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Ants on swollen-thorn acacias: species coexistence in a simple system

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Abstract On the black cotton soils of the Laikipia ecosystem in Kenya, two swollen-thorn acacia species support nine ant species, four of which are apparently obligate plant-ants. Among the ants, there are five species of *Crematogaster*, two species of *Camponotus*, and one each of *Tetraponera* and *Lepisota*. *Acacia drepanolobium* is host to four ant species that are both common and mutually exclusive. These four ant species, and an additional non-exclusive ant species, tend to occur on trees of different sizes, implying a succession of ant occupants. Nonetheless, all four exclusive species occur in substantial proportions on trees of intermediate size. There is direct evidence that an early successional ant species (*Tetraponera penzigi*) is actively evicted by two late successional ant species in the genus *Crematogaster*. There was also some evidence of height differentiation among ant species resident on *A. seyal*. Different acacia-ant species had different direct effects on *A. drepanolobium*. Extrafloral nectaries were eaten and destroyed only on trees inhabited by *Tetraponera*. Axillary shoots were eaten only on trees inhabited by *C. nigriceps* (potentially another early successional ant). This was associated with more new terminal shoots and healthier leaves than other trees, but also the virtual elimination of flowering and fruiting. Different resident acacia-ant species also had characteristic relationships with other insects. Among the four mutually exclusive ant species, only *Crematogaster sjostedti* was associated with two species of *Camponotus*, at least one of which (*C. rufoglaucus*)

appears to be a foraging non-resident. *A. drepanolobium* trees occupied by *C. sjostedti* were also far more heavily infested with leaf galls than were trees occupied by other ant species. *A. drepanolobium* trees occupied by *C. mimosae* and *C. sjostedti* uniquely had tended adult scale insects. This diversity of ant inhabitants, and their strikingly different relationships with their hosts and other insect species, are examples of coexisting diversity on an apparently uniform resource.

Key words Succession · Mutualism · Symbiosis · *Crematogaster* · *Acacia drepanolobium*

Introduction

Species coexistence remains one of the central puzzles of modern ecology (Chesson 1991; Taper 1993). The principle of competitive exclusion asserts that no two species sharing the same limiting resource can co-exist for long. It has been suggested that there is a limiting similarity between species in order for co-existence to be stable. Attempts to show niche separation among similar species sometimes meet with success (reviewed in Losos et al. 1989; Taper and Case 1992), but often do not, leading to alternative theories for species coexistence (Chesson and Warner 1981; Hubbell and Foster 1986; Zhang and Jiang 1993; Eriksson 1994). Particularly troubling are multiple species that coexist on a single, apparently uniform resource.

The biotic community found on “black cotton” soils of the Laikipia ecosystem in Kenya is an example of a superficially uniform and simple system. Across thousands of square kilometers, the overstory is essentially limited to one (or occasionally both) of two swollen-thorn *Acacia* species: the dominant *A. drepanolobium* Sjöstedt, and the less common *A. seyal* Del. var. *fistula* (Schweinf.) Oliv. In many areas *A. drepanolobium* forms a virtual overstory monoculture. Five grass species and five herb species account for > 97% of the herbaceous cover (see below).

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Both *Acacia* species have bipinnate leaves with extrafloral nectaries, traits shared by most African *Acacia* spp. (Brennan 1959; Coe and Beentje 1992). Paired stipular thorns occur at the nodes of their branches. In *A. drepanolobium* and *A. seyal* var. *fistula*, approximately one pair of stipular thorns in five is swollen at the base to produce a hollow structure 1–3 cm in diameter (Monod and Schmitt 1968; Hocking 1970). In addition to long terminal shoots, these acacias produce a short axillary shoot at each node. The axillary shoots, the “cushions” of Coe and Beentje (1992), produce new leaves and often inflorescences throughout their lives, but produce no visible internodes.

African swollen thorn acacias have been the subject of considerable research and speculation concerning relationships with their ant inhabitants (Burt 1942; Brown 1960; Monod and Schmitt 1968; Hocking 1970; Coe and Beentje 1992; Madden and Young 1992; Davidson and McKey 1993a, b). Hocking (1970) described the rich invertebrate fauna associated with this symbiosis, and noted that several ant species were mutually exclusive, without quantitative descriptions of differences among ant occupants. Only Davidson and McKey (1993b) directly address the question of coexistence among different acacia ants.

The ability of occupant ants to defend acacias against large mammalian herbivores is often assumed (Brown 1960; Hocking 1970; Coe and Beentje 1992), but evidence for it is still preliminary (Janzen 1967; Madden and Young 1992), and thorns may play a more important role here (Young 1987; Milewski et al. 1991).

The benefit of the symbiosis to the ants is more obvious. Like Central American ant acacias, African ant acacias provide housing in the form of swollen thorns. These domatia are produced even in the absence of ants (Monod and Schmitt 1968; Hocking 1970; T.P. Young, personal observations). Although African ant acacias lack the Beltian bodies characteristic of Central American ant acacias, ants on *A. drepanolobium* can meet the majority of their caloric needs by harvesting the nectar produced by extrafloral nectaries on the leaves and to a lesser extent the scale insects that some ant species tend (Hocking 1970). Myrmecophytic acacias generally have larger nectaries and hold their leaves more uniformly through the seasons than do their non-mutualistic congeners. Our review of the species in Coe and Beentje (1992) revealed that in none of the six swollen-thorn acacias found in Kenya are populations occasionally leafless (during dry seasons), but that in 23 of 39 (60%) of the acacias without swollen thorns populations are sometimes leafless ($X^2 = 5.07$, $P < 0.025$).

It is common for extrafloral nectaries to attract large numbers of non-obligate insect species to a given host (Hocking 1970; Oliveira and Brandao 1992). Particularly intriguing is the maintenance on a particular tree species of multiple obligate ants that are mutually exclusive (Davidson and McKey 1993b). The two swollen-thorn acacias we studied support no less than nine ant species, at least four of which appear to be mutually exclusive and

obligate associates specializing in this niche. All but two of the nine occur on *A. drepanolobium*. Here we report results of investigations into the nature of coexistence in this system, and of the different strategies of these plant-ants. *Acacia drepanolobium* was by far the most common ant-acacia, and we concentrated our efforts on this species.

