



## Responses of Ground-Foraging Ant Communities to Three Experimental Fire Regimes in a Savanna Forest of Tropical Australia<sup>1</sup>

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### ABSTRACT

Ants were sampled using pitfall traps in two replicate 1 ha plots of each of three experimental fire treatments (annually burned, biennially burned, and unburned for over 14 years) in a eucalypt-dominated savanna of tropical northern Australia. The ant fauna was extremely diverse, with 81 species from 24 genera recorded. Species were classified into functional groups based on habitat requirements and competitive interactions, with the most important groups being dominant species of *Iridomyrmex* (11 species, 14–63% total ants in traps); generalized myrmicines (mostly species of *Monomorium* and *Pheidole*; total of 22 species, 11–61% total ants in traps); hot climate specialists (species of *Melophorus*, *Monomorium* ("Chelaner") and *Meranoplus*; total of 14 species, 1–16% total ants in traps); cryptic species (many genera; total of 13 species, 2–27% total ants in traps); and, opportunists (mostly species of *Rhytidoponera* and *Tetramorium*; total of 11 species, 3–12% total ants in traps). Ant communities in the annually burned plots were characterized by relatively high numbers of dominant *Iridomyrmex*, hot climate specialists and opportunistic *Rhytidoponera aurata*, and low numbers of generalized myrmicines and cryptic species. The reverse was true for unburned plots. Many species were common under one fire regime, but were rarely or never recorded under the other. These differences were attributed to structural changes in the habitat caused by fire, and in particular to the levels of litter accumulation and insolation on the ground. These changes influenced ants directly, but also had important indirect effects through their influence on the abundance of dominant *Iridomyrmex*, and therefore on competitive interactions. The ant communities in the biennially burned plots were generally intermediate to those of the unburned and annually burned plots. However, one was more similar to those in the annually burned plots, while the other resembled those in the unburned plots.

These results demonstrate that different fire regimes have a major influence on one of the most important faunal groups in tropical savannas, and this has important implications for conservation management in these ecosystems.

FIRE IS AN IMPORTANT LAND MANAGEMENT TOOL in many ecosystems throughout the world (Naveh 1975, Gill 1977, Hobbs & Gimingham 1987, Moore 1987), but especially in tropical savannas (Gillon 1983, Murphy & Lugo 1986, Stott 1986), where fires are often annual and lit almost exclusively by humans (Braithwaite & Estbergs 1985, Gillon 1983). Studies of the effects of fire in tropical savannas have largely focused on the responses of grasses (Stocker & Mott 1981, Gillon 1983) and, to a lesser extent, woody plants (Miyanishi & Kellman 1986, Stark 1986), with little attention paid to the fauna. Indeed, some recent reviews of the ecological effects of fire in tropical savannas ignore the fauna completely (Coutinho 1982, Lacey *et al.* 1982, Sarmiento 1984). Moreover, most faunal studies have been concerned with responses to single fires (Gillon 1983, Gandar 1982, Frost 1985), rather than to different fire regimes. This lack of information on the influence of different fire regimes on faunas makes it difficult for managers of tropical

savannas to devise appropriate fire management plans, especially in areas like national parks where conservation is the prime management objective.

Here I report on the effects of three experimental fire regimes on communities of ground-foraging ants in a forested savanna in Kakadu National Park, in tropical northern Australia. Ants are a dominant faunal group in most tropical savannas (Levieux 1983), but are particularly abundant and diverse in those of northern Australia, where more than 100 species can occur within 500 m<sup>2</sup> (Andersen, in press a, b). Kakadu savannas have been burned by aboriginal people for at least 20,000 years (Jones 1969, Haynes 1985, Kershaw 1985), but details of the frequency, timing, and extent of their burning are poorly understood (see Horton 1982). The contemporary fire regime is one of dry season burning at least once every three years, and, typically, annually (Braithwaite & Estbergs 1985, Day 1985). The fires include both prescription burns by management authorities, which usually occur early during the dry season (May/June) and are often relatively low in intensity and small in area, and unprescribed burns lit by the public, which tend to

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occur later in the season and are often more severe. Different fire regimes are known to have important influences on the bird (Woinarski 1990) and lizard (Braithwaite 1987) faunas of Kakadu, but there have been no studies of their effects on invertebrates.

## STUDY SITES

The predominant vegetation types in the Kakadu region are heavily wooded savannas dominated by species of *Eucalyptus* (Braithwaite & Estbergs 1985, Taylor & Dunlop 1985), as is the case for much of northern Australia (Gillison 1983, Mott *et al.* 1985). Rainfall is highly seasonal, with 80 percent of the annual mean of 1000–1400 mm falling between December and March (Taylor & Dunlop 1985). Compared with tropical savannas elsewhere in the world, vertebrate biomass is exceptionally low, and invertebrates in general assume far greater functional importance (Mott *et al.* 1985, Andersen & Lonsdale, 1990).

