A role for indirect facilitation in maintaining diversity in a guild of African acacia ants

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Abstract. Determining how competing species coexist is essential to understanding patterns of biodiversity. Indirect facilitation, in which a competitively dominant species exerts a positive effect on one competitor by more strongly suppressing a third, shared competitor, is a potentially potent yet understudied mechanism for competitive coexistence. Here we provide evidence for indirect facilitation in a guild of four African *Acacia* ant species that compete for nesting space on the host plant *Acacia drepanolobium*, showing that a competitively dominant acacia ant species indirectly creates establishment opportunities for the most subordinate species that may help to maintain diversity. Using long-term observational data and field experiments, we demonstrate that the competitively dominant ant species outcompetes two competitively intermediate species, while tolerating colonies of the subordinate competitor; this creates opportunities for local colonization and establishment of colonies of the subordinate species within the dominant species' territories. Host plants occupied by this subordinate species are then more likely to be colonized by the intermediate species, which in turn are more likely to be displaced by the dominant species. This process has the potential to generate a cyclical succession of ant species on host trees, contributing to stable coexistence within this highly competitive community.

Key words: acacia ants; Acacia drepanolobium; *ant–plant interactions; competition; indirect facilitation; species coexistence.*

INTRODUCTION

Understanding the mechanisms that promote and maintain biological diversity has always been a core problem in community ecology, and the problem has assumed particular importance with the intensification of human environmental impacts. Groups of competing species, called "guilds," are often characterized by hierarchies in competitive ability (reviewed in LeBrun 2005). These competitive inequalities underlie the central paradox of diversity: how do lesser competitors coexist within the same habitat as their stronger competitors? Over the past decades, multiple mechanisms have been

proposed to explain the coexistence of groups of competing species, which variously invoke resource partitioning, trade-offs in performance under different environmental conditions, differences among species in recruitment ability, and natural enemies that target more abundant species (reviewed in Chesson 2000, Holt 2001, Palmer et al. 2003).

While much of species-coexistence theory assumes that competition results in direct negative interactions among species, competitors may also exert indirect positive effects on one another via suppression of a shared competitor (Levine 1976). Referring to this phenomenon of "indirect" or "apparent" facilitation, Levine (1999) later proposed that indirect facilitation is more likely to operate when different pairs of species within a guild compete for slightly different sets of resources, or have different resource-acquisition strategies. For example, Davidson (1980) documented body-size-based seed preferences in three harvester ant species of varying size in the Chihuahuan desert. By suppressing the abundance of an intermediate-sized competitor, the largest harvester ant species had net positive effects on the smallest harvester ant species. While a variety of theoretical models (Levine 1976, Stone and Roberts

1991, Roberts and Stone 2004, Allesina and Levine 2011) suggest that indirect facilitation could be common within competitive networks, there are relatively few experimental studies that document indirect facilitation and its underlying mechanisms (Brooker et al. 2008), especially within animal communities (but see Davidson 1980, 1985, Thompson et al. 1991, Steiner et al. 2005).

In this paper, we investigate the potential for indirect facilitation to promote coexistence in a guild of four acacia ant species that compete intensely for exclusive occupancy of *Acacia drepanolobium* host trees in central Kenya. Within this system, individual trees are occupied by a single colony of symbiotic ants, although colonies may occupy more than one host plant. Experimental manipulations (Palmer 2004) and long-term monitoring of ~1800 marked trees (Stanton et al. 1999, Palmer et al. 2000) demonstrate a consistent, linear hierarchy in competition among mature colonies for host plants, where competitive success is a direct function of colony size (Palmer 2004). In this hierarchy, *Crematogaster sjostedti* > *C. mimosae* > *C. nigriceps* > *Tetraponera penzigi*, and competition occurs via direct takeover of host plants by neighboring colonies. Despite intense interspecific competition for host plants, the four symbiotic ant species coexist at fine spatial scales, with all four species typically found within any given 30×30 m area. Although the relative frequency of different species varies among sites throughout Kenya's Laikipia County, all four species are likely to be found within most 0.25-ha areas of *A. drepanolobium* habitat.

Although they are all members of a single guild, these four acacia ant species occupy host trees in contrasting ways. *Tetraponera penzigi*, *C. nigriceps*, and *C. mimosae* nest entirely within swollen-thorn domatia produced by the plant, and are specialists on *A. drepanolobium* in our study area. The fourth species, *C. sjostedti*, nests principally within stem cavities on larger trees excavated by long-horn beetle (Cerambycidae) larvae, but its workers occasionally occupy swollen thorns on smaller trees (whether *C. sjostedti* abundance is limited by the abundance of these beetles is not known). Individual *Crematogaster* colonies usually span multiple trees consisting of a core group of relatively large trees (≥ 1.0 m tall) and a variable number of smaller "satellite" trees (<1.0 m tall), whereas *T. penzigi* colonies typically control only a single, contiguous canopy (number of trees per colony is 1.14 ± 0.20 [mean $\pm$ SE]; see also Palmer 2004). Trees up to 6 m in height occur in the study area, but most trees are <2.5 m tall, and all four species of acacia ants can be found on trees 1–2 m tall (Young et al. 1997, Palmer 2001).