Methods

Study site and species

This research was carried out in the Laikipia ecosystem (36° 50' E, 0° 15' N) in north-central Kenya, on Segera Ranch and Mpala Farm. The majority of the surveys were carried out between November 1992 and November 1993, with additional surveys in March 1996. Rainfall averages 500–600 mm per year. Approximately 43% of the Laikipia ecosystem (4200 out of 9700 km², calculated from Taiti 1992) is underlain with “black cotton” vertisol soils characteristic of impeded drainage, and supporting a characteristic flora. The vegetation on these soils is wooded grassland with different densities of two species of swollen-thorn acacias (*A. drepanolobium* and *A. seyal* ssp. *seyal*). Occasional additional woody species include *Cadaba farinosa* Forssk., *Balanites aegyptiaca* (L.) Del., *Rhus natalensis* Krauss, *A. mellifera* (Vahl) Benth., *A. brevispica* Harms and *Lycium europaeum* L. The dominant grasses are *Lintonia nutans* Stapf., *Bracharia lachnantha* (Hochst.) Stapf., *Themeda triandra* Forssk., *Pennisetum mezianum* Leeke, and *P. stramineum* Peter. The dominant herbs are *Aerva lanata* (L.) Juss., *Rhinacanthus ndorensis* Schweinf., *Dyschoriste radicans* Nees, and *Commelina* sp.

Most of the study area is *Acacia drepanolobium* wooded grassland. This is the commonest plant community in Laikipia, covering 2700 km² (28%) of the ecosystem (Taiti 1992). *Acacia drepanolobium* is locally restricted to black cotton soils. All individuals produce swellings at the bases of some of their stipular thorns that are red when young and black when mature. Unswollen thorns and the unswollen (distal) parts of swollen thorns are white or pale gray, and are narrow and sharp. At some locations there are also smaller populations of *A. seyal* var. *fistula* within *A. drepanolobium* wooded grassland. *A. seyal* occurs in two forms: var. *fistula* occurs on black cotton soils and produces swollen stipular thorns that are white when mature; var. *seyal* occurs on other soil types and does not produce swollen thorns (Brennan 1959; Coe and Beentje 1992). It is not known whether this difference is genetic or facultative.

At least four ant species in the genus *Crematogaster* live in the swollen thorns on these trees. Vouchers of all ant species found in this system have been examined by P. Ward and are on deposit at the University of California at Davis. *Crematogaster* is a difficult and diverse genus currently under review, and our specimens have been assigned provisional designations (P. Ward, personal communication). Scale insects were sent for identification by P. Ward to P. J. Gullan of the Australian National University.

Seven ant species are found on *A. drepanolobium* (Table 1). Four species are common and mutually exclusive. *Crematogaster mimosae* Santschi has a red head and thorax and a black abdomen. *C. nigriceps* Emery has a black head and thorax and a red abdomen. *C. sjostedti* Mayr has a black head and abdomen and a reddish-black thorax. *Tetraponera penzigi* Mayr is a long thin ant, entirely black and readily recognizable.

An additional mutually exclusive ant species, *Crematogaster* (*Orthocrema*) sp. was found in swollen thorns on only one *A. drepanolobium* tree. *Camponotus braunsi* Mayr and *C. rufoglaucus* Jerden (*sensu lato*) were non-exclusive, and found on trees that were occupied by other ant species, although *C. braunsi* did enter swollen thorns on some of these trees. These three ant species are apparently generalists, i.e. not obligately limited to swollen thorn acacias (P. Ward, personal communication).

Table 1 Ants found on *Laikipia* swollen thorn acacias. The first seven species appear to be mutually exclusive on an individual tree. All species except *Camponotus rufoglaucus* and sometimes *C. braunsi* were residents, living inside thorns

Ant species	Tree species	Obligate?	Abundance
<i>Crematogaster mimosae</i>	<i>A. drepanolobium</i>	Probably	Common
<i>C. nigriceps</i>	<i>A. drepanolobium</i>	Probably	Common
<i>C. sjostedti</i>	Both species	Probably	Common
<i>Crematogaster (Orthocrema) sp.</i>	<i>A. drepanolobium</i>	Probably not	One occurrence
<i>C. castanea</i>	<i>A. seyal</i> var. <i>fistula</i>	No	Common
<i>Tetraponera penzigi</i>	<i>A. drepanolobium</i>	Probably	Common
<i>Lepisota canescens</i>	<i>A. seyal</i> var. <i>fistula</i>	Probably not	Common
<i>Camponotus braunsi</i>	<i>A. drepanolobium</i>	Probably not	Occasional
<i>C. rufoglaucus</i>	Both species	No	Common

The swollen thorns of *A. seyal* var. *fistula* are inhabited by *Crematogaster sjostedti* and two additional species. *C. castanea* F. Smith (*sensu lato*) has all body parts honey-colored. *Lepisota canescens* Emery (*sensu lato*) is a tiny entirely black ant that is not aggressive. "This genus has been referred to as *Acantholepis* in most literature" (P. Ward, personal communication). P. Ward (personal communication) suggests that latter two species are probably not obligate acacia ants. We have seen *C. castanea* in other habitats and foraging on camp structures.

Vegetation surveys

We carried out vegetation surveys at three different *A. drepanolobium* sites that were within 1.5 km of each other, and were representative of *A. drepanolobium* sites in the area. At each site we established regular survey points every 20 m on gridded plots totaling 6 ha. At each point, we measured the nearest tree (including juveniles) in each of four compass directions, recording the distance to the tree, its height, and its species. In addition, we sampled 1 square meter of herbaceous vegetation at each point. Using a pin frame with 25 regularly spaced vertical pins, we counted the number of pins that touched any living vegetation. At one site, we also counted the number of times pins touched each plant species. At all sites, we recorded presence/absence of each plant species in each square meter. In all, we surveyed 1800 trees and shrubs, and placed 450 pin frames.