The study was conducted at an experimental fire site at Munmarlary (12°28'S, 132°30'E), which was established jointly by CSIRO and the Conservation Commission of the Northern Territory (CCNT) during 1972 (Hoare *et al.* 1980). The site consists of a series of replicated treatment plots with annual, biennial, and fire-exclusion (unburned) burning regimes. The plots are each 1 ha, and located within a total area of approximately 20 ha. The vegetation is an open forest of *Eucalyptus tetradonta* and *E. miniata* over a tall grassland of annual *Sorghum intrans* on well-drained, sandy loam soils, and is described in detail by Bowman *et al.* (1988). There are some fire-induced floristic differences between plots, but the major effect of fire regime on vegetation has been structural, with unburned plots having far greater mid-story development (predominantly *Acacia* spp. and *Erythrophloeum chlorostachys*) than all others (Fig. 1; Bowman *et al.* 1988). Such mid-story development is a feature of unburned savannas both in Australia (Stocker & Mott 1981) and elsewhere (Kellman & Miyashita 1982, Gillon 1983).

## METHODS

Ants were studied in six plots, representing two replicates of each of three fire regimes. The plots will subsequently be referred to as A1 and A2 (burned annually), B1 and B2 (burned every two years), and C1 and C2 (unburned). The CCNT codes for the plots were B1P2, B2P2, B1P3, B2P3,

B1P4 and B3P4, respectively. All fires were lit early during the dry season (May/June).

In each plot, ants were sampled using 20 pitfall traps (5 cm diameter), located in a 5 × 4 grid with 10 m spacing. Traps were partly filled with a 70 percent ethanol-glycerol mixture as a preservative, and operated for 48 hr from 9–11 June 1986. Two traps in plot A1 were disturbed and consequently excluded from analysis. The weather was dry throughout, with temperatures ranging from 15 to 31°C.

Results from similar sites elsewhere in Kakadu show that trapping at this intensity provides a good indication of the relative abundance of the major ant species on the ground (Andersen, in press a). Pitfall trapping is not so effective for cryptic species, and of course does not sample arboreal species. Moreover, catches are influenced by the structure of ground vegetation and litter (Greenslade 1964), with catches likely to be disproportionately lower in areas of heavy litter (*i.e.*, unburned plots). When comparing catches from different sites, it was therefore necessary to consider the relative as well as absolute abundances of species in traps.

Ants were sorted to species level, but most species were unable to be named with certainty due to the generally poor species-level taxonomy of Australian ants. Unnamed species within a genus were distinguished by a number code following, and extending where necessary, the nomenclature of Andersen (in press a, b). A complete collection of voucher specimens is held at the CSIRO Tropical Ecosystem Research Centre in Darwin.

The great diversity of ants collected, combined with an absence of information on their specific biology, made it impractical to interpret their responses to fire at the species level. Both these problems were overcome by assigning species to functional groups according to their habitat requirements and competitive interactions, based on studies of related species elsewhere. This functional group scheme was originally derived by P. J. M. Greenslade from studies of the Australian arid zone (Greenslade 1978, Greenslade & Halliday 1983), but has since been widely applied elsewhere in Australia (Greenslade & Thompson 1981, Greenslade 1985, Andersen 1986). The groups are as follows:

1. Dominant species (*Iridomyrmex* spp. throughout most of Australia, but also *Oecophylla smaragdina* in tropical regions), which are highly abundant and aggressive ants having a strong competitive influence on other species. *Iridomyrmex* is especially abundant in open habitats, where high levels of ground insolation and unimpeded foraging

