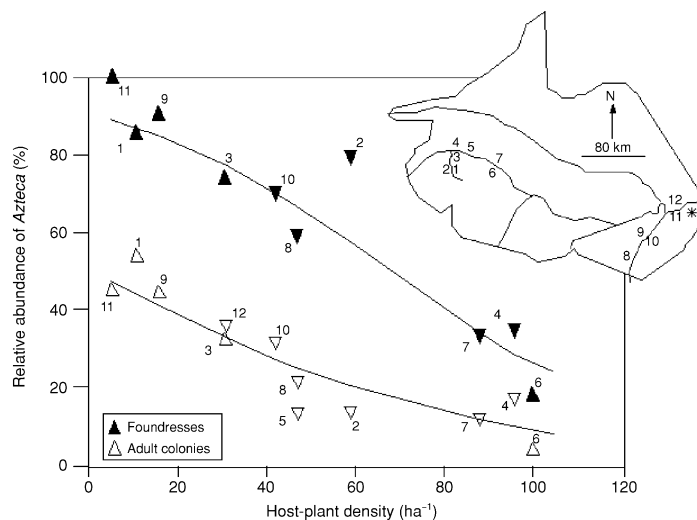
a role in the *C. nodosa* system, because viable *C. nodosa* saplings exist only in the forest interior.

PREVIOUS RESULTS

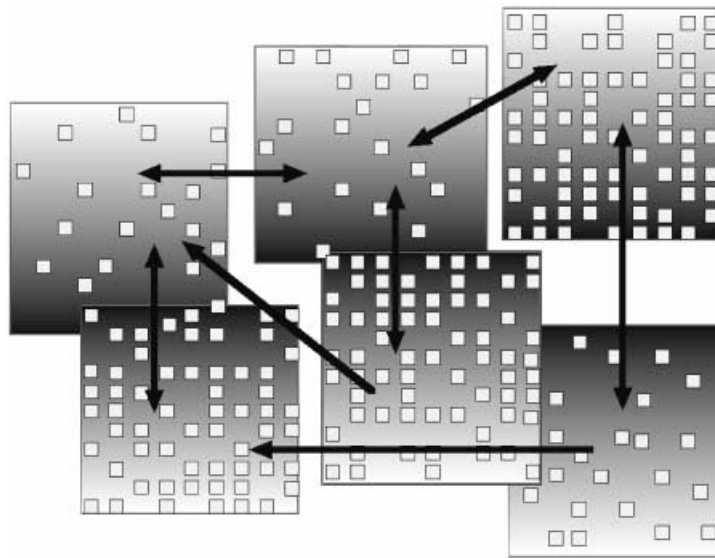
Attempts to explain the coexistence of *Azteca* and *Allomerus* have concentrated on spatial processes (Yu *et al.* 2001), for which the *C. nodosa* system is ideal. Spatial structure is defined by the distribution of plants, each of which is a single patch. Dispersal limitation is the failure of alates to arrive at saplings (empty patches) and found new colonies. In addition, multiple life-history traits have been measured quantitatively, including foundress (ant queen) mortality during colony establishment, and adult colony mortality and growth (Yu *et al.* 2001).

Most importantly, across the landscape of the Department of Madre de Dios, Peru where our studies have been located (Yu & Pierce 1998; Yu *et al.* 2001), host-plant density varies spatially by over an order of magnitude. We can use this natural experiment to measure how relative abundances change as patch density varies, in effect, measuring how habitat loss determines extinction trajectory.

Such a landscape-level census has revealed that variance in the relative abundances of the two genera is almost completely explained by patch density (Fig. 2, Yu *et al.* 2001). The three key features of this graph are that (i) the relative abundances of both *Azteca* foundresses and colonies rise with decreasing host-plant density, (ii) in all locations, the relative abundance of *Azteca* foundresses in saplings is greater than that of adult colonies, and most importantly (iii) *Azteca* foundress relative abundance rises significantly more steeply with decreasing host-plant density than does colony relative abundance.



**Fig. 2.** Host-plant density and ant relative abundance across locations. Relative abundances of *Azteca* colonies and foundresses increase as host-plant density drops across locations (in some locations, foundresses were not censused). The foundress line is significantly steeper than the colony line, indicating increasing dispersal advantage as patch density drops. The asterisk indicates the location with uniformly low host-plant density (4.2–6.7 plants ha<sup>-1</sup>), where *Azteca* was the sole symbiont. Terra firme and lowland floodplain forests are indicated by up and down triangles. Inset: map of census locations across Madre de Dios Province. Location and statistical details in Yu *et al.* (2001).



**Fig. 3.** Schematic representation of patch density variation across sites in one location. A site is defined as an area small enough that no species suffers dispersal limitation within. A location is a collection of sites varying in average patch density. In Fig. 2, each density census took place over a single location and averaged the densities over several sites. In Fig. 4, censuses took place across sites within a single location. Better dispersing species are favoured in low-density sites, but stronger competitors or more fecund species are favoured in high-density sites. Dispersal across sites (arrows) leads to local mixing throughout a location.

Figure 2 is consistent with two models for spatial niche partitioning: (1) a competition–colonization trade-off and (2) a dispersal–fecundity trade-off (Yu & Wilson 2001). Under both scenarios, stable coexistence is obtained over a spatial mosaic of sites with variable host-plant densities (which we call a ‘location’), with a site defined as an area small enough so that the patches occur at a relatively uniform density and total mixing occurs within (Fig. 3, Yu & Wilson 2001). Total mixing implies that all competitors can easily disperse across the site.