The competitive hierarchy among mature colonies manifests as a quasi-successional sequence of ant symbionts on individual trees over time, as the small colonies of *T. penzigi*, which are most common on small trees, are gradually displaced by successively larger multi-tree colonies of *Crematogaster* species as the host trees grow. Some young trees are directly colonized by

C. nigriceps and *C. mimosae*, but these colonies are also vulnerable to take-over by larger, multi-tree colonies of higher-ranking competitors.

Our investigation into indirect facilitation was motivated by observations that small colonies of *T. penzigi* (the most subordinate species) often are found in very close proximity to large colonies of the *C. sjostedti* (the competitive dominant), despite evidence for strong interference competition among neighboring colonies in this highly space-limited community. We hypothesized that this pattern might result from three differences in patterns of resource use by these species. First, unlike the three *Crematogaster* species, *T. penzigi* does not forage off of their host trees, instead gleaning pollen and fungus from the surfaces of host plants. Second, *T. penzigi* destroys all nectaries on its host plants; in contrast, while *C. mimosae* and *C. nigriceps* depend heavily on *A. drepanolobium*'s extrafloral nectar, *C. sjostedti* workers rarely visit nectaries and appear to incorporate little nectar into their diet (Palmer et al. 2008). The majority of *C. sjostedti*'s diet is composed of insect parts and prey they obtain from foraging on the ground around their host plants. Finally, *C. sjostedti* is typically found on large-stemmed trees where creamby-cid beetles can excavate large cavities that this ant species uses to house brood, workers, and reproductives; contrastingly, *T. penzigi* colonies often occupy very young acacias that are too small to be tunneled by cerambycids. As a result, *T. penzigi* may not compete strongly with *C. sjostedti* for nest space or food (as do *C. nigriceps* and *C. mimosae*), raising the possibility that *C. sjostedti* might tolerate neighboring small *T. penzigi* colonies.

To evaluate whether *C. sjostedti* indirectly facilitates *T. penzigi*, we examined spatial patterns of establishment, persistence, and displacement at two critical stages in the life cycles of these acacia ants: (1) colony initiation, when foundress queens and their young offspring are sealed within swollen thorn domatia on prospective host plants, and (2) colony establishment, when young independent colonies resulting from successful founding events have fully occupied small trees.

METHODS

All research was conducted at the Mpala Research Centre, part of a private conservancy in Laikipia County ($0°17'$ N, $37°52'$ E). Our study area was situated on black-cotton vertisol soils where *A. drepanolobium* constitutes $>95\%$ of the overstory cover (Young et al. 1997).

Stem diameter surveys: Is an ant species' position in the competitive hierarchy correlated with the average stem diameter of its host plants?—We conducted stem-diameter surveys of all host plants ≥ 1.0 m in height in six permanently marked 1-ha plots within our study area. For each host plant, we recorded the identity of the ant occupant, and the diameter of the host plant at 30 cm height.

Swollen thorn surveys: Do the three Crematogaster *species vary in the degree to which their colonies use swollen thorns on small trees within their multi-tree colonies?*—Foundress queens are unable to initiate colonies in thorns already occupied by plant-ant workers, so underutilized trees (i.e., those with empty swollen thorn domatia) represent opportunities for colonization. Along randomly oriented transects, we located 60 focal trees <1 m tall and determined whether these trees were "satellite" trees (small trees within a colony's territory, and controlled and/or occupied by that colony) of neighboring colonies by performing experimental transplants of workers between focal trees and neighboring trees occupied by the same species and watching for aggressive behavior (workers from different colonies are always aggressive toward one another [Palmer 2004]). Independent colonies on small trees were excluded from this analysis. If transplanted workers were not mutually aggressive, we concluded that the occupants of the focal tree were members of the same colony as on the neighboring tree. For each focal satellite tree, we opened five swollen thorns and counted the number of workers in each swollen thorn, also recording the presence of brood, winged reproductive adults, scale insects, and other insects. For analysis, we pooled worker numbers for all five swollen thorns on a given tree. We tested for differences in the number of workers per swollen thorn and the proportion of swollen thorns containing brood for the three Crematogaster species using one-way ANOVA. Tukey's HSD tests were used for pairwise comparisons among the ant species.

Claustral queen surveys: Are claustral queens of a given species differentially successful within territories controlled by the three Crematogaster *species?*—Along transects through the study area, we located sites within or immediately adjacent to the boundaries of multi-tree colonies (determined by experimental transplants of workers as for *Methods: Swollen thorn surveys.*..) of the three Crematogaster species. Each collection area was identified a priori as a *C. sjostedti*, *C. mimosae*, or *C. nigriceps* territory, and we avoided making collections in sites with neighboring trees occupied by more than a single species. Colonized swollen thorns were identified by the presence of small sealed entry holes on the surface of the thorn. We searched exhaustively for sealed swollen thorns on young trees and coppices within these sites and collected those thorns without knowing what species of foundress queen was inside. Sealed swollen thorns ($N = 180$ thorns) were later opened in the laboratory, and each foundress was identified as either *C. mimosae*, *C. nigriceps*, or *T. penzigi* (we have never discovered a foundress *C. sjostedti* queen sealed within a swollen thorn). Because *C. nigriceps* colonies control very little ground area, we found very few sealed swollen thorns within their territories. Thus, we pooled thorns from *C. nigriceps* and *C. mimosae* territories, and then tested for independence between foundress species and the two types of local neighborhoods (*C. sjostedti* vs.

other Crematogaster spp.) using a chi-squared statistic for a 3×2 contingency analysis.

