SPATIAL HABITAT HETEROGENEITY INFLUENCES COMPETITION AND COEXISTENCE IN AN AFRICAN ACACIA ANT GUILD

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Abstract. Spatial mosaics in resource productivity may facilitate competitive coexistence when species differ in their ability to exploit resource-rich vs. resource-poor conditions. In this study, I investigated the influence of a termite-generated spatial mosaic in resource productivity on the dynamics of competition and coexistence in a guild of four acacia ants that reside on *Acacia drepanolobium*. Near termite mounds, both new shoot production of *A. drepanolobium* and densities of litter-dwelling invertebrates (an important food source of the acacia ants) are higher than in "matrix" habitats between mounds. This resource variation is spatially correlated with the outcome of competition among acacia ants for host trees; near the mounds, competitively dominant species are more likely to supplant subordinates, whereas the likelihood of subordinates replacing dominants on host trees increases with distance from mounds. Variation in competitive outcomes among patch types appears to result from differential responses among acacia ant species to resource heterogeneity. Analysis of average tissue $\delta^{15}N$ levels indicated that acacia ant colonies near termite mounds had higher ratios of animal prey in their diets than colonies in matrix areas. Bait trials and analysis of average nest size in mound and matrix habitats suggest that competitively dominant species are disproportionately successful in exploiting higher prey densities near termite mounds. Increased dietary uptake of nitrogen-rich prey may fuel more rapid colony growth in competitively dominant acacia ants, resulting in more pronounced asymmetries in colony size between dominant and subordinate species in mound areas. Because colony size asymmetry is a key determinant of interspecific competitive outcomes, colonies of subordinate species near termite mounds may be more vulnerable to aggressive take-overs by dominants. In lower-productivity matrix habitats, increased tolerance to low-resource conditions may afford subordinate species greater persistence. Overall, these results suggest that termite-induced habitat heterogeneity plays a significant role in the dynamics of the acacia ant community, and may contribute to species coexistence in this intensely competitive community.

Key words: acacia ants, Acacia drepanolobium; *ant–plant mutualism; colony size;* Crematogaster; *Kenya; patch dynamics; resource competition; spatial heterogeneity; species coexistence; stable isotope;* Tetraponera.

INTRODUCTION

Spatial heterogeneity is a ubiquitous feature of natural ecosystems. Classic experiments over five decades ago (e.g., Gause 1932, Park 1948) convincingly demonstrated that this patchiness is crucial to the coexistence of competing species, and ecologists in the ensuing decades have done much to elaborate how and when spatial variability in habitats may promote the maintenance of species diversity (reviewed in Tilman and Kareiva 1997, Tokeshi 1999).

Patchiness in nature takes many forms. At the landscape level, habitat patches may be relatively uniform, or may differ from one another either qualitatively (e.g., wooded areas vs. grassland) or quantitatively (e.g., varying levels of productivity in a single habitat type). Different patch characteristics lead to differing

expectations of the mechanisms that may promote species coexistence (Hanski 1995). In relatively uniform habitats, competing species may coexist through intraspecific aggregation (e.g., Hanski and Cambefort 1991, Ives 1991), trade-offs in colonization and competitive ability (e.g., Levins and Culver 1971, Tilman 1994, but see Yu and Wilson 2001), or via priority effects (Wilbur and Alford 1985) that lead to alternative local equilibria (e.g., Levin 1974, Barkai and McQuaid 1988). At the other extreme, patches may differ qualitatively from one another, and variation in habitat selection among species can reduce the probability of competitive exclusion (e.g., Schoener 1974).

Structurally homogeneous habitats may consist of a mosaic of patches that vary with respect to quantitative factors such as resource level or productivity. In this case, spatial variation in resources may facilitate coexistence if there are interspecific trade-offs in the ability of species to exploit resource-rich vs. resource-poor patches (Kotler and Brown 1988, Hanski 1989). For example, different species may be superior competitors

at different resource levels (Jitts et al. 1964, Tilman et al. 1981), or species may differ in their tolerance to low resource conditions (Grime 1979). Inverse correlations among species in the ability to exploit rich vs. poor resource conditions have been reported for a variety of taxa (algae, Sommer 1989; invertebrates, Kohler 1992, Schmitt 1996, Amarasekare 2000, Tessier et al. 2000; vertebrates, Brown et al. 1994), and may play an important role in supporting species coexistence in mosaic habitats.

Interspecific trade-offs in competitive ability play a key role in the organization of ant communities (Hölldobler and Wilson 1990). For example, trade-offs in the ability to locate resources and the ability to dominate resources once located (Fellers 1987) often lead to a temporal succession of ant species at baits in experimental studies (e.g., Fellers 1987, Savolainen and Vepsäläinen 1988, Morrison 1996, Holway 1999, and reviewed in Hölldobler and Wilson 1990). While temporal partitioning of resources among ants is well documented (reviewed in Cerdá et al. 1998), fewer studies have documented the influence of spatial variation in resource abundance on ant coexistence and community structure (Davidson 1977, Kaspari 1996, Schooley et al. 2000). Nonetheless, the apparent generality of competitive trade-offs among ants (Davidson 1998) suggests that spatial variation in resource levels may play an important role in competitive coexistence in some ant communities.

In this study, I examined the influence of spatial variation in resource availability on patterns of competition and coexistence in a widespread guild of acacia ants residing on *Acacia drepanolobium* in Laikipia, Kenya. In this guild, four ant species coexist despite a strong dominance hierarchy (*Crematogaster sjostedti* > *C. mimosae* > *C. nigriceps* > *Tetraponera penzigi*) when colonies compete for limiting host trees (Stanton et al. 1999, Palmer et al. 2000). These ant species are generally mutually exclusive (only one ant species is found on a given tree), and competition for trees is intense. More than 99% of trees >1.0 m tall are occupied by ants (Young et al. 1997), interspecific turnover of ants on host trees can be as high as 7% in a six-month period, and violent interspecific take-overs of host trees by adjacent colonies are common (Palmer et al. 2000). Because these four acacia ant species exploit the same species of host tree, and the three *Crematogaster* species exploit the same food resources and forage actively during similar hours (A. E. Evans, *unpublished manuscript,* and see *Study System and Methods*), opportunities for conventional resource partitioning (e.g., via niche displacement) are lessened. However, the ecosystem is characterized by strong spatial heterogeneity in resource abundance, and this feature may contribute to species coexistence if acacia ant species differ in their ability to exploit resource-poor vs. resource-rich patches.

