Effects of fire management and grazing by cattle on ant communities in south-east Queensland open forests

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ABSTRACT

Forest management practices, such as prescribed burning and cattle grazing, have come under increasing scrutiny due to their potential to cause damage to local ecosystems. This study examined the impacts of these practices on ant communities at Bauple State Forest in south-east Queensland. Ant community structure was studied at three locations subjected to different long-term burning frequencies (fire protected, low intensity spring burns at 2-3 year intervals and annual low intensity spring burns). Within the annually burned area, the effects of fire and grazing exclusion for a three-year period were also examined. The results indicate that fire frequency has a significant impact on ant community structure, most probably through its influence on the structural environment (alterations to insolation and ground cover). Ant abundance, species richness and the relative abundance of Dominant Dolichoderines were significantly lower in areas of lower fire frequency, while the relative abundance of Opportunists increased. Ant community data at the two burned areas were significantly different from the long-term unburned area, suggesting regular fire events have a considerable impact on ant community structure. After three years of experimental fire exclusion, both the environmental and ant community structure resembled the long-term infrequently burned site, suggesting a rapid response by the ant community to changes in vegetation structure and the related abiotic characteristics. A significant reduction in ant abundance and species richness was observed by the third year and a trend to reduced abundance of Dominant Dolichoderines and increased Opportunists was observed in fire-protected plots. Experimental release from grazing pressure for a period of 36 months did not result in any significant differences in ant community, possibly indicating that grazing impacts were not readily reversible in the short term.

Key words: fire, forest management, ant community, grazing, *Corymbia variegata*, disturbance

Introduction

The invertebrate fauna of forest ecosystems are often ignored when considering how forests should be managed, yet invertebrates are amongst the most important components of these environments (Campbell and Tanton 1981; Olembo 1991; Kremen *et al.* 1993; Stork 1994; Friend 1995; New 1995). They are essential to ecological processes such as nutrient cycling, decomposition of organic matter, trophic transfers and provision of prey for wildlife (Hurditch 1986; Rosenberg *et al.* 1986; Anderson 1993; Kim 1993), and easily comprise the major portion of biological diversity. This contribution to biological diversity has made them difficult to study because the taxonomic knowledge required for their identification is often not available. Hence, many investigations of invertebrates and their responses to disturbance concentrate on only a portion of the fauna, usually on selected focal taxonomic groups.

Quite possibly, no single group of organisms will prove to be a suitable indicator of ecological condition at a scale beyond a few hectares. However, there has been much discussion about ant communities as an interesting and informative focal group for monitoring forest ecosystems, especially open forests and woodlands (Andersen 1987; Paoletti *et al.* 1991; Andersen 1997a, 1997c; Bestelmeyer 1998; Folgarait 1998). Ants are abundant and diverse, sensitive to environmental change, ecologically and functionally dominant in most terrestrial environments, their stationary nesting habits allow re-sampling over time, and they are easily collected and identified to generic level (Alonso and Agosti 2000; Wilson 2000). Consequently an understanding of their response to various environmental disturbances is of great relevance to the interpretation of ecological monitoring data.

In this chapter we describe how ant communities are affected by some of the human-induced disturbances commonly experienced in forest ecosystems, and in doing so, shed a little light on the bewildering complexity of invertebrate communities that live within these environments. By understanding how the actions of forest managers alter the structure and dynamics of ant communities, we may be able to make more informed decisions about how these ecosystems can be managed to fulfil the requirements of ecologically sustainable forest management.

Historically, tall open forests have been an important regional source of hardwood timber in south-east Queensland (DPI Forestry 1998). They have been intensively managed to maximise timber production while at the same time providing other values such as

places where cattle and sheep have been grazed, amenity, and water-catchment areas. Fire has been managed to maximise timber production as well as minimise the risk of wildfire with its attendant potential for damage to property and human life. In common with all production forests in Australia, open forest management in south-east Queensland has come under closer scrutiny in recent years (National Forest Policy Statement Implementation Sub-committee 1995) to ensure that long-term ecological sustainability of the forests is not compromised by poor land management decisions.

Timber harvesting in native forests is likely to decline or cease in the foreseeable future but fire management will be an ongoing issue. Even active exclusion of fire is a form of fire management. Furthermore, the promotion of cattle grazing as a secondary forest use may also continue. Despite this, fire and grazing management practices are poorly understood and may influence the ecological sustainability of forest ecosystems as much as timber harvesting (Christensen 1998). Management of fire and grazing in open forests will be critical in maintaining the integrity of these ecosystems.

Fire management

Before the arrival of Europeans to the Australian continent, it is speculated that indigenous Australians deliberately lit forest fires to improve hunting conditions by increasing access and providing grazing areas for macropods. In south-east Queensland, these fires appear to have been regular (typically every 2-4 years), of low intensity (<500 kW/m) and most likely initiated during winter (Fensham 1997). Burning remained a management tool in forests after European settlement with a shift to late winter and early spring as the preferred ignition times (Just 1980; Guinto et al. 1998; 1999). Today, such fires are normally uniform across the landscape with little or no heterogeneity and, as a result, the mosaic of burned and unburned patches that one would expect from a wildfire are not evident. Many ecologists recognise that fire is a vital and necessary component of open forest ecosystems (Swain 1924; Florence 1977; Lamb et al. 1980; Walker 1981; Garthe 1983; Andersen 1988; Whelan 1995; Florence 1996), and that fire exclusion may well be detrimental to the normal functioning of many forests and the survival of species therein (Christensen 1998).

Ant community responses to a single fire event have been well documented (Majer 1984; O'Dowd and Gill 1984; Andersen 1988; Neumann 1992; Jackson and Fox 1996). However, fire regime (frequency, intensity and timing) may be of greater importance to the persistence and structure of ecosystems (Andersen 1996). In tropical savannas, increased ant abundance and distinctly different functional composition have been recorded as a result of frequent burning compared with no burning imposed over a 14 year period (Andersen 1991). Similar trends of increased ant abundance, ant species richness and distinctly different functional composition were observed in a baseline investigation of fire frequency at an open forest in south-east Queensland (Vanderwoude et al. 1997a; 1997b).