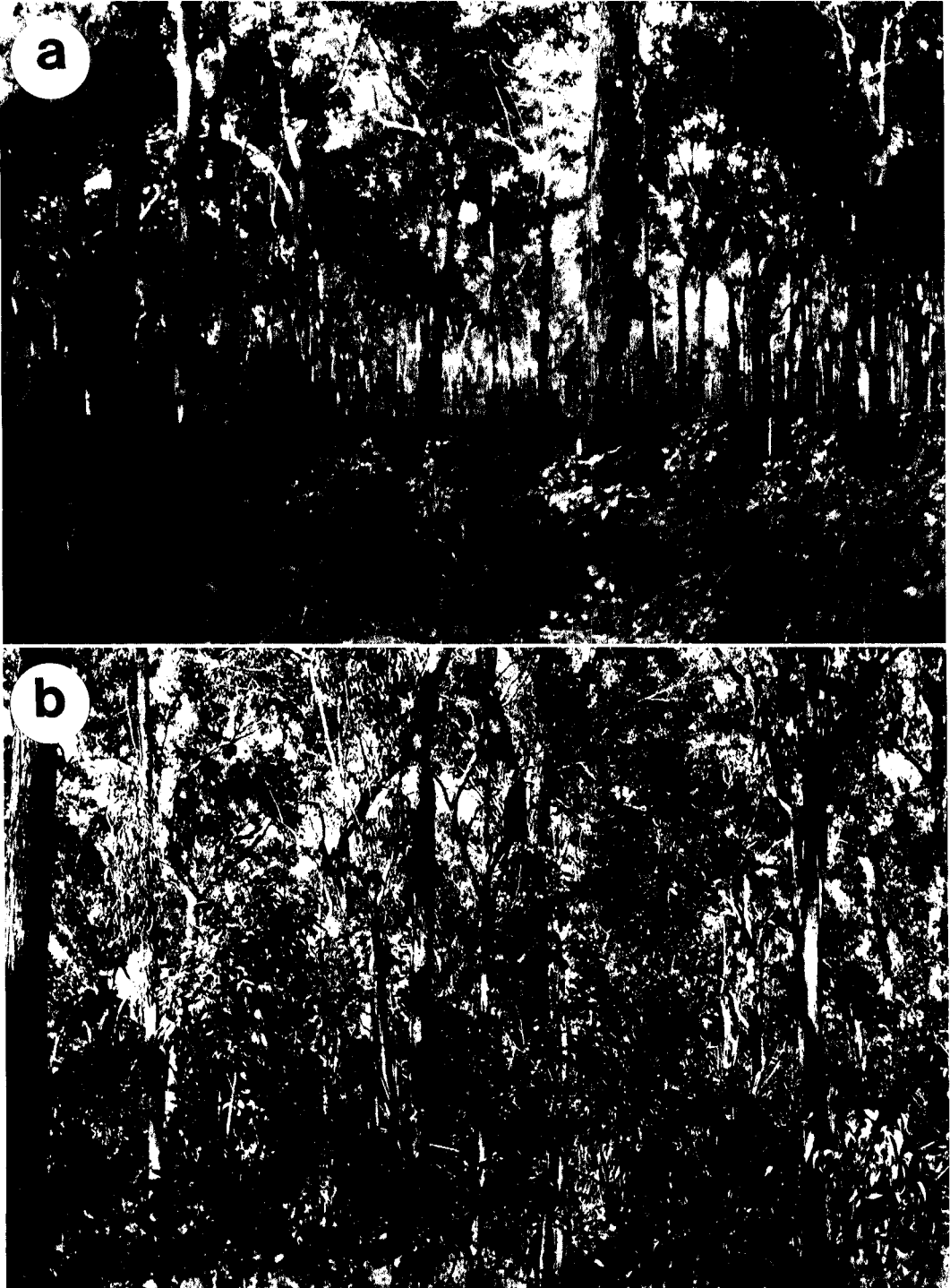


FIGURE 1. Photographs of study plots burned annually (a) and totally unburned (b) over the 14 year treatment period.

surfaces allow for rapid surface movement and recruitment to food sources.

2. Associated subordinate *Camponotini* (particularly species of *Camponotus*), which coexist successfully with dominant species through differences in body size, time of activity, and submissive behavior.

3. Climate specialists, which in this case are taxa restricted to hot environments (e.g., *Melophorus*, *Meranoplus*). These taxa possess physiological (*Melophorus*) or morphological (*Meranoplus*) and associated behavioral specializations which reduce their interaction with *Iridomyrmex*.

4. Cryptic species (mostly small Ponerinae and Myrmicinae), which nest and forage predominantly within soil and litter, and therefore do not interact greatly with other ants.

5. Opportunists (predominantly species of *Rhytidoponera*, *Tetramorium* and *Paratrechina*), which are unspecialized and poorly competitive species that are often abundant in disturbed habitats.

6. Generalized myrmicines (mostly species of *Monomorium*, *Pheidole*, and *Crematogaster*), which are unspecialized but highly competitive taxa occurring in most Australian habitats.

7. Large, solitary foragers (in this case larger Ponerinae), whose large body size and low foraging densities suggest that they do not interact strongly with other ants.

For each of the seven functional groups, ANOVA and LSD tests were performed on absolute abundance data from individual pitfall traps, to test for differences between plots. For each plot, species abundances were used to calculate Shannon–Wiener coefficients of diversity ( $H'$  decits), and coefficients of species evenness ( $J'$ ), defined by  $H'/\log S$  where  $S$  is the total number of species (see Pielou 1975). Bray–Curtis similarity coefficients were calculated for each pair of plots. The coefficients take into account the abundance of shared species, therefore reducing distortion caused by inadequately sampled rare species. Frequencies, rather than total abundances, in pitfall traps were used to reduce the influence of highly abundant species (see Southwood 1978, pp. 432–443).