Throughout the *A. drepanolobium* habitat at our study site, there are strong gradients in the productivity of resources upon which the acacia ants depend. These resource gradients are highly spatially correlated with mounds of the subterranean termite *Odontotermes* spp. Through their activities (e.g., concentration of organic materials and coarse soil particles), these termites locally enrich soils in nitrogen, phosphorus, and organic carbon, and increase soil drainage and water availability at termite mounds (T. Palmer, *unpublished data*). Relative to the surrounding matrix areas, production of nectary-bearing new shoots on *A. drepanolobium* is 60% higher on host trees near termite mounds (<10 m from mound edges). In addition, areas near termite mounds support 2.5 times higher densities of litter-dwelling invertebrates, a common food of the three *Crematogaster* species (T. Palmer, *unpublished data*). Consequently, termite activity in this habitat appears to generate a spatial mosaic of relatively more productive mound areas (~21% of the habitat; T. Palmer, *unpublished data*) embedded within less productive matrix areas.

This spatial variation in productivity caused by termites may strongly influence species coexistence in this intensely competitive community. In a prior study, Palmer et al. (2000) demonstrated that variation in *A. drepanolobium* growth rate was correlated with the outcome of competition among acacia ants competing for limiting host trees; more subordinate species were replaced by dominants on faster growing trees, while more dominant species tended to be replaced by subordinates on slower growing trees. However, whether variation in host tree growth rate is a cause or correlate of competitive outcomes was not determined.

In this study, I addressed several questions to determine how spatial variation in habitat productivity may influence the dynamics of competition and coexistence among the acacia ants: (1) Do patterns of host tree occupancy differ among acacia ant species in mound vs. matrix areas? (2) Do the dynamics of competition (e.g., direction of competitive outcomes) and/or the intensity of competition (e.g., risk of interspecific take-over on any given tree) differ for the acacia ants in mound vs. matrix areas? (3) Do interspecific asymmetries in colony size, the critical determinant of competitive outcomes (T. Palmer, *unpublished manuscript*), vary between mound and matrix habitats? (4) Can interspecific differences among acacia ants in the ability to exploit high productivity areas explain spatial variation in competitive outcomes? More specifically, do foraging trials, stable ^{15}N isotope analysis, and a resource addition experiment indicate differential responses of acacia ant species to resource heterogeneity?

Study System and Methods

This research was conducted in the semi-arid Laikipia ecosystem (37° E, 0° N; 1800 m elevation) in north-central Kenya, at the Mpala Research Centre. Ap-

proximately 43% of the Laikipia ecosystem (Taiti 1992), and much of upland East Africa, is underlain with poorly drained ''black cotton'' vertisol soils that support wooded grassland. In these habitats, *A. drepanolobium* forms a virtual monoculture in the overstory, accounting for over 97% of canopy cover (Young et al. 1997).

Three of the four acacia ant species (*C. mimosae, C. nigriceps, T. penzigi*) that reside on *A. drepanolobium* are obligate associates of this tree species. The fourth, *C. sjostedti*, is also found on *A. seyal*, which is rare at this study site. *Tetraponera penzigi, C. mimosae,* and *C. nigriceps* all rely on swollen thorns produced by the tree for nesting space, while *C. sjostedti* generally nests in hollowed-out cavities within the tree's twigs and stem. Colonies of the three *Crematogaster* species typically occupy multiple trees, while each *T. penzigi* colony usually controls only a single contiguous canopy.

With the exception of *T. penzigi*, all of these acacia ants consume virtually the same food resources and forage actively during similar hours (A. E. Evans, *unpublished data*). Nectar is harvested from extra-floral nectaries present on the leaflets of host trees, and invertebrates dwelling in the litter and soil around host trees are scavenged and occasionally preyed upon by the acacia ant workers (Hocking 1970, T. Palmer, *personal observation*). Both *C. sjostedti* and *C. mimosae* tend scale insects on host trees (Young et al. 1997). In contrast to the *Crematogaster* species, *Tetraponera penzigi* destroys the nectaries on its host trees (Young et al. 1997, Palmer et al. 2002), and does not appear to forage off host trees. Instead, this species gleans small food particles (e.g., pollen, fungal spores) from the surfaces of host trees, a trait common to other pseudomyrmecines (Wheeler and Bailey 1920).

Determining the presence of termite mounds, and delineating their boundaries

Odontotermes construct circular mounds that are generally 10–20 m in diameter, but no more than 0.5 m high (Darlington and Bagine 1999). Although they are low in profile, they can readily be delineated from the surrounding area through a combination of vegetation, soil, and other characteristics. At this study site, the perennial grass *Pennisetum stramineum* grows abundantly on mounds (60–80% cover), and declines sharply >1 m from the mound edge to <25% cover (T. Palmer, *unpublished data*). Equally sharply, *Pennisetum mezianum* increases in abundance across a fairly short distance (1–2 m) at the mound's edge, increasing from <20% cover on top of mounds to >50% cover beyond the mound boundaries. These two grass species differ strongly in appearance and texture, making the identification and delineation of mounds more straightforward (T. Palmer, *unpublished data*). I used this strong contrast in plant species composition to delineate mound ''edges'' from the surrounding vertisol soils. Strong changes in vegetation across mound

boundaries appear to indicate equally abrupt changes in underlying soil characteristics; across this boundary between dominance by *P. stramineum* and *P. mezianum*, soil physical and chemical characteristics change dramatically. Mound soils are higher in silt and sand than the surrounding heavy clay vertisols, and therefore are noticeably different in texture, and lack the characteristic deep cracks present in surrounding vertisols (T. Palmer, *unpublished data*). In addition, mound soils have markedly higher levels of organic carbon, phosphorus, and nitrogen relative to the surrounding soils (T. Palmer, *unpublished data*).

Measuring acacia ant species composition on A. drepanolobium *host trees along transects intersecting termite mounds*

To determine whether the composition of the acacia ant community might be influenced by proximity to termite mounds, I recorded ant species occupying trees along 40-m transects originating in the center of termite mounds. I randomly selected 15 mounds for this analysis. If any termite mound selected was within 30 m of another mound, it was discarded and another chosen for study. At each termite mound, I located the center (defined as the point of intersection of two diameters running in the N–S and E–W cardinal directions), and ran two 4-m wide belt transects out in two randomly chosen cardinal directions. Transects were run from the center of mounds to a distance of 30 m outside the mound edge. Along belt transects, I recorded the distance along the transect where *A. drepanolobium* trees were encountered, the heights of the trees, and their resident ant species. For each mound, I then calculated the percentage of trees occupied by each ant species adjacent to (≤10 m) and distant from (>10 m) mound edges.