Ant surveys

At nearby sites, we carried out ant surveys of two types. In simple surveys, we recorded the height of each tree to the nearest 0.5 m and the identity of its resident ant occupants ($n = 536$ trees). In detailed surveys, we also recorded numerous other traits for each tree ($n = 285$ trees). We subjectively classified the condition of the leaves as average, below average, or above average, in terms of the size and color of leaves, and the number of leaflets that were missing from the leaves. We also counted the number of new shoots.

We sampled 10–20 nectaries per plant, and classified the nectaries as active, dried, eaten, or absent. Active nectaries were green and completely formed. Dried nectaries were present, but brown and shriveled. Eaten nectaries were indicated by (usually indented) scars at the locations where nectaries normally occur (at the base of the petiole). Nectaries were classified as absent when there were neither nectaries nor scars at the locations where nectaries normally occur. We also recorded the presence of other, apparently non-resident, ant species, and the presence of scale insects and aphids.

Initially we surveyed all individuals in 10 m × 10 m quadrats at sites either at or within 400 m of the vegetation plots. Later we surveyed the nearest tree at 10 m or 20 m intervals along line transects in a variety of sites in this ecosystem, all within 5 km of the earlier survey sites. These different survey methods and sites produced similar results, and are combined below. We surveyed 441 trees of *A. drepanolobium* and 95 trees of *A. seyal* var. *seyal*.

At an additional site approximately 2 km from the vegetation plots, we opened four thorns on each of 105 randomly sampled *A. drepanolobium* trees and recorded their contents. We sampled one

swollen thorn at random on each of four branches per tree. We recorded tree height to the nearest 0.5 m, branch height, and the relative position of the sampled thorn along the branch (proximal, medial, distal). We sampled two reddish thorns and two gray-black thorns on each tree. Reddish thorns are always distal, because they are younger. We recorded the identity of ants in each thorn, and the presence of adults, pupae, larvae, and eggs. We also noted whether the thorn contained adult scale insects.

In 1996, we recorded whether the axillary shoots had been eaten on 220 *A. drepanolobium* trees between 1.0 and 2.5 m tall. We also surveyed 90 individuals (1.0–2.0 m tall) of *A. drepanolobium* in a reproductive population, recording ant species, flowering class, and the number of pods present. Flowering classes were as follows: 0 = no flowers; 1 = inflorescences present, but on fewer than one-third of the branches; 2 = inflorescences on one-third to two thirds of the branches; 3 = inflorescences on more than two-thirds (but not all) of the branches; 4 = inflorescences on all branches.

Results

Accacia drepanolobium

Height structure and ant distribution

In the *A. drepanolobium* sites surveyed for plant species composition, this species formed a virtual monoculture in the overstory (Table 2). Its height distribution approximated a negative exponential, consistent with a stable age structure (Fig. 1). The understory was also poor in species. Five grass species and five forbs comprised 97.4% of the relative cover and 86.6% of the relative frequencies in the understory (Table 2). Consistent frequencies of these species across sites imply community homogeneity on a large scale. Bare ground averaged $51.6 \pm 2.2\%$ (SE, $n = 3$ sites). Plant cover and bare ground total to more than 100% because multiple hits per pin were common. Species richness per one 1-m² quadrat averaged 5.52 ± 0.09 .

Host trees occupied by different species of mutually exclusive ants had characteristic height distributions (Fig. 2, Table 3). If tree height is an approximation of tree age, the horizontal axis in Fig. 2 can be viewed as representing changes in ant occupancy through an average tree's lifetime. Initially, many trees are uninhabited, though *Crematogaster mimosae* is common and *T. penzigi* and *C. sjostedti* occur at low frequency. In the next size class, the proportion of uninhabited trees drops to nearly zero, with *T. penzigi* and *C. nigriceps* becoming more common. Thereafter, there is a steady increase in

Table 2 Absolute and relative abundance among the trees and shrubs (density) and among the herbs (cover and frequency), averaged over 18 ha in three sites. Cover was only measured at one site (6 ha), and frequency was measured at all three sites (18 ha)

Trees and shrubs	All heights		>1 m	
	Density (per ha)	Relative density (%)	Density (per ha)	Relative density (%)
<i>Acacia drepanolobium</i>	1335	98.1	602	99.8
<i>Cadaba farinosa</i>	9.8	0.7	0	0
<i>Balanites aegyptiaca</i>	5.3	0.4	1.2	0.2
<i>Rhus natalensis</i>	4.5	0.3	0	0
<i>A. mellifera</i>	3.0	0.2	0	0
<i>A. brevispica</i>	1.5	0.1	0	0
<i>Lycium europaeum</i>	0.8	<0.1	0	0
<i>Maerua</i> sp.	0.8	<0.1	0	0
Total	1361	100.0	603	100.0

Understory	Cover (%)	Relative cover (%)	Frequency (%)	Relative frequency (%)
Grasses				
<i>Lintonia nutans</i>	12.92	18.6	82.9	14.8
<i>Pennisetum mezianum</i>	17.28	24.9	69.6	12.5
<i>Brachiaria lachnantha</i>	11.88	17.1	73.3	13.1
<i>Themeda triandra</i>	7.36	10.6	65.9	11.8
<i>P. stramineum</i>	6.76	9.7	46.7	8.4
All others (>5 spp.)	0.40	0.1	8.8	1.6
Forbs				
<i>Aerva lanata</i>	6.12	8.8	55.2	9.9
<i>Commelina</i> sp.	0.36	0.5	36.6	6.6
<i>A. drepanolobium</i>	2.64	3.8	20.6	3.7
<i>Rhinacanthus ndorensis</i>	1.24	1.8	19.7	3.5
<i>Dyschoriste radicans</i>	0.28	0.4	13.1	2.3
All others (>32 spp.)	1.72	2.5	65.9	11.8
Total	69.36	100.0	558.3	100.0