Grazing

Grazing has been specifically promoted as a desirable secondary forest use in state-controlled forests in south-east Queensland (Queensland Government 1992), with almost all open forests in this region used for grazing by cattle or sheep since European settlement. Few data are available to make an assessment of the impacts of grazing on the ecosystem, but such practices are now thought to be detrimental to the ecological sustainability of forests (Commonwealth of Australia 1992). The introduction of cattle and sheep may cause mortality of grass species susceptible to defoliation (Mott et al. 1992; Walker et al. 1997), habitat simplification (Majer 1978) and a reduction of soil permeability (Abbott et al. 1979).

Ant communities may also be affected by grazing. Some Australian studies report reduced ant diversity and abundance in grazed areas compared with similar sites that had not been grazed (Majer 1978; Davieson and Majer 1983; Majer and Beeston 1996). Functional composition of ant communities may also change in response to grazing (Andersen 1987; Andersen and McKaige 1987; Scougall et al. 1993). In addition, the presence of cattle has been implicated in the spread of invading pest ant species (Anthony et al. 1991) and associated with shifts in ant species dominance (Bromham et al. 1999).

Aims of study

The broad aim of this study was to establish how fire frequency and grazing by cattle affect ant community structure in open forests of south-east Queensland. More specifically, we aimed to examine:

- ant community structure at sites subjected to (i) long term protection from fire, (ii) infrequent, low intensity late winter-spring burning and (iii) frequent, low intensity late winter-spring burning,

- the effects of experimental exclusion of fire from previously frequently-burned areas on ant community structure, and

- the effects of experimental release of grazing pressure on ant community structure.

Methods and materials

Site description

Bauple State Forest (State Forest 958, 22° 55'S, 152° 40'E) is located approximately 200 km north of Brisbane in south-east Queensland. The climate is sub-humid with a mean annual rainfall of 1125 mm per annum with over 50% of the rain falling during the summer months from December to March.

The vegetation is typical of tall open forests (Specht 1970) in south-east Queensland and is dominated by spotted gum Corymbia variegata and grey ironbark Eucalyptus siderophloia (both commercially important timber species). A discontinuous shrub layer is present, composed chiefly of wattles Acacia leiocalyx, Acacia aulacocarpa, and soap bush Alphitonia excelsa. Where the shrub layer is sparse

or absent, a grassy ground layer dominated by kangaroo grass *Themeda triandra,* spear grass *Aristida holathera* and panic grass *Entolasia* spp. is also present. Two distinct soil types are present. Brown and red kurosols are found on the majority of sites, with small areas of red kandosols occurring on some shallow ridges (Isbell 1996). Kurosols are characterised by loamy surface textures, moderate texture contrasts between A and B horizons, strongly acidic B horizons (Isbell 1996) and are regarded as being of low agricultural value. Kandosols possess no texture contrast between A and B horizons and the B horizon is massively structured (Isbell 1996).

This study was located within three forest areas that formed part of the southern and western boundary of the reserve. One area (314 ha) had been prescribed-burned every year since 1952 with low intensity late winter-early spring fires of <500 kW/m (Guinto *et al.* 1998). The second area (423 ha) had been burned less frequently (every 2–3 years) since 1973. The third area (296 ha) had remained unburned since at least 1946. Adjacent farm land (pasture and light forest) to the west and south had been burned every 1-3 years while the remainder of Bauple State Forest to the north and east was burned at intervals of 5-7 years. The effect of fire on plant regeneration at this site was described by Henry and Florence (1966).

The forest had been utilised for grazing by cattle for at least 40 years prior to this study. Grazing continued for the duration of the experiment, which began in September 1995 and ended in October 1998, with the exception of a short period from late 1997 to mid 1998 when the site was de-stocked by the lessee in response to low cattle prices. (The destocking was beyond the control of the study, which relied on the assumption of a continuation of normal grazing management). From mid 1998 the site was stocked once again. Stocking rates during this time were between 80 and 110 adult beasts over the total area of 1033 ha which is typical for this region.

Experimental design, establishment of plots and imposition of treatments

Two experiments were conducted over a three year period to examine 1) the differences between ant community composition within the unburned, infrequently burned and frequently burned areas, and 2) the effects of release from grazing and burning treatments on the ant community within the annually (frequently) burned site.

Ant Community Composition

Ant community composition was determined by repeated sampling within four 50 m x 50 m plots established in each of the three areas (unburned, infrequently burned and frequently burned). Due to the scarcity of sites exposed to similar long-term fire regimes in open forests, true replication was not possible and pseudoreplication was employed to estimate variance.

Fire and Grazing

Studies of fire and grazing were limited to the annually burned area where two representative sites were selected – one site on a kurosol soil type and the other on a kandosol soil type. At each of the soil-type sites, two main plots (100 m x 50 m) were established in an arrangement that minimised visible between plot differences, such as large canopy gaps. One of each pair of main plots was randomly designated 'not-grazed' and fenced using steel pickets and timber corner posts with three plain low-tensile wires strained at 0.25 m, 0.75 m and 1.2 m above ground – preventing cattle from entering plots but not impeding any native rodents or marsupials that may have been present (large numbers of which were not observed during the course of this study). The 'not-grazed' treatment therefore represented a release from grazing pressure rather than representing a truly ungrazed condition, which means only reversible ecological properties could be measured (see Fleischner 1994).

The main plots were further divided into two sub-plots (50 m x 50 m), of which one was randomly designated 'not-burned' and fire was actively excluded. Prescribed burning, was conducted in late winter/early spring in August 1996 and August 1997. One plot designated as unburned was unintentionally ignited in 1996 and also partially burned in 1997. Data from this plot were not used in statistical analyses. Prescribed burning was also attempted unsuccessfully after a relatively damp winter in August 1998. In this case the plots were burned separately to ensure the research project was not jeopardized.