Examining spatial variation in the dynamics of competition among acacia ants

To assess whether interspecific competitive outcomes vary spatially with respect to proximity to termite mounds, I compared the distance from termite mound edges of trees that had undergone transitions in ant occupancy in the direction of the competitive hierarchy (i.e., dominant species replaced more subordinate species) with trees where transitions had occurred against the competitive hierarchy (i.e., subordinate species replaced more dominant species). I identified 80 trees that had undergone transitions in ant occupancy (61 in the direction of the competitive hierarchy and 19 against the competitive hierarchy) between July 1998 and July 1999 from a long-term monitoring transect of 1773 trees (Palmer et al. 2000). The distance of each tree to the nearest termite mound edge was measured using a meter tape.

Examining spatial variation in ''risk'' of host tree take-over by more dominant competitors

To determine whether proximity to termite mounds influences a colony's risk of losing a host tree to take-

over by more dominant species, I compared the distance from termite mound edges of ''transitioning to dominant'' and ''stable'' trees from the long-term monitoring transect. ''Transitioning to dominant'' trees were defined as trees undergoing a change in ant occupant from a subordinate species to a more dominant species over a 12-month period. ''Stable'' trees were defined as trees not undergoing changes in ant occupant over a 24-month period. The same ''transitioning to dominant'' trees ($N = 61$) used in the preceding analysis were used for this analysis. For each of these 61 trees, I randomly selected a size-matched (± 5 cm height and ± 3 cm basal diameter), ''stable'' tree that had been continually occupied over the past 24 months by the original ant occupant of the transitioning tree. For each of these trees, I measured the distance to the edge of the nearest termite mound. Matching trees by size is critical for this analysis, since species turnover rate is much higher on smaller trees (Palmer et al. 2000). Because I used the same set of 61 trees in both of the above analyses, I used a Bonferroni correction for both analyses to minimize the probability of Type I error.

Measuring spatial variability in acacia ant colony size

Because colony size is a major determinant of interspecific competitive outcomes among these acacia ants (T. Palmer, *unpublished manuscript*), I assessed whether proximity to termite mounds affected colony sizes for the four acacia ant species. Focal colonies were chosen randomly along five parallel 1-km transects, each running N–S and separated by at least 100 m. Two observers walked along each transect until a termite mound was intersected. At each mound, I measured colony size for the first colony of each species encountered within 10 m of the mound edge. When a particular ant species was absent from an encountered mound, I moved to the next species. After measuring colony size for the different species at mounds, I ran a perpendicular 30-m transect either due east or west (determined by coin toss). At the end point of this transect (30 m from the mound edge), I measured colony sizes for the first colonies of each species encountered within 10 m, provided there were no termite mounds within 10 m of that point. When a termite mound was encountered within 10 m of the endpoints of perpendicular transects, I established a transect in the opposite cardinal direction for colony size measurements. Again, when a particular species was not encountered, I moved on to the next species.

Colony size was estimated by measuring the total height of all trees occupied by a given colony, which provides a reliable surrogate for relative colony size within and among the four acacia ant species (T. Palmer, *unpublished manuscript*). To determine which trees were occupied by a single colony, I used a modification of methods given in Hölldobler (1979). Workers from

randomly chosen focal trees were transferred in clipped swollen thorns to all neighboring trees within 10 m occupied by conspecifics. I then assessed whether workers from the two trees fought (indicating that trees were occupied by different colonies) or not. Cases where workers from neighboring trees fought were unambiguous. When neighbors appeared not to fight, I performed a reciprocal transfer to ensure that the trees belonged to the same colonies. Each interaction from the transfer of swollen thorns was observed for ~10 min. When colonies occupied more than two trees, I performed a number of reciprocal transfers between different pairs of trees to ensure that identification of same-colony trees was correct. When conflicting results were obtained, all trees were re-tested until I obtained an unequivocal result. After all host trees occupied by a colony were identified, I measured the height of each tree using a meter tape. I measured fewer *C. sjostedti* colonies because their colonies often occupied >20 trees, and identifying a single colony usually took at least a full day.

Measurements of foraging ability of the three Crematogaster *species*

Spatial variation in invertebrate prey resources associated with termite mounds may differentially influence acacia ant species if they vary in their ability to discover and recruit to these resources off of their host trees. To assess the relative foraging abilities of the acacia ant species, I conducted foraging trials using tuna baits. Only the three *Crematogaster* species (see Plate 1) were studied, since *T. penzigi* appears to be strictly arboreal, and has not been observed foraging off of host trees (T. M. Palmer, M. Stanton and T. Young, *unpublished data*). I randomly selected trees 1.5–2.0 m in height occupied by each of the three *Crematogaster* species ($N = 26$, 29, and 27 focal trees for *C. sjostedti*, *C. mimosae* and *C. nigriceps*, respectively) in matrix habitats. Each focal tree was chosen from a different colony. I then placed 5 g of tuna bait on the ground at the base of each focal tree, at a distance of 40 cm in a westerly direction from the stem. Prior observations indicated that these three *Crematogaster* species seldom recruit to baits at distances over 1.0 m from host trees within a 2-h observation period (A. E. Evans, *unpublished data*). Hence, I positioned baits at 40 cm from trees to increase the probability that baits would be discovered by focal colonies, while reducing the likelihood that workers from nearby trees (generally >2.0 m distant) would discover baits. I then revisited baits at 30-min intervals, and recorded the number of workers present in a 10-cm radius around each bait, in addition to recording the presence and number of any other ant species. After counting the number of workers at baits, I observed the movements of foragers carrying food items to determine whether they were returning to the focal tree or to other nearby host trees. Trials were discontinued after 150 min of observation. I re-

PLATE 1. (Left) A column of *Crematogaster mimosae* workers departing from and returning to the host *A. drepanolobium* tree during off-tree foraging for insect parts and prey. (Right) *Odontotermes* spp. mound in *Acacia drepanolobium* wooded grassland. The termite mound is in the foreground, delineated by the abrupt transition from darker (more green) vegetation to lighter vegetation (less green) in the background. Note the absence of trees on the mound, and the presence of taller trees at the mound periphery. Photographs by Todd M. Palmer.

plenished baits as they were removed by ants to keep the abundance of the resource approximately constant throughout the trials. If one or more workers from the focal tree discovered the bait, it was noted that the colony had ''discovered'' the bait. Successful ''recruitment'' was noted when >10 workers from a focal tree were present on experimental baits at a single time. A colony was successful at ''defending'' baits when workers were present on baits with other ground-dwelling ant species, and then were capable of completely displacing these other ant species from baits.