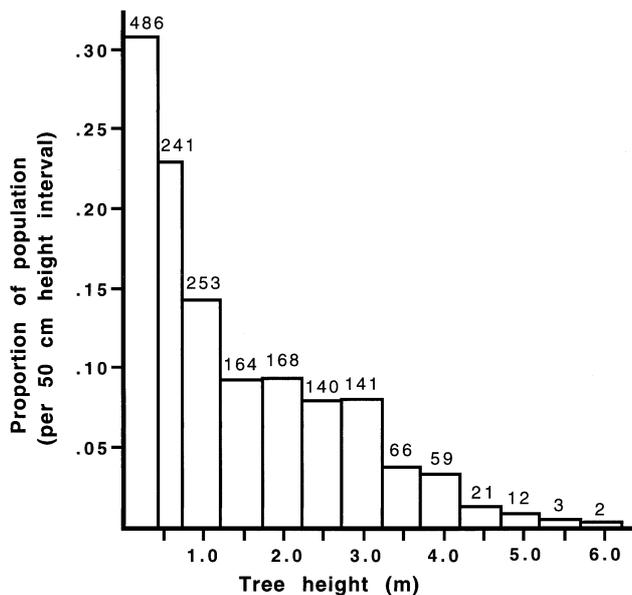


Fig. 1 Size distribution of *Acacia drepanolobium*, based on a survey of 1774 individuals. Trees were measured to the nearest 0.5 m. The proportion in each size class is reported "per 50-cm interval" because the two shortest size classes spanned height intervals (0–0.45 m, called < 0.5 m); and 0.45–0.75 m, called 0.5 m) different from the others (each of which spanned exactly 0.5). For example, there were 241 individuals in the 0.5-m height class, which spans 0.3 m (0.45–0.75 m). Therefore, the proportion of the population per 50 cm height interval is $241/1774 \times 0.50/0.30 = 0.226$

C. mimosae and *C. sjostedti* at the expense of *T. penzigi* and *C. nigriceps*. In the trees over 5 m, *C. sjostedti* may supplant *C. mimosae*. All species were relatively common in trees of intermediate heights. At least 15% of the trees 0–1.5 m tall were occupied by each of the four common resident ant species.

It is possible that some of these differences in heights of trees occupied by different ant species could be due to differential tree mortality (higher in unoccupied, *T. penzigi* and *C. nigriceps* trees), to differential growth rates (lower in trees occupied by *T. penzigi* and *C. nigriceps*; see below), or to historical effects (a recent increase in *T. penzigi* and *C. nigriceps* occupancy in general). However, there is both indirect and direct evidence that a succession occurs among ant species. Most convincingly, we have seen active eviction of one species by another on six different trees.

Direct observations of interspecific aggression and supplantation among ant species

We located and marked two trees (2.5 and 3.0 m tall) in which the upper canopy was occupied by *T. penzigi*, and on lower branches were occupied by *C. mimosae*. In addition, we located and marked four trees (0.7, 0.7, 1.0, and 2.5 m tall) in which older branches were occupied by *T. penzigi*, and newer branches were occupied by *C.*

Table 3 Comparison of *A. drepanolobium* trees occupied by four different ant species (or unoccupied). Ant species are presented in order of increasing mean tree height on which the ant species is found. All mean tree heights not sharing a superscript are significantly different ($p < 0.05$, Tukey-Kramer Honestly Significant Test,

JMP 3.1 Software). Frequencies of characteristics were compared among trees occupied by different ant species were compared with Chi-square tests. There were four degrees of freedom for all comparisons, except 'Proportion fruiting', where d.f = 3. Unless otherwise noted, sample sizes are the same as in the first line of the table

Trait	Proportion of trees with trait, based on ant occupant					χ^2	P
	Unoccupied	<i>T. penzigi</i>	<i>Crematogaster nigriceps</i>	<i>C. mimosae</i>	<i>C. sjostedti</i>		
<i>n</i> (for most traits)	37	50	33	122	43		
Plant traits							
Mean height (+ SE)	0.33+0.09	0.85+0.11 ^a	1.07+0.12 ^{a,b}	1.63+0.12 ^{b,c}	2.28+0.22 ^c		
Some nectaries eaten	0.11	0.90	0.48	0.33	0.21	44.53	<0.001
No nectaries active	0.38	0.92	0.33	0.27	0.26	41.15	<0.001
Some leaves without nectaries	0.49	0.24	0.03	0.11	0.23	27.16	<0.001
Some leaves without nectaries among trees <0.5 m tall (<i>n</i>)	0.62 (34)	0.55 (11)	0.00 (2)	0.30 (33)	0.33 (9)	5.12	~0.30
Short shoots eaten (<i>n</i>)	0.00 (5)	0.00 (30)	0.97 (72)	0.00 (172)	0.00 (22)	222.0	<0.001
Proportion flowering	0.67 (3)	0.62 (13)	0.10 (21)	0.89 (38)	0.80 (15)	14.21	<0.01
Proportion fruiting	n.a.	0.45 (11)	0.00 (12)	0.67 (9)	0.29 (7)	7.95	<0.05
Insect associations							
Scale insects present	0.00	0.02	0.00	0.45	0.28	49.93	<0.001
Scale insects inside swollen thorns (<i>n</i>)	0.00 (35)	0.00 (9)	0.00 (16)	0.15(41)	0.00(4)	9.45	~0.06
Leaf galls present	0.05	0.18	0.06	0.11	0.44	28.62	<0.001
Other galls present	0.05	0.02	0.09	0.05	0.14	6.27	~0.20
<i>Camponotus rufoglaucus</i> ants present	0.00	0.00	0.00	0.02	0.44	87.70	<0.001
<i>Camponotus braunsi</i> ants present	0.00	0.00	0.00	0.01	0.14	27.32	<0.001