Species abundances in each trap were then transformed to a six point scale (i.e., 0–5), range standardized, and analyzed using the multivariate analysis package PATN (Belbin 1987a). A Bray–Curtis association matrix of data from individual traps was constructed, and a nonhierarchical clustering strategy (ALOC program, Belbin 1987b) used to generate six groups of trap data, and to identify the ten ant species best discriminating each group. Trap

data were then ordinated using hybrid multidimensional scaling (two axes; KYSP and KYST programs, Belbin 1987a), which is considered to be more robust than the widely used, but somewhat unreliable, detrended correspondence analysis (Minchin 1987, Wartenberg *et al.* 1987, Oksanen 1988). KYST was unable to process the entire data set, so analysis was restricted to the first 15 traps of each plot. Correlation coefficients were calculated for the KYST scores of both axes and the abundance of each functional group. ANOVA and LSD tests were performed on KYST scores to test for differences between plots.

Finally, PATN was used to cluster the ant species according to their distribution in traps. An association matrix of the 32 most abundant species (those with a total of 15 or more individuals recorded) was constructed using the TWO STEP program (Belbin 1987a). TWO STEP employs an asymmetric, modified Bray–Curtis similarity measure, avoiding the problem of forming groups that depend largely on species frequency (e.g., grouping rare species simply because of their rarity; Belbin 1980). ALOC was used to generate five groups of species based on this association matrix.

## RESULTS

A total of 81 ant species from 24 genera were recorded in pitfall traps, with the richest genera being *Monomorium* (14 species), *Iridomyrmex* (11), *Meranoplus* (8), *Pheidole* (7), and *Rhytidoponera* (5) (Table 1). The most commonly trapped ants were unidentified species of *Iridomyrmex*, *Monomorium*, *Pheidole*, *Melophorus*, *Solenopsis*, and *Paratrechina* (*minutula* gp.), as well as *Rhytidoponera aurata*.

The overall composition of the fauna (Table 1) is similar to that in other wooded savannas of the region (cf. Greenslade 1985, Andersen, in press a, b), with dominant species of *Iridomyrmex* and generalized myrmicines (mostly species of *Monomorium* and *Pheidole*) combined comprising about 70 percent of total ants captured in traps. Hot climate specialists (up to 16% total ants) and cryptic species (up to 27% total ants) were also locally abundant. Although the fauna contains many tropical taxa, including species of *Oecophylla*, *Aenictus*, *Glamyromyrmex*, *Quadristuma*, *Bothroponera*, *Leptogenys* and *Odontomachus*, none of these were frequently recorded, and the overall faunistic composition bears a strong resemblance to that in arid central and semiarid southern Australia (see Greenslade 1978; Greenslade & Halliday 1983; Andersen 1983,

TABLE 1. Composition of ant species collected in pitfall traps. Data are numbers of species per taxon, with percent total ants per plot in brackets. Taxa are arranged into functional groups according to a generalized model of ant community organization in Australia (see text for details).

	Plot						Total
	A1	A2	B1	B2	C1	C2	
1. Dominant species							
<i>Iridomyrmex</i>	6 (63)	6 (52)	7 (47)	4 (14)	1 (15)	1 (19)	11 (33)
<i>Oecophylla</i>	—	—	1 (<1)	—	1 (<1)	1 (<1)	1 (<1)
2. Associated subordinate Camponotini							
<i>Camponotus</i> , <i>Opisthopsis</i> + <i>Polychachis</i>	2 (<1)	3 (1)	4 (1)	—	—	3 (1)	7 (<1)
3. Climate specialists							
<i>Monomorium</i> ( <i>'Chelaner'</i> )	2 (7)	1 (4)	2 (1)	2 (4)	1 (<1)	—	3 (3)
<i>Melophorus</i>	3 (7)	3 (7)	3 (6)	2 (2)	1 (3)	1 (<1)	3 (4)
<i>Meranoplus</i>	5 (2)	4 (1)	4 (1)	1 (1)	1 (1)	1 (<1)	8 (1)
Subtotal	10 (16)	8 (11)	9 (8)	5 (7)	3 (4)	2 (1)	14 (8)
4. Cryptic species							
<i>Aenictus</i> , <i>Gnamptomyrmex</i> + <i>Quadristruma</i>	—	1 (<1)	1 (1)	1 (<1)	2 (1)	—	4 (<1)
<i>Solenopsis</i> , <i>Acropyga</i> , <i>Stigmacros</i> , <i>Tapinoma</i> + <i>Paratrechina minutula</i> gp.	2 (2)	4 (3)	7 (10)	5 (23)	4 (26)	4 (14)	9 (14)
5. Opportunists							
<i>Paratrechina</i>	1 (<1)	—	—	1 (1)	1 (3)	1 (<1)	1 (1)
<i>Rhytidoponera</i>	3 (4)	5 (9)	3 (5)	2 (3)	2 (1)	—	5 (4)
<i>Tetramorium</i>	3 (4)	2 (3)	3 (3)	2 (5)	—	1 (3)	3 (3)
<i>Cardiocondyla</i>	—	—	—	1 (1)	—	—	1 (<1)
<i>Odontomachus</i>	1 (<1)	—	—	—	1 (<1)	—	1 (<1)
Subtotal	8 (9)	7 (12)	6 (8)	6 (9)	4 (4)	2 (3)	11 (9)
6. Generalized Myrmicinae							
<i>Crematogaster</i>	1 (1)	2 (1)	—	3 (1)	1 (2)	1 (2)	4 (1)
<i>Monomorium</i>	7 (8)	6 (17)	9 (12)	9 (31)	7 (33)	5 (50)	11 (25)
<i>Pheidole</i>	3 (2)	4 (4)	4 (14)	4 (13)	4 (15)	3 (9)	7 (10)
Subtotal	11 (11)	12 (21)	13 (26)	16 (46)	12 (50)	9 (61)	22 (36)
7. Large, solitary foragers							
<i>Bothroponera</i> + <i>Leptogenys</i>	1 (<1)	1 (<1)	2 (<1)	1 (<1)	—	—	2 (<1)
Total no. ants	807	606	772	354	375	282	3196
Total no. species	38	42	49	38	27	22	81
Mean no. species per trap	7.8	8.1	8.4	5.7	4.9	4.0	6.5
Species diversity ( $H'$ )	0.89	1.25	1.30	1.35	1.22	0.95	1.16
Species evenness ( $J'$ )	0.55	0.76	0.75	0.85	0.82	0.70	0.74