Measurements of $\delta^{15}N$ levels and percent nitrogen in acacia ant body tissues

To estimate the importance of invertebrate prey in the diets of these acacia ants, I analyzed ratios of stable nitrogen isotopes in all four ant species, adjacent to (<10 m) and distant from (>20 m) termite mound edges. Higher $\delta^{15}N$ ratios are thought to indicate a greater ratio of prey to plant resources in the diet (Minegawa and Wada 1984, Davidson and Patrell-Kim 1996, Vasconcelos and Davidson 2000). The same samples were analyzed for percentage of nitrogen content, which may reflect a species' investment in costly, protein-rich exoskeleton (see Davidson and Patrell-Kim 1996). I randomly selected 10 colonies for each species located <10 m from termite mound edges, and 10 colonies for each species located at distances >20 m from termite mound edges. Samples were collected between 0700 and 0900 hours, before colonies began intensive foraging. Using latex gloves, I disturbed a single tree in each colony and collected ~20 workers. Workers were placed in marked paper envelopes, and transferred to a freezer. After killing the ants in the freezer, I dried

each sample in a muffle furnace for 48 h at 60°C. These samples were then re-frozen until they were analyzed for percentage of nitrogen and $\delta^{15}N$ using a mass spectrometer (PDZ Europa Hydra 20/20 Mass Spectrometer, Davis, California, USA) at the isotope analysis facility at University of California, Davis. Just prior to isotopic analysis, ants from each sample were ground using a mortar and pestle, pooling individuals within each colony. I used whole ants for these analyses, so $\delta^{15}N$ ratios may reflect both tissue and gastric content isotope levels.

STATISTICAL ANALYSES

All statistical analyses were performed using JMP (SAS Institute 1996). Data on the proportion of trees occupied by each species in mound and matrix areas were arcsine square-root transformed prior to analysis. I pooled data from the two transects run at each mound. MANOVA was used to determine whether overall differences in species occupancy on *A. drepanolobium* existed between mound and matrix areas. I then assessed whether there were differences in the proportion of trees occupied by each species in mound and matrix areas using paired *t* tests. Data for empty trees were analyzed separately. Significance levels for multiple *t* tests were adjusted using a sequential Bonferroni correction (Rice 1989).

I used logistic regression to determine whether the direction of competitive outcomes (transitions with and against the competitive hierarchy) on host trees differed as a function of distance from termite mounds. The independent variable in this analysis was distance from termite mounds (square-root transformed), regressed against alternative transition outcomes (i.e., transitions
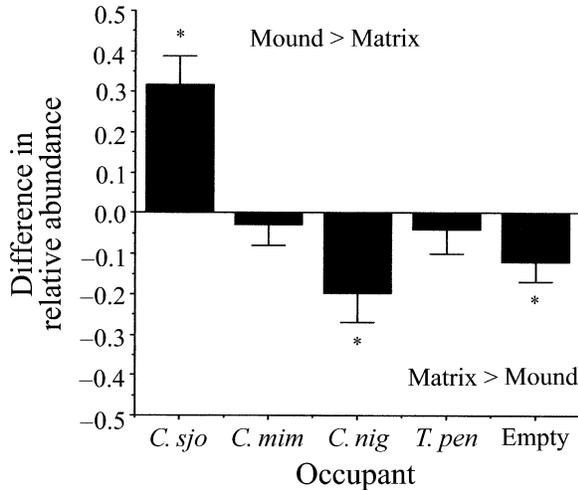
FIG. 1. Variation in acacia ant community structure in response to termite-induced habitat heterogeneity. Each bar represents the mean difference (± 1 SE) between the percentage of trees occupied by a given species near mounds (≤ 10 m from mound edges) and in matrix areas (>10 m from mound edges) for 15 transects. Percentage data were arcsine square-root transformed for statistical analysis, and to generate this figure. Asterisks indicate significant variation ($P < 0.05$) in percentage occupancy between mound and matrix habitats for a given species. Abbreviations are: *C. sjo*, *Crematogaster sjostedti*; *C. mim*, *C. mimosae*; *C. nig*, *C. Nigriceps*; and *T. pen*, *Tetraponera penzigi*

occurring in the direction of or against the competitive hierarchy). I also used logistic regression to determine whether distance from termite mounds was a significant predictor of risk of host tree take-over, where "stable" and "transition to dominant" tree states were alternative outcomes.

The relationship between proximity to termite mounds and colony size was assessed using a two-way ANOVA. Within each species I compared average colony size at mound vs. matrix areas using planned contrasts. Repeated-measures ANOVA was used to assess differences in worker recruitment to baits over time among the three *Crematogaster* species. ANOVA was used to examine variability in both $\delta^{15}N$ levels and

percentage of nitrogen in body tissues among ant species and sites (mound and matrix).

RESULTS

Acacia ant species composition along transects intersecting termite mounds

The community composition of the acacia ants varied spatially with respect to termite mounds (Fig. 1, Table 1). The proportion of trees occupied by the competitively dominant *C. sjostedti* was three times higher near termite mounds, while the proportion of unoccupied trees, and trees occupied by the competitively subordinate *C. nigriceps*, was approximately three times higher in matrix habitats (Table 1). There were no significant differences between mound and matrix areas in the proportion of trees occupied by *C. mimosae* or *T. penzigi* (Table 1). Unoccupied trees were relatively rare, but were found significantly more frequently in matrix (6.5% of trees) than in mound (1.7% of trees) habitats (Table 1).

Spatial variation in competitive outcomes among acacia ants

Proximity to termite mounds was a significant predictor of competitive outcomes among the acacia ants. Near the mounds, dominants were more likely to supplant subordinates on host trees, whereas the likelihood of subordinates replacing dominants on host trees increased with distance from mounds (logistic regression: $\chi^2 = 20.01$, df $= 1$, $P < 0.0001$; Table 2a).

Spatial variation in risk of host tree take-over by more dominant competitors

The risk that a colony would lose a host tree to a more dominant species varied with proximity to termite mounds. Colonies occupying host trees closer to termite mounds were more likely to be supplanted from those trees by more dominant competitors than colonies on host trees located at greater distances from mounds (logistic regression: $\chi^2 = 23.76$, df $= 1$, $P < 0.0001$; Table 2b).

TABLE 1. Comparison of ant species occupancy rates on trees at mound and matrix areas.

