

COMPETITION–COLONIZATION TRADE-OFFS IN A GUILD OF AFRICAN ACACIA-ANTS

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Abstract. In systems where disturbance creates colonization opportunities, competition–colonization trade-offs can lead to coexistence between competitors sharing a single, limiting resource. In upland East Africa, four species of obligate acacia-ants compete for possession of *Acacia drepanolobium* host trees but still coexist at fine spatial scales. Previous experiments revealed a hierarchy of competitive dominance among mature ant colonies in battles over occupied trees (*Crematogaster sjostedti* > *C. mimosae* > *C. nigriceps* > *Tetraponera penzigi*), and the pattern of ant species turnover on single host trees over time is consistent with this hierarchy. Here we present evidence that competition–colonization trade-offs are likely to facilitate coexistence within this guild. The population of host trees is highly dynamic. Although most suitable host trees are occupied by ants, mature *A. drepanolobium* trees may be vacated after fire, extensive damage, or drought. Smaller host trees with limited nesting space become available when they recruit into the population as saplings or coppices. These unoccupied trees may be colonized by expansion of nearby, mature colonies as well as by foundress queens attempting to initiate new colonies. We identified competition–colonization trade-offs between two stages of colony development: competitive colony expansion onto nearby trees, and competition among foundress queens for nest-initiation sites. All three *Crematogaster* species readily occupy nearby, empty trees by colony expansion. In contrast, *T. penzigi* colonizes empty trees almost exclusively by dispersive foundress queens. Colonies of *C. sjostedti* are competitively dominant over those of all other species, but foundress queens of this species rarely attempt to start independent colonies. Foundress queens of the secondary competitive dominant (*C. mimosae*) are restricted mostly to low-quality, small saplings. In contrast, competitively subordinate colonies of *T. penzigi* and *C. nigriceps* produce foundress queens that disproportionately colonize empty mature trees, the highest quality host plants that are available. Competition between foundress queens is intense. Queens are significantly hyper-dispersed among potential nest-initiation sites, indicating that the presence of resident foundresses deters subsequent colonization attempts, and competitive dominance among foundresses who fight during colony founding is the reverse of that seen among mature colonies. Coexistence within this guild may therefore be promoted by ontogenetic reversals in relative competitive ability between early and late stages of colony development, a pattern that is consistent with the niche hypothesis for competition–colonization trade-offs.

Key words: acacia-ants, Kenya; *Acacia drepanolobium*; ant–plant mutualism; coexistence of species; colonization, acacia-ant strategies; competition–colonization trade-offs; *Crematogaster*; dispersal-limitation hypothesis; foundress queens; niche hypothesis; patch dynamics; *Tetraponera*.

INTRODUCTION

A major goal of ecology is to understand the mechanisms that promote and maintain diverse ecological communities. Of special interest is the fact that many communities include multiple species that appear to utilize the same resources or, at the very least, a broadly overlapping set of resources (Hutchinson 1961). Theoretical analyses suggest that a number of factors can promote equilibrium or nonequilibrium coexistence among competing species (e.g., Levins 1979, Hastings

1980, Tilman 1982, Chesson 1985, Pacala and Rees 1998). These treatments have inspired a number of empirical studies (reviewed in Yodzis [1986], Wilson [1990], Ricklefs and Schluter [1993], and Tokeshi [1999]), but our understanding of coexistence mechanisms in natural communities has lagged behind theoretical developments.

Patch-dynamics models, in which new patches of a limiting resource are continually being created by local disturbance, have consistently shown that local successional replacement among competing species can lead to prolonged, fine-grained coexistence, even though those species utilize the same resource base (Levins and Culver 1971, Huston 1979, Yodzis 1986). According to the dispersal-limitation hypothesis and

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the niche hypothesis, two types of competition–colonization trade-offs can promote coexistence (Pacala and Rees 1998). In each case, species that are competitively dominant during later stages of succession are underrepresented in early successional, post-disturbance sites, but for different reasons. Under the dispersal limitation hypothesis, species that dominate in late-successional stages could potentially succeed in, but rarely disperse to, recent disturbances (Levins and Culver 1971, Horn and MacArthur 1972, Hastings 1980, Tilman 1994, Hurtt and Pacala 1995, Young et al. 2001). Poor dispersal by late-successional competitive dominants may arise from lower allocation to dispersal, i.e., low propagule number, and/or limited dispersal distance, compared with early successional dispersal specialists (e.g., Werner and Platt 1976, Denno et al. 1989). In contrast, the “niche hypothesis” for competition–colonization trade-offs (Pacala and Rees 1998) proposes that colonization of post-disturbance sites by late-successional competitive dominants is not limited by dispersal ability. Instead, post-disturbance conditions favor colonists of early successional species over late-successional species (Tilman 1990, Pacala et al. 1996, Brewer et al. 1998). Competition–colonization trade-offs arise in this case because the phenotypic traits favored in recent disturbances are disadvantageous during later successional stages, and vice versa.

According to the dispersal-limitation hypothesis, limited resources make fugitive colonists vulnerable to competition, and so their success hinges on escaping from established competitors by arriving early at disturbed microhabitats (e.g., Platt 1975, Del Moral 1999). Species adapted to this fugitive life history tend to display a suite of traits that includes early reproduction and the production of large numbers of relatively small, highly dispersive propagules. High investment in dispersive propagules limits investment for resource capture and defense, leading to an allocation-based trade-off between colonization success and competitive ability (MacArthur and Wilson 1967, Turnbull et al. 1999). The potential importance of dispersal limitation in community patch dynamics is shown by studies in which the propagules of community dominants fail to reach suitable, available sites (e.g., Schupp et al. 1989, Quintana-Ascencio et al. 1998, Losos and Spiller 1999, Young et al. 2001). Competition–dispersal trade-offs have been particularly well documented in terrestrial plants (Platt 1975, Platt and Weiss 1985, Bertness and Ellison 1987, Tilman 1994) and benthic invertebrates (Grosberg 1988, Tokeshi and Romero 1995, Barnes and Clarke 1998), but also occur in other organisms (e.g., Denno et al. 1989).

Under the “niche hypothesis,” species coexistence within disturbed habitats is not driven by trade-offs between competitive ability and dispersal success, but by species differences in the ability to compete or survive in recent disturbances vs. in undisturbed microhabitats (Pacala and Rees 1998). The reversal in species

performance between early and late-successional patches is ascribed to trade-offs between competitive ability and tolerance for stressful, post-disturbance conditions (e.g., during primary succession, Connell and Slatyer 1977, Grime 1979), or to trade-offs in competitive ability under contrasting resource regimes (Tilman 1988). Support for the niche hypothesis comes from experiments in terrestrial plant (Wedin and Tilman 1993, Pacala et al. 1996) and benthic (e.g., Bertness and Ellison 1987) communities showing that conditions in recently disturbed patches are less suitable for species characteristically found in undisturbed microsites.

Patch-dynamics models have most often been applied to communities of sedentary organisms in which space represents a limiting resource (Dayton 1975, Platt 1975, Connell 1978, Paine 1979, Bertness and Ellison 1987, Schupp et al. 1989). In such systems, when disturbance creates vacant space, the newly available resource patch may be filled in by growth of established individuals nearby, or may be colonized by small, competitively vulnerable propagules. Over time, if disturbance does not recur, the early successional specialists tend to be overgrown by late-successional competitive dominants. The pattern of species occupancy, and the mode of patch colonization during post-disturbance succession may depend on patch size (Keough 1984, Rice 1987), proximity to established individuals (Morse and Schmitt 1985, Schupp 1992), the type of disturbance (Rice 1987), and local, edaphic conditions (Bertness and Ellison 1987, also see Moloney and Levin 1996).

Competition–colonization trade-offs, broadly defined, have also been suggested to be important in maintaining species diversity in ant communities (Janzen 1975, Davidson et al. 1989, Holldobler and Wilson 1990, Davidson and McKey 1993*b*). However, we know very little about the critical relationships between coexisting ant species with respect to the competitive ability of mature colonies, production of dispersing queens, success of queens at locating suitable colonization sites, and the post-dispersal success of incipient colonies.

Specialized ant–plant symbioses offer an excellent opportunity for studying the consequences of dispersal, colonization, and competition on coexistence among competing species. Within any given geographic area, it is common to find that a single species of host plant is associated with more than one species of plant–ant, although mature plants typically harbor only a single active colony (e.g., Janzen 1975, Davidson and McKey 1993*a*). Dispersive foundress queens belonging to different plant–ant species can be monitored within above-ground domatia (Perlman 1992, Yu and Davidson 1997), allowing investigators to compare frequencies of queens and mature colonies and to determine if foundresses preferentially colonize empty host plants within different microhabitats (Yu and Davidson 1997). Fi-

nally, competition among foundresses and incipient colonies is likely to occur, as new shoots are often colonized by multiple queens (Janzen 1975, McKey 1984, Perlman 1992, Vasconcelos 1993, Maschwitz and Fiala 1995, Yu and Davidson 1997).

In this paper we investigate the potential role of competition–colonization trade-offs in promoting coexistence within a guild of obligate acacia-ants in central Kenya. The four ant species that coexist at a fine spatial scale, within our study area (Young et al. 1997) and over much of East Africa (Hocking 1970), all live in symbiotic association with a single species of myrmecophytic tree, *Acacia drepanolobium*. The low frequency of unoccupied trees over 0.5 m tall (Young et al. 1997, Palmer et al. 2000), battles between mature ant colonies for sole possession of host trees (Stanton et al. 1999), and relatively high rates of species turnover on trees (Palmer et al. 2000) all indicate that *A. drepanolobium* is a limiting resource for which ant species within this guild compete intensively.