Queen detection tests: Do mature colonies of C. sjostedti *and* C. mimosae *differ in the efficiency with which they detect and kill claustral queens of different species?*—To test for differences between *C. sjostedti* and *C. mimosae* in the ability to detect and kill claustral queens of different species, as well as for interspecific differences in the ability of claustral queens to escape detection and death, we conducted queen-detection tests in July 2006. We collected swollen thorns containing claustral queens from small saplings and coppices within the grass layer of a recently burned site. In the lab, we drilled a small hole in each thorn on the side opposite the queen's sealed entry hole, and inserted a lighted borescope (RBAC series; UXR, Simi Valley, California, USA) to determine the species of claustral queen in residence. Independent foundress queens of *C. sjostedti* are extremely rare (Stanton et al. 2002), and so our sample included only claustral colonies of the other three ant species. We then sealed the drilled holes using rope caulking and labeled each swollen thorn with a unique identification number. Early on the following morning, before resident plant-ants became active, resealed thorns were attached to the trunks of 10 large *A. drepanolobium* trees (five occupied by *C. mimosae* and five occupied by *C. sjostedti*) using the sticky caulking. Nine sealed claustral colonies (three each of *T. penzigi*, *C. nigriceps*, and *C. mimosae*) were placed on each tree in random positions. Observers each watched a pair of nearby trees, one occupied by a mature colony of *C. mimosae*, the other by *C. sjostedti*. In this blind test, the observers did not know the identity of the claustral colony inside sealed thorns. Observers recorded the numbers of resident ants attacking the seal of each claustral thorn at frequent intervals for several hours, noting times at which the seals were breached. The *C. sjostedti* colony on one experimental host tree was unusually inactive and did not show any interest in the claustral colonies. This tree was excluded from the sample. After 2 days, all thorns were collected and opened to determine whether there was still a living claustral queen inside. Chi-squared contingency tests were used to test two null hypotheses: first, that the proportion of surviving claustral queens was equivalent between "host" colonies of *C. mimosae* and *C. sjostedti*, and second, that foundress queens of the three colonist species were equally likely to escape detection and survive.

Young colony surveys: Are small, independent T. penzigi *colonies more successful in* C. sjostedti-*controlled territories?*—We compared the expected vs. observed neighboring ant species composition around small independent colonies of *T. penzigi*. To generate an expected distribution for ant species composition around small independent colonies, we surveyed the relative abundance of neighboring ant species around randomly encountered colonies along a series of 4 m

wide belt transects through the study area. Surveys included all *A. drepanolobium* trees ≤1.5 m tall until we had sampled a total of 82 small independent colonies of *C. mimosae*, *C. nigriceps*, and *T. penzigi*. (*Crematogaster sjostedti* are virtually never found as independent colonies on small trees.) We established whether each encountered colony was either independent or a satellite of a nearby mature colony using ant-transplant aggression assays, as described in *Methods: Swollen thorn surveys* .... Small trees without active colonies (e.g., young coppices with only sealed claustral colonies) and satellite trees belonging to larger colonies were not included in this survey. Around each independent colony that we found, we surveyed all *A. drepanolobium* trees within 2 m and recorded resident ant species and tree height as a spatial estimate of the surrounding neighborhood. We then summed the tree heights of neighbors occupied by each species to estimate the relative abundance of neighboring ant species (following Palmer 2004). We continued this survey method to characterize the immediate neighborhoods around an additional 73 small independent *T. penzigi* colonies. We then compared the neighborhoods surrounding these 73 small independent colonies of *T. penzigi* with those surrounding the 82 randomly sampled small independent colonies (comprising *C. mimosae*, C. *nigriceps*, and *T. penzigi*) using ANOVA. The dependent variable in the model was the height-weighted abundance of a given neighboring ant species around a focal colony, and we tested for an interaction between focal colony type (*T. penzigi* sample vs. random sample) and neighboring ant species. The interaction term in the model was significant ($F = 15.92$, df = 3, $P < 0.0001$), so we proceeded to conduct four separate one-way ANOVAs for each of the neighboring ant species comparing neighbor abundance around young *T. penzigi* colonies to that around randomly sampled independent colonies. Significance levels for these multiple comparisons were adjusted using a sequential Bonferroni correction (Rice 1989).