Occupant	Percentage of trees occupied		t	P
	Mound	Matrix		
Crematogaster sjostedti	30.58 (5.06)	11.04 (3.08)	4.55	<0.001***
C. mimosae	48.57 (4.23)	51.03 (5.07)	−0.01	0.991
C. nigriceps	4.82 (2.26)	14.81 (3.27)	−2.74	0.015*
Tetraponera penzigi	13.90 (2.57)	16.60 (2.09)	−0.74	0.470
Empty	1.76 (0.68)	6.51 (1.84)	−2.34	0.034*

Notes: Values are means with 1 SE in parentheses. MANOVA results for overall comparisons of occupancy data for mounds vs. matrix areas: Wilks' lambda $= 0.55$, df $= 5$, $P = 0.0098$. Paired t tests were used to compare mean percentage occupancy (arcsine square-root transformed) between mound and matrix areas for each species. $N = 15$ for each species at each site.

* $P < 0.05$; *** $P < 0.001$.

TABLE 2. Relationship between distance from termite mound edges and transition direction for ant colonies on trees from the long-term monitoring transect, and the relationship between distance from termite mound edges and ''risk'' of interspecific takeover for ant colonies on trees from the long-term monitoring transect.

Competitive outcome	Distance from mound edge (m)	
	≤5.0	>5.0
a) Transition direction		
Subordinate supplants dominant	3	16
Dominant supplants subordinate	39	22
b) Transition history		
No transition in past 24 months	15	46
Dominant supplants subordinate	39	22

Spatial variation in average colony size

Colonies adjacent to termite mounds were on average twice as large (as measured by the total height of trees occupied) than colonies located in matrix areas for all three *Crematogaster* species (Table 3, Fig. 2). Colonies of *T. penzigi* did not differ significantly in average size between mound and matrix areas (Fig. 2). Increases in average colony size near termite mounds were strongest for *C. sjostedti* (120% increase) and *C. mimosae* (100% increase), and weakest for *C. nigriceps* (45% increase) and *T. penzigi* (29% decrease). Consequently, disparity in colony size between dominant and subordinate species was stronger near termite mounds than in matrix areas (Fig. 2).

Foraging trials for the three Crematogaster species

Workers of the three *Crematogaster* species differed strongly in their abilities to locate and recruit to tuna baits placed near their host trees. In all foraging trials where *Crematogaster* workers successfully discovered and recruited to baits, workers were observed returning to focal trees, indicating that workers originated from the focal trees under study. In 2.5-h bait trials, *C. sjostedti* located and recruited to 92% of baits (24 out of 26 baits), while *C. mimosae* and *C. nigriceps* recruited to only 59% (17 out of 29) and 18% (5 out of 27) of baits, respectively ($\chi^2 = 33.14$, df = 2, $P < 0.0001$). Once baits were discovered, the three *Crematogaster* species differed significantly in the number of workers recruiting to baits over time (Table 4). *Crematogaster*
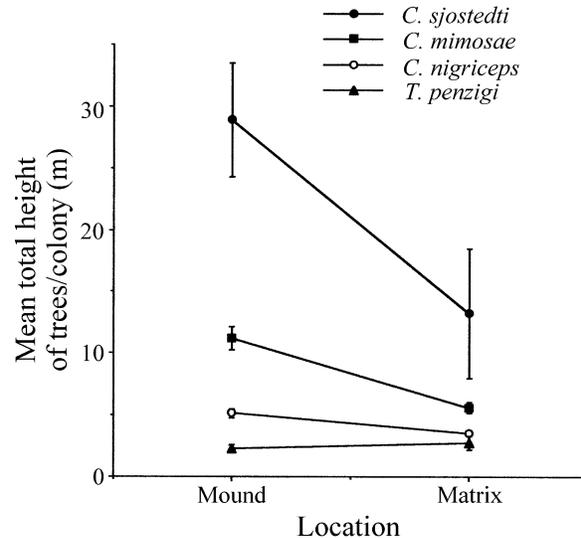

FIG. 2. Responses of acacia ant colony size to termite-induced habitat heterogeneity. Colony size is estimated by measuring the total height of trees occupied by a given colony (T. Palmer, *unpublished manuscript*). Each point represents the mean total height of trees ±1 SE occupied by colonies of a given species. Near termite mounds, N = 7, 33, 31, and 7 colonies for *C. sjostedti*, *C. mimosae*, *C. nigriceps*, and *T. penzigi*, respectively. In matrix areas, N = 4, 36, 40, and 7 colonies for *C. sjostedti*, *C. mimosae*, *C. nigriceps*, and *T. penzigi*, respectively.

mimosae had the strongest recruitment response, followed by *C. sjostedti* and *C. nigriceps* (Fig. 3). *Crematogaster sjostedti* and *C. mimosae* were better able to defend baits from exploitation by other ground-dwelling ant species than was *C. nigriceps*. The former two species displaced ground-dwelling ants in 92% (24 out of 26 cases) and 94% (17 out of 18) of cases when they located baits, respectively, while *C. nigriceps* only displaced soil-dwelling ant competitors in 36% (5 out of 14) of cases where they located baits ($\chi^2 = 19.06$, df = 2, $P < 0.0001$).

Stable N isotope ratios and percentage of nitrogen in acacia ant body tissues

Ant $\delta^{15}N$ showed both strong interspecific and spatial variation (Fig. 4, Table 5). Among the three *Crema-*

TABLE 3. Two-factor ANOVA on average acacia ant colony size at two locations (mound and matrix).

Source	df	ss	F ratio	P
Ant species	3	5.11	35.46	<0.0001
Location	1	1.02	18.33	<0.0001
Species × location	3	0.62	3.66	0.013
Error	157	8.79		
Total	164	18.21		<0.0001

Note: Colony size was estimated as log(total height of trees occupied) for each colony.

TABLE 4. Repeated-measures ANOVA on the number of ants observed at experimental baits during 2.5-h foraging trials.

Source	ss	df	F ratio	P
Ant	1159.46	2	43.23	<0.0001
Time	1191.04	4	22.21	<0.0001
Ant × time	243.813	8	2.27	0.02
Error	3700.78			
Total	6476.81			<0.0001

Note: The number of workers observed at baits was (square-root + 0.5)-transformed to satisfy normality requirements.
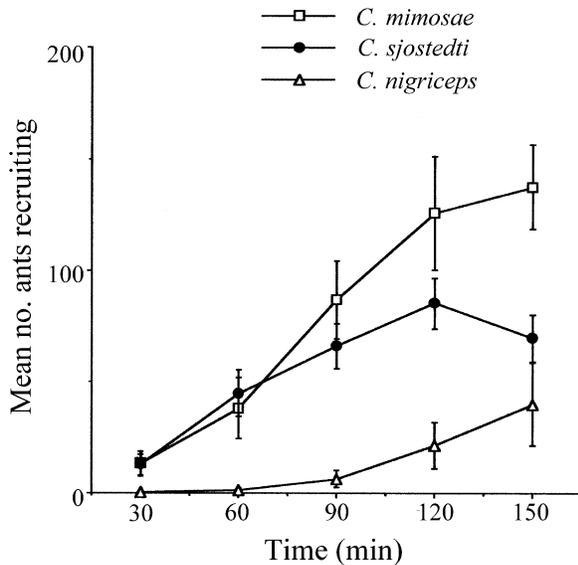
FIG. 3. The mean number of workers recruiting to tuna baits over time for the three *Crematogaster* species. Each point represents the mean number of workers at baits ±1 SE in scans at 30-min intervals. This figure represents only trials where ants successfully located baits (i.e., at least one worker was seen at the experimental bait). $N = 26$, 18, and 14 trials for *C. sjostedti*, *C. mimosae*, and *C. nigriceps*, respectively.