The upland habitats underlain by heavy clay vertisols (Ahn and Geiger 1987) in this region of East Africa are dominated by *A. drepanolobium*, which often accounts for over 95% of the overstory (Taiti 1992, Young et al. 1997, 1998). Densities of trees and acacia-ants are often high (~2000 trees/ha), leading Hocking (1970) to estimate that acacia-ants may account for up to 25% of the animal biomass in this ecosystem. The *A. drepanolobium* population is extremely dynamic, even at fine spatial scales, and “open space” for colonization by acacia-ants is created in several ways. After damage due to fire or the activities of elephants kills resident ants, previously healthy *A. drepanolobium* trees can produce vigorous new shoots from stem tissues that survive above- or belowground (Okello et al. 2001). These emergent shoots quickly produce swollen thorns and leaves with nectaries, becoming attractive targets for colonization by expansion of nearby mature colonies or by foundress queens. Smaller trees recruit into the *A. drepanolobium* population as saplings or as coppices from small, apparently browsed underground stems. These shoots occur at high densities (typically 500–1200 shoots/ha); they produce leaves and swollen thorns relatively slowly, and are often intermixed with under story vegetation.

There is a linear competitive hierarchy among mature colonies of the four species of acacia-ants in this system. Healthy, mature trees are virtually all occupied by colonies with patrolling workers (Young et al. 1997, Palmer et al. 2000). Taller, presumably older trees are most often occupied by one of two *Crematogaster* species (*C. sjostedti* or *C. mimosae*), whereas shorter trees tend to be occupied by either *C. nigriceps* or *Tetraponera penzigi*. Experiments and long-term monitoring (Stanton et al. 1999, Palmer et al. 2000) show that *C. sjostedti* colonies are uniquely capable of displacing colonies of *C. mimosae*, and that trees occupied by *C. nigriceps* are very vulnerable to takeover by both of

the other *Crematogaster* species. *Tetraponera penzigi* very rarely displaces other ants from host trees, and natural takeovers of *T. penzigi* trees by mature *Crematogaster* colonies are relatively common. Given this linear competitive hierarchy (*C. sjostedti* > *C. mimosae* > *C. nigriceps* > *T. penzigi*) we would expect *C. sjostedti* and *C. mimosae* to dominate the system in the absence of disturbance.

We addressed several questions, to determine whether patch colonization dynamics play an important role in facilitating coexistence within this acacia-ant guild (Huston 1979, Yodzis 1986, Pacala and Rees 1998). We found that patterns of colonization observed for unoccupied, mature trees sometimes contrasted with those observed for smaller saplings and coppicing shoots, and so we discuss these two types of colonization “targets” separately.

1) Does the frequency of colony expansions onto available trees by the four acacia-ant species differ from that expected from the local abundance of mature colonies? In particular, are ant species that are competitively dominant as mature colonies also more likely to colonize unoccupied trees by “clonal” expansion?

2) Does the frequency of foundress queens belonging to particular species differ from that expected from the local abundance of mature colonies? In particular, are ant species that are competitively dominant as mature colonies underrepresented within the pool of foundress queens, as would be expected if competitive dominants are dispersal limited?

3) Are foundress queens distributed at random among available swollen-thorn nesting sites? Alternatively, is there a significant pattern of aggregation or hyper-dispersion of queens that might indicate either cooperation or competition among foundresses?

4) Do foundress queens of the acacia-ant species vary with respect to demographic measures of colonization ability, such as survival after combat with other queens, speed of nest site location, and the speed with which eggs are laid and new workers are produced?

STUDY SITE AND METHODS

The study system

Our research is being conducted at the Mpala Research Centre, in the Laikipia District of central Kenya (0°17' N, 37°52' E). Vegetation within the semiarid, uplands research site (1800 m elevation) is bushland savanna, in which the canopy is dominated by a single species of swollen-thorn acacia tree, *Acacia drepanolobium*. The fire-prone habitat hosts numerous large herbivores and browsers, and is also an important cattle-producing region for Kenya (Young et al. 1998). *Acacia drepanolobium* produces a formidable pair of stipular thorns up to 7 cm long at each node along its branches. On a portion of these nodes (5–40%), the

paired thorns share a hollow, inflated base that is usually 1.5–3.5 cm in diameter. Acacia-ants, and occasionally other insects, chew holes through the wall of each swollen thorn and nest inside the cavity. The bipinnate leaves of *A. drepanolobium* bear 1–3 extrafloral nectaries along their central axis, but do not produce food bodies (Holldobler and Wilson 1990). Accordingly, the resident ants of *A. drepanolobium* require other protein sources for colony growth (Palmer 2001). Acting in concert, ants and sharp thorns form a quite effective defense against browsing by small to medium-sized herbivores (Milewski et al. 1991, Madden and Young 1992, Stapley 1998).

Throughout the Laikipia district, four species of acacia-ants are the principal symbionts of *A. drepanolobium* (Hocking 1970, Young et al. 1997, Stanton and Young 1999). *Tetraponera penzigi*, *Crematogaster nigriceps*, and *C. mimosae* depend entirely on the interiors of swollen thorns for nesting space, and are specialists on *A. drepanolobium* within this ecosystem. *Crematogaster sjostedti* also occurs on a locally less common swollen-thorn acacia, *A. seyal* var. *fitula*. This latter species nests principally within dead acacia tissues, but its workers may also occupy swollen thorns. Single *Crematogaster* colonies often span multiple trees, but *T. penzigi* colonies typically control only a single, contiguous canopy (Palmer 2001). Trees up to 6 m in height occur, but most trees are <2.5 m tall, and all four species of acacia-ants are common on trees 1–2 m tall (Young et al. 1997, Palmer et al. 2000). The four principal ant species are intolerant of one another. In any given survey, <1% of trees are occupied by more than one ant species, but these are transient co-habitations (also see Hocking 1970). Despite this mutual exclusivity, the species coexist at a very fine spatial scale, so that all four acacia-ants are likely to be found within any given 0.1–0.2 ha area.

Alate queens and males are commonly found within swollen thorns on trees occupied by colonies of *T. penzigi*, *C. nigriceps*, and *C. mimosae*, and also occur within the stem nesting cavities of *C. sjostedti* trees. Mating flights are especially likely to occur on still mornings following rainfall, although newly mated foundress queens can be found year-round. Many alate reproductives are captured by spider webs on *A. drepanolobium* canopies, suggesting that new queens suffer significant predation pressure during the dispersal stage. The following description applies to queens of *T. penzigi*, *C. nigriceps*, and *C. mimosae*, which commonly establish independent, new colonies. Newly mated, winged queens of these species can be found exploring the exterior surfaces of *A. drepanolobium* trees. We have observed these individuals being attacked by resident ant colonies when they are encountered. Before attempting to colonize a swollen thorn, a foundress queen removes her wings, initiating a conversion of the flight muscles into food for brood production (Holldobler and Wilson 1990). The queen

chews an entry hole into the swollen thorn, plugs up the hole from the inside, and then remains sealed within the swollen thorn until her first nuptial workers are produced. Queens of *T. penzigi* and *C. nigriceps* are completely intolerant of other foundresses, but we occasionally encounter pleometrotic groups of 2–5 *C. mimosae* queens that appear to be cooperating in founding a colony within a single swollen thorn (M. Stanton, unpublished data). Dissections of *A. drepanolobium* canopies (T. Palmer, M. Stanton, and B. Barringer, unpublished data) indicate that mature colonies of *T. penzigi* and *C. nigriceps* have only a single laying queen, whereas multiple laying queens are found in trees inhabited by *C. sjostedti*. The polygynous habit of *C. sjostedti* may explain why we rarely find independent foundress queens of this species.

Monitoring patterns of colonization

In three experiments conducted from 1996 to 2001 we observed how members of this acacia-ant guild colonize unoccupied trees, which represent “patches” of available resource. Most unoccupied *A. drepanolobium* trees fall into one of three categories: (1) relatively small (≤ 0.5 m) understory saplings or coppices with few leaves and swollen thorns; (2) relatively large trees recently singed by fire, or regrowing following heavy damage due to fire or elephants; and (3) mature, drought-stressed trees abandoned by former ant inhabitants (T. Palmer, T. Young, and M. Stanton, unpublished data). We used two types of experimental manipulations to create relatively large, unoccupied *A. drepanolobium* trees, and then monitored colonization by foundress queens and/or nearby colonies. Concurrently, we documented patterns of colonization on naturally occurring, small saplings within permanently marked plots.