The experimental design therefore consisted of four replicates of the grazing-release treatment and four replicates of the burning-release treatment. Choice of the design was partly based on the desire to test for grazing-fire interactions, which are known to occur in Australian forest ecosystems for vegetation (Leigh and Holgate 1979) and hypothesised to also occur in ant communities.

Ant sampling and identification

At the centre of each 50 m x 50 m plot, a 3 x 3 grid of pitfall traps (~20 mm diameter and 5 metres apart) was installed. These were partially filled with an ethanol/water preservative. Ants were sampled by pitfall trapping over a four-day period on each of nine occasions: December 1995 (summer), August (winter) and November (spring) 1996, February (summer), August (winter) and October (spring) 1997, March (summer), July (winter) and October (spring) 1998, with the traps remaining in the same position for the entire survey period.

Ants in pitfalls were identified using a verified voucher collection now housed at the DPI Fire Ant Control Centre, Brisbane. The poor state of species-level ant taxonomy in Australia prevented the identification of many specimens to species-level. Wherever possible, species names were determined, or their species-group affiliation identified. In other cases, morphospecies were labelled with species-codes that identified them in the context of this study. Voucher specimens were identified and their biogeographic affiliation determined.

Ant species were also grouped according to their functional behaviour and their interactions with other ant species. Similar approaches have been used to

describe ant community dynamics in Ghana (Majer 1972; 1976a; 1976b; Dejean *et al.* 1994); Papua New Guinea (Room 1975); Argentina (Bestelmeyer and Wiens 1996) and North America (Fellers 1987; Andersen 1997b). Functional groups have also been used to classify other terrestrial invertebrate groups, for example Collembola (Dindal and Metz 1977), arboreal insects (Simandl 1993) and spiders (Churchill 1996). These functional groupings are determined largely at genus-level for ants (Andersen 1990; 1995; 1997a). Classification of Australian ant genera to these functional groups was based on work by Greenslade (1978), and Greenslade and Thompson (1981), which was later substantially extended by Andersen (1990; 1992).

Nine ant functional groups were found in open forest ecosystems of south-east Queensland. Dominant Dolichoderines (chiefly species of *Iridomyrmex*) control ant community structure by their aggressive behaviour and monopolisation of resources (Greenslade 1976; Fox *et al.* 1985). Subordinate Camponotini (for example, species of *Camponotus*, *Polyrhachis*, *Opisthopsis*) are subordinate to *Iridomyrmex* but become dominant in their absence. The abundance of these two groups, in turn, determines to a large extent the abundance of Opportunists (disturbance-adapted species including those from the genera *Aphaenogaster* and *Rhytidoponera*) and Generalised Myrmicines (unspecialised species including *Pheidole*, *Crematogaster* and some species of *Monomorium*). Other groups display strategies that reduce contact with Dominant Dolichoderines. These include Climate Specialists (sub groups of Hot, e.g. *Melophorus*, Cold e.g. *Prolasius* and Tropical e.g. *Tetraponera*), which avoid interaction with Dominant Dolichoderines by foraging at different times, Cryptic Species (e.g. species of *Hypoponera*), which occupy different niches and Specialist Predators (e.g. species of *Myrmecia*), which are normally present in only small numbers. The relationships between these groups may provide valuable insights into the dynamics of ecosystems and have been demonstrated to be sensitive to mining restoration (Andersen 1987), fire (Andersen 1991; Vanderwoude *et al.* 1997a) and grazing (Andersen and McKaige 1987).

Vegetation assessments

Shrub cover was measured by the line intersect method at each plot. Ground-level vegetation and abiotic variables were measured at eight 1 m² quadrats placed at four metre intervals along a line that bisected each plot.

Analytical methods

Abundance counts of ant species in each pitfall were square root transformed in order to avoid bias caused by a mildly contagious data set (Southwood 1978). Assessments of ant species richness and ant community composition based on single pitfall traps were not likely to reflect site species richness and site community composition in sub-tropical environments (Andersen 1997c) due to the high species turnover commonly observed at warmer and less mesic sites in Australia (Andersen and Burbidge 1992).

A better estimate of species richness was obtained by summing the abundances of all pitfalls in a plot to more adequately represent the ant community being sampled. Seasonal variation in abundance, species composition and community structure is an expected feature of ant data (Whitford 1978; Briese and Macauley 1981; Andersen 1983; Abensperg-Traun 1992; 1992) and a summer peak in abundance is expected (Vanderwoude *et al.* 1997b). In order to avoid bias caused by this effect, pitfall trapping data within each year (summer, winter, and spring samples) were combined to allow comparisons between sites.

Analysis of variance (ANOVA) was used to compare treatment effects on ant species richness, ant abundance and ant functional group composition. Ant community data (species x abundance matrices) were analysed by ordination of non-metric multi dimensional scaling (NMDS) of the Bray-Curtis similarity matrix (Bray and Curtis 1957) using PRIMER v4, a software package developed by Plymouth Marine Laboratories (Clarke 1993). Differences between treatments were tested by ANOSIM, a procedure within PRIMER. The contribution of each ant species to the similarity matrices was calculated using SIMPER which is also a routine within PRIMER. The species abundance data were not further transformed beyond the square-root transformations conducted on individual pitfall data as further transformation was unlikely to have improved the resolution of the resulting ordinations (Pik *et al.* 1999). Otherwise, the default options were selected in all PRIMER routines.

Seasonal changes in ant community composition were also examined by condensing the species abundances for each sampling period (summer, winter and spring, over three years) to two values: burned and fire-protected. This permitted an examination of the combined effects of time and treatment on the ant communities. Differences between the abundance of individual ant species was calculated using the Wilcoxon rank sum test.

Results

General differences between long-term burning regimes

A total of 122 ant morpho-species was recorded over the three-year sampling period. One hundred and eight ant species were identified from the annually burned area, 104 from the periodically burned area and 73 from the long-term unburned area. Ten ant species were recorded only in the annually burned area, nine only in the periodically burned area and five only in the unburned area.