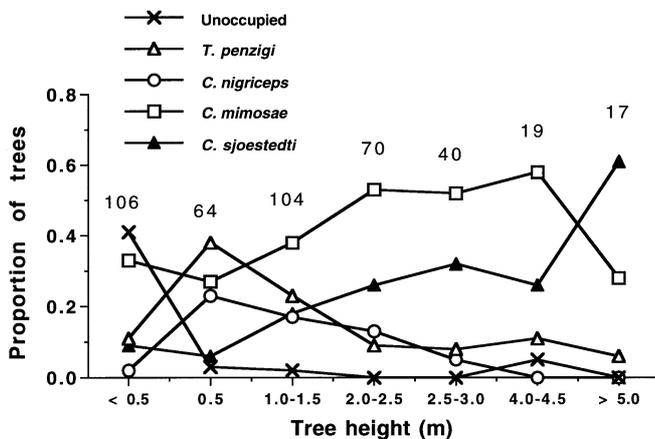


Fig. 2 The relative abundance of different species of mutually exclusive acacia-ants on *A. drepanolobium* trees of different heights. Trees were measured to the nearest 0.5 m. The number of trees sampled at each height is shown. The two *Camponotus* species are not included, because they occurred on the same trees with other ant species (especially *Crematogaster sjostedti*, see Fig. 3)

sjostedti, *Crematogaster mimosae* and *C. sjostedti* ants move between trees by going down trunks and along the ground, a behavior not seen in *T. penzigi*. All six trees in our surveys that had both *T. penzigi* and another ant species (four *C. sjostedti* and two *C. mimosae*) were marked in July-August 1993. Two trees that were occupied by both *C. sjostedti* and *T. penzigi* on 5 July 1993 were occupied only by *C. sjostedti* on 16 August 1993. By November 1993, all six trees were inhabited by only one ant species, with *T. penzigi* being supplanted in each case. All of

these observations indicate that *T. penzigi* ants are competitively subordinate to *C. mimosae* and *C. sjostedti* ants and that succession within trees is taking place.

On 13–14 August 1993, T.P. Young observed the following on one of these trees. *C. sjostedti* ants were the only species in evidence, and were resident in most swollen thorns. *C. sjostedti* ants were clustered in large numbers around several swollen thorns, each bearing the multiple small holes characteristic of *T. penzigi*. The *C. sjostedti* ants were enlarging these holes. Two of these swollen thorns were cut open (by T.P.Y.), and *T. penzigi* ants emerged. These were set upon by *C. sjostedti* ants, and one after another fighting pair dropped off the tree in combat.

On a different tree occupied by both *T. penzigi* and *C. mimosae*, T.P.Y. observed the following along the trunk at the "boundary" between the two species' distributions. Two *T. penzigi* ants had ventured down to the upper limits of *C. mimosae* activity, which in this case was the attack of a swollen thorn presumably occupied by *T. penzigi*. Whenever either of the two *T. penzigi* ants encountered an *C. mimosae* ant, it immediately flattened itself against the tree trunk and became motionless. The *C. mimosae* ants invariably moved on soon thereafter. The *T. penzigi* ants thus confronted did not leave the area immediately, but continued to wander in the vicinity, and this resulted in multiple encounters. Similar interactions were observed on the other trees that housed both *T. penzigi* and *Crematogaster* spp.

There may also be a replacement by *Camponotus braunsi* on taller trees occupied by *Crematogaster sjost-*

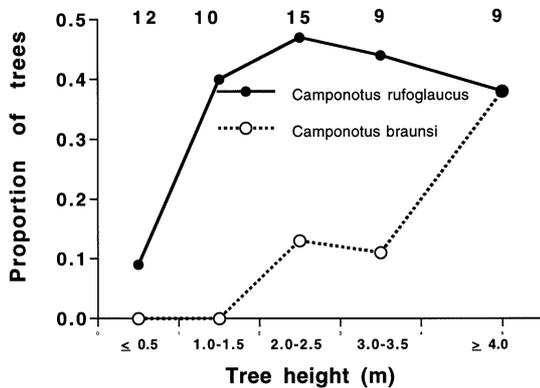


Fig. 3 The proportion of *A. drepanolobium* trees occupied by *C. sjostedti* on which non-resident *Camponotus rufoglaucus* ants (closed circles) and *C. braunsi* ants (open circles) were observed. Trees were measured to the nearest 0.5 m

edti. These large ants were commonly seen on taller trees with *C. sjostedti* (Fig. 3). We observed no aggression between these ants. On the tallest tree in our sample (6.0 m) *Camponotus braunsi* were the only ants in residence. When their swollen thorns were molested by an observer, the ants inside did not exit, but instead blocked the entrance holes with their gasters (see also Davidson and McKey 1993b). Under similar circumstances, all other resident ants on *A. drepanolobium* will come out and act aggressively (though to differing degrees). Even on smaller trees occupied by *Crematogaster sjostedti*, *Camponotus braunsi* ants were occasionally seen entering swollen thorns, and it is possible that these ants were resident in the trees on which we saw them.

Trees with *Crematogaster sjostedti* ants were also unique in commonly having *Camponotus rufoglaucus* ants on them (about half of all larger trees, Fig. 3). We have seen these *Camponotus* ants in other settings and other habitat types. We do not know if they were living in some of the swollen thorns, and consider them to be only foragers on *A. drepanolobium*. In any case, there was no observed aggression between these two ant species.

Traits of trees with different ant occupants

In addition to height, numerous other traits varied significantly among trees with different ant occupants (Table 3). The tendency for unoccupied trees to have at least some leaves that had never produced any nectaries was largely a height effect: nearly half of all very small trees had such leaves, which were rare or absent from taller trees (Fig. 4; $X^2 = 45.77$, $P < .001$).

Among trees that had produced nectaries, there were significant differences in the presence of active nectaries. Trees occupied by *T. penzigi* were 2–9 times more likely to have at least some leaves with their nectaries eaten than were other trees (Table 3). In fact, most of the nectaries were eaten on these trees, and more than 90% of

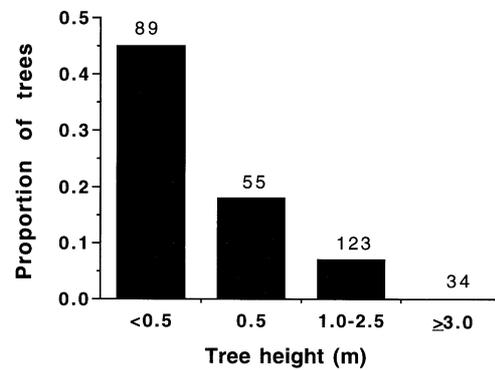


Fig. 4 The proportion of trees of different heights with at least some leaves that had not produced any nectaries. Trees were measured to the nearest 0.5 m. Sample sizes are shown