Colonization following moderate damage to trees (Experiment 1).—To mimic the natural creation of empty trees by drought stress or by moderate fires that kill resident ants but do not catastrophically damage living stems, we removed ants from *A. drepanolobium* canopies using a minimally destructive technique. In April 1996 we removed all ants from 122 randomly selected trees between 0.75 and 2.0 m in height along four 100-m transects through the study site. Stratified sampling was used to ensure that trees occupied by each of the four acacia-ant species were common ($\geq 20\%$) in the subsample of trees along each transect. Resident ants were removed by cutting open all swollen thorns on the host tree, brushing ants from inside the thorns as well as from leaves and stems, and installing a sticky barrier (Tanglefoot [The Tanglefoot Company, Grand Rapids, Michigan, USA]) on the stem to prevent recolonization by crawling ants. To characterize the local community of acacia-ant species along the transects, we used the cardinal (compass) directions to define four quadrants around each ant-removal tree. We then recorded the occupying ant species and canopy

height for the three nearest neighbor trees within each quadrant. These neighborhood data were pooled across the ant removal trees along all four transects to calculate expected frequencies for each ant species that might colonize target trees (see Statistical analyses: Testing for nonrandom colonization . . . , below). Over the next year, while sticky stem barriers were being continuously maintained, 85 of the ant-removal trees began to produce new branches and swollen thorns. Beginning in April 1997 the sticky stem barriers were allowed to degrade naturally; this gradually made trees accessible to crawling ants. In July 1997 we examined each regrowing experimental tree canopy for the presence of mature colonies and/or foundress queens. Fifty-one trees had been fully occupied by workers and brood derived from established ant colonies nearby. We recorded the species of ant for each such expansion. Swollen thorns that are actively patrolled and inhabited by workers never contain foundress queens, and we did not examine the contents of such thorns. Seventeen tree canopies had been only partially occupied by nearby colonies; on these trees, we cut open all swollen thorns not occupied by actively patrolling workers to look for foundress queens ($n = 59$ thorns). The remaining tree canopies ($n = 17$) lacked patrolling workers altogether. On these trees, we opened all swollen thorns and examined their contents ($n = 184$ thorns).

Colonization following severe damage to trees (Experiment 2).—In two replicates of a second colonization experiment, we removed ants from *A. drepanolobium* trees by simulating severe fire or elephant damage. In October 1998 we identified four sites within the study area. In each site, we selected eight healthy trees 1.5–2.5 m in height, including two trees occupied by each of the acacia-ant species. All ant-inhabited parts of each tree were removed by cutting off the main stem 0.75 m above the ground and dragging the canopy and its irate inhabitants to a location >100 m away. At each site, one of the two trees formerly occupied by each ant species was randomly assigned to the exclusion treatment; sticky barriers were placed on these stems to inhibit recolonization by nearby acacia-ant colonies. No barrier was placed on the stem of the other tree within each pair. Five of these “disarmed” stems were heavily damaged by wild ungulates that used them as scratching posts. To minimize this problem, we set up a second replicate of this experiment in October 1999, involving eight trees at each of two sites, within a large mammal enclosure (Young et al. 1998). In this second replicate, sticky barriers were maintained on the stems of all 16 trees within the study, increasing opportunities for colonization by foundress queens. By December 1999 some of these trees were producing coppicing shoots and swollen thorns, but drought conditions over the next 10 mo reduced rates of regrowth, compared with the first replicate. Because of compromised barriers, several coppicing trees were occupied by workers from mature colonies on nearby trees. On

the remaining eight trees we conducted longitudinal surveys of foundress queens through August 2000. For each replicate of the experiment, we characterized the local acacia-ant community by recording the height and ant occupant of the five *A. drepanolobium* trees nearest to each experimental tree. These data were used to calculate the expected frequency of colonization by each of the four acacia-ant species (see Statistical analyses: Testing for nonrandom colonization . . . , below).

Unlike the “moderate-disturbance” experiment, in which each swollen thorn was destroyed when surveyed, in this experiment we carefully opened new swollen thorns and then resealed them (also see Perlman 1992). By doing so, we could gather longitudinal demographic data on foundress queens colonizing swollen thorns on these coppicing tree stems. In surveys conducted twice each month from January 1999 to December 2000, observation windows 1 cm in diameter were cut into newly produced but mature swollen thorns using a portable drill. Occupant queens and their brood were observed inside each thorn using a lighted borescope (RBAC series [UXR, Simi Valley, California, USA]). In each opened thorn, we recorded the species of foundress queen(s), whether each queen was alive or dead, and the presence of other insects. Queens are protective of eggs and brood, and avoid the light produced by the borescope, making it difficult to make accurate counts of eggs, brood, or workers without seriously disrupting the incipient colony. Accordingly, we recorded only the presence or absence of eggs, brood, and/or new (nanitic) workers. After making observations, thorn windows were immediately resealed with a small pad of reusable window caulking.

Colonization of naturally occurring saplings and small coppicing shoots (Experiment 3).—In July 1998 we established four 20 × 40 m plots within the study area, separated from one another by ≥0.5 km. Each plot was divided into a pair of 20 × 20 m subplots, and then one subplot within the pair was randomly assigned to a sapling-removal manipulation. In June 1998, January 1999, and January 2000 the species of acacia-ant active on all *A. drepanolobium* trees within each subplot were counted, and each tree was assigned to one of five height categories: <0.5 m, 0.5–0.99 m, 1.0–1.49 m, 1.5–3.0 m, and ≥3 m. In the experimental sapling-removal subplot all trees <0.5 m tall (“saplings”) were cut off at ground level, removed from the site, and carefully examined for active workers and/or foundress queens. Some of these saplings had been fully occupied by large workers from nearby colonies, and we did not open swollen thorns that were patrolled and occupied by such mature workers. (To check the validity of this approach, we opened all swollen thorns on >25 saplings with mature workers. In no case did we find a laying queen, although swollen thorns often contained brood imported from the mother colony.) Other saplings lacked patrolling, occupant workers, but had sealed swollen thorns (indicating claustral queens

inside) and, in a few cases, tiny nanitic workers (indicative of newly establishing colonies). On these saplings, all swollen thorns were opened and their contents catalogued. Saplings present in the control subplots were surveyed for actively patrolling workers, but were left in place.

Statistical analyses

Testing for nonrandom colonization by ant species.—We used chi-square analysis to test the null hypothesis that colonization of available *A. drepanolobium* trees occurs at random with respect to the species composition of the local acacia-ant community. We specifically compared the two major modes of colonization, by colony expansion vs. by foundress queens, and also contrasted patterns of colonization seen for the different types of available trees: moderately damaged mature trees (Experiment 1); severely damaged mature trees (Experiment 2); and saplings <0.5 m tall (Experiment 3).

For Experiments 1 and 2, expected frequencies of the four ant species were calculated from the proportions of neighboring trees occupied by each species, weighted by the canopy height of each tree. Tree height was used as a weighting factor because the available nesting space on a tree, as estimated by the numbers of swollen thorns, increases significantly with canopy height (least-squares linear regression for all ant species pooled: $F_{1,118} = 46.83$; $P < 0.0001$; $R^2 = 0.284$). We pooled these neighborhood data for all trees within each experiment, and then calculated the expected proportion of colonizations by ant species i (E_i) as follows:

$$E_i = \frac{\sum_{j=1}^n H_{ij}}{\sum_{i=1}^4 \sum_{j=1}^n H_{ij}}$$

where H_{ij} is the height of the j^{th} neighboring tree occupied by the i^{th} ant species. Observed frequencies of colonization (either by colony expansion or by foundress queens) were compared to these expected frequencies using χ^2 analysis (Zar 1996).

For the small saplings and coppicing shoots surveyed in Experiment 3, we calculated the expected colonization frequency by each acacia-ant species using the local frequency of trees ≥ 0.5 m tall occupied by that ant, weighting each tree by the lower boundary of its height class (0.5 m, 1 m, 1.5 m, or 3 m). All saplings within each pair of subplots were nondestructively surveyed for the active, mature workers that indicate expansionist colonization by nearby colonies. Accordingly, the height-weighted frequencies of all trees ≥ 0.5 m tall, pooled across both subplots, were used to calculate expected frequencies of colonization by expansion of mature ant colonies in that site. In contrast, claustral foundress queens were counted only within the 20×20 m sapling-removal subplot within each 20

$\times 40$ m plot. Observed frequencies of foundress queens belonging to each species were compared to expected values calculated from the weighted frequencies of trees ≥ 0.5 m within each sapling-removal subplot only.

We used chi-square goodness-of-fit tests to determine whether the observed, overall frequency of sapling colonization events by each ant species differed significantly from that expected, based on the weighted frequencies of trees ≥ 0.5 m occupied by each species, summed across all plots and averaged across years (Zar 1996). Colonizations by colony expansion vs. by foundress queens were analyzed separately. Next, we asked whether plot-to-plot and year-to-year variation in the local abundance of mature ant colonies affected the proportion of colonization events by each ant species within each plot.

All four ant species occupied saplings by colony expansion. For this type of colonization event, we used ANCOVA (SAS Institute 1992) to determine how the proportion of saplings colonized by mature colonies of a given acacia-ant within a plot was influenced first by the local, weighted frequency of trees ≥ 0.5 m occupied by that species (the covariate) and second, by ant species (4 levels). Each plot was surveyed in three different years, yielding 48 observations for this analysis (4 plots \times 3 surveys \times 4 ant species). Ant-species turnover on saplings is frequent, and substantial changes in the occupancy of larger trees also occurred over the three-year period. However, because subsequent surveys within a single plot are not independent samples of the community, the significance values reported for this analysis should be interpreted cautiously. Moreover, because only three of the four ant species' frequencies can vary independently within any given plot survey, the interaction term between local frequency and ant species is biased. Accordingly, the consistency of the spatial pattern among species was checked by repeating the ANCOVA for subsets of the data, excluding one ant species at a time.