Ant abundance and species richness were both lower at sites with lower burning frequency, and substantially lower at the unburned sites (Figure 1a). The lower species richness in the unburned plots relative to those that were burned annually or periodically were independent of ant abundance. The relative abundance of ants in each functional group is compared in Figure 1b. Dominant Dolichoderines were most abundant in the annually burned area and least abundant in the long-term unburned area, corresponding with higher relative
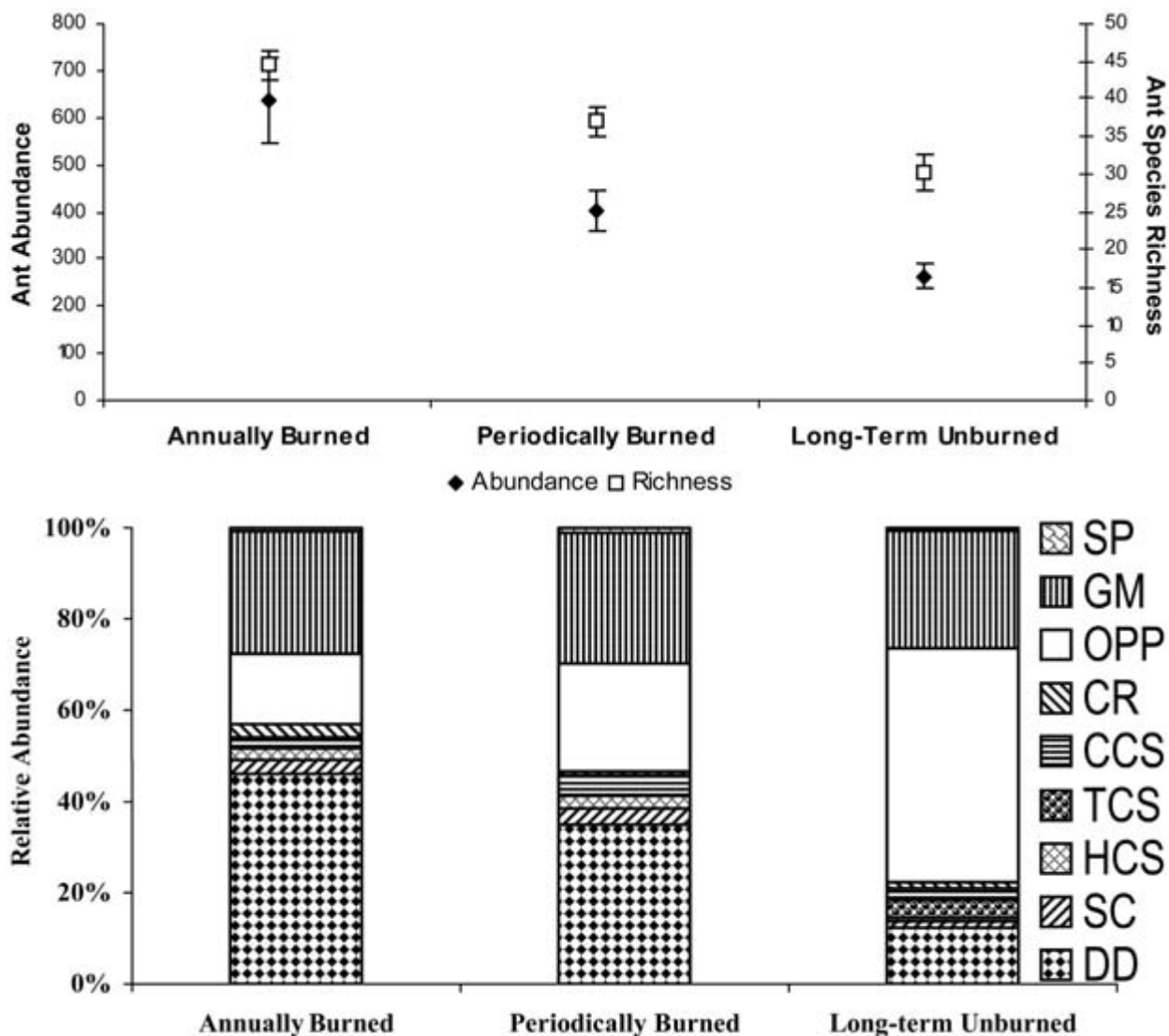
Figure 1. Ant abundance, species richness and functional group composition as measured at the annually burned, periodically burned and long-term unburned areas.

abundances of Opportunists in the long-term unburned area and lower relative abundances in the annually burned area. The relative abundance of Generalised Myrmicines and minor functional groups remained relatively constant at all three areas.

Ant community data, analysed by non-metric multi-dimensional scaling is represented in Figure 2. There were significant differences between the two burned areas when compared with the unburned area (P<0.05, Global R = 0.899), suggesting that regular fire events have a considerable impact on ant community structure. No significant differences were observed between the ant communities at the two burned areas.

Experimental manipulation of burning regimes

When plots in the annually burned area were protected from fire for three years, ground-layer characteristics, shrub-layer vegetation and the ant community changed. The normal management regime of low-intensity, prescribed burning in spring maintained an open grassy

structure characterised by little or no understorey layer and high amounts of bare ground. Plots that were protected from fire for the duration of the experiment developed increased shrub cover from a mean of 4% to 21% (Table 1). Ground cover characteristics also changed when fire was excluded (Figure 3). Most notably, the amount of bare ground decreased (F=16.3, P<0.05).