A competition–colonization trade-off can produce coexistence if *Allomerus* foundresses are superior competitors for saplings and if *Azteca* foundresses are better colonizers of saplings. Under this scenario, Fig. 2 is explained by a process analogous to the Habitat Destruction Effect of Tilman *et al.* (1994): decreasing patch density favours the better colonizer *Azteca* (Yu & Wilson 2001). We emphasize that because colonies are invulnerable to competitive displacement by alates of either taxon, a competition–colonization trade-off requires variation in patch density if it is to produce coexistence (see Yu & Wilson 2001, for a full exposition).

In contrast, a dispersal–fecundity trade-off can produce coexistence if *Allomerus* colonies are more fecund and if *Azteca* alates are the better individual dispersers. Under this scenario, coexistence is obtained because *Allomerus*’ superior fecundity makes it less dispersal-limited in high-density sites, while *Azteca*’s superior flying ability makes it less dispersal-limited in low-density sites. The result is mutual dispersal limitation and stable coexistence (Yu & Wilson 2001; Yu *et al.* 2001). Again, *Azteca*’s relative abundance

should rise with decreasing patch density, as seen in Fig. 2 (Yu *et al.* 2001).

Under either trade-off, dispersal between high and low density sites produces local mixing. However, both mechanisms have difficulty explaining coexistence in locations characterized by very high mean patch density. A parameterized model has found that heavy immigration of *Allomerus* from the many high-density sites can overwhelm *Azteca* in the few low-density sites (Yu & Wilson 2001; Yu *et al.* 2001).

We therefore consider two other coexistence mechanisms. The first is regeneration niche partitioning of saplings over some axis such as sapling size or local light regime. The second is negative density dependence. Foundresses of both genera are attacked by taxon-specific natural enemies after arrival at saplings: the fungus *Hirsutella cf. formicarum* (Fungi Imperfecti) in the case of *Allomerus*, and the parasitoid wasp *Compsobraconoides* sp. Quicke (Braconidae) (Yu & Quicke 1997) in the case of *Azteca*. Neither of these two enemies attacks adult colonies. However, foundress mortality cannot explain the landscape-scale patterns seen in Fig. 2, because previous work has found that post-arrival foundress mortalities do not vary with host-plant density across locations (Yu *et al.* 2001). Thus, we examine the potential contribution of density dependence to coexistence only at smaller spatial scales.

In summary, we have four hypotheses explaining coexistence: (1) a competition–colonization trade-off, (2) a dispersal–fecundity trade-off, (3) niche partitioning of saplings and (4) negative density dependence. We emphasize that these are not mutually exclusive, as the former two appear not to explain why *Azteca* persists in

the highest density locations, and the latter two appear not to explain why relative abundance varies with host-plant density. We test these hypotheses using a series of experimental and observational studies.

## Methods

### SETTING

Work was conducted in Madre de Dios, Peru (Fig. 2), characterized by extensive, mesic to seasonal lowland tropical rain forest (~2100 mm rain/year, Yu, Hendrickson & Castillo 1997, Yu *et al.* 2001).

### FECUNDITY

Entire colonies of *Azteca* ( $n = 109$ ) and *Allomerus* ( $n = 59$ ) were collected in both rainy (December and January 2000) and dry seasons (July 2000, June 2001) and scored for size (number of domatia) and numbers of alates by sex. Results are pooled.

### DISPERSAL ABILITY

#### $\chi^2$ dispersion tests

In 1999, we mapped all *C. nodosa* to the nearest  $m^2$  in a 16-ha quadrat in lowland tropical forest at location 10 (Fig. 2). Natural density of *C. nodosa* there is 65 plants  $ha^{-1}$ . Colonies of the poorer disperser should show a more clumped distribution, reflecting a greater propensity to colonize nearby saplings. We subdivided the 16-ha quadrat into  $k = 4, 9, 16, 25$  and 36 subquadrats. If  $X$  is the count of objects in a subquadrat, then the index of dispersion  $I = \text{Var}(X)/E(X) = 1$  when objects are distributed randomly (null),  $I < 1$  when dispersed, and  $I > 1$  when clustered. The test statistic  $T = (k - 1) I$  is approximately  $\chi^2$  distributed with d.f. =  $k - 1$  (Lewis 1988), allowing us to test for significant two-tailed deviation from the null. The test was performed for all host-plants containing an adult colony, and containing *Allomerus* and *Azteca* separately.

#### Isolation experiments

In October 2000 we removed all the ant colonies from the quadrat and planted equally spaced saplings in concentric squares at 0, 25, 100, 125, 150 and 175 m from the plot edge, as well as allowing the original trees to regenerate domatia. Sixty days later, 484 foundresses were collected from the experimentally planted saplings ( $n = 210$ ) and from a distance-stratified random sample of the naturally regenerating saplings ( $n = 162$ ) and identified to species. Each sapling was scored for distance from plot edge, number of domatia and light environment (understorey or canopy gap). We repeated the experiment in 2001 by removing all domatia in mid-July and allowing saplings to regrow and be recolonized. A total of 289 foundresses were collected

in early October from the naturally established saplings ( $n = 138$ ). Wing muscle mass for *Allomerus* and three *Azteca* species was estimated by measuring the depth of the alitrunk using an ocular micrometer on a stereoscope.

### COMPETITIVE ABILITY

#### 'Gladiator' experiments

We measured competitive ability by subjecting foundresses to 16 'gladiator' trials in which one *Azteca* and between one and four *Allomerus* foundresses were placed in a glass vial arena and allowed to fight.