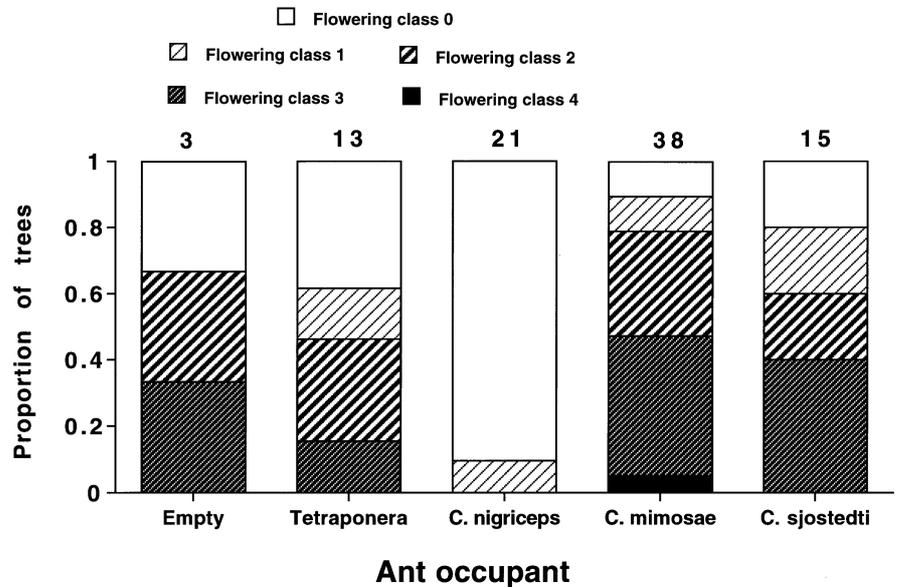
them lacked any active nectaries, whereas only 26–38% of other trees lacked active nectaries (Table 3). The fact that unoccupied trees were much less likely to have nectaries eaten (Table 3) implies that *T. penzigi* themselves were doing the eating, rather than merely not defending the trees as well as other ants against species that eat nectaries.

On virtually every tree with *Crematogaster nigriceps*, all of the axillary shoots at nodes with unswollen thorns were eaten (Table 3). On every tree, a variable proportion, but never all, of the axillary shoots at nodes with swollen thorns were eaten. No other species ate these axillary shoots, and the fact that this was also not seen in unoccupied trees implies that *C. nigriceps* ants were directly responsible. Only about 20% of thorn pairs are swollen (Hocking 1970), and inflorescences are produced at only at axillary shoots. In contrast to trees inhabited by other ant species, few *A. drepanolobium* trees inhabited by *C. nigriceps* flower or set fruit (Table 3, Fig. 5).

Overall, taller trees occupied by *C. nigriceps* also had significantly more new terminal shoots than did trees not occupied by *C. nigriceps* ($F = 3.07$, $P = 0.03$; Fig. 6). Trees occupied by *C. nigriceps* were half as likely to be judged as having leaves less healthy than normal, and twice as likely to have leaves judged more healthy than normal ($P < 0.05$), compared with other classes of trees (Fig. 7), although the overall number of leaves may be less (due to fewer axillary shoots). Among trees occupied by each ant species, there were no tendencies for trees of different heights to differ in leaf condition. Of 33 trees occupied by *C. nigriceps*, only one had at least some leaves that failed to produce nectaries, whereas 11–43% of the trees occupied by other ants or unoccupied had at least some leaves that failed to produce nectaries (Table 3).

Altogether 45% of trees with *C. mimosae* and 28% of trees with *C. sjostedti* had adult scale insects on the undersides of younger branches, and these scales were virtually absent on other trees (Table 3). These scales have been tentatively identified as *Ceroplastes* sp. ("wax scales", Coccidae; P. Gullan, personal communication).

Fig. 5 Proportion of trees in different flowering classes, relative to identity of ant occupant. Sample sizes are shown. From a sample of trees 1.0–2.5 m tall



These scales are often tended by one to several ants in direct contact with each scale insect. Only in sampled trees with *C. mimosae* ants were adult scale insects found inside swollen thorns. However, only four trees occupied by *C. sjostedti* were included in this sample (Table 3), and M. Stanton (personal communication) reports that scale insects occur in swollen thorns with this species, although at a lower rate than with *C. mimosae*. As mentioned above, *C. sjostedti* was the only species commonly associated with the two *Camponotus* species (Table 3). In trees occupied by *Crematogaster sjostedti*, both *Camponotus* species were more likely to be found on taller trees than on shorter trees (Fig. 3). In addition, trees occupied by *Crematogaster sjostedti* were two and a half to nine times more likely to be infested with leaf galls (Table 3) than trees occupied by other ants (or un-

occupied). For each species of occupant ants, the presence of scale insects or leaf galls was not significantly related to tree height.

Acacia seyal var. *fistula*

Three ants were commonly found in *A. seyal* var. *fistula*. One of them, *Lepisota canescens*, was found only on *A. seyal*. The other common species, *C. sjostedti*, was found on *A. drepanolobium* and *A. seyal*, but not elsewhere in the environment. The third species, *C. castanea*, was found in other habitats, including our research camp (on trees and tents) along the Ewaso Nyiro River, on red soils.

There was only limited evidence of different ant species inhabiting *A. seyal* trees of different heights (Fig. 8).