Only three ant species (*C. mimosae*, *C. nigriceps*, and *T. penzigi*) produced the vast majority of foundress queens found on naturally occurring saplings. To identify causes of local variation in foundress queen frequency, we used an ANCOVA model in which the proportion of new queens within a sapling-removal plot belonging to one of those three species of acacia-ant was predicted first by the weighted relative frequency of trees ≥ 0.5 m occupied by that species (excluding *C. sjostedti* from the sample), and second, by ant species (3 levels). This analysis was based on 36 observations (4 plots \times 3 surveys \times 3 ant species). Because all saplings were destructively harvested in these samples, foundress queens and shoots were never resurveyed in subsequent years. Much as for the analysis of colony expansion onto saplings, only two of the three ant species' frequencies could vary independently within a plot, invalidating analysis of the interaction between local frequency and ant species. To check for

consistency in the pattern among ant species, the ANCOVA was repeated by excluding one ant species at a time.

Testing for nonrandom distribution of foundress queens among available swollen thorns.—During the destructive surveys used in Experiments 1 and 3, we noted the numbers of queens inside each available swollen thorn at the time of the census. A thorn was classified as “available” if it was not brittle with age, broken open, occupied by mature acacia-ant workers, or occupied by other insects (mostly spiders and lepidopteran larvae). The mean number of queens per available swollen thorn was calculated, and then the observed distribution of queens was compared to that expected based on a random, Poisson distribution with that same mean, using a chi-square goodness-of-fit test (Zar 1996). This analysis was done separately for swollen thorns on moderately damaged mature trees (Experiment 1) and for naturally occurring saplings (Experiment 3).

Analysis of survival during interspecific queen-to-queen combat.—When foundress queens cannot avoid contact with each other, the ensuing combats are often fatal. We have observed a number of fights in progress, but it is more typical to find the aftermath of these struggles, in which one queen remains alive inside a thorn with the body of another queen she has defeated. When queens of more than one species have attempted to colonize a single swollen thorn, the resulting pattern of queen mortality can be used to construct a competitive hierarchy among queens of the three ant species for which foundresses are commonly encountered. (Only three *C. sjostedti* foundress queens have been found in our surveys, and none of these occurred in thorns occupied by another queen.) For these encounters, we used χ^2 analyses to compare the survival of queens involved in contests with other acacia-ant species. Overall survival probabilities in these interspecific encounters were used to rank the competitive abilities of queens belonging to different species.

Comparing the demographic attributes of foundress queens.—We used observation windows to gather longitudinal demographic data on foundress queens that colonized coppicing shoots on the mature trees that were severely damaged in Experiment 2. During semi-weekly surveys we placed a numbered tag on each mature swollen thorn and recorded the survey date on which it first appeared. We also recorded the first date on which that swollen thorn was occupied by a foundress queen. “Days to colonization” was calculated as the difference between these dates. To determine whether acacia-ant species vary with respect to the efficiency with which they locate potential nest sites, we used analysis of variance (SAS Institute 1992: ANOVA procedure) to test whether the estimated number of days to colonization varied significantly among ant species. We continued to monitor queens within swollen thorns through August 2000. Most foundress queens

died over this 30-mo interval; some remained alive, while others were lost from the study when branches were inadvertently broken, window caulking plugs fell off, or numbered tags disappeared. Because we did not mark individual queens, subsequent colonizations of a single swollen thorn by queens of the same species sometimes meant that we could not determine whether the initial foundress or the newcomer had died in the conflict. When multiple colonizations led to ambiguity in assigning dates to death, egg production, or worker production, these data were eliminated from the analysis. Because dates of survival, egg production, and worker production are right-censored, we used failure-time analysis (Fox 1993) to compare the demographic attributes of queens belonging to the acacia-ant species. The LIFETEST procedure (SAS Institute 1992) was used to determine whether queens of three acacia-ant species showed significant variation in survival, time to laying of the first egg, and time to production of the first nanitic worker, based on the product-limit method (SAS Institute 1992).

RESULTS

Expansion of mature ant colonies onto empty trees

Although occupation of experimentally vacated trees by colony expansion roughly paralleled the abundance of the four acacia-ant species along the transects, there were consistent deviations from random expectation in Experiments 1 and 2 (Fig. 1A and B). Among colonies that took over moderately damaged, mature trees by expansion in Experiment 1, *Tetraponera penzigi* was underrepresented and *Crematogaster nigriceps* was overrepresented, when compared with their local frequencies (Fig. 1A: $\chi^2 = 9.59$, $df = 3$, $P = 0.023$; $n = 51$ trees). This same pattern was repeated even more dramatically for colony expansion onto severely damaged, coppicing trees in experiment 2 (Fig. 1B: $\chi^2 = 25.951$, $df = 3$, $P < 0.0001$; $n = 32$ trees). *Crematogaster* species, especially *C. nigriceps*, tend to occupy empty, mature *Acacia drepanolobium* trees by colony expansion, whereas *T. penzigi* does not.

In contrast to *Crematogaster*-dominated colony expansion onto empty, mature trees, all four ant-acacia species are likely to occupy small saplings and coppicing shoots growing near their established colonies. Pooled across three annual surveys conducted in the four 20×40 m sapling-removal and control plots, we found 73 *A. drepanolobium* trees <0.5 m tall that were occupied by mature workers. The proportions of saplings occupied by each of the four ant species were very similar to those expected, based on overall frequencies of mature colonies, averaged across all plots and years (Fig. 2A: $\chi^2 = 0.752$, $df = 3$, $P = 0.860$). Spatial and temporal variation in the frequency with which the four ant species expanded onto local saplings was explained, to a great extent, by variation in the local frequencies of mature acacia-ant colonies within

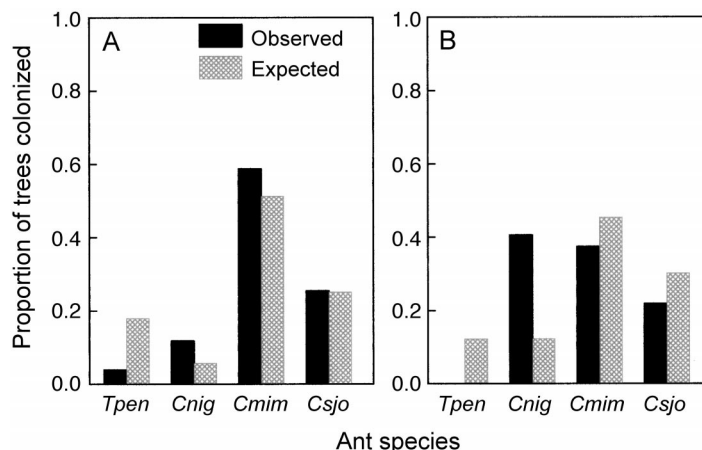


FIG. 1. Colonization of mature trees by expansion of nearby acacia-ant colonies. (A) The proportion of moderately damaged, empty trees occupied by expansion of mature colonies belonging to each of the four acacia-ant species (Experiment 1: $N = 51$ trees). (B) The proportion of severely damaged, regrowing trees occupied by expansion of mature colonies (Experiment 2: $N = 32$ trees). Ant species are ordered left to right, from the least competitive to most competitive, as measured by contests between mature colonies (*Tpen* = *Tetraponera penzigi*, *Cnig* = *Crematogaster nigriceps*, *Cmim* = *C. mimosae*, *Csjo* = *C. sjostedti*). Expected frequencies of expansionist colonization were calculated from the local, size-weighted frequencies of trees occupied by each acacia-ant species (see *Statistical analyses: Testing for nonrandom colonization . . .*). Chi-square tests were used to compare observed to expected frequencies of colony expansions.

each plot. The proportion of saplings occupied by colonies of each ant species in a given plot survey increased significantly with the local, weighted frequency of trees ≥ 0.5 m occupied by that species (Table 1A; Fig. 2B). Once plot-to-plot variation in the species composition of the local acacia-ant community was accounted for in the ANCOVA model, ant species had a nonsignificant effect on colonization frequency (R^2 for the ANCOVA = 0.331; R^2 for a linear regression on local species abundance alone = 0.247). Subsequent analysis of partially independent subsets of the data suggest that spatial variation in the abundance of mature *C. sjostedti* colonies is largely responsible for site-to-site variation in colony expansion frequencies. When *C. sjostedti* is dropped from the analysis (making frequencies of the other three species independent within plots), the positive relationship between local species abundance and frequency of colony expansion onto saplings is no longer statistically significant (ANCOVA $R^2 = 0.145$, $P = 0.4247$). For all subsets of the data that include *C. sjostedti*, both the overall ANCOVA and the effect of local species frequency are highly significant ($P < 0.005$).