#### Sapling invasion experiments

*Allomerus* foundresses were collected from wild saplings, allowed to enter the domatia of cultivated saplings and left to acclimate for at least 24 h. In 41 cases we used one *Allomerus* foundress per domatium and in 26 cases, two. *Allomerus* foundresses exhibit facultative, primary pleometrosis (multiple queen founding), and we wanted to test the hypothesis that a benefit of multiple founding might be a better defence against *Azteca*. We used the three species of *Azteca* that could be wild-collected in sufficient numbers for testing.

For each replicate, a single *Azteca* foundress was placed on a sapling and observed for an hour. *Allomerus* foundresses could be observed defending domatia entrances against *Azteca*, which pushed in with their heads and attempted to lock mandibles. If, at the end of an hour, the *Azteca* foundress had left the plant or was no longer attempting to enter the domatium, then the invasion attempt was scored as a failure. We confirmed subsequently that all the failed foundresses were able to enter empty domatia. In 32 of the 40 successful invasions, we also opened domatia and scored *Allomerus* mortality 24 h later. The results from saplings with one and two *Allomerus* foundresses were indistinguishable and have been pooled. Head sizes of foundresses of *Allomerus* and three *Azteca* species were measured using an ocular micrometer on a stereoscope.

### LANDSCAPE PATTERNS OF RELATIVE ABUNDANCE

#### Within-location density census

*C. nodosa* were mapped for density and scored for ant inhabitant in five 1-ha quadrats varying in host-plant density within location 7 in Fig. 2.

#### Deterministic extinction

If spatial variation in patch density is allowing coexistence within locations, *Allomerus* should go extinct in areas where host-plant density is *uniformly* low and no high-density sites can act as sources. The requirement

for uniformity derives from a basic asymmetry: the presence of even a few high-density sites is sufficient to maintain *Allomerus*' presence in a location, but a large amount of low-density habitat is needed to maintain *Azteca* (Yu *et al.* 2001; Fig. 3). We have found one location where *C. nodosa* density ranges between only 4.2 and 6.7 plants ha<sup>-1</sup> over an area of at least 1500 ha (Fig. 2), and we used a 14.5 km-long transect to census the abundances of *Azteca* and *Allomerus*.

#### DENSITY DEPENDENCE AND REGENERATION NICHE PARTITIONING

We can take advantage of three data sets. First is a collection of foundresses from the 290 naturally occurring saplings in the 16-ha quadrat. We measured the percentage of open canopy (an index of light level) over each sapling using a canopy crown densiometer and scored sapling size by the number of domatia. Second is a collection of foundresses from naturally occurring ( $n = 86$ ) saplings in five 1-ha quadrats set within the trail system (Fig. 4 inset) of the Cocha Cashu Biological Station in Manu National Park (location 7 in Fig. 2). Details of the planting are in Yu *et al.* (2001). Third is a collection of foundresses from naturally occurring saplings taken during the density censuses in locations 1, 3, 4, 6 and 8 (Fig. 2).

We use the first two of these data sets to test whether *Azteca* and/or *Allomerus* foundress mortality caused by taxon-specific natural enemies increases with either congeneric foundress or colony density, at either the within-sapling or 1-ha scale. The test using congeneric foundress density is analogous to Harms *et al.* (2000) for tropical trees.

We use all three data sets to test whether the relative abundance of *Azteca* foundresses within a sapling

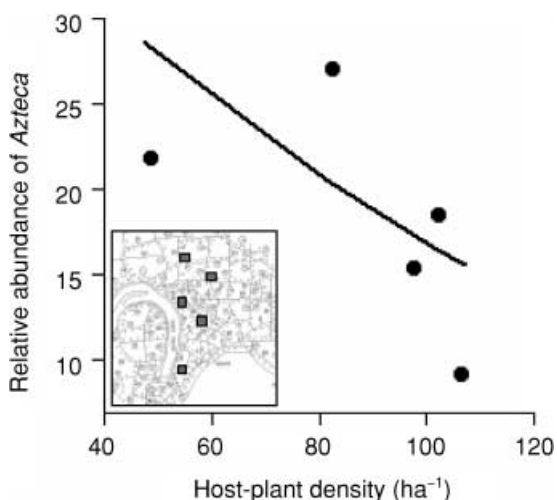


Fig. 4. Host-plant density and relative abundance of *Azteca* across five 1-ha quadrats set within the trail system of location 7 (Fig. 2). The relative abundance of *Azteca*-inhabited *C. nodosa* increases as host-plant density decreases (logistic regression,  $\chi^2 = 3.861$ ,  $P = 0.049$ ). Inset: map of the quadrats.

changes in response to sapling size and/or light regime. Because both *Azteca* and *Allomerus* are claustral founders (they exclusively utilize internal resources during egg laying and brood maturation), *C. nodosa* saplings effectively provide only space during this life-history stage, minimizing the ways in which saplings might be partitioned by the two genera.

## Results

#### FECUNDITY

*Allomerus* colonies are more than twice as fecund as *Azteca* colonies (20.4 vs. 9.1 mean female alates per colony, Mann–Whitney  $U = 1893.5$ ,  $P < 0.0001$ ), even though *Allomerus* colonies are typically smaller (Fig. 5a). This fecundity difference is due to zero female alate production in 96.3% of the *Azteca* colonies censused. In contrast, only 54.2% of *Allomerus* colonies did not produce female alates. Male alate production did not differ significantly (Fig. 5b).