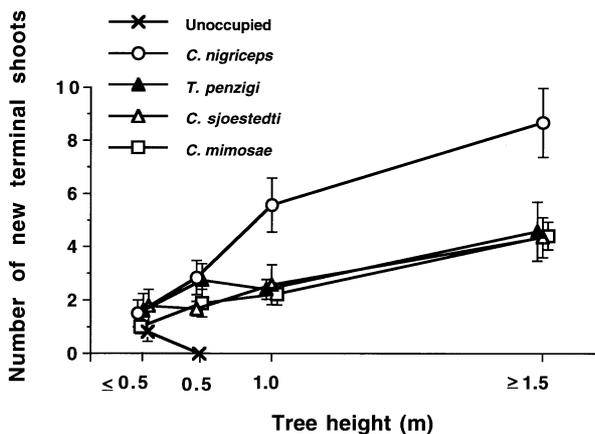


Fig. 6 Number of new terminal shoots per tree (± 1 SE.), relative to ant occupant and tree height. Trees were measured to the nearest 0.5 m. The numbers of new shoots were similar across heights above 2.0 m, so all these data were combined; *n* ranges from 34 to 127 per ant species

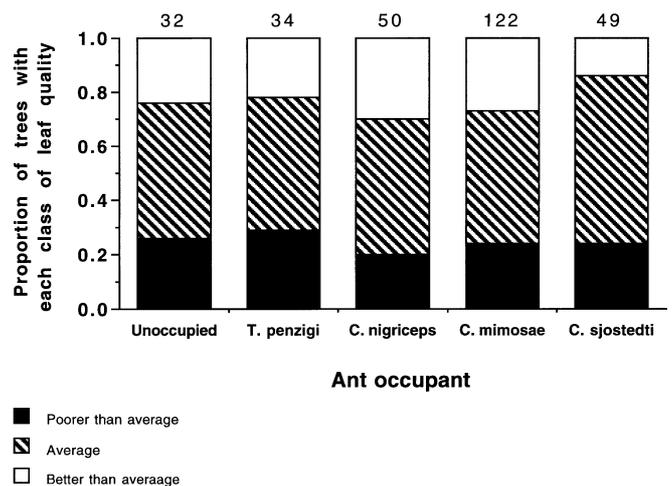


Fig. 7 Proportion of trees judged to have leaves better than average (*open*), average (*shaded*), or worse than average (*closed*), relative to identity of ant occupant. Sample sizes are shown. For each ant species, occupied trees of different heights did not differ in leaf quality

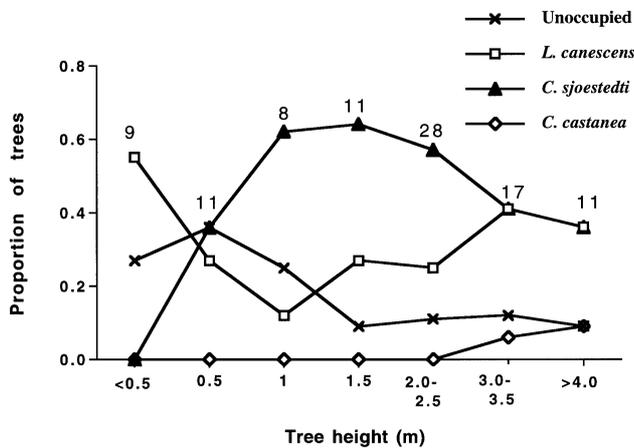


Fig. 8 The relative abundance of different species of acacia-ants on *A. seyal* var. *fistula* trees of different heights. Trees were measured to the nearest 0.5 m. The number of trees sampled at each height are shown

Lepisota ants were the most common occupants of shorter trees, and *C. sjostedti* ants were the most common occupants on trees of intermediate height. The less common *C. castanea* occurred only in the taller size classes. Although the proportion of unoccupied trees dropped off above 0.5 m, there were unoccupied trees in all size classes.

C. sjostedti ants were often seen tending immature scale insects concentrated at leaf bases and were also found in small excavations in young branches. It was not possible to identify the immature scale insects to species, but they belong to the family Pseudococcidae (P. Gullan, personal communication). Again, *Camponotus rufoglaucus* was associated with *Crematogaster sjostedti*. However, there were relatively few leaf galls or scale insects on *A. seyal*, regardless of the identity of the ant occupant.

Discussion

Species coexistence on a simple resource

Few natural terrestrial habitats appear as uniform as the *A. drepanolobium* wooded grasslands in East Africa. There is little topographic or soil heterogeneity, and a single tree species accounts for virtually the entire overstory. Nonetheless, this single tree species supports at least four mutually exclusive resident ant species and numerous associated insect species. A number of predatory arthropods also inhabit these trees, including at least three species of spiders, and three species of mantids. The coexistence of several obligate ant species in this habitat is made more problematic by their intolerance of each other; more than 99% of all trees had only a single species of resident ant. Host populations in different habitats have been shown to support different ant mutualists (Davidson and McKey 1993b), but in this system coexistence occurs within an unusually uniform ecosystem and

on a very fine spatial scale. There are at least four possible explanations for this apparent violation of the principle of competitive exclusion.

First, it is possible that several ant species are able to share the same niche because acacia trees are not a limiting resource for resident acacia ants. For example, Byrne (1994) has suggested that among twig-dwelling ants in Costa Rica, neither nest sites nor food are apparently limiting. In our study, the occurrence of unoccupied *A. seyal* trees of all sizes suggests this possibility. On the other hand, virtually the only unoccupied *A. drepanolobium* trees were in the smallest size class, and it appears that the environment of suitable colony sites (trees) is mostly saturated in this tree species.

Second, there may be some niche separation among resident ants based on tree size, with two ant species restricted to smaller trees, and two ant species more common on taller trees (Fig. 2). Differences in ant occupants based on plant size have been demonstrated before (see Davidson and McKey 1993b). Our results strongly suggest that this pattern is at least partly related to a succession of ants on *A. drepanolobium* trees of increasing height, and therefore presumably increasing age. We have seen active evictions in progress of some *Tetraponera* ant colonies by others, and have documented similar species replacements that are consistent with a successional change. The early successional status of *C. nigriceps* remains uncertain. Similar ant species replacements through time have been observed in several myrmecophytes (Davidson and McKey 1993b).

Differences in mean height of trees occupied by different ant species are less likely to be caused by the ants themselves, e.g., through differential rates of herbivory or tree growth, at least for three of the four ant species. All of our measures of vegetative vigor were similar for unoccupied trees and trees hosting three of the four ant species. The exception was for trees hosting *C. nigriceps*, which showed greater vegetative vigor. However, this ant species was typically found on smaller trees, a pattern opposite to that which one might expect if differential growth rates were the cause of different characteristic tree heights of different ants. On the other hand, this greater vegetative vigor need not have a simple relationship with height growth, and a more thorough test of this hypothesis awaits estimates of growth rates of *A. drepanolobium*.