Colonization of empty trees by foundress queens

Colonization of mature trees by foundress queens contrasted markedly with the pattern of host tree occupation by expansionist colonies (Fig. 3A and B; compare with Fig. 1A and B). On mature trees from which resident ants had been extirpated, foundress queens of *T. penzigi* and, to a lesser extent, *C. nigriceps* were far more common than would be expected from their local frequencies, whereas foundress queens of *C. mimosae* were rarer than expected, and *C. sjostedti* queens were

virtually absent (Experiment 1: Fig. 3A: $\chi^2 = 773.53$, $df = 3$, $P \ll 0.0001$; Experiment 2: Fig. 3B: $\chi^2 = 840.62$, $df = 3$, $P \ll 0.0001$). Only one *C. sjostedti* queen was found on the mature trees used as colonization targets in Experiment 2. Moreover, mature workers and nanitic workers were seen attending that queen, suggesting that she and her brood had been transplanted from a nearby, mature colony. Because it appears that foundress *C. sjostedti* queens very rarely establish independent colonies, we excluded this species in a second set of goodness-of-fit tests. These analyses confirmed that, among the three acacia-ant species producing independent foundresses on mature trees, *T. penzigi* queens and *C. nigriceps* queens are much more common than expected from the local frequencies of their colonies (Experiment 1: $\chi^2 = 515.56$, $df = 2$, $P \ll 0.0001$; Experiment 2: $\chi^2 = 507.27$, $df = 2$, $P \ll 0.0001$). New, independent colonies on empty trees are least likely to be founded by the two acacia-ant species that form competitively dominant colonies (*C. sjostedti* and *C. mimosae*), and disproportionately founded by the two species that are competitively subordinate as mature colonies (*C. nigriceps* and *T. penzigi*).

On small saplings, the frequencies of foundress queens are again strongly nonrandom, but differ instructively from the pattern seen on mature trees (Experiment 3: Fig. 4A: $\chi^2 = 726.908$, $df = 3$, $P \ll 0.0001$). As for foundress queens on mature trees (Experiments 1 and 2; Fig. 3A and B), queens of *C. sjostedti* were extremely rare. However, in contrast to the pattern for mature trees, *C. mimosae* queens were much more frequent on small saplings than expected, based on frequencies of mature colonies in the plots, while *T. penzigi* foundresses were somewhat less common

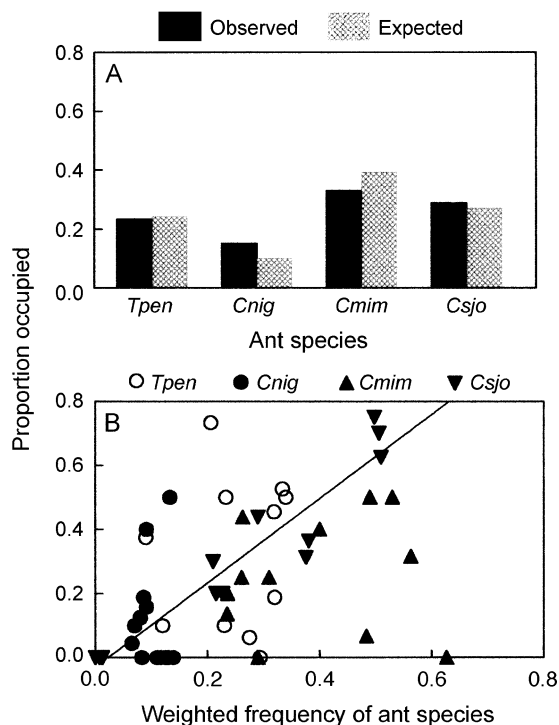


FIG. 2. Colonization of saplings by expansion of nearby acacia-ant colonies. (A) The proportion of naturally occurring saplings occupied by workers from nearby mature colonies of each acacia-ant species (Experiment 3: $N = 73$ saplings). Expected colonization frequencies were calculated from size-weighted frequencies of trees occupied by each acacia-ant species across all survey plots and annual surveys (see *Statistical analyses: Testing for nonrandom colonization . . .*). Chi-square tests were used to compare observed to expected frequencies. (B) Spatial variation in the colonization of naturally occurring saplings by workers from nearby colonies. Each point represents the pool of saplings found in a single survey conducted in one of four permanent 20×40 m plots in Experiment 3. Weighted frequencies of mature colonies belonging to each ant species were calculated, as described in the text (reference given above), for each plot sample. See Fig. 1 for species codes.

than expected (excluding *C. sjostedti*, $\chi^2 = 49.20$, $df = 2$, $P \ll 0.0001$). Local variation in the acacia-ant community explained a significant amount of plot-to-plot variation in the frequencies of foundress queens (Table 1B; Fig. 4B). However, there was a highly significant effect of ant species in the ANCOVA model, even after accounting for variation in the local composition of the acacia-ant community (R^2 for the ANCOVA = 0.740; R^2 for a linear regression on local species abundance = 0.421). As suggested by the goodness-of-fit analysis for pooled plot data (Fig. 4A), foundress queens of *C. mimosae* and *C. nigriceps* were more abundant than predicted from local frequencies of their colonies, whereas queens of *T. penzigi* were underrepresented (Fig. 4B). Subsequent analyses of partially independent subsets of the data suggest that the effect of local frequency on colonization by foundress queens

is due largely to *C. mimosae*. When this species is dropped from the analysis (making the local frequencies of *C. nigriceps* and *T. penzigi* independent), there is no relationship between local colony frequency and the abundance of foundress queens from each species (ANCOVA: $R^2 = 0.250$, $P = 0.891$). In subsets of the data including *C. mimosae*, both the overall ANCOVA and the effect of local species frequency are highly significant ($P < 0.0001$). The dramatic effect of removing *C. mimosae* from the analysis indicates that foundresses of this species are most likely to establish new colonies on small saplings relatively close to their natal colonies. Foundresses of *C. nigriceps* and *T. penzigi* apparently disperse further from their colonies of origin.

Distribution of foundress queens among thorns

The nonrandom distribution of foundress queens among available swollen thorns implies strong competition among foundresses for potential colony-initiation sites. In our 1997 census of new swollen thorns on moderately damaged trees from which resident ant colonies had previously been removed (Experiment 1),

TABLE 1. Consequences of local variation in the frequency of acacia-ant colonies for species representation in two types of sapling colonization. (A) Results of ANCOVA for the proportion of saplings colonized via colony expansion by each of the four acacia-ant species. (B) Results of ANCOVA for colonization of saplings and small coppicing shoots by foundress queens.

Source of variation	df	Type I			
		SS	MS	F	P
A) Colony expansions					
Overall model	4	0.793	0.198	5.33	0.0014
Local frequency	1	0.592	0.592	15.90	0.0003
Ant species	3	0.201	0.067	1.80	0.1607
Error	43	1.600			
B) Foundress queens					
Overall model	3	1.731	0.577	24.16	<0.0001
Local frequency	1	0.986	0.986	42.11	<0.0001
Ant species	2	0.746	0.373	15.93	<0.0001
Error	26	0.609			

Notes: (A) For each of four 20×40 m permanent plots surveyed in 1998, 1999, and 2000 we recorded canopy height and ant occupant for all trees ≥ 0.5 m tall within each plot. We then calculated a local, size-weighted frequency for the four ant species. The weighted frequency for each ant species within each plot was used as the covariate in the analysis ($N = 48$). (B) For each of four 20×20 m sapling-removal subplots in three annual surveys, we recorded the numbers of foundress queens found on destructively sampled saplings and calculated a frequency of foundresses for the three acacia-ants that produce independent queens (*Tetraponera penzigi*, *Crematogaster nigriceps*, and *C. mimosae*). In each survey (except for one subplot in 1998), we also recorded canopy height and ant occupant for all trees ≥ 0.5 m tall within each subplot. Local, size-weighted frequencies of trees occupied by each of the same three acacia-ant species were calculated, then used as a covariate in the analysis ($N = 30$, due to missing frequency data in 1998 and no saplings in one subplot in 2000). Type I sums of squares (SAS Institute 1992) were used for hypothesis testing in both models, to enter local frequency into the analysis first, followed by ant species.

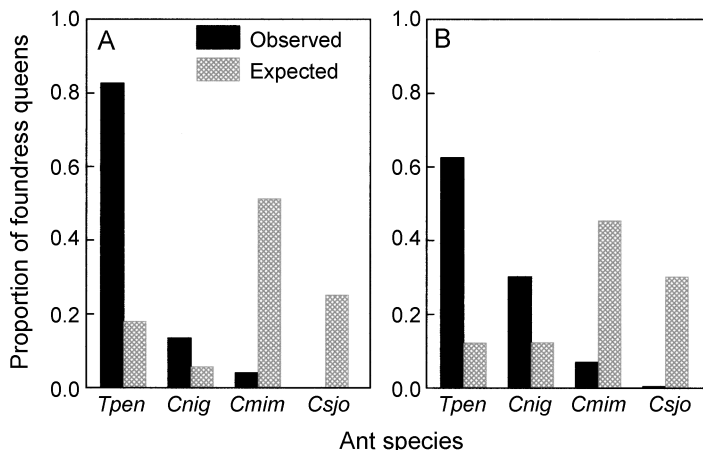


FIG. 3. Colonization of mature trees by acacia-ant foundress queens. (A) The proportion of foundress queens belonging to each ant species found on moderately damaged, empty trees (Experiment 1: $N = 247$ queens). (B) The proportion of foundress queens belonging to each species found on severely damaged, regrowing trees (Experiment 2: $N = 285$ queens). Totals include queens found on trees that had been partially occupied by workers from nearby colonies. Expected frequencies of foundresses were calculated from the local, size-weighted frequencies of trees occupied by each acacia-ant species (see *Statistical analyses: Testing for nonrandom colonization . . .*). Chi-square tests demonstrated highly significant differences between observed and expected frequencies. See Fig. 1 for species codes.

only 22.3% (41/184) of the thorns available to queens were not yet occupied; 56.5% of the thorns contained a single foundress queen, and the remainder (21.2%) contained multiple queens. In thorns with multiple queens, we found either two queens engaged in combat, or only a single queen that remained alive. On average, there were 1.180 queens (dead or alive) per swollen thorn. Comparing the observed numbers of foundress queens per thorn to the distribution expected for a Poisson distribution with a mean and variance of 1.18 revealed that foundress queens were significantly hyperdispersed among thorns (for five classes: $n = 184$ thorns; $\chi^2 = 37.48$, $df = 4$; $P < 0.0001$; Fig. 5A). Similarly, destructive surveys of naturally occurring saplings revealed an average of 0.918 queens per available swollen thorn, with 32.4% (134/414) of the available swollen thorns not yet occupied. Comparing expected frequencies of queens per available thorn to those expected for a random Poisson distribution again revealed significant hyperdispersion of foundresses among thorns ($n = 414$ thorns; $\chi^2 = 54.38$, $df = 4$; $P < 0.0001$; Fig. 5B). For both mature trees and saplings, there are fewer multiply colonized thorns than would be expected if queens colonized thorns at random with respect to the presence of other queens. However, even though potential foundresses avoid each other when possible, apparent nest site limitation leads to frequent struggles between queens. In Experiment 1, we found 17 *T. penzigi* queens inside a single swollen thorn, with only one queen remaining alive. This is an extreme example, but the overall picture that emerges from our surveys is one in which competition among foundress queens for nest-initiation sites is very intense.