A decrease in the number of ants caught in pitfall traps (Figure 4a) was observed following the cessation of regular burning over the three year period of this study relative to burned plots. This reduction was significant by the third year (F=17.9, P<0.05). Ant species richness at fire-protected plots also declined significantly over the course of the study, but this decline was small (F=5.9, P<0.1). Comparison of relative abundances of functional groups for burned and fire-protected plots (Figure 4b) revealed no significant differences between the relative abundance of Dominant Dolichoderines, Opportunists or Generalised Myrmicines in any year. However, a non-significant trend of reducing abundance of Dominant Dolichoderines and increasing abundance of Opportunists during this time can clearly be observed for fire-protected plots.
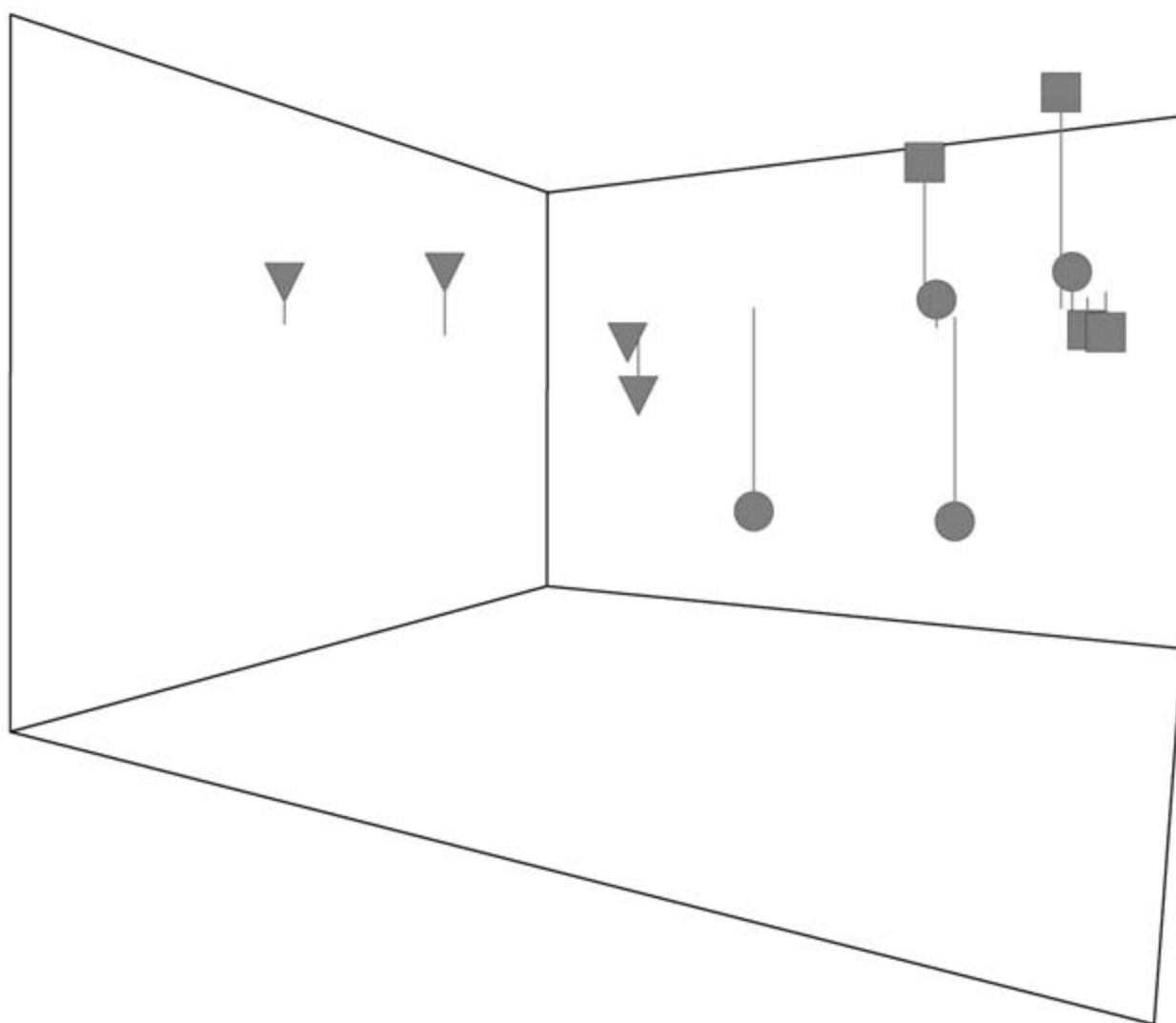
Figure 2. Ordination of ant community similarity scores for the annually burned area ■ the periodically burned area ●
and the long-term unburned area ▼ (stress = 0.06).

Table 1. Mean percentage foliage cover of *Eucalyptus, Acacia, Alphitonia, Lantana, Lophostemon, Angophora* and other species, total foliage cover (m) and mean shrub species richness in burned and fire protected plots (*Eucalyptus* cover includes *Corymbia* cover).

Shrub genus	burned	± sem	unburned	± sem
Eucalyptus	2.8	1.2	4.4	1.4
Acacia	0	0	15.1	6.9
Alphitonia	0.2	0.2	0	0
Lantana	0	0	1.4	1.3
Lophostemon	0	0	0	0
Angophora	0.8	0.7	0.2	0.1
Other	0.5	0.4	0.2	0.1
Total	4.2	1.3	21.3	6.2
mean species richness	1.1	0.30	3.0	0.46

Before the burning treatment was implemented, ant community structure appeared to be strongly influenced by its location relative to each other (Figure 5). However, over the three years that sampling took place, treatment became increasingly important and by the third year, ant communities in burned plots were significantly different from those in unburned plots (Global R=0.574, P<0.05). There were also pronounced seasonal changes in ant community composition in burned plots (Figure 6) that were not apparent for unburned plots.

When the burned and fire protected plots were compared, 14 ant morpho-species were found to be responsible for 80% of the dissimilarity between burning treatments (Table 2). The most notable of these, contributing over 34% to total dissimilarity, was *Iridomyrmex* sp B. (*rufoniger* gp.) (Figure 7). This species was significantly more abundant in burned plots (mean transformed abundance 86.3) than in fire-protected plots (mean transformed abundance 24.6) (Wilcoxon rank sum test $n_1=7$, $n_2=8$, U=5, P<0.05).