1984). This suggests that seasonal aridity is a major determinant of faunistic composition in the region.

Ant abundance, diversity, and composition in traps varied markedly between fire treatments. There was good separation between annually burned and unburned plots according to the ordination of trap data, with only slight overlap (Fig. 2). This separation was primarily across the first axis, where scores

were similar within each burning treatment, but different between treatments (Table 2). Ordination scores on the first axis were positively correlated with the abundances of dominant *Iridomyrmex* ( $r = 0.35$ ,  $P < 0.005$ ), hot climate specialists ( $r = 0.21$ ,  $P < 0.05$ ), and opportunists (primarily *Rhytidoponera aurata*;  $r = 0.49$ ,  $P < 0.05$ ), and negatively correlated with the abundance of cryptic

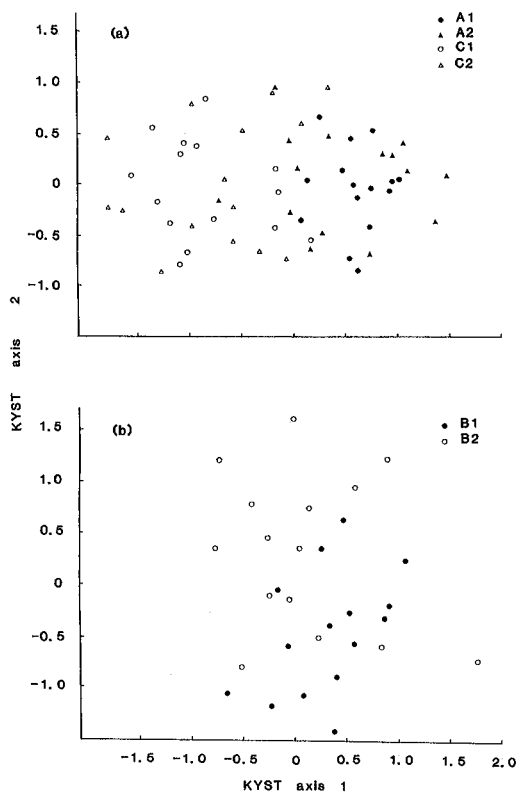


FIGURE 2. Scatter plots of ordination of pitfall traps using hybrid multidimensional scaling (HMDS) across two dimensions (two plots have been used for improved clarity).

species ( $r = -0.21$ ,  $P < 0.05$ ) and generalized myrmicines ( $r = -0.22$ ,  $P < 0.05$ ). This suggests that the former taxa were most abundant in the annually burned plots, with the latter most abundant in unburned plots. This was in fact the case, when considering either absolute (Table 2) or relative (Table 1) abundance of ants in traps. The relative abundance of *Iridomyrmex* spp. (63 and 52% of total ants), hot climate specialists (16, 11%) and opportunists (9, 12%) were all considerably higher in the annually burned plots than in the unburned plots (15, 19%; 4, 1%; and 4, 3%, respectively). Generalized myrmicines and cryptic species, on the other hand, were more abundant in the unburned than annually burned plots (50, 61% and 26, 14% total ants, respectively, compared with 11, 21% and 2, 3%) (Table 1).

The biennially burned plots were intermediate between the annually burned and unburned plots, but B1 was more similar to the former, with B2 resembling the latter (Fig. 2, Table 2). Compared

to B2, B1 had a higher relative abundance of dominant *Iridomyrmex* (47 vs 14%), but lower relative abundances of generalized myrmicines (26 vs 46%) and cryptic species (10 vs 23%) (Table 1).