Mortality of foundresses in interspecific queen-to-queen combat

Our surveys of swollen thorns on trees from which ant colonies had previously been extirpated, as well as of thorns on naturally occurring saplings and coppicing shoots of *A. drepanolobium*, located 568 thorns that had been colonized by foundress queens. Of these, 67 thorns contained queens of two different species. Both queens died in three of these thorns; in the remainder, one queen survived the conflict. No *C. sjostedti* queens occurred in thorns occupied by another queen, and so this species is excluded from the following analyses.

The outcomes of queen-to-queen encounters were biased in favor of *T. penzigi* queens, which defeated *C. nigriceps* queens in 26 of 41 battles ($\chi^2 = 2.95$, $df = 1$, $P = 0.089$), and defeated *C. mimosae* queens in all 16 of the encounters we observed ($\chi^2 = 16.00$, $df = 1$, $P < 0.0001$). Although *C. nigriceps* queens defeated *C. mimosae* in 5 out of the 7 encounters in which one queen survived, this difference was not significant ($\chi^2 = 1.29$, $df = 1$, $P = 0.26$). Pooled over all fatal queen-to-queen encounters, foundresses of *T. penzigi* survived most often, whereas *C. mimosae* foundresses were least likely to survive (Fig. 6). Among these three species, the ranking of acacia-ant species by the combative ability of their foundress queens is the reverse of the ranking seen among mature colonies in staged conflicts (Stanton et al. 1999, Palmer et al. 2000).

Phenology and demography of foundress queens

Through the course of Experiment 2, 281 foundress queens were monitored in longitudinal surveys of 106 swollen thorns on 8 heavily damaged, coppicing trees.

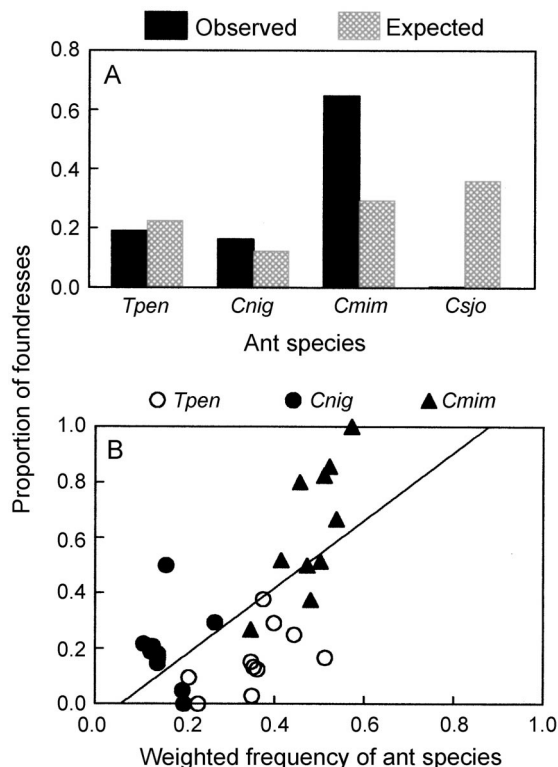


FIG. 4. Colonization of saplings by foundress queens. (A) The proportion of foundress queens belonging to each acacia-ant species that were found on small saplings (Experiment 3: $N = 364$ queens). Queens found in one plot survey were excluded in this analysis because the local abundances of mature colonies were not recorded. Expected colonization frequencies of trees occupied by each acacia-ant species, pooled across plots and annual surveys (see *Statistical analysis: Testing for nonrandom colonization* . . .). Chi-square tests were used to compare observed to expected frequencies. (B) Spatial variation in colonization of saplings by foundress queens. Each point represents the pool of foundress queens found in a destructive harvest of saplings in one of four permanent 20×20 m plots. New saplings within the same plots were destructively harvested in each survey. Weighted frequencies of mature colonies belonging to each ant species were calculated, as described in the text, for each plot sample. See Fig. 1 for species codes.

Although the numbers of foundress queens often differed from those expected based on the local frequencies of acacia-ant colonies (see above), there is no evidence that foundresses of some species discover new swollen thorns more quickly than others. On average, 35 d elapsed between the first census in which a swollen thorn was mature and the arrival of any given foundress queen at that thorn. ANOVA demonstrated that the timing of a queen's arrival does not vary significantly among the three acacia-ant species that produce independent foundresses ($P = 0.2828$; Table 2). Similarly, the proportions of queens arriving first at each new swollen thorn mirrored the frequencies of foundress queens belonging to the three species overall ($\chi^2 = 1.03$; $df = 2$; $P > 0.50$).

Overall survival rate did not vary significantly among foundresses of *T. penzigi*, *C. nigriceps*, and *C. mimosae* (Table 2), and the nearly linear survivorship curves (Fig. 7) suggest that per capita rates of mortality are relatively constant during the claustral period of colony founding. Although there is a tendency for *C. mimosae* foundresses to die sooner, high demographic variability and the small sample size for this species preclude a powerful statistical comparison with the other species.

There is marked variation among acacia-ant species in the rate at which critical benchmarks in colony development are attained. Foundress queens of *T. penzigi* tend to be slowest in initiating new colonies once they have sealed themselves within a swollen thorn (Table 2; Fig. 7). *C. nigriceps* queens laid eggs sooner than *T. penzigi* queens ($\chi^2 = 8.42$; $df = 1$; $P = 0.0037$), but the difference between *T. penzigi* and *C. mimosae* was not significant ($\chi^2 = 0.21$; $df = 1$; $P = 0.6460$). It takes 2–4 mo for surviving claustral queens to produce their first nanitic workers, and *T. penzigi* queens are slower in reaching this stage than their competitors. *Crematogaster nigriceps* and *C. mimosae* queens produce their first workers in just over half the time it takes *T. penzigi* queens (Table 2: for the pairwise comparisons with *T. penzigi*, $\chi^2 = 16.63$; $df = 1$; $P = 0.0001$; and $\chi^2 = 12.94$; $df = 1$; $P = 0.0003$, respectively). On average, 14.8% of foundress queens survived to produce new workers, and the probability of surviving to this stage was nearly identical among the three species of foundress queens ($\chi^2 = 0.21$; $df = 2$; $P = 0.91$).

DISCUSSION

Relatively little attention has been paid to the factors that promote local diversity within communities of tropical plant-ants (but see Davidson and Fisher 1991, Davidson 1997, Yu and Davidson 1997). Even though different ant colonies very rarely cohabit a single host plant, it is common to find that multiple, obligately symbiotic plant-ant species share host species within any given geographic region (reviewed in Hocking [1970], Davidson and McKey [1993b], and McKey and Davidson [1993]). Two principal mechanisms have been proposed for the maintenance of species diversity within these intensively competing guilds: niche partitioning along habitat productivity gradients and competition-colonization trade-offs. Davidson and co-workers (Davidson and Fisher 1991, Davidson 1997, Yu and Davidson 1997) consistently find that competitively dominant ants tend to be most abundant in productive microhabitats, and suggest that habitat heterogeneity facilitates species coexistence. This same pattern occurs in our acacia-ant study system, and will be the focus of future publications (Palmer 2001). In this paper, we have focused exclusively on the second pro-

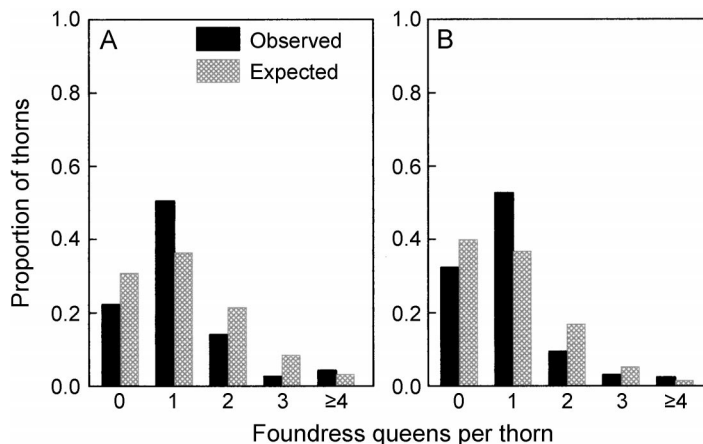


FIG. 5. Numbers of foundress queens per available swollen thorn on unoccupied host trees. (A) Distribution of queens on moderately damaged, mature trees from which resident ants had been extirpated previously (Experiment 1: $N = 184$ thorns). (B) Distribution of queens surveyed on naturally occurring saplings < 0.5 m tall (Experiment 3: $N = 414$ thorns). For both surveys, the observed frequencies of queens per thorn were found to deviate significantly from random Poisson frequencies using a chi-square goodness-of-fit test for five classes. Data include all queens of the four acacia-ant species, both living and dead, found on trees that had not been fully occupied by mature workers from mature colonies.

posed mechanism, competition–colonization trade-offs.