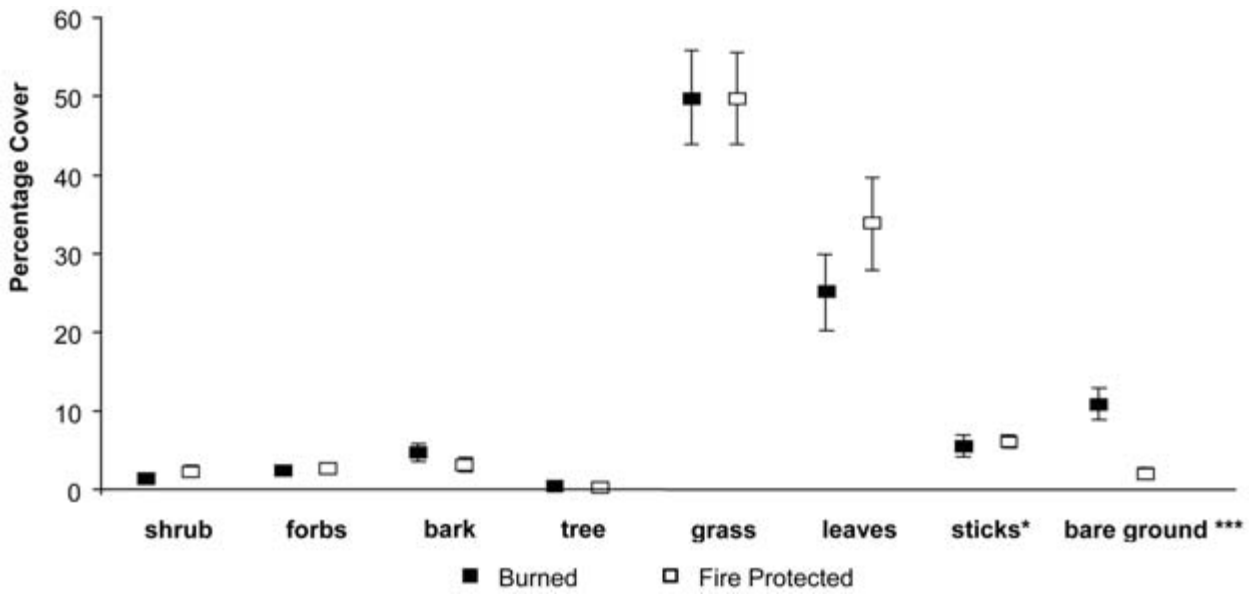**Figure 3.** Percentage of ground cover at burned and fire protected plots within the annually burned area.
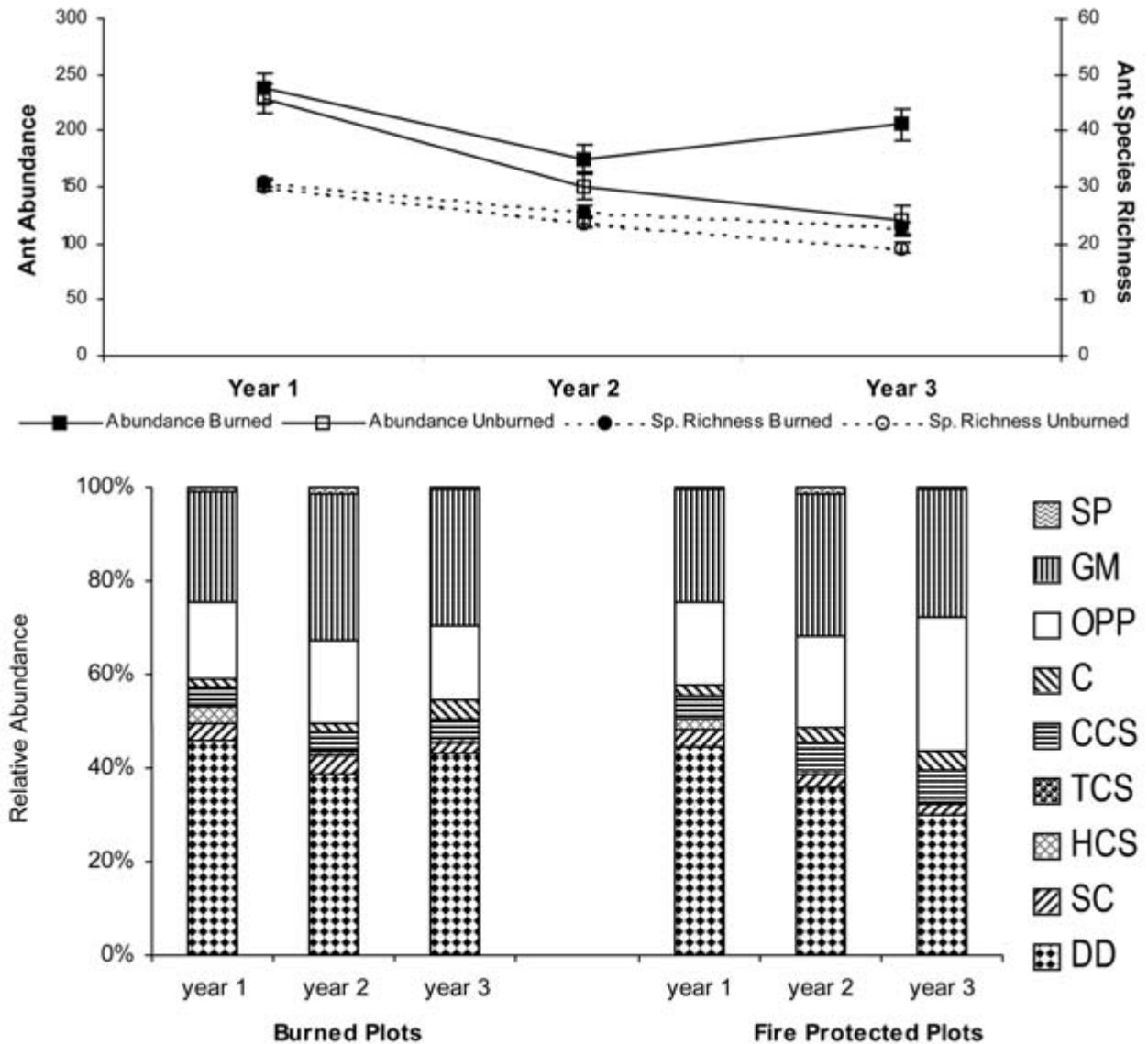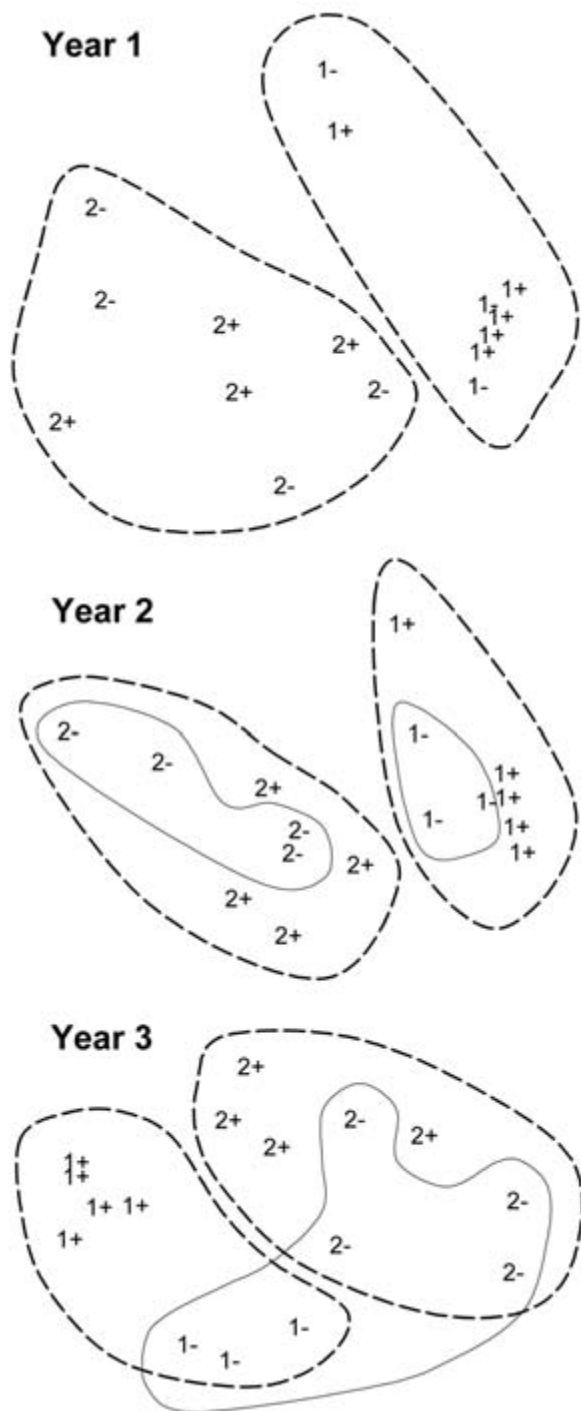