#### DISPERSAL ABILITY

##### $\chi^2$ dispersion tests

For spatial scales  $\leq 100$  m, *Allomerus*' spatial distribution is significantly clumped, whereas *Azteca* colonies are not significantly clumped at any scale, and colony-containing host-plants overall are significantly clumped for only subquadrats of 80 m per side (Fig. 6).

#### ISOLATION EXPERIMENT

Both collections revealed that the relative abundance of *Allomerus* foundresses fell off significantly 100–150 m from the plot edge (Fig. 7). In contrast, *Azteca* showed indications of dispersal limitation only for the first-arriving foundresses (those collected with brood in larval or later stages), and even then, only in the first year's collection (logistic regression,  $\chi^2 = 5.838$ ,  $P = 0.016$ ). *Allomerus*' poorer dispersal ability is consistent with its significantly smaller wing muscle mass, as revealed by alitrunk depth (Fig. 8).

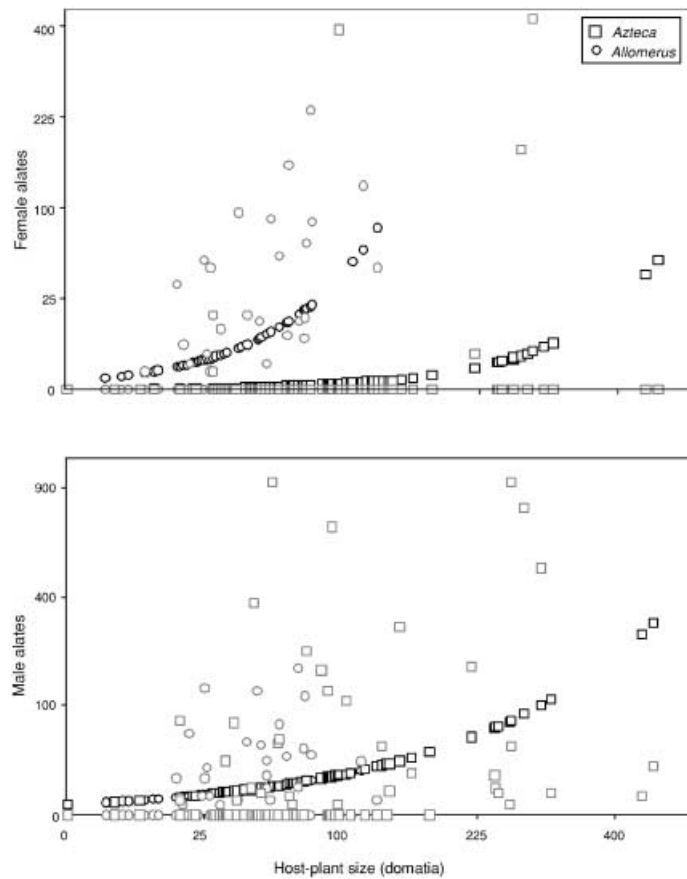
#### COMPETITIVE ABILITY

##### 'Gladiator' experiments

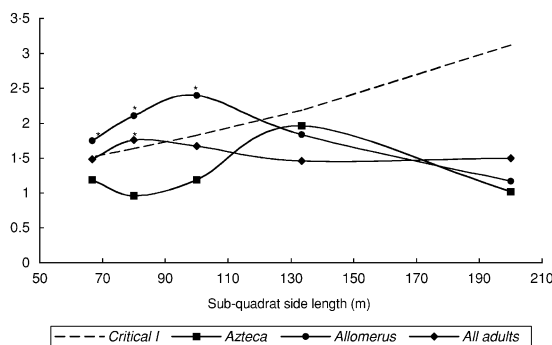
In 12 of the 16 trials, the *Azteca* foundress attacked and killed the *Allomerus* foundress(es) within minutes. In the remaining cases, no fights took place.

##### Sapling invasion experiments

Foundresses of all three *Azteca* species were able to push their way into domatia already inhabited by *Allomerus* foundresses, but with significant differences



**Fig. 5.** Fecundity. A generalized linear model with Poisson errors and a log link was used to find the best-fit models for alate production, as a function of genus and host-plant size, both square-root transformed. Bold symbols represent fitted values. (a) Colonies in larger host-plants produce more female alates ( $F = 48.92, P < 0.0001$ ), and *Allomerus* colonies produce significantly more female alates per domatium ( $F = 75.30, P < 0.0001$ ), despite inhabiting smaller host-plants. The interaction effect was not significant.  $P$ -values have been re-scaled to correct for moderate overdispersion. The size difference between host-plants inhabited by the two genera is due to predation on the largest *Allomerus*-inhabited hosts by a specialist Cerambycid beetle (Yu & Pierce 1998). (b) Male alate production rate is not significantly higher in *Azteca* ( $F < 0.01, P = 0.94$ ).