Sapling colonization experiments: Do foundress queens of different species vary in their ability to locate and successfully colonize saplings in C. sjostedti- *vs.* C. mimosae-*controlled territories?*—We compared foundress queen establishment and survival on experimental saplings planted within both *C. sjostedti*- and *C. mimosae*-controlled territories. Saplings were reared from field-collected seeds within screen houses until they were 0.75–1.25 m tall. Only saplings with at least two fully formed swollen thorns were used in this experiment. We then identified 13 *C. sjostedti*- and 13 *C. mimosae*-controlled territories (non-overlapping), and identified all trees belonging to each colony using methods described for *Swollen thorn surveys* .... For each multi-tree colony, we selected the most "active" tree, using the number of workers moving up and down host-plant stems during 30-s scans as an index of activity. We placed pairs of experimental saplings, matched for height and swollen thorn number, in close

proximity (<1.5 m) to the most active host plant within each colony. For each pair, one sapling was randomly chosen to receive a sticky-barrier treatment around the base of the planting bag, to preclude access by worker ants from the adjacent colony. The second sapling was designated as a control sapling, and did not receive a sticky barrier. To prevent damage to saplings by mammalian browsers (such as eland, Grant's gazelle, and steinbuck), we placed a single wire-mesh cage (1.5 × 1.4 × 2 m) around each pair of saplings. One-inch (2.5-cm) mesh was used to allow access to saplings by aerially colonizing foundress queens, while preventing damage to saplings by mammalian herbivores. After three weeks, we destructively sampled all swollen thorns on saplings, and counted the number of foundress queens of each ant species therein. We analyzed the number of queens of *T. penzigi* and *C. nigriceps* colonizing experimental saplings placed within *C. mimosae* and *C. sjostedti* territories using MANOVA. We then compared the numbers of queens of each species colonizing sticky-barrier protected saplings vs. control saplings in each territory type using ANOVA. The number of swollen thorns per sapling was included as a covariate in these analyses, and the success of queens of each species in colonizing saplings in *C. sjostedti*- vs. *C. mimosae*-controlled territories was tested using planned contrasts.

Spatial patterns of interspecific transitions on A. drepanolobium *host plants: comparing frequency of takeover of* T. penzigi-*occupied trees by the three* Crematogaster *species.*— If, as hypothesized, facilitation of *T. penzigi* colony establishment promotes the coexistence of all four acacia ant species, then *T. penzigi* colonies must in turn be displaced by *Crematogaster* colonies. We used two methods to assess how frequently *T. penzigi* colonies are displaced from host plants by *Crematogaster* neighbors. First, we examined six years of annual census data on 1800 permanently marked trees along five 200-m transects in our study area. In particular, we focused on trees ≤1.5 m in height that were occupied by *T. penzigi* when we started conducting annual censuses in 1998. We then tallied the number of those trees that underwent transitions to *C. sjostedti* as opposed to either *C. mimosae* or *C. nigriceps* over the next six years. Because transient cohabitations of host trees are occasionally found between species, we scored trees as having undergone transitions only when the displacing species was recorded as the sole occupant on the tree for two consecutive annual surveys following the displacement of *T. penzigi*. We then generated expected frequencies of *T. penzigi* displacement using neighborhood data (height-weighted abundances of neighboring species, expressed as a proportion) from our surveys of 73 independent *T. penzigi* colonies on trees <1.5 m tall (detailed in *Methods: Young colony surveys*...). Observed and expected frequencies of transitions from *T. penzigi* to *C. sjostedti*, or to *C. mimosae* and *C. nigriceps*, were compared using a chi-squared statistic with a 3 × 2 contingency analysis.

TABLE 1. Mean stem diameter (recorded at 30 cm height) for host trees occupied by each acacia ant species ($N = 692$, 1990, 292, and 202 host plants for *C. sjostedti*, *C. mimosae*, *C. nigriceps*, and *T. penzigi*, respectively).

Ant occupant	Mean stem diameter	95% CI
Crematogaster sjostedti	5.42	5.29–5.55
C. mimosae	5.25	5.17–5.33
C. nigriceps	4.49	4.29–4.70
Tetraponera penzigi	3.81	3.57–4.07

In addition, we conducted a field survey of host plants occupied by the three *Crematogaster* species to determine whether *T. penzigi* had previously occupied these trees. *Tetraponera penzigi* characteristically makes numerous (typically >4), small entry holes across the entire surface of their swollen thorns, in contrast to the *Crematogaster* species, which create only one or two larger entry holes at the base of each stipular thorn. Consequently, it is possible to detect recent past occupancy of trees by *T. penzigi* based on the presence of old swollen thorns with these distinctive entry holes (also see methods in Palmer [2004]). We examined 80 *C. mimosae*-occupied trees, 54 *C. nigriceps*-occupied host plants, and 46 *C. sjostedti*-occupied trees along randomly oriented transects for signs of previous *T. penzigi* occupation.

RESULTS

Stem diameter surveys.—Average stem diameters were smallest for *T. penzigi*-occupied host plants, and increased with increasing dominance rank among the three *Crematogaster* species ($N = 3176$ stems, *C. nigriceps* < *C. mimosae* < *C. sjostedti*; Table 1).