Figure 4. Ant abundance, species richness (a) and relative abundance of ant functional groups (b) at experimentally burned and fire-protected plots within the annually burned area over a period of three years.

Figure 5. (above) Ordination of NMDS for ant community data for year one, two and three showing ant community relatedness at burned and unburned plots. Sites ("1" and "2") are enclosed with a stippled line and treatments (where there was an obvious effect, with a solid line). The **+** symbols represent burned plots while the **–** symbol represents unburned plots. In the third year, ant communities in burned plots were significantly different from those in unburned plots (Global R=0.574, P<0.03).

Figure 6. (right) Ordination of ant community data at burned and fire-protected plots as a time sequence ✷ = summer sample, ⬡ = winter sample, and ◯ = spring sample at the fire-protected sites. ✱ = summer sample, ■ = winter sample, ● = spring sample at the burned plots. Arrows indicate time trajectories.

Nine other ant species exhibited non-significant increased abundance in burned plots compared with fire-protected plots: *Crematogaster* sp A, *Pheidole* sp. F, *Rhytidoponera* nr *rufithorax*, *Monomorium* sp. A, *Solenopsis* sp. A, *Pheidole* sp. I, *Crematogaster* sp. C, *Iridomyrmex* sp. A, and *Paratrechina* '*vaga*'. Four ant species recorded non-significant decreased abundance in burned plots compared with fire-protected plots: *Rhytidoponera* '*metallica*', *Notoncus enormis*, *Iridomyrmex* nr. *gracilis* and *Pheidole* sp. C. The three most abundant ant species to exhibit an increase in response to burning treatment in the third year were *Iridomyrmex* sp B, *Pheidole* sp. F and *Crematogaster* sp A. The three most abundant species to exhibit a decrease in response to burning treatment in year 3 were *Rhytidoponera* '*metallica*', *Notoncus enormis* and *Iridomyrmex* nr *gracilis*.

Experimental release of grazing pressure

After 36 months of release from grazing pressure, the amount and composition of shrub cover did not change significantly. Mean total shrub cover was lower in grazed plots but the difference was not significant. Also, release from grazing pressure did not result in significant differences in any ground layer characteristics (Table 3).

Mean ant abundance and species richness (Figure 8a) in each year was not significantly affected by grazing treatment. Ant functional group comparisons between grazed and ungrazed plots (Figure 8b) showed no significant differences between the relative abundance of Dominant Dolichoderines, Opportunists or Generalised Myrmicines in any year. In year 2, there were detectable changes in ant community similarity as a result of release of grazing pressure (Figure 9) when similarity matrices were compared (Global R = 0.193, P<0.05). However, these differences were not apparent in the third year.