The relationships between plots outlined above were supported by Bray-Curtis similarity coefficients. Greatest similarities were between the replicates of the annually burned plots (coefficient of 0.63), and unburned plots (0.56), with the lowest similarities being between the annually burned and unburned plots (0.23–0.29). Plot B1 had highest similarities with the annually burned plots (0.51, 0.54), whereas B2 was more similar to the unburned plots (0.46, 0.50). The annually burned plots and B1 had more ants and more species recorded in traps than did the unburned plots and B2, but there were no systematic differences in species diversity or evenness indices (Table 1).

Cluster analysis of traps (Table 3) also showed a clear separation between annually burned and unburned plots, with B1 grouping with the former, and B2, the latter. The largest cluster (group 1) comprised 41 traps, and included 15 each from A1 and A2, and nine from B1. The ants best discriminating this group were species of *Iridomyrmex* (dominant species), *Melophorus* (hot climate specialists) and *Rhytidoponera aurata* (opportunist). The next two largest clusters (group 6 with 31 traps, and group 5 with 24 traps), on the other hand, consisted almost entirely of traps from C1, C2 and B2. The ants best discriminating these two groups were mostly generalized myrmicines (species of *Monomorium* and *Pheidole*) and cryptic species (*Solenopsis* sp. 1 and *Paratrechina (minutula* gp.) sp. 1). The characterization of annually burned plots by *Iridomyrmex* spp., hot climate specialists and *Rhytidoponera aurata*, and of unburned plots by generalized myrmicines and cryptic species, is also shown by cluster analysis of species (Table 4; in particular, see groups 1 and 4).

Many species that were common under one fire treatment were uncommon or even absent from others. For example, of the 32 most abundant species (Table 4), nine (*Iridomyrmex* spp. 1 and 3, *I. sanguineus*, *Monomorium* ("Chelani") sp. 1, *Meranoplus (diversus* gp.) sp. 1, *Paratrechina (minutula* gp.) sp. 1, *Monomorium* spp. 8 and 13, and *Rhytidoponera trachypyx*) were not recorded at all in the unburned plots. Similarly, several species that were common in the unburned plots (e.g., *Monomorium* sp. 14, *Crematogaster* sp. 2, *Pheidole* spp. 4, 8 and 14) were rarely recorded in the annually burned plots.

The data presented here only relate to ground-

TABLE 2. Mean numbers of ants per pitfall trap for each functional group, and mean ordination scores (KYST axes 1 and 2) for each plot. In each case, numbers followed by the same letter are not significantly different ( $P > 0.05$ ) from each other (ANOVA and LSD).

	A1	A2	B1	B2	C1	C2	F
Dominant <i>Iridomyrmex</i>	27.6 <sup>A</sup>	14.9 <sup>B</sup>	20.2 <sup>AB</sup>	2.6 <sup>C</sup>	3.3 <sup>C</sup>	3.6 <sup>C</sup>	11.27
Associated subordinate Camponotini	0.2 <sup>A</sup>	0.1 <sup>A</sup>	0.3 <sup>A</sup>	0 <sup>A</sup>	0 <sup>A</sup>	0.2 <sup>A</sup>	1.16
Hot climate specialists	6.2 <sup>A</sup>	4.0 <sup>AB</sup>	3.1 <sup>BC</sup>	1.1 <sup>CD</sup>	1.9 <sup>BCD</sup>	0.1 <sup>D</sup>	6.09
Cryptic species	1.0 <sup>A</sup>	1.1 <sup>A</sup>	5.0 <sup>B</sup>	5.1 <sup>B</sup>	4.8 <sup>B</sup>	2.7 <sup>AB</sup>	2.73
Opportunists	2.7 <sup>AB</sup>	3.6 <sup>A</sup>	3.7 <sup>A</sup>	1.8 <sup>BC</sup>	0.8 <sup>C</sup>	0.5 <sup>C</sup>	6.44
Generalized myrmicines	5.2 <sup>AB</sup>	4.5 <sup>A</sup>	9.8 <sup>BC</sup>	8.3 <sup>ABC</sup>	10.9 <sup>C</sup>	8.3 <sup>ABC</sup>	1.85
Large, solitary foragers	0 <sup>A</sup>	0.1 <sup>A</sup>	0.1 <sup>A</sup>	0.1 <sup>A</sup>	0 <sup>A</sup>	0 <sup>A</sup>	0.67
KYST 1	0.53 <sup>A</sup>	0.48 <sup>AB</sup>	0.39 <sup>AB</sup>	0.09 <sup>B</sup>	-0.72 <sup>C</sup>	-0.83 <sup>C</sup>	17.55
KYST 2	-0.02 <sup>AB</sup>	0.11 <sup>B</sup>	-0.43 <sup>A</sup>	0.34 <sup>B</sup>	0.03 <sup>B</sup>	-0.03 <sup>AB</sup>	2.77

TABLE 3. Composition of the six groups of pitfall trap data generated by cluster analysis. Figures are the number of traps contributed to each group by each plot. The five most abundant of the ten species best discriminating each group are also given, with their functional group (Table 2) in brackets.