Swollen thorn surveys.—The abundance of unoccupied swollen thorns within colonies varied strongly among the three *Crematogaster* species. Within *C. sjostedti* colonies, swollen thorns on smaller satellite trees (<1.0 m in height) are dramatically underutilized, containing on average 80% fewer workers ($N = 60$ trees, ANOVA, $F_{2,57} = 19.87$, $P < 0.0001$) and >90% less brood (ANOVA, $F_{2,57} = 23.77$, $P < 0.0001$) than swollen thorns on satellite trees controlled by *C. mimosae* and *C. nigriceps*.

Claustral queen surveys.—Surveys of 180 sealed swollen thorns containing claustral queens revealed disproportionate numbers of *T. penzigi* queens on the smallest trees within *C. sjostedti*-controlled areas, compared with areas controlled by the other two *Crematogaster* species (Fig. 1; $\chi^2 = 8.88$; df = 2; $P = 0.012$).

Queen detection tests.— Overall, mature colonies of *C. sjostedti* were less likely to detect and kill foundress queens (pooled across species) from host-plant stems than were colonies of *C. mimosae* (Fig. 2; 59% vs. 81% of all foundress queens placed on stems killed by each species, respectively; $\chi^2 = 4.47$, 1 df, $P < 0.05$). Across host species, founder colonies of *T. penzigi* were less

likely to be discovered and killed on host-plant stems than were founder colonies of *C. nigriceps* and *C. mimosae* (Fig. 2; 63% surviving to 3 days for *T. penzigi* queens vs. 29.5% and 10.5% for *C. nigriceps* and *C. mimosae* queens, respectively; $\chi^2 = 16.78$, 2 df, $P < 0.001$). Survival of claustral foundress queens did not differ significantly for *T. penzigi* vs. the other two (pooled) *Crematogaster* species on *C. sjostedti*-occupied hosts (67% vs. 28% for *T. penzigi* queens vs. *C. nigriceps* and *C. mimosae* queens combined, respectively; $\chi^2 = 3.28$, 1 df, $P = 0.07$), but was significantly higher for *T. penzigi* queens vs. the other two *Crematogaster* species on *C. mimosae*-occupied hosts (60% vs. 6.3% for *T. penzigi* queens vs. *C. nigriceps* and *C. mimosae* queens combined $\chi^2 = 14.28$, 1 df, $P < 0.001$).

Young colony surveys.—Our surveys of independent colonies on small trees <1.5 m tall revealed that *T. penzigi* colonies were twice as likely to occur within *C. sjostedti*-dominated neighborhoods than expected by chance (ANOVA, $F_{1,153} = 16.1$, $P < 0.0001$; Fig. 3), and were significantly more likely to have other *T. penzigi* colonies as neighbors as well (ANOVA, $F_{1,153} = 7.48$, $P = 0.007$). By contrast, small *T. penzigi* colonies were under-represented near colonies of *C. mimosae* (ANOVA, $F_{1,153} = 5.39$, $P = 0.021$) and *C. nigriceps* (ANOVA $F_{1,153} = 21.02$, $P < 0.0001$; Fig. 3).

Sapling colonization experiments.—We found significant variation in the success of colonizing *C. nigriceps* and *T. penzigi* queens within *C. sjostedti*- and *C. mimosae*-controlled territories (MANOVA, Wilks' lambda = 0.72, df = 8, 90; $P = 0.005$). *Crematogaster nigriceps* queens were significantly more likely to successfully colonize saplings with sticky barriers than control saplings to which neighboring plant-ants had access (Fig. 4a; ANOVA, treatment $F = 4.13$, df = 1, $P <$
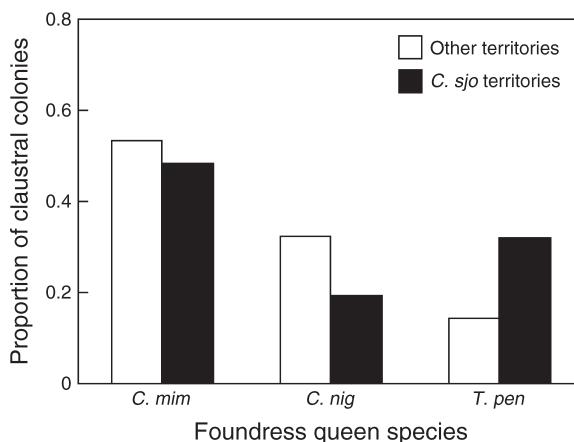

FIG. 1. The proportion of claustral queen colonies of three acacia ant species found in swollen thorns within territories occupied by *Crematogaster sjostedti* vs. territories occupied by the three other acacia ant species. Ant species are *C. sjo*, *C. sjostedti*; *C. mim*, *C. mimosae*; *C. nig*, *C. nigriceps*; *T. pen*, *Tetraponera penzigi*.
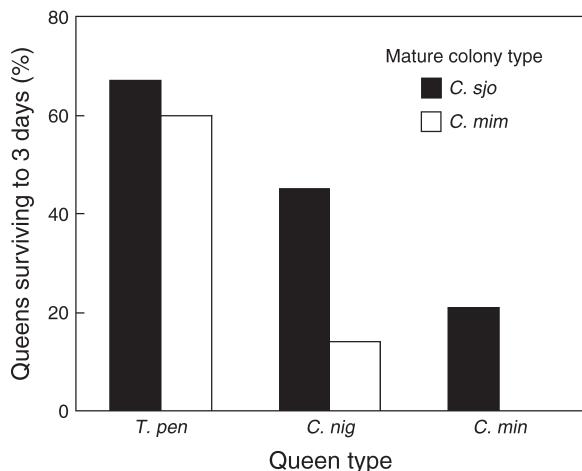
FIG. 2. The percentage of sealed claustral foundress queens of three species surviving to day 3 when placed on host plants occupied by mature colonies of *C. sjostedti* and *C. mimosae*.