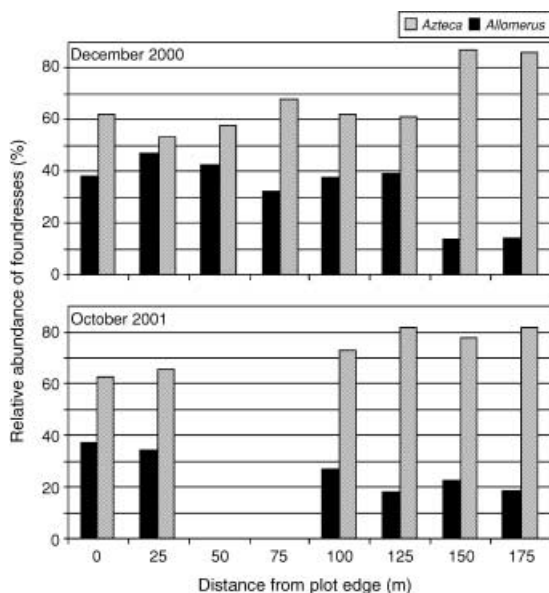
**Fig. 6.** Clumping analysis. The 16-ha quadrat was subdivided into  $k = 4, 9, 16, 25,$  and  $36$  subquadrats, and for each subquadrat scale, a  $\chi^2$  dispersion test was used to assess deviation from the null hypothesis of random distribution for all host-plants containing an adult colony, and *Allomerus*-, *Azteca*-inhabited plants separately (see Methods). The two-tailed  $P < 0.05$  critical value of the dispersion parameter  $I$  at each spatial scale is given by the dashed line. *Allomerus*-inhabited host-plants are significantly clumped at smaller spatial scales (\*), all adult plants are marginally significantly clumped at only one spatial scale (80-m per side subquadrats) and *Azteca*-inhabited plants are never significantly clumped.

among species (Table 1). Consistent with the gladiator experiments, in 26 of the 34 successful invasions for which we later scored mortality, *Allomerus* foundresses were found dead, often in pieces and sometimes pushed out of the domatium. Morphology again appears to play an important role in providing *Azteca* with its advantage; all three species have much larger heads than does *Allomerus*, and the *Azteca* species best able to displace *Allomerus* has the biggest head, and so on down the line (Table 1).

#### LANDSCAPE PATTERNS OF RELATIVE ABUNDANCE

##### *Within-location density census*

The results of the isolation experiment suggest that the size of a single site (Fig. 3) is on the order of one to several hectares. This implies that censuses of individual hectares within a single location should also detect a density effect, and as expected *Azteca*'s relative abundance declines as host-plant density increases (Fig. 4).



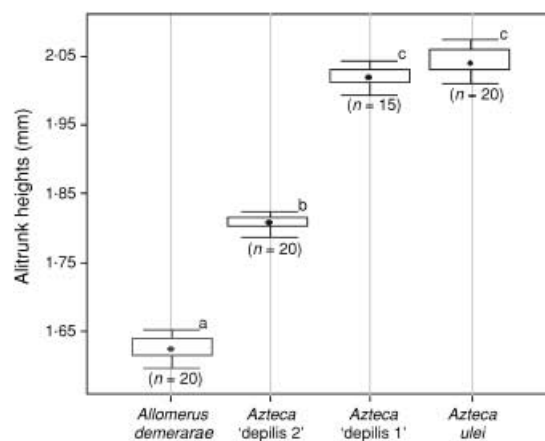
**Fig. 7.** Isolation experiment. (a) December 2000. *Allomerus*' relative abundance declines significantly with distance from plot edge ( $\chi^2 = 9.95$ ,  $P = 0.0016$ ), as well as in larger plants ( $\chi^2 = 7.55$ ,  $P = 0.006$ ) and in the understorey ( $\chi^2 = 4.61$ ,  $P = 0.032$ ). There are no significant interactions. (b) October 2001. *Allomerus*' relative abundance again declines significantly with distance ( $\chi^2 = 9.64$ ,  $P = 0.002$ ), but there are no other significant effects or interactions. Data were analysed using logistic regression, with total foundresses in the binomial denominator. We also analysed the results using (total foundresses + empty domatia) in the denominator, which allows separate analyses of the two genera. In both collections, *Allomerus*' abundance declines significantly with distance, whereas *Azteca*'s abundance does not (results not shown). Analysis of individual *Azteca* species also fails to reveal negative effects of distance (results not shown). Previous work has found that *Azteca* foundresses suffer a two-times higher post-arrival mortality (Yu *et al.* 2001), meaning that a numerical advantage for *Azteca* begins 125–150 m from the plot edge. In both collections, the relative abundance of *Azteca* foundresses at the plot edge ( $\approx 60\%$ ) is consistent with a previous measure taken in 1993 from non-isolated saplings in the forest proper (69.8%, Fig. 2).

#### Deterministic extinction

In the uniformly low-density location, we found 30 *Azteca*-inhabited and zero *Allomerus*-inhabited host-plants, as opposed to the expected 50% relative abundance from Fig. 2 (two-tailed binomial,  $P < 0.0001$ ).

**Table 1.** Invasion experiment and head-size comparisons. All three *Azteca* species are able to invade domatia and kill resident *Allomerus* foundress(es). Additionally, the three *Azteca* species show a marked hierarchy in their relative invasion abilities, correlated with relative head sizes. After sequential Bonferroni correction, all pairwise contrasts are significantly different at the  $P = 0.05$  level for the invasion experiment (two-tailed Fisher's exact test) and at the  $P = 0.01$  level for the head-length comparisons (mm, hind margin to ventral edge of clypeus, Kruskal–Wallis,  $n = 20$  per species)

Invading species	<i>Azteca</i> vs. 1 or 2 <i>Allomerus</i>		Head length (SE)
	Invasion	Failure	
<i>Azteca</i> 'depilis1'	12	0	1.90 (0.014)
<i>Azteca</i> <i>ulei</i> var. <i>cordiae</i>	20	9	1.75 (0.018)
<i>Azteca</i> 'depilis2'	8	18	1.61 (0.007)
<i>Allomerus octoarticulatus demerarae</i>	–	–	1.26 (0.008)



**Fig. 8.** Foundress morphology. Alitrunk depths (mesoscutum to ventral mesopleuron) of *Allomerus* and three *Azteca* species. Superscripts denote significant differences at the  $P < 0.0005$  level (ANOVA, Tukey's HSD *post-hoc* test for unequal sample sizes). *Azteca* 'depilis1' and *Azteca* *ulei* are not significantly different at  $P = 0.725$ . Sample sizes are indicated in parentheses, boxes enclose one standard error, and whiskers 1.96\* SE.