TABLE 5. Two-factor ANOVA on $\delta^{15}N$ levels in acacia ant body tissues.

Source	df	SS	F ratio	P
Ant species	3	59.08	11.60	<0.0001
Location	1	42.25	24.89	<0.0001
Species × location	3	10.05	1.97	0.12
Error	69	117.14	1.69	
Total	76	229.12		<0.0001

onies near termite mounds than colonies located further from mounds. Percentage of nitrogen in body tissues varied among ant species (Fig. 5), but did not vary between mound and matrix habitats (Table 6).

DISCUSSION

Results from this study suggest that the spatial mosaic of resource productivity associated with *Odontotermes* mounds strongly influences the dynamics of competition and community structure in the acacia ants of *A. drepanolobium* (see Plate 1). In relatively productive termite mound microhabitats, competitively dominant species are disproportionately successful in displacing more subordinate species from host trees, while subordinate species are more successful in less productive matrix areas. This spatial variation in competitive outcomes appears to contribute to coexistence in this intensely competitive guild. Spatial heterogeneity in competitive dominance likely plays a role in maintaining species coexistence in other species assemblages (reviewed in Dunson and Travis 1991), and may correlate with gradients in both abiotic (e.g., soil acidity, Tansley 1917) and biotic factors (e.g., seed

togaster species, average $\delta^{15}N$ was positively correlated with differences in off-tree foraging ability; *Crematogaster sjostedti* had the highest tissue $\delta^{15}N$, while levels in *C. nigriceps* were lowest. $\delta^{15}N$ in *T. penzigi* was also high. Average $\delta^{15}N$ was 33% higher for col-
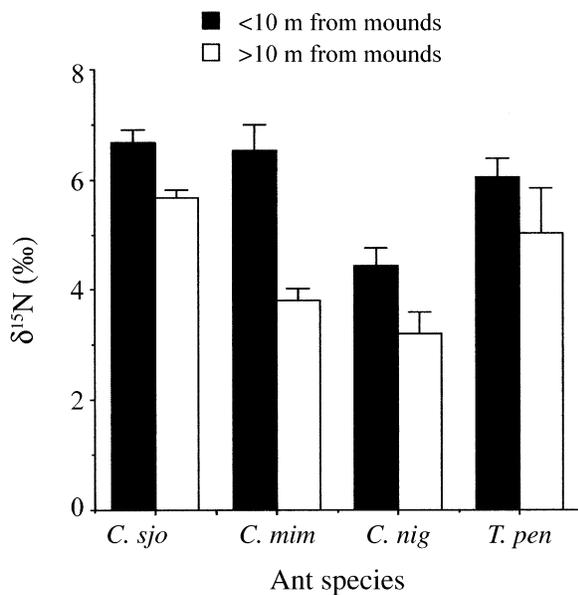

FIG. 4. Mean $\delta^{15}N$ levels for acacia ant tissues collected from colonies in mound and matrix habitats. Bars represent the average of $\delta^{15}N$ values +1 SE. $N = 10$ samples for each species at each location. See Fig. 1 for species abbreviations.
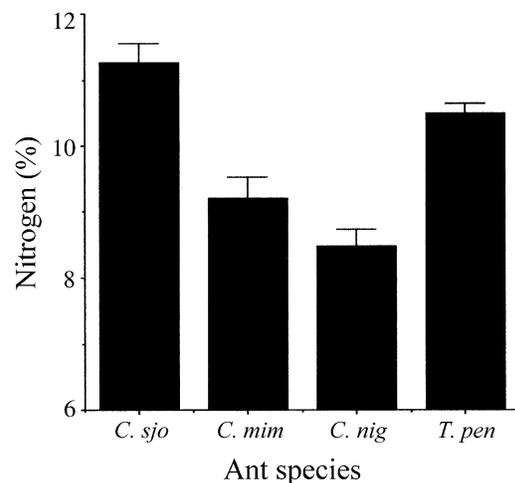

FIG. 5. Mean percentage of nitrogen for acacia ant tissues collected from colonies in mound and matrix habitats. Bars represent the average of percentage nitrogen values +1 SE. Because there was no significant effect of spatial location (e.g., mound vs. matrix) on percentage of nitrogen, data from both locations were combined for each species for this figure. $N = 20$ samples for each species at each location. See Fig. 1 for species abbreviations.

TABLE 6. Two-factor ANOVA on percentage of nitrogen levels in acacia ant body tissues.

Source	df	ss	F ratio	P
Ant species	3	0.005	21.88	<0.0001
Location	1	0.00002	0.39	0.53
Species × location	3	0.00007	0.33	0.80
Error	32	0.002		
Total	39	0.007		<0.0001

density, Brown et al. 1994). In ant communities, most research examining the influence of habitat heterogeneity on species coexistence has focused on niche partitioning in factors such as resources or nest sites (reviewed in Hölldobler and Wilson 1990). Productivity has been suggested as a major structuring force in ant communities at geographical scales (Kaspari et al. 2000), but the role of local spatial variation in resource productivity on the dynamics of ant competition and community structure is not well known. Davidson and colleagues (Davidson and Fisher 1991, Davidson et al. 1991, Davidson and McKey 1993, Yu and Davidson 1997) have suggested that productivity mosaics driven by light regimes may influence competitive dynamics in Neotropical and Asian plant–ant assemblages, based on observations and experiments demonstrating that competitive dominants tend to successfully occupy faster growing hosts and more productive habitats, while subordinates are generally restricted to slower growing hosts and less productive habitats (but see Vasconcelos and Davidson 2000). This study adds to a growing body of evidence that productivity mosaics may play an important role in mediating species coexistence among plant–ant assemblages.