0.05), but did not differ in overall colonization success between *C. sjostedti*- vs. *C. mimosae*-controlled territories (territory $F = 0.07$, df = 1, $P = 0.80$). There was no significant territory × treatment interaction effect on the number of *C. nigriceps* queens colonizing saplings ($F = 0.07$, df = 1, $P = 0.80$). By contrast, we found that *T. penzigi* queens were disproportionately successful in colonizing unprotected saplings within *C. sjostedti*-controlled territories (Fig. 4b; ANOVA, territory × treatment $F = 10.39$, df = 1, $P = 0.002$).

Spatial patterns of interspecific transitions on A. drepanolobium host plants.—Whereas the establishment of *T. penzigi* is favored on satellite trees within *C. sjostedti* foraging territories, long-term (six-year) annual surveys of transitions in ant occupancy show that *T. penzigi* is more likely to be displaced from its host trees by the competitively intermediate *C. nigriceps* and *C. mimosae* than by the guild-wide dominant competitor, *C. sjostedti* (Fig. 5; $\chi^2 = 11.04$; df = 2; $P < 0.01$). In addition, a substantial proportion of host plants occupied by *C. mimosae* and *C. nigriceps* show evidence of past occupation by *T. penzigi*. In our survey of transition histories of trees <2 m tall, we found that 24.1% of trees occupied by *C. nigriceps* ($N = 54$ trees) and 32.5% of trees occupied by *C. mimosae* ($N = 80$ trees) still possessed some swollen thorns with the multiple, small entry holes that are uniquely made by *T. penzigi*, vs. only 6.5% ($N = 46$ plants) of host plants occupied by *C. sjostedti*. All of these values likely underestimate transitions from *T. penzigi* to other competitors, since the *Crematogaster* species occupy host trees in this size range for 5–10 years, on average, and swollen thorns on older growth become brittle and disappear after several years (T. M. Palmer, T. P. Young and M. L. Stanton, *unpublished data*).

DISCUSSION

Our results demonstrate that the most subordinate species within this intensely competitive guild, *T. penzigi*, fares better at early life history stages in areas controlled by the most dominant species, *C. sjostedti*, than in areas controlled two *Crematogaster* species that are intermediate in the dominance hierarchy. Indirect facilitation of *T. penzigi* thus flows from the competitive suppression by *C. sjostedti* of *C. nigriceps* and *C. mimosae*, creating opportunities for the foundation of young *T. penzigi* colonies and likely contributing to the persistence of this subordinate species and the maintenance of species diversity within the guild.

Spatial patterns of claustral foundress queens in the field suggest that *T. penzigi* is disproportionately successful at colonizing small saplings within territories of *C. sjostedti* (Fig. 1). Mature *C. sjostedti* and *C. mimosae* colonies were equally likely to find and kill claustral *T. penzigi* queens placed directly on their host plants in queen-detection trials (Fig. 2), but *T. penzigi* queens were significantly more successful at establishing colonies on experimental saplings in *C. sjostedti* territories than in *C. mimosae* territories (Fig. 4). Together, these results suggest that although *C. sjostedti* is capable (or at least as capable as *C. mimosae*) of detecting and killing *T. penzigi* queens on high-value
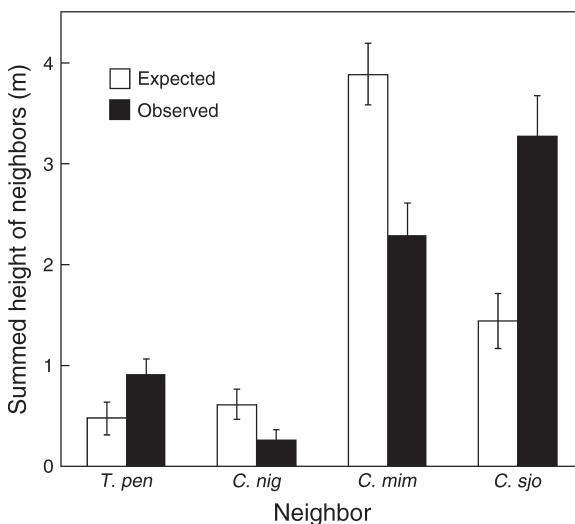