#### DENSITY DEPENDENCE AND SAPLING PARTITIONING

##### Density-dependent mortality

In the 16-ha quadrat, neither *Allomerus* mortality due to fungal attack nor *Azteca* mortality due to wasp predation rose significantly with congeneric foundress density within saplings (Table 2). Similarly, across the 1-ha quadrats in location 7 (Fig. 4), neither *Allomerus* nor *Azteca* foundress mortality rose significantly in hectares with more congeneric foundresses or colonies (Table 2).

##### Regeneration niche partitioning

In the 16-ha quadrat, the relative abundance of *Azteca* foundresses was significantly higher in larger saplings, and this effect was significantly stronger in plants located in lower light microsites (logistic regression,  $n = 166$  saplings with foundresses, total variance explained = 21.3%,  $F = 14.63$ , d.f. = 3,  $P < 0.0001$  after rescaling for moderate overdispersion; parameter estimates are domatia number =  $0.092 \pm 0.019$  SE, light =  $16.5 \pm 6.92$

**Table 2.** Density-dependent mortality of foundresses. Analyses were conducted at two spatial scales: across 290 saplings in the 16-ha quadrat in location 10 and across five 1-ha quadrats in location 7. In all analyses, logistic regression was used to relate congeneric density with the proportion of dead foundresses. At the 1-ha scale, we were able to use both congeneric colonies and foundresses as explanatory variables. Negative density dependence is indicated if slopes are positive (mortality rises with density). In three of six analyses the slopes were positive, but none of the regressions was statistically significant

Spatial scale of analysis	Explanatory variable	n	<i>Azteca</i>		<i>Allomerus</i>	
			Slope of relationship	P	Slope of relationship	P
Across saplings in 16-ha quadrat	Foundresses	290	Negative	0.286	Positive	0.268
Across 1-ha quadrats	Foundresses	5	Negative	0.280	Positive	0.836
	Colonies	5	Positive	0.533	Negative	0.458

SE, interaction effect =  $-1.00 \pm 0.455$  SE). Light by itself does not have a significant effect ( $F = 3.069$ , d.f. = 1,  $P = 0.082$ ). Most of this sapling size effect is driven by *Azteca ulei* var. *cordiae*, although the two other *Azteca* species for which we have sufficient sample size also show positive trends (data not shown).

However, in only one other location (1) is this size effect also significantly positive, and only if we do not correct for multiple comparisons. In four other locations (3, 4, 6, 7), the relative abundance of *Azteca* foundresses trends higher in larger saplings, but not significantly, and in location 8 *Azteca* relative abundance trends lower in larger saplings, also non-significantly (Table 3).

**Table 3.** Regeneration niche partitioning. Logistic regression was used to relate the relative abundance of *Azteca* foundresses to sapling size (number of domatia). Light measurements over saplings were not available for these data sets. In four locations the relationship is positive but not significant, and in one location (8) the relationship is negative and not significant. Only in location 1 is the relationship positive and significant (but without correcting for multiple comparisons)

Location	Host-plant density (ha <sup>-1</sup> )	n saplings	Slope of relationship	P
1	11	20	Positive	0.040
3	31	20	Positive	0.541
4	96	30	Positive	0.427
6	100	6	Positive	0.626
7	88	83	Positive	0.072
8	47	16	Negative	0.257

**Table 4.** Summary of direct and indirect evidence supporting the three hierarchies in fecundity, dispersal and competition. Bold indicates *Azteca*'s superiority, and italics *Allomerus*' superiority. Arrows indicate which trade-off is thought to contribute more to coexistence in low- and high-density locations. Note that competition here refers only to direct foundress–foundress interference during colonization of host-plant saplings

	Dispersal	Fecundity	Competition
Direct evidence	<b>Isolation experiment</b>	<i>Colony collections</i>	<b>Invasion experiment</b>
Indirect evidence	<b>Alitrunk sizes, Extinction of <i>Allomerus</i></b>	<i>Allomerus' castration behaviour</i>	<b>Head sizes</b>

### Discussion

These results provide evidence for the existence of three hierarchies between *Azteca* and *Allomerus* (Table 4).

- Allomerus* colonies are more fecund. *Allomerus*' superior fecundity is consistent with its status as a castration parasite, because the advantage of castration is thought to be increased colony fecundity (Yu & Pierce 1998).
- Azteca* foundresses are better long-distance dispersers, as shown experimentally by the isolation experiment, and as suggested by their larger wing muscle masses and lack of colony clumping. Note that the clumping patterns go against the expectation that *Allomerus* should show less clumping than does *Azteca*, as *Allomerus*-inhabited host-plants produce few fruit and thus have fewer neighbouring saplings (unpublished data). Importantly, *Allomerus*' demonstrated high fecundity allows us to ascribe its dispersal disadvantage to poor dispersal *per se* rather than to a simple lack of propagules (i.e. source limitation is not as important as dispersal limitation, Dalling *et al.* 2002).
- Azteca* foundresses are superior competitors for saplings, as shown experimentally by the 'gladiator' and isolation experiments and as suggested by their larger head sizes.