	Group					
	1	2	3	4	5	6
Total	41	6	10	6	24	31
A1	15	0	1	0	2	0
A2	15	4	0	1	0	0
B1	9	1	6	3	1	0
B2	2	1	2	1	11	3
C1	0	0	1	1	5	13
C2	0	0	0	0	5	15
Discriminating species	<i>Iridomyrmex</i> sp. 14 (1) <i>Rhytidoponera aurata</i> (5) <i>Iridomyrmex</i> sp. 3 (1) <i>Melophorus</i> sp. 10 (3) <i>Melophorus (aeneovirens</i> gp.) sp. 1 (3)	<i>Paratrechina (minutula</i> gp.) sp. 2 (4) <i>Monomorium</i> sp. 8 (6) <i>Iridomyrmex sanguineus</i> (1) <i>Tetramorium</i> sp. 1 (5) <i>Monomorium</i> ('Chelacner') sp. 6 (3)	<i>Melophorus</i> sp. 10 (3) <i>Iridomyrmex (nitidus</i> gp.) sp. (1) <i>Monomorium</i> sp. 21 (6) <i>Pheidole</i> sp. 8 (6) <i>Solenopsis</i> sp. 1 (4)	<i>Pheidole</i> sp. 4 (6) <i>Pheidole</i> sp. 8 (6) <i>Iridomyrmex</i> sp. 1 (1) <i>Rhytidoponera aurata</i> (5) <i>Rhytidoponera (turneri</i> gp.) sp. 3 (5)	<i>Iridomyrmex</i> sp. 14 (1) <i>Solenopsis</i> sp. 1 (4) <i>Monomorium</i> sp. 24 (6) <i>Monomorium</i> sp. 17 (6) <i>Tetramorium</i> sp. 1 (5)	<i>Monomorium</i> sp. 24 (6) <i>Paratrechina (minutula</i> gp.) sp. 1 (4) <i>Pheidole</i> sp. 8 (6) <i>Monomorium</i> sp. 14 (6) <i>Solenopsis</i> sp. 1 (4)

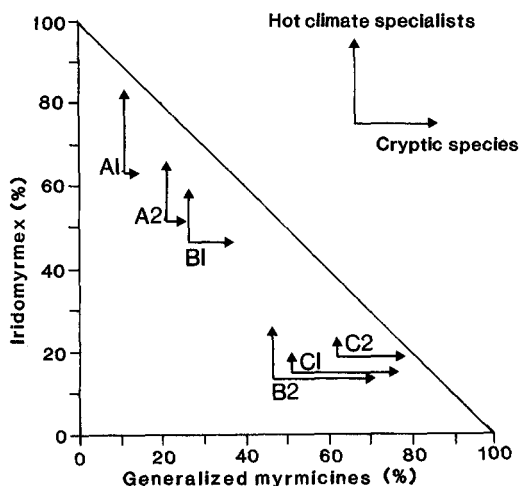


FIGURE 3. Vector diagram (Lamacraft 1979) illustrating relative abundances of major functional groups of ants in experimental fire plots (A1, A2: burned annually; B1, B2: burned biennially; C1, C2: unburned).

foraging ants, but my field observations show that arboreal ants were also severely affected by different fire regimes. In particular, leaf-nesting *Oecophylla smaragdina*, a dominant ant of the Asian and Australian tropics, was extremely abundant in the mid-story of the unburned plots, but was uncommon elsewhere.

## DISCUSSION

The different fire regimes had a major influence on ground-foraging ant communities. The annually burned and fire-exclusion treatments produced two distinctive communities, the first characterized by high proportions of dominant *Iridomyrmex*, hot climate specialists, and opportunistic *Rhytidoponera aurata*, and the second by high proportions of generalized myrmicines and cryptic species. These differences therefore involved gross changes in community organization, rather than simple changes in species composition. The ant communities of the biennially burned plots were generally intermediate between those of the annually burned and unburned plots, but interestingly one was more similar to those in the annually burned plots, while the other resembled those in the unburned plots. The relationships between the ant communities of each plot are summarized in Figure 3.

Fire can directly affect many arthropod groups by killing them, or by forcing them to disperse to unburned sites (Gillon 1983). However, fire often seems to have little direct effect on communities of ground-foraging ants because of the protection afforded by soil nests, and because ants are unable to disperse away from the fire front. The effects of fire occur indirectly, through fire-induced modifications to habitat, food supplies, and interspecific competition (Levieux 1983, Andersen & Yen 1985, Andersen 1988). The effects of fire regime on ant

TABLE 4. Composition of the five groups of species generated by cluster analysis (TWO-STEP program). The functional group (Table 1) of each species is given in brackets.