Until recently, the case for competition–colonization trade-offs among plant-ants has been based principally on the observation that aggressive species tend to be found on larger (presumably older) hosts, while smaller or more docile species predominate on smaller plants (Janzen 1975, Davidson et al. 1989, Longino 1991, Davidson and McKey 1993b, Young et al. 1997). Stud-

ies documenting ant species turnover on single host plants over time (McKey 1984, Palmer et al. 2000) are also consistent with the idea that competition–colonization trade-offs lead to successional replacement among plant-ants. However, we know of no previous studies that have used experimental approaches to test for the existence of competition–colonization trade-offs in these communities.

Acacia drepanolobium host trees appear to be a limiting resource for the four species of symbiotic acacia-ants that coexist within black cotton habitats in East Africa (also see Longino 1989). In our study site and elsewhere (Hocking 1970), vacant trees over 0.5 m tall are relatively rare (Young et al. 1997), and acacia-ant colonies frequently battle for the possession of occupied trees (Palmer et al. 2000). Even so, disturbance, stress, and host recruitment create empty trees that are targets for colony expansion or initiation. Low-intensity ground fires kill off many acacia-ant colonies, while incurring only moderate damage to taller host trees (T. Palmer, unpublished data). After elephant feeding or severe fire causes catastrophic damage to the main stem of a mature tree, displacing the occupying colony, a new canopy can be produced by vigorous coppicing during the subsequent rainy season. During drought periods, ant colonies occupying multiple trees may abandon the least productive host trees (Palmer et al. 2000). After recovery from disturbance or stress, any of these larger trees can potentially support many plant-ants. In contrast, while there are many new host trees recruiting into the population as saplings or coppices, these small trees have high rates of mortality (Palmer et al. 2000) and produce domatia and leaves relatively slowly. As is commonly reported in other myrmecophytes (Schupp 1986, Vasconcelos and Casimiro 1997), young host plants are often unoccu-

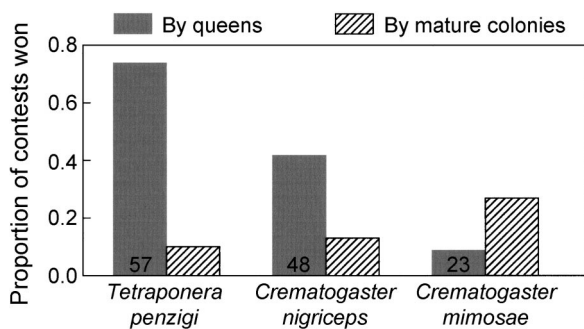


FIG. 6. Survival of acacia-ant foundress queens after interspecific combat over nest-initiation sites. Solid grey bars summarize the outcome of fatal struggles between foundress queens of different species that attempted to colonize the same swollen thorn. Numbers of queens involved in interspecific fights for each species are shown. Overall survival rates, pooled across adversary species, differed significantly ($P < 0.05$) between all pairs of acacia-ants, according to chi-square tests. The hatched bars summarize the results of an earlier experiment, in which conflicts were experimentally staged between neighboring colonies of different acacia-ant species (Stanton et al. 1999, Palmer et al. 2000). A colony was scored as a “winner” in these conflicts if its workers fully occupied the adversary’s host tree within 320 d. Proportions of wins in intercolony conflicts do not sum to 1, since some staged conflicts did not result in a host-tree take-over.

TABLE 2. Phenology and demography of three species of acacia-ant foundress queens.

Demographic or phenological parameter	Foundress species			Results of H_0 test		
	<i>Tetraponera penzigi</i>	<i>Crematogaster nigriceps</i>	<i>Crematogaster mimosae</i>	Test statistic	df	P
Days to arrive at thorn	36.51 ± 3.98 (177)	29.10 ± 5.02 (84)	48.20 ± 14.20 (20)	$F = 1.27$	2, 278	0.2828
Days alive	79.86 ± 6.43 (170)	101.28 ± 13.12 (79)	34.52 ± 7.46 (15)	$\chi^2 = 1.360$	2	0.5067
Days to first egg	22.17 ± 2.58 (117)	11.71 ± 2.78 (59)	9.00 ± 2.98 (14)	$\chi^2 = 9.372$	2	0.0092
Days to first workers	120.16 ± 5.81 (65)	68.21 ± 4.44 (39)	55.20 ± 11.75 (5)	$\chi^2 = 20.856$	2	<0.0001

Notes: Data are means ± 1 SE; sample sizes for each estimate are given in parentheses. Means and standard errors were derived either from ANOVA (for days to arrival at a swollen thorn, an uncensored variable) or from product-limit estimates of right-censored failure functions (for days alive, days to first egg, and days to first nanitic worker; SAS Institute 1992; LIFETEST procedure). Sample sizes for each estimate decrease in subsequent stages of the colony life cycle due to mortality of foundress queens, loss of thorn markers, or loss of queen identification due to multiple colonizations of the same swollen thorn. For each statistical analysis, the tested null hypothesis was that the three acacia-ant species do not vary with respect to a given demographic or phenological parameter.

pied by mature colonies, but repeatedly colonized by foundress queens.

Our analysis indicates that strong trade-offs exist between success at two stages of the colony life cycle in these ant species: (1) competition between mature colonies for possession of host trees, and (2) the initiation of new colonies by foundress queens. *Crematogaster sjostedti*, the ant species producing the most competitively dominant mature colonies (Stanton et al. 1999, Palmer 2001), is very rare within the pool of foundress queens attempting to establish new, independent colonies on vacant trees or saplings of *A. drepanolobium*. Conversely, the two acacia-ant species that are least likely to vanquish neighboring colonies in battles over host trees, *Tetraponera penzigi* and *C. nigriceps*, are significantly overrepresented among foundress queens colonizing available, mature trees. *Crematogaster nigriceps* queens also colonize small saplings disproportionately. Moreover, the apparent competitive hierarchy among queens of *T. penzigi*, *C. nigriceps*, and *C. mimosae* is the reverse of that among mature colonies. Although mature colonies of *T. penzigi* are competitively subordinate to *Crematogaster* colonies, direct encounters between foundress queens strongly favor *T. penzigi* over competing foundresses. Similarly, although mature colonies of *C. mimosae* tend to be competitively dominant over mature colonies of *T. penzigi* and *C. nigriceps*, *C. mimosae* queens are the most likely to die in queen-to-queen competition for colonization sites. Our longitudinal surveys of claustral foundresses within swollen thorns revealed that ~40% of these young queens were killed by other queens. Thus, the reversal of the competitive hierarchy we observed during colony establishment could be important in maintaining high species diversity within this guild of acacia-ants.

In contrast to the formation of new colonies by foundress queens, the tendency of colonies to expand onto nearby, empty trees roughly parallels the competitive hierarchy between the three *Crematogaster* species and *T. penzigi*. *Crematogaster* are more likely to take over empty trees by colony expansion, just as they tend to

displace resident *T. penzigi* colonies in battles over occupied trees (Palmer et al. 2000). The expansionist tendencies of *Crematogaster* explain why most mature colonies of these species encompass multiple trees, while *T. penzigi* colonies most often occupy only a single, contiguous canopy (Stanton and Young 1999, Palmer 2001).

There is some evidence for a trade-off between intercolony competition and expansive colonization, even among the *Crematogaster* species. *Crematogaster nigriceps*, which is competitively subordinate to the other *Crematogaster* species in intercolony conflict over occupied trees, shows the greatest tendency to expand onto empty trees, suggesting that this ant species is especially opportunistic when "empty space" becomes available nearby. Given this tendency, the smaller average size of *C. nigriceps* colonies in our primary study site is probably due to their poor ability to compete with larger colonies of *C. mimosae* and *C. sjostedti* in battles over the trees they occupy (Palmer et al. 2000, Palmer 2001).