### SORTING THROUGH THE TRADE-OFFS

The three hierarchies give us three possible trade-offs (Fig. 9), two of which potentially produce coexistence and only one of which, the dispersal–fecundity

$$\frac{dp_1}{dt} = [(\text{fecundity})(\text{dispersal})(\text{survival})(\text{growth})][\text{competition}](\text{adults})(\text{empty patches}) - [\text{mortality}_{\text{adult}}][\text{competition}]$$

$$\frac{dp_2}{dt} = [(\text{fecundity})(\text{dispersal})(\text{survival})(\text{growth})][\text{competition}](\text{adults})(\text{empty patches}) - [\text{mortality}_{\text{adult}}][\text{competition}]$$

**Fig. 9.** A verbal schematic of replacement competition, with the three identified trade-offs from the *C. nodosa* system. Colonization rate is broken into four stages [fecundity, dispersal (= successful arrival), propagule survival and growth to reproductive maturity]. Coexistence can be achieved by a trade-off between any of the colonization, competition or mortality terms over the appropriate form of environmental heterogeneity (Yu & Wilson 2001). The competition–dispersal, competition–fecundity and dispersal–fecundity trade-offs are indicated by dashed, bold and thin lines, respectively. Similarly, other trade-offs identified in the literature can be summarized in this diagram (Table 5, Yu & Wilson 2001).

trade-off, explains the observed landscape-level patterns in relative abundance (Fig. 2).

1. A competition–dispersal trade-off. This is one form of a competition–colonization trade-off but cannot produce coexistence, as *Azteca* is both the better competitor and the better disperser.

2. A competition–fecundity trade-off. This is the other form of a competition–colonization trade-off, with *Allomerus* being the better colonizer, since fecundity is a component of colonization ability (Bolker & Pacala 1999; Levine & Rees 2002, Fig. 9). We must reject the hypothesis that this trade-off produces coexistence in this system, because *Azteca*'s relative abundance rises rather than falls with decreasing host-plant density (Figs 2 and 4), in direct contradiction of theoretical expectations (Tilman *et al.* 1994; Yu & Wilson 2001).

3. A dispersal–fecundity trade-off. This trade-off is consistent with (i) the relative abundance patterns in Figs 2 and 4 (Yu *et al.* 2001), (ii) the spatial scale at which changes in relative abundance can be detected locally (Fig. 4) and (iii) the deterministic extinction of *Allomerus* in a location characterized by uniformly low patch density. We are therefore left with this trade-off as the most probable explanation for coexistence, as hypothesized previously (Yu & Wilson 2001; Yu *et al.* 2001).

#### DENSITY DEPENDENCE AND SAPLING NICHE PARTITIONING

We found no evidence in either genus to support the hypothesis that increased foundress or colony density leads to increased mortality caused by taxon-specific natural enemies (Table 2). On the other hand, there is strong evidence for niche partitioning across sapling size in location 10, even though the effect is almost absent elsewhere. The most straightforward explanation for the lack of significance in other locations is that the range of sapling size is greater in the 16-ha quadrat data set (unpublished data), due to more thorough sampling, suggesting that it is mainly the very largest saplings that are preferentially attractive to *Azteca*. We hypothesize that larger saplings might be more 'apparent' to long-distance dispersing *Azteca* alates.

If, for the sake of argument, we accept the existence of a sapling size effect, then this could drive the density effect seen in Fig. 2 if saplings were also generally bigger in low-density locations. However, a census of

saplings in nine locations ( $n_{\text{tot}} = 473$ ) has found that sapling size [as measured by  $\log(\text{domatia})$ ] is not related significantly to host-plant density across locations (linear regression, variance explained = 0.6%, density parameter estimate =  $-0.004 \pm 0.002$  SE,  $P = 0.076$ ).

#### ARE HIGH-DENSITY LOCATIONS A LARGE SINK FOR *AZTECA*?

What coexistence roles might be played by *Azteca*'s superior competitive ability and preferential colonization of larger saplings? Recall that a dispersal–fecundity trade-off is insufficient to explain *Azteca* persistence in the highest-density locations, due to excessive immigration of *Allomerus* from high-density sites (Yu *et al.* 2001). We therefore hypothesize that *Azteca*'s ability to displace *Allomerus* from saplings and/or regeneration niche partitioning of saplings could allow *Azteca* continually to invade high-density locations from low-density locations, maintaining a presence throughout the landscape (Table 4).

#### ALTERNATIVE EXPLANATIONS FOR COEXISTENCE

One caveat is that we have had to take advantage of natural variation in patch density, as there is no way to manipulate it experimentally at a landscape scale. It is possible that some other factor correlated with plant density could be driving ant abundances. However, we can rule out three alternatives. First, *Azteca* foundress mortality does not decrease in the low-density locations where it is relatively more abundant (Yu *et al.* 2001). Secondly, across-genus differences in adult colony growth or mortality rates cannot account for the significantly steeper foundress slope seen in Fig. 2 because under this scenario, colonization rates should reflect changes in adult relative abundance only passively, and the slopes would be equal (Yu *et al.* 2001). Thirdly, as we have seen, sapling size does not increase in low-density locations. We can suggest one more alternative, as follows.