FIG. 3. Ant species composition of neighborhoods in which small independent colonies of *T. penzigi* are found (observed), compared to a separate survey of independent colonies of all ant species (yielding expected neighborhood profiles if *T. penzigi* were establishing in random neighborhoods). Ant species: *C. sjo*, *C sjostedti*; *C. mim*, *C. mimosae*; *C. nig*, *C. nigriceps*; *T. pen*, *T. penzigi*. Only independent colonies on trees <1.5 m in height were included in these surveys. $N = 73$ colonies for *T. penzigi*, $N = 82$ colonies for the survey conducted for colonies of all species. Error bars show ±SE. For all four species, there was a significant difference between expected vs. observed neighbor frequencies from separate ANOVAs for each neighbor species, with significance levels adjusted using a sequential Bonferroni (Rice 1989).
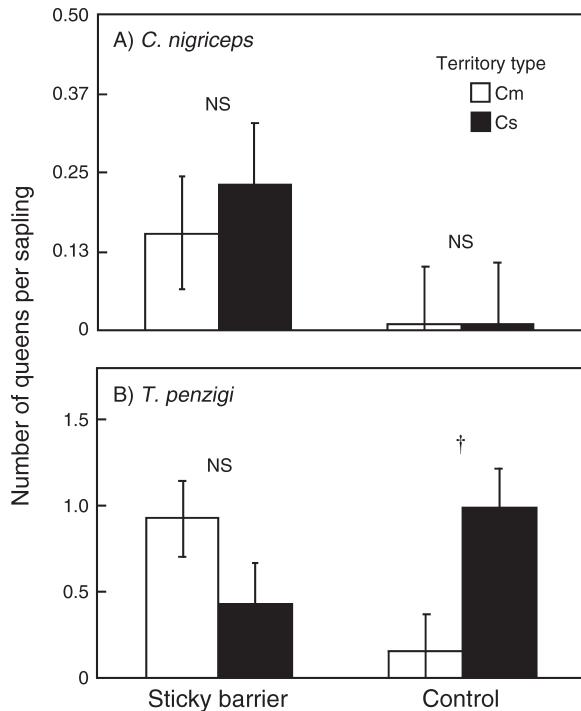
FIG. 4. (a) The mean number of *C. nigriceps* queens successfully colonizing saplings protected from local ant workers by sticky barriers vs. unprotected saplings within territories controlled by *C. mimosae* and *C. sjostedti*. Abbreviations are: NS, no significant differences in mean number of queens colonizing sticky barrier vs. unprotected saplings in two territory types, planned contrasts, $P > 0.70$; Cm, *C. mimosae*; Cs, *C. sjostedti*. (b) The number of *T. penzigi* queens successfully colonizing sticky-barrier-protected saplings vs. unprotected saplings within territories controlled by *C. mimosae* and *C. sjostedti*. A dagger (†) shows $P = 0.016$, planned contrasts; NS stands for no significant difference, planned contrasts, $P = 0.09$. Error bars show ±SE.

resources such as primary nest sites, *C. sjostedti* is not as aggressive as *C. mimosae* in protecting low-value resources, such as small satellite saplings that cannot be used for nest space by this cavity-nesting species. *Crematogaster nigriceps* queens established on saplings in both territory types only when sticky barriers were present to block access by *C. sjostedti* and *C. mimosae* workers; otherwise establishment was close to zero.

Our results further suggest that once established, small *T. penzigi* colonies are comparatively successful within the enemy-free domain of *C. sjostedti* territories. Our analyses of neighborhoods around small independent colonies revealed that small *T. penzigi* colonies are significantly underrepresented in both *C. mimosae* and *C. nigriceps* territories, and occur more frequently than expected within territories controlled by *C. sjostedti* (Fig. 3). These spatial patterns indicate that young colonies of *T. penzigi* are highly susceptible to takeover by nearby *C. mimosae* and *C. nigriceps*, but are disproportionately able to exploit colonization oppor-

tunities in territories held by the competitively dominant *C. sjostedti*.

Disproportionate success of small *T. penzigi* colonies within *C. sjostedti* territories likely results from two aspects of *T. penzigi*'s ecology. First, *T. penzigi* does not forage on the ground around its host plants, and thus ground-foraging *C. sjostedti* workers are less likely to encounter *T. penzigi* within the boundaries of the dominant colony. However, it is not immediately clear why this would not also be true for *T. penzigi*'s interactions with *C. nigriceps* and *C. mimosae*. Thus, a more compelling hypothesis is that the lower rate of displacement of *T. penzigi* by *C. sjostedti* reflects the low value to *C. sjostedti* colonies of small trees, many of which are occupied by *T. penzigi*. Field dissections of *A. drepanolobium* trees (67 trees, 1.5–9.0 cm stem diameter) indicate that stem excavations by long-horn beetle larvae, which produce most of the primary nesting spaces used by *C. sjostedti* colonies, are rarely found on trees with stem diameters ≤4.0 cm (excavated cavities found in only 2 of 34 small trees surveyed), and are very common on trees with stem diameters >4.0 cm (excavated cavities found in 27 of 33 large trees surveyed). The average stem diameter for *T. penzigi*-occupied host trees is below this threshold size (Table 1). By contrast, the average stem diameters for *C. nigriceps*- and *C. mimosae*-occupied host plants exceed the size threshold at which *C. sjostedti* is observed nesting within twig and stem cavities (Table 1). Colonies of *T. penzigi* occurring on *C. sjostedti* satellite trees may persist simply because the stems of these smaller host plants are too small to be excavated by long horn beetles, and thus provide little (if any) nesting space for *C. sjostedti*.