Odontotermes termite mounds in this habitat are associated with both increased shoot production by *A. drepanolobium* and increased densities of the invertebrate prey of the acacia ants (Palmer et al., in prep). New shoot production by *A. drepanolobium* should result in increased nectar availability on host trees, since active nectaries are found primarily on new growth (T. Palmer, M. Stanton, and T. Young, *unpublished data*). In addition, increased host tree vigor near mounds may fuel greater exudate production by the scale associates of *C. sjostedti* and *C. mimosae*. $\delta^{15}N$ levels in all four acacia ant species were positively correlated with proximity to mounds, suggesting that mound sites are rich in the animal prey of these acacia ants. In addition, all three *Crematogaster* species showed increases in average colony size near mounds. By contrast, there were no significant differences in average colony size between mound and matrix areas for *T. penzigi* perhaps because this species destroys host tree nectaries (Young et al. 1997, Palmer et al. 2002) and does not forage off of host trees. It is not clear why *T. penzigi* showed increases in $\delta^{15}N$ near termite mounds. One possibility is that this species may feed on very small prey (e.g., mites), which may also be more abundant near termite

mounds. Further investigation is required to clarify this pattern.

These results suggest that increased resource availability both on and off of host trees near termite mounds promotes increased colony growth in the *Crematogaster* species. Because colony growth depends on the availability of protein (Hölldobler and Wilson 1990, Tobin 1995), while tree-provisioned resources (e.g., extrafloral nectar and homopteran exudates) are typically carbohydrate rich and nitrogen and protein poor (Baker et al. 1978, Davidson and McKey 1993, Davidson and Patrell-Kim 1996), increased invertebrate prey densities may play a larger role in facilitating *Crematogaster* spp. colony growth near termite mounds. However, excess carbohydrates provided by nectar may ''fuel'' ant activity that can be directed towards locating, recruiting to, and defending nitrogenous resources on the ground (Davidson 1997).

Differences among *Crematogaster* species in the ability to exploit nitrogen-rich off-tree resources appear to underlie differential colony growth among the three species. While all three *Crematogaster* species showed significant increases in average colony size near termite mounds relative to matrix areas, colony size increases were of the greatest magnitude in the competitively dominant *C. sjostedti* and *C. mimosae* These differences suggest that competitive dominants are better able to exploit the increased prey availability near termite mounds, which may lead to more rapid colony growth by these species in high productivity areas. Consistent with this hypothesis, *Crematogaster sjostedti* and *C. mimosae* located, recruited to, and defended baits more effectively than did the subordinate *C. nigriceps* suggesting that the former two species are not constrained by trade-offs in exploitation and interference competitive ability at concentrated resources similar to those represented by experimental baits (e.g., vertebrate and large invertebrate carcasses, carnivore dung, termite colonies, etc.). High carbohydrate yields from both extra-floral nectaries and scale exudates may afford these species high tempo activity (Oster and Wilson 1978) and high dynamic density (workers/m², Hölldobler and Wilson 1990) in off-tree foraging areas, leading to more effective resource discovery, harvesting, and defense (Davidson 1998). In a number of other ant communities, access to excess carbohydrates may enable species to ''break'' the trade-off in exploitation and interference competition, enhancing their ecological dominance (Davidson 1998).

The mechanisms underlying competitive outcomes among these acacia ants may differ between mound and matrix areas. Near termite mounds, high resource availability appears to fuel more rapid colony growth of competitively dominant species, increasing colony size asymmetry between dominants and subordinates. In this community, interspecific wars between adjacent colonies were won through a process of attrition, and competitive outcomes were primarily determined by

asymmetries in colony size (T. Palmer, *unpublished manuscript*). More rapidly growing colonies of dominant species may experience a greater degree of space limitation on host trees (e.g., if colony growth exceeds the production of new domatia), leading to take-overs of adjacent trees occupied by the considerably smaller colonies of subordinates. These results are consistent with a model proposed by Davidson et al. (1991), who suggested that poor competitors should be displaced on fast-growing host plants by superior competitors whose high energy demands could be met by more vigorously growing trees. As an extension to their model, data from this study suggests that increased plant vigor may be positively spatially correlated with increased productivity of nitrogen-rich food resources that are critical for colony growth. When plant ants forage both on and off their host trees, these enhanced nitrogen-rich resources may further fuel the expansion of competitively dominant species.

In lower productivity matrix areas, reversals in transition outcomes (i.e., subordinates increasingly replacing dominants on host trees) may result either from true competitive reversals, or from subordinates colonizing trees that have been abandoned by competitive dominants (Palmer et al. 2000). Data from this study suggest that the latter explanation is more likely to underlie most reversals in transition outcomes. First, almost 60% of reverse transitions involved either *C. mimosae* or *C. nigriceps* replacing *C. sjostedti* on host trees. However, even in matrix areas, *C. sjostedti* colonies are ~2.5 times larger on average than *C. mimosae* colonies, and almost six times larger than *C. nigriceps* colonies. This large disparity in average colony size suggests that more subordinate *C. mimosae* and *C. nigriceps* colonies are unlikely to usurp trees occupied by *C. sjostedti* in direct conflict. More likely, *C. sjostedti* may abandon lower productivity satellite trees in these low-resource areas, especially during times of environmental stress. Average tissue nitrogen concentrations are highest in *C. sjostedti* suggesting that this ant species may invest more nitrogen in costly, protein-rich exoskeleton (see Davidson and Patrell-Kim 1996). As a consequence, this species may be less able to maintain positive colony growth during stressful periods (e.g., droughts) when resource levels are low, since the cost of producing workers is relatively high. By contrast, the competitively subordinate *C. nigriceps* had the lowest average tissue nitrogen concentrations, suggesting that this species may require lower overall dietary nitrogen to maintain positive colony growth. Consequently, this species may be at an advantage in resource-poor areas, or during prolonged periods of environmental harshness. Consistent with this hypothesis, while *C. nigriceps* has the lowest rank abundance among the acacia ants at this study site (occupying 9% of host trees), the same species has the highest rank abundance (53%) at a nearby site (<5 km distant) where invertebrate densities, vegetative cover, and *A.*

drepanolobium height growth are markedly lower (T. Palmer, *unpublished manuscript*). Further, the proportion of unoccupied *A. drepanolobium* trees was significantly higher in matrix relative to mound areas. Combined, these observations suggest that tolerance to stress (e.g., the ability to maintain positive growth rate under low-resource conditions) may be more important than competition in structuring this community in unproductive matrix environments (e.g., Grime 1973, 1979). Unproductive microhabitats may provide a "competitive refuge" for subordinate species such as *C. nigriceps*, increasing their persistence in the community. The fact that the risk of host tree take-over by more dominant species declines with distance from termite mounds lends support to this interpretation.