Third, even though there may be a niche gradient among ants associated with tree size, all resident ant species occur in substantial numbers on trees of intermediate height (1.5 m). This coexistence may merely be due to time lags and individual variability, such as in intermediate successional stages in plant communities, where both early successional and late successional species temporarily co-exist. It may also reflect underlying environmental variation that we have not yet discovered.

Fourth, there may be multiple persistent ("quasi-stable") states for ant-acacia relationships on trees of intermediate height or age. Once established, *C. nigriceps* and *T. penzigi* may be difficult to dislodge. We have al-

readily mentioned “destructive” behaviors of these two ant species that (at least in *T. penzigi*) may make their trees less attractive for takeovers. In addition, the holes in swollen thorns occupied by *T. penzigi* are considerably smaller than the holes in thorns occupied by species of *Crematogaster* (Hocking 1970), and it appears necessary for a supplanting *Crematogaster* colony to enlarge them before successful eviction of *Tetraponera*. Even in thorns with the larger holes characteristic of *Crematogaster*, the defensive positions inside thorns with a limited number of entrances (usually one or two) may put invaders at a considerable disadvantage (Davidson and McKey 1993b).

Multiple persistent states have been reported for other ant communities. In a pattern that is similar to that reported here, Cole (1983a,b) found that ant communities in a mangrove ecosystem were driven by priority effects, interspecific competition, and island size. Multiple persistent states have also been found in bird communities (Diamond 1975), and terrestrial (Niering et al. 1986; Young 1990; Young and Peacock 1992) and aquatic (Scheffer et al. 1993) communities (reviewed in Whittaker and Levin 1977; Drake 1990; Pimm 1991). Invasion resistance (priority effect) appears to be a key factor in some of these systems (e.g., Barkai and McQuaid 1988), but the presence or absence of key herbivores or predators can also result in alternative communities (reviewed in Sutherland 1974).

Overall species richness in this system is increased by the ability of particular ant species to provide opportunities for additional insect species. The loss of *C. sjostedti* from this system would apparently be accompanied by the loss of *Camponotus rufoglaucus*, *C. braunsi*, the insects producing leaf galls, and several unidentified arthropod species found living in their swollen thorns. If *C. mimosae* were also lost, the scale insect would disappear from the system. The various predator species may also rely on the presence of resident ants. Hocking (1970) lists many more invertebrate symbionts (many living inside swollen thorns, and some as ant mimics) that may rely on these ant-plant relationships for their success.

Costs and benefits of ant occupancy

Mutualistic relationships evolve to maximize the fitness of each partner separately (Janzen 1966; Howe and Westley 1988). In each species, adaptations are favored that maximize the overall reproductive success of individuals, largely independently of the effects on fitness of the other species (although these may be secondarily linked). The result may very well include particular adaptations in one partner that are less than beneficial to the other, even when both benefit overall from the relationship. Parasites of these mutualisms can also occur.

We do not as yet have quantitative measures of ant aggression. *C. mimosae*, a late successional species, appears to swarm most quickly after a disturbance to the

tree. *Tetraponera*, an early successional species, is the least reactive. The other two species are intermediate. It is still not clear what defensive function these ants serve. In a previous study lumping all ant species, *A. drepanolobium* trees with more active ants had more foliage than did trees with less active ants, and were less heavily browsed by immature, but not mature, giraffes (Madden and Young 1992).

The tending of scale insects and the tolerance of other “damaging” insects are not consistent with the classic view of a co-evolved mutualism. More aggressive ants may be more likely to defend a tree against attackers (Fiala et al. 1994), but they may also be better defenders of tended scale insects (Buckley and Gullan 1991). The two ant species that tend scale insects on *A. drepanolobium* (*C. mimosae* and *C. sjostedti*) and *A. seyal* (*C. sjostedti*) are the “late successional” species. Their trees have relatively high reproductive fitness (Table 3, Fig. 7) despite these scale insects. *Crematogaster sjostedti* is also associated with leaf galls, two species of *Camponotus*, and several unidentified residents of swollen thorns.

It has been suggested that the production of extrafloral nectaries may be an adaptation to discourage the tending of sucking insects by ants (Becerra and Venable 1989, 1991). The presence of scale insects on both tree species, many of them tended by resident ants, implies that the alternative food sources provided by plant nectaries are not sufficient to eliminate the tending by ants of potentially deleterious insect parasites (see also Davidson and McKey 1993b, Del-Claro and Oliveira 1993).

The unique destruction of most axillary shoots by *Crematogaster nigriceps* is associated with two very different plant traits. First, at the time of our surveys, *A. drepanolobium* trees occupied by *C. nigriceps* ants had more young shoots and healthier leaves than did other trees (Figs. 5 and 6). These trees were also less likely to have leaves lacking active nectaries (Table 3), and the nectaries that were present were generally far larger than on other trees (personal observation). It is not known how the eating of axillary shoots would produce more shoots or healthier leaves, but the reallocation of resources is an obvious possibility. The long-term consequences for growth form of this “pruning” of axillary shoots are currently being explored.

Second, the destruction of axillary shoots by *C. nigriceps* prevented virtually all trees occupied by this ant species from flowering or fruiting, at least at the time of this survey. This may be part of a trade-off between reproductive effort (at axillary shoots), and the increased vegetative vigor described above. As such, *C. nigriceps* appears to be an evolutionary parasite, harvesting (and even perhaps enhancing) its nectar rewards while greatly reducing its hosts’ reproductive fitness. The other occupant ant species may also differ in their effects on the evolutionary fitnesses of their host plants, but in less dramatic ways (Table 3, Fig. 5).

These obligate plant-ants provide an ideal system in which to ask questions about community structure, species coexistence, and the uneasy co-evolution of mutual-

ists. Research currently underway includes experimental manipulation of ant occupancy, further measurement of the evolutionary fitness of trees with different ant symbionts (and of the ants themselves), and long-term monitoring of trees to document turnover of ant symbionts and the demography of their host trees.

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