There are strong parallels between the patch dynamics we documented within this acacia-ant guild and those seen in highly productive and highly competitive terrestrial (e.g., Grime 1973, Platt 1975, Harper 1977, Hartshorn 1980) and marine (e.g., Dayton 1975, Sale 1977, Paine 1979, Bertness and Ellison 1987, Barnes and Clarke 1998, Brewer et al. 1998) communities of sessile organisms (also see Holldobler and Wilson 1990, Anderson 1991). Several generalizations have emerged from such systems (Horn 1974, Tilman 1994). Competitive dominants are often characterized by larger stature, greater allocation to resource acquisition, the ability to spread vegetatively, and, in some cases, a dense "phalanx" growth form (Lovett-Doust 1981, Platt and Weiss 1985, Bertness and Ellison 1987, Tokeshi and Romero 1995). Individuals of these species are difficult to displace once established, infrequently recruit from sexual propagules, and usually occupy nearby, vacant patches by vegetative spread. Conversely, species found principally in recently disturbed microhabitats tend to have smaller stature, are less likely

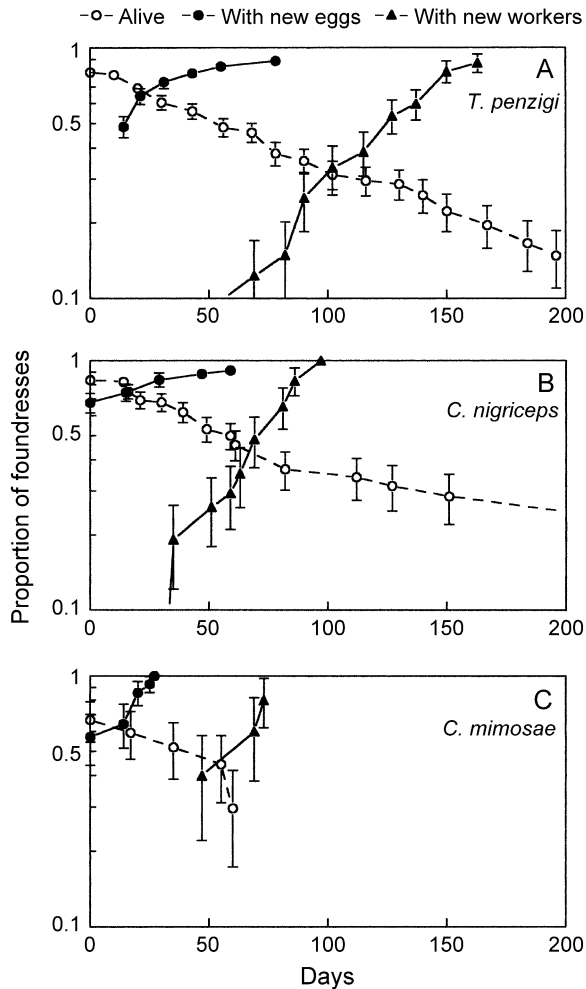


FIG. 7. Survivorship of foundress queens and rates of development in incipient colonies of three acacia-ant species. Data are from longitudinal surveys of foundress queens colonizing severely damaged, coppicing trees in Experiment 2: (A) *Tetraponera penzigi* ($n = 170$); (B) *Crematogaster nigriceps* ($n = 79$); (C) *C. mimosae* ($n = 15$). Data (means \pm 1 SE) are plotted on a logarithmic scale to facilitate comparison of slopes between species and across time periods. The first census in which a queen was discovered within a swollen thorn was scored as day 0. Uncensored survival values and standard errors for each day were derived from the LIFETEST procedure (SAS Institute 1992).

to occupy space by lateral expansion, and produce larger numbers of highly dispersive sexual propagules (e.g., Werner and Platt 1976, Tilman and Wedin 1991). In part because of these varying dispersal strategies, the species composition of new colonists within recent disturbances only loosely parallels that of the surrounding, mature community (Harper 1977, Ribbens et al. 1994).

A number of these same life-history trait associations characterize the four species of acacia-ants that coexist within populations of *A. drepanolobium*. Large colonies of the competitively dominant acacia-ants *C. sjostedti*

and *C. mimosae* proliferate principally by the expansion of existing colonies, rather than through the founding of new, independent colonies on vacant trees. *C. sjostedti* exhibits the most extreme "perennation" strategy of all the species. Its queens are virtually absent from the pool of independent foundresses, and dissection of its mature colonies has revealed the presence of multiple, laying queens within a single tree (T. Palmer, unpublished data). As observed in other polygynous ant species (Hollдобler and Carlin 1985, Keller 1991), foundresses of *C. sjostedti* may establish principally within the confines of existing colonies. *C. mimosae*, whose mature colonies are competitively subordinate only to *C. sjostedti*, displays an intermediate colonization strategy. Its foundress queens are underrepresented on mature, empty trees (representing empty patches of potentially high value), but appear to be overrepresented on young saplings close to their natal colony. Small colonies of *C. mimosae* appear to have only a single laying queen, but it is possible that large colonies may be polygynous. In contrast, a disproportionately high number of *T. penzigi* and *C. nigriceps* foundresses colonize large, empty trees, suggesting that colonies of these species make an unusually high investment in dispersive sexual reproductives. Dissections of *T. penzigi* and *C. nigriceps* colonies consistently yield only a single laying queen (T. Palmer, M. Stanton, and B. Barringer, unpublished data), suggesting a purely monogynous strategy in which proliferation of the species hinges on the founding of new colonies.

Although it is tempting to rank these acacia-ant species along a strict life-history continuum from r -selected to K -selected strategies (MacArthur and Wilson 1967), there are some intriguing exceptions to this generalization. For example, it would be misleading to characterize *T. penzigi* as a poorly competing fugitive, since foundress queens of this species dominate in direct competition with queens of other species. The overrepresentation of these queens on vacant, mature trees, compared with saplings, may reflect their ability to exclude the queens of other species from the best potential nesting sites. Moreover, unlike "weedy" fugitives in some other ant-plant systems (Janzen 1975), incipient colonies of *T. penzigi* actually develop more slowly than those of their *Crematogaster* competitors. We found no evidence that individual foundress queens of *T. penzigi* are more effective dispersers than the queens produced by other species, as they do not appear to discover available swollen thorns faster than would be predicted from their abundance. Similarly, *C. nigriceps* displays some classic r -selected traits, including rapid early colony development and consistent overrepresentation within the pool of colonizing queens, but is also an opportunist that readily colonizes nearby, vacant trees by colony expansion. The rapidity with which colonies of *C. nigriceps* and *C. mimosae* produce their first nanitic workers suggests that these

species may experience a competitive advantage when multiple, new colonies initiate in separate swollen thorns and compete for possession of the same tree (also see Davidson et al. 1989, Perlman 1992, Vasconcelos 1993). Finally, queens produced by competitively dominant *C. mimosae* colonies compete poorly with queens of the other species; their foundresses are rare on large, vacant trees, quite possibly because interference competition limits their access to the most valuable nest-initiation sites.

Our results strongly support the niche hypothesis as a basis for competition–colonization trade-offs in this guild of acacia-ants, but we cannot exclude the possibility that dispersal limitation may also be operating. According to the dispersal-limitation hypothesis, colonization success is principally dictated by dispersal ability, rather than by competitiveness within new resource patches (Ribbens et al. 1994, Hurtt and Pacala 1995). In this view, open resource patches are seen as refuges from competition, and competition–colonization trade-offs arise because competitive dominants produce fewer successful propagules (Schupp et al. 1989). Alternatively, the niche hypothesis suggests that competition–colonization trade-offs occur because species that are superior competitors in undisturbed habitat are poorer competitors under the conditions that prevail early in the colonization process (Tilman 1990, Pacala et al. 1996).

These acacia-ant species vary in their ability to compete for nest-initiation sites, a pattern that is consistent with the niche hypothesis. Among the species that produce independent foundresses, the competitive ranking among fighting queens is the reverse of that between mature colonies fighting for possession of *A. drepanolobium* trees. Moreover, queens of the three species contributing to the pool of independent foundresses are most common on different types of trees. Queens produced by the competitively subordinate colonies of *T. penzigi* are overrepresented on vacant trees of high potential quality, whereas queens of *C. mimosae*, a competitive dominant, are most often found on smaller saplings. This pattern of distribution is consistent with the hypothesis that *T. penzigi* queens are able to exclude most *C. mimosae* queens from the most attractive take-over targets. However, in contrast to most articulations of the niche hypothesis, the resulting competition–colonization trade-off reflects ontogenetic changes in competitive ability within acacia-ant species, rather than uniquely challenging environmental conditions on vacant host trees. Competition among the workers of young colonies for possession of multiply colonized trees is also likely have important consequences for species coexistence, but we have yet to compare the performance of the different acacia-ant species at this stage in colony development.

Some variation in the propensity to found new colonies among these four acacia-ant species may reflect dispersal limitation. Possibly because *T. penzigi* col-

onies make a greater allocation to reproductives, *T. penzigi* queens occupy the vast majority of available swollen thorns on empty trees, the high-quality resource “patches” in our system. Conversely, lower allocation to dispersing reproductives in more dominant acacia-ant species (especially *C. sjostedti*) may limit their discovery of empty trees. However, in contrast to the dispersal-limitation hypothesis, our data indicate that empty *A. drepanolobium* trees are not refuges from competition. Foundress queens are significantly hyperdispersed among available swollen thorns, indicating strong competition for nest-initiation sites. Moreover, fatal battles between foundresses are a major source of mortality for incipient colonies. Thus, competition among foundress queens for nesting sites may be no less intense and important than competition among mature colonies for possession of trees.

Symbiotic ant–plant associations are promising systems in which to test alternative hypotheses for the coexistence of species that compete strongly for a single, limiting resource. The intrinsically dynamic nature of myrmecophyte plant populations suggests that competition–colonization trade-offs could be a potent force promoting species coexistence, especially in host plants that occupy early to mid-successional niches. Documenting these trade-offs, and evaluating their importance relative to other mechanisms for species coexistence, will require experimental studies of colonization and competition, in concert with long-term longitudinal data on host-plant demography, colony allocation strategies, and patterns of host-plant occupancy by ants over space and time.

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