A further consequence of spatially contingent competitive outcomes is that the degree of intraspecific aggregation among the acacia ants may increase if a single species is disproportionately successful at any given site. Aggregation serves to increase the intensity of intraspecific, relative to interspecific, competition (Atkinson and Shorrocks 1981, Ives and May 1985), which may further facilitate coexistence among these acacia ants. Development of spatially implicit and explicit models of competition in this community is underway.

While host tree occupancy by *C. sjostedti* and *C. nigriceps* differed significantly (in opposite directions) between mound and matrix areas, there were no significant differences in occupancy by *C. mimosae* or *T. penzigi*. *Crematogaster mimosae* is a competitively intermediate species, and in transitions on marked trees between July 1998 and July 1999, lost nearly as many trees to the more dominant *C. sjostedti* ($N = 22$ trees) near termite mounds as it gained in take-overs of the more subordinate *C. nigriceps* and *T. penzigi* ($N = 26$ trees total; T. Palmer, M. Stanton, and T. Young, *unpublished data*). In matrix areas, *C. mimosae* lost six host trees to other species, and gained five. Consequently, this species did not increase or decrease significantly in abundance between the two subhabitat types. The lack of significant variation in the proportion of trees occupied by *T. penzigi* between mound and matrix habitats may result from the strong priority effects exerted by this species on host trees; nectary destruction and the maintenance of small entry holes in swollen thorn domatia by *T. penzigi* dramatically reduce the probability of aggressive take-over of their host trees by competitively dominant species (Palmer et al. 2002). Similar occupancy on host trees in mound vs. matrix areas may result because *T. penzigi* does not aggressively expand onto neighboring trees, nor succumb easily to aggressive take-over.

Despite habitat-dependent variation in competitive outcomes, all four of the acacia ant species were found in both mound and matrix habitats. This observation begs the question: What maintains species diversity in both of these locations? For example, why are host trees

in mound areas not completely dominated by *C. sjostedti* colonies? The answer to this question likely includes consideration of temporal environmental variability. If the larger colonies (analogous to larger body size) of more dominant species require higher protein intake to maintain positive growth (see Kotler and Brown 1988, Davidson and McKey 1993), then, during periods of environmental harshness (e.g., droughts), the highly polydomous (i.e., multi-tree) colonies of these species may ''contract'' from peripheral host trees, opening up the trees to colonization by subordinate species with superior colonization abilities (Palmer et al. 2000, Stanton et al. 2002). Similarly, in favorable (e.g., high rainfall) years, colonies of dominant species may spread outward from mounds, usurping host trees of subordinate species within matrix habitats. Preliminary data from a long-term monitoring transect are consistent with this hypothesis, showing increases in abundance of *C. sjostedti* during the year following El Niño events, and decreases of this species in the subsequent drought year (T. Palmer, M. Stanton, and T. Young, *unpublished data*). It is interesting to note that drought negatively affected *C. sjostedti* despite the fact that this species tends scale insects, suggesting that the trophobionts did not provide a strong buffer against strong environmental variability. East Africa is typified by strong spatial and temporal variation in rainfall (McClanahan and Young 1996), which may contribute to coexistence in this system by favoring different ant species under different rainfall regimes. We are currently developing models to examine the influence of strong temporal variation in environmental conditions on long-term coexistence among these acacia ants.

In addition, ''spatial mass effects'' (Shmida and Ellner 1984) may help to maintain high diversity in mound and matrix areas, if local diversity in either patch type is augmented by immigration from neighboring patches with a different equilibrium community. These effects might be significant if the recruitment of new host trees in mound habitats is rapid enough to allow substantial establishment by strongly colonizing subordinate species. Further data are needed to evaluate the plausibility of this hypothesis.

Because the spatial mosaic in acacia ant resources is closely correlated with *Odontotermes* mounds, the relative density of termite mounds in this ecosystem is an important determinant of ant community processes and structure. The factors that mediate termite mound densities include competitive interactions among termite colonies and resource availability to termites. *Odontotermes* mounds in black cotton habitats are generally over-dispersed, a pattern thought to result from the maintenance of foraging territories by termite colonies (Darlington 1985). The spatial pattern of mounds is stable, and probably persists over hundreds of years through repeated recolonization of established nest sites (Darlington 1985, see also Watson 1967). The overall density of mounds in a habitat is also likely limited by habitat productivity (Darlington 1985). Habitats with higher mound densities should support a higher proportion of competitively dominant acacia ant species, while those with lower mound densities should be characterized by increases in the abundance of subordinate species. This hypothesis is supported by observations that the relative abundance of *C. nigriceps* on *A. drepanolobium* trees increases more than fivefold between our study site and a nearby site where termite mound densities are much lower (*personal observation*).

The repeatable patterns between local variation in habitat productivity and competitive outcomes among the acacia ants observed in this study may be useful in understanding the mechanisms that underlie variation in the composition of this acacia ant community at geographical scales. Elsewhere in Laikipia, and more broadly across East Africa, subsets of the same four ant species are present on *A. drepanolobium*. At most other sites surveyed (Hocking 1970, T. M. Palmer, *personal observation*), at least three of the four ant species can be found, indicating that the mechanisms promoting coexistence in this ant community are widespread. However, species composition can vary dramatically from site to site, at both local (<3 km) and regional scales. Geographic-scale surveys of this acacia ant community currently underway will help to determine whether biogeographic patterns in this arboreal ant community are associated with large-scale variation in habitat productivity.

Results from this study provide evidence that termite-generated environmental heterogeneity plays a strong role in structuring the acacia ant community, influencing patterns of interspecific competition for nest sites and contributing to coexistence among the four ant species. As in other African savanna communities (Dangerfield et al. 1998), termites act as ''ecosystem engineers'' (sensu Jones et al. 1994) in black cotton savannas, dramatically altering soil physical and chemical properties. These soil changes, in turn, have strong ''upward cascading'' impacts on the trophic dynamics of the aboveground community. Links between ecosystem engineers and trophic ecology are understudied (Jones et al. 1997), but potentially very important to the structure and function of ecosystems (e.g., Estes and Duggins 1995). This study provides an example of how habitat modification by an ecosystem engineer influences ecological patterns (e.g., variation in community structure, intraspecific variation in colony size) and processes (e.g., competitive outcomes) in acacia ants at both the population and community level. Since trees occupied by the different ant species differ strongly in growth form (Stanton et al. 1999; T. Palmer, M. Stanton, and T. Young, *unpublished data*), suites of associated invertebrate species (M. L. Stanton, *unpublished data*), leaf tannin levels (Ward and Young 2002), and patterns and rates of herbivory (T. M. Palmer, *unpublished data*), the determinants of acacia ant

community structure have a substantial impact on the broader black cotton ecosystem.

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