Niche differentiation is common within ant communities, allowing subordinate species to coexist with competitive dominants (Schoener 1983) through differences in life-history traits such as thermal tolerance (Cerda et al. 1997, 1998), food-particle-size preferences (Fellers 1987, Savolainen and Vepsalainen 1989, Vep-
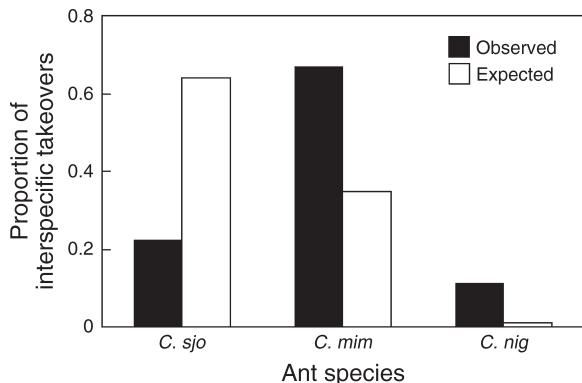

FIG. 5. Expected vs. observed ($N = 45$ observations) proportion of takeovers of small (≤1.5 m) *T. penzigi*-occupied trees by the three *Crematogaster* species. Expected takeover rates were based on the neighborhood data observed around young *T. penzigi* colonies shown in Fig. 4.

salainen and Savolainen 1990), exploitation vs. interference competitive ability (Davidson 1998, Holway 1999, Adler et al. 2007), or susceptibility to enemies (Lebrun and Feener 2007). In some cases, these trade-offs may afford subordinate species protection from competitors and enemies when they exploit habitats occupied by more behaviorally dominant species with whom they have less niche overlap (e.g., Savolainen and Vepsalainen 1989, Czechowski and Vepsalainen 2001, Czechowski 2004, Czechowski and Marko 2006). Our findings corroborate these earlier studies, in that reduced niche overlap (in particular, for nesting space with *C. sjostedti* colonies) allows *T. penzigi* to exploit colonization and establishment opportunities within enemy-free space provided by mature *C. sjostedti* colonies.

Intriguingly, we found that *T. penzigi* host plants are ultimately more likely to be competitively displaced by the intermediate competitors *C. nigriceps* and *C. mimosae* than by *C. sjostedti* (Fig. 5). As small *T. penzigi*-occupied satellite trees grow and produce new leaves, they become attractive targets for nearby colonies of *C. mimosae* and *C. nigriceps*, both of which require swollen-thorn nesting space and the nectaries produced on new leaves (Palmer et al. 2002). These intermediate competitors are in turn more likely to be displaced by *C. sjostedti* (Palmer et al. 2010), which then facilitates colonization and establishment of *T. penzigi*; the consistency of this successional replacement of ant species as host plants age is indicated by an increase in average stem diameter of host plants occupied by acacia ant species of increasing dominance rank (Table 1; see also Young et al. 1997). This stage-dependent pattern of facilitation and competition has the potential to generate a cyclical succession (sensu Watt 1947) of ant species on acacias as host plants grow older.

Contrary to the conventional view of competitive dominants as antagonists of diversity, in the acacia ant system, differences in resource use between the most dominant and least dominant species could allow for an overall increase in guild-level diversity. In the absence of the competitive dominant, establishment opportunities for the subordinate would be diminished, potentially collapsing diversity within the system. Consistent with this hypothesis, at a nearby site with differing soil, where average *A. drepanolobium* size is smaller and *C. sjostedti*-occupied host plants are rare, *T. penzigi* is also virtually absent (both species <1% of host plants surveyed along randomly oriented 4 m wide belt transects, $N = 300$ trees). However, because several different mechanisms are known to operate to support coexistence in this guild (e.g., priority effects, habitat heterogeneity, and competition–colonization trade-offs [Palmer et al. 2002, Stanton et al. 2002, Palmer 2003]), establishing the magnitude of the effect of indirect facilitation on species coexistence will require additional manipulative experiments.

While theoretical models suggest that positive interactions may be as common as negative ones in large communities (Dodds 1997), positive interactions are less often invoked to explain species coexistence within guilds (Stachowicz 2001, Holbrook and Schmitt 2004). It may not be uncommon for competitive dominants to utilize a shared resource very differently from competitively subordinates (e.g., where competition and resource partitioning are both mediated by body size). In such situations, de facto facilitation of the subordinate by the dominant may result from selective competitive exclusion of competitively intermediate species (e.g., Davidson 1985). Our results demonstrate that such facilitative interactions can play an important role in the maintenance of diversity within an entire guild of competitors, and echo the call for a more thorough incorporation of positive interactions into ecological theory (Bruno et al. 2003).

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