	Species	Distribution in plots
Group 1 (12 spp.)	<i>Iridomyrmex</i> spp. 3 and 14 (1), <i>Monomorium</i> ( <i>rothsteini</i> gp.) sp. 2 (3), <i>Monomorium</i> (' <i>Chelaner</i> ') sp. 13 (3), <i>Melophorus</i> sp. 10 (3), <i>M. (aeneovirens</i> gp.) sp. 1 (3), <i>Meranoplus</i> ( <i>diversus</i> gp.) sp. 1 (3), <i>Tetramorium</i> sp. 1 (5), <i>Rhytidoponera aurata</i> (5), <i>Monomorium</i> sp. 23 (6), <i>Solenopsis</i> sp. 1 (4), <i>Paratrechina</i> ( <i>minutula</i> gp.) sp. 2 (4)	Predominantly in annually burned plots, many completely absent from unburned plots
Group 2 (6 spp.)	<i>Iridomyrmex</i> sp. 1 (1), <i>I. sanguineus</i> (1), <i>Pheidole</i> sp. 4 (6), <i>Monomorium</i> spp. 8 and 13 (6), <i>Rhytidoponera trachypyx</i> (5)	Equally abundant in annually and biennially burned plots; absent from unburned plots
Group 3 (6 spp.)	<i>Iridomyrmex</i> sp. 2 (1), <i>I. (nitidus</i> gp.) sp. (1), <i>Tetramorium</i> sp. 2 (5), <i>Rhytidoponera</i> ( <i>turneri</i> gp.) sp. 3 (5), <i>Monomorium</i> sp. 21 (6), <i>Pheidole</i> sp. 6 (6)	Predominantly (3 spp. exclusively) in biennially burned plots
Group 4 (5 spp.)	<i>Monomorium</i> spp. 14 and 24 (6), <i>Pheidole</i> sp. 8 (6), <i>Solenopsis</i> sp. 2 (4), <i>Paratrechina</i> ( <i>minutula</i> gp.) sp. 1 (4)	Predominantly in unburned plots; uncommon in annually burned plots
Group 5 (3 spp.)	<i>Monomorium</i> spp. 13, 17, and 19 (6)	Widely distributed across plots



community structure reported here are easily accounted for by the indirect effects of fire-induced changes to habitat, in particular to vegetation structure. In the annually burned plots, a mid-story is virtually absent, the ground layer is sparse, and there is considerable bare ground (Fig. 1; Bowman *et al.* 1988). These open conditions are ideal for *Iridomyrmex*, hot climate specialists, and opportunistic *Rhytidoponera aurata*. Generalized myrmicines are also favored by open, well-insolated conditions, but in this case are limited by competition with *Iridomyrmex*. In the unburned plots, on the other hand, the well-developed mid-story shades the ground, which is also covered with litter. These conditions are less favorable for *Iridomyrmex* and hot climate specialists. Generalized myrmicines predominate because they can tolerate a much broader range of physical conditions (Greenslade & Thompson 1981, Greenslade 1985), and are not so limited here by competition from *Iridomyrmex*. Cryptic species are favored by the heavy litter development.

The marked differences between the two biennial replicates are noteworthy, and show that the effect of a biennial burning regime can vary considerably. There are two associated explanations that possibly account for this. Soil properties vary considerably between the Munmarlary plots (Bowman *et al.* 1988), and this is likely to affect vegetation structure and therefore ant distribution. Bowman *et al.* report that the responses of many plant species to fire varied markedly between the plots. It is possible that the communities typical of annually burned and unburned sites represent two opposing equilibrium states, with only relatively minor environmental changes being sufficient to flip a community from one state to the other. Gross changes in ant communities, apparently mediated by dominant species, following relatively minor changes in

vegetation structure have been reported elsewhere in Australia (Fox & Fox 1982, Majer 1985).

Ants are one of the most important groups of animals in tropical savannas (Levieux 1983), and are closely linked with soils, vegetation, and other fauna. The effects of fire on ants are therefore likely to indicate broader effects on the ecosystem (see Greenslade & Greenslade 1984, Andersen 1990). For example, the responses of ants to environmental change can be correlated with the responses of other faunal groups (Majer 1983). Similarly, the response of cryptic ants is likely to be similar to that of a great many other soil and litter invertebrates, and consequently, to processes operating at the soil-litter interface, such as nutrient cycling. The sensitivity of ants to different fire regimes documented here has important implications for conservation management in tropical savannas. A management policy of long-term fire exclusion is unrealistic on a large scale in most tropical savannas because it is not possible to control ignition by humans, and, in the longer term, by lightning strikes. However, the results of this study suggest that fire-free intervals of only a few years can have important ecological consequences. The maintenance of areas with such fire frequencies should therefore be an objective of savanna management.

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