#### Temporal cycling and successional coexistence

Because *Azteca* is a mutualist, in theory it could 'sow the seeds of its own demise'. That is, fruit production

**Table 5.** Trade-off models of plant species coexistence translated into replacement competition model terms, with the enabling environmental heterogeneity, showing that seemingly disparate models can be summarized in a single schematic (Fig. 9)

Key trade-off identified	Replacement competition analogue	Environmental heterogeneity	Reference
Low palatability–high competitive ability	Survival–growth/direct competition	Herbivore density	Pacala & Crawley (1992)
‘Torch’ trees–‘damp’ trees	Fecundity/direct competition–mortality <sub>adult</sub>	Tree density	Bond & Midgley (1995)
‘Rain forest’–‘eucalypt’ (no ‘flammability effects’)	Survival–growth	Non-fire-caused/ fire-caused gaps	Possingham, Comins & Noble (1995)
High flammability, susceptibility and reproduction rates vs. low F, S, R	Growth–mortality <sub>adult</sub>	Frequency of forest fires as a function of abundance of ‘high flammables’	Possingham <i>et al.</i> (1995)
High susceptibility and low death rate – low S and high D	Mortality <sub>adult</sub> –mortality <sub>adult</sub>	Relative abundances of ‘eucalypt’ and ‘rain forest’ trees	Possingham <i>et al.</i> (1995)
Calcicole–calcifuge	Growth–survival	Soil pH	Tansley (1917)
Nutrient 1 limited–nutrient 2 limited	Growth/mortality <sub>adult</sub> –growth/mortality <sub>adult</sub>	Soil nutrient ratios	Tilman (1982)
Seed number–seed size	Fecundity/arrival–survival/ growth/direct competition	Patch density or ambient light	Foster & Janson (1985)
Pioneer–advance regeneration	Fecundity/arrival/growth–survival	Ambient light	Horn (1971); Whitmore (1989), Kohyama (1993)
Root–shoot	Direct competition–fecundity/arrival	Soil N concentration	Tilman (1994)
Per-size fecundity–absolute fecundity	Fecundity–fecundity	Forest vertical structure	Kohyama (1993, 1984)

could convert a low-density site favouring *Azteca* to a high-density one favouring *Allomerus* (and vice versa), thus bringing about coexistence. However, for this to occur, seeds must generally fall close to natal plants, but this is unlikely because *C. nodosa* fruits are dispersed by monkeys over hundreds of metres, eliminating any correlation between ant abundance and seed fall.

For this reason, and because so much of the variance in ant relative abundance can be explained by host-plant density (Figs 2 and 4), suggesting that the system is in equilibrium (Yu *et al.* 2001), we doubt that cycling is occurring. Instead, we take variation in host-plant density to be driven mainly by exogenous factors such as soil (Fig. 2). In any event, note that the temporal cycling hypothesis also relies on a dispersal–fecundity trade-off for coexistence, the only difference being the source of variation in patch density.

In summary, the dispersal–fecundity trade-off is currently the best supported and the most parsimonious explanation of coexistence.

#### OTHER ANT–PLANT SYSTEMS

Dispersal–fecundity trade-offs (McKey 1984; Vasconcelos 1993), ecological succession (Fonseca & Ganade 1996) and niche partitioning (Yu & Davidson 1997) are implicated as coexistence mechanisms in other ant–plant systems (reviewed in Yu 2001; Yu *et al.* 2001), but the only other ant–plant system in which coexistence-enabling trade-offs have been investigated thoroughly is the *Acacia drepanolobium* (Harms) Sjöstedt ant–plant symbiosis in Kenya (Young, Stubblefield & Isbell 1997; Palmer, Young & Stanton 2002; Stanton,

Palmer & Young 2002). The key difference between the *C. nodosa* and *A. drepanolobium* systems is that only in the latter are established ant colonies regularly displaced from host-plants by colonies of the most competitively superior species (Stanton *et al.* 1999; Palmer *et al.* 2002). This results in a well-defined, adult-stage dominance hierarchy across four ant species (Stanton *et al.* 2002). The most competitively inferior ant species appears to persist because its queens are the best at colonizing and fighting for larger saplings, and the middle-ranking ant species are better at colonizing small saplings (Stanton *et al.* 2002). All this results in a series of displacement competition–colonization trade-offs reminiscent of competition among grasses (Wedin & Tilman 1993; Yu & Wilson 2001).

#### STABILITY OF MUTUALISMS

Finally, the invocation of spatial structure to explain the maintenance of mutualisms in the face of parasites (Nowak & May 1992; Doebeli & Knowlton 1998; Kinzig & Harte 1998; Stanton *et al.* 1999; Denison 2000; Hochberg *et al.* 2000; Yu 2001) and the maintenance of coexistence in the face of competition (Chesson 1985; Comins & Noble 1985; Bolker & Pacala 1999; Yu & Wilson 2001; Mouquet & Loreau 2002) have traditionally been treated as intellectually separate endeavors. However, they can both be seen as attempts to explain the coexistence of multiple life-history strategies (Law, Bronstein & Ferriere 2001; Yu 2001). Seen in this light, we can equate the persistence of this mutualism with the persistence of *Azteca*, and the importance of the dispersal–fecundity trade-off leads us to speculate that

castration behaviour might even have evolved as a competitive response to *Azteca*. Thus, we suggest that much future progress toward explaining the evolutionary stability of mutualisms will hinge on explaining the factors that produce evolutionarily stable trade-offs in life-history traits, such as have led to extraordinarily low fecundity in *Azteca* and poor dispersal ability in *Allomerus*.

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