Discussion

Climate, in combination with biogeographical factors, determines ant community structure (Greenslade and Thompson 1981) by influencing levels of activity (productivity) and the pool of species available for colonisation of a particular site at macro– and micro– scales. Immediate environmental factors, such as soil type (Lobry de Bruyn 1993), vegetation (Burbidge *et*

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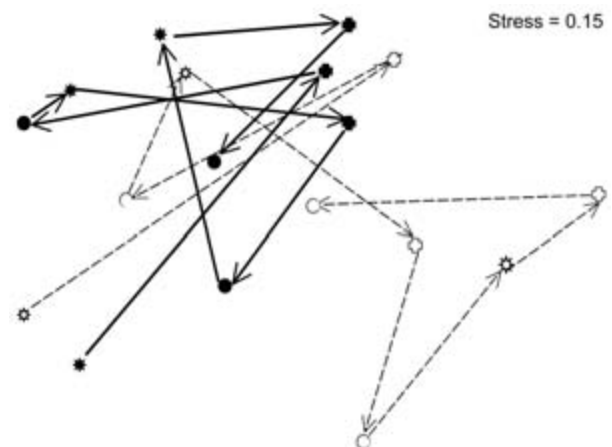
Table 3. Mean percentage foliage cover of *Eucalyptus, Acacia, Alphitonia, Lantana, Lophostemon, Angophora* and other species, total foliage cover (m) and mean shrub species richness in grazed and ungrazed plots (*Eucalyptus* cover includes *Corymbia* cover).

Shrub genus	grazed	± sem	ungrazed	± sem
Eucalyptus	4.2	1.3	3	1.2
Acacia	2.5	1.3	11.2	7
Alphitonia	0.2	0	0	0
Lantana	0	0	1.1	1.2
Lophostemon	0	0	0	0
Angophora	1.1	0.7	0	0
Other	0.5	0.4	0	0
Total	8.7	1.5	15.7	7
mean species richness	2.5	0.39	1.6	0.56

al. 1992) and structural differences further fine-tune ant community structure by determining activity levels and therefore productivity (Greenslade 1981; 1985). The interaction of individual ant species through interspecific competition for resources and nesting sites (Fox and Fox 1982; Fox *et al.* 1985) is also a determinant of ant community structure.

The experimental manipulation of fire frequency for over 45 years at Bauple State Forest has resulted in large and easily detectable differences in the vegetation structure, with reduced fire frequency resulting in increased litter, less bare ground, decreased grass cover and fewer plant species found at ground level. The study results allow the suggestion to be made that corresponding differences have developed in ant community structure at these sites. In areas of lower fire frequency, ant species richness and ant abundance was substantially lower, in accordance with a

Table 2. Species that contributed most to the dissimilarity between burned and unburned plots at the annually burned compartment.

Species	Functional Group	Abundance		% Dissimilarity
		Unburned Plots	Burned Plots	
Iridomyrmex sp B.	DD	24.61	86.26	34.42
Crematogaster sp A.	GM	7.74	14.44	8.37
Rhytidoponera 'metallica'	OPP	21.19	16.88	6.72
Pheidole sp F.	GM	8.99	15.40	5.03
Rhytidoponera nr rufithorax	OPP	2.69	7.74	3.93
Notoncus enormis	CCS	6.00	4.01	3.50
Monomorium sp A.	GM	1.71	5.41	2.66
Solenopsis sp A.	OPP	3.81	6.88	2.59
Pheidole sp I.	GM	2.73	6.07	2.56
Crematogaster sp C.	GM	2.55	3.80	2.24
Iridomyrmex sp A.	DD	0.49	4.41	2.24
Iridomyrmex nr gracilis	DD	3.16	1.11	1.98
Pheidole sp C.	GM	2.78	1.03	1.94
Paratrechina vaga	OPP	2.28	3.67	1.83
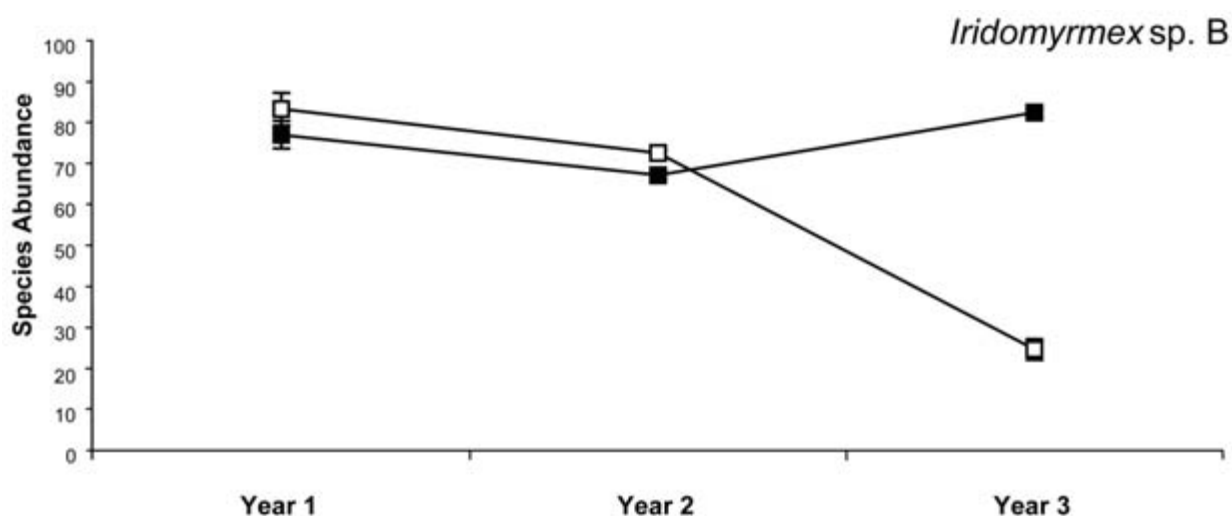
Figure 7. Mean abundance of *Iridomyrmex* sp. B at burned and fire protected plots within the annually burned area for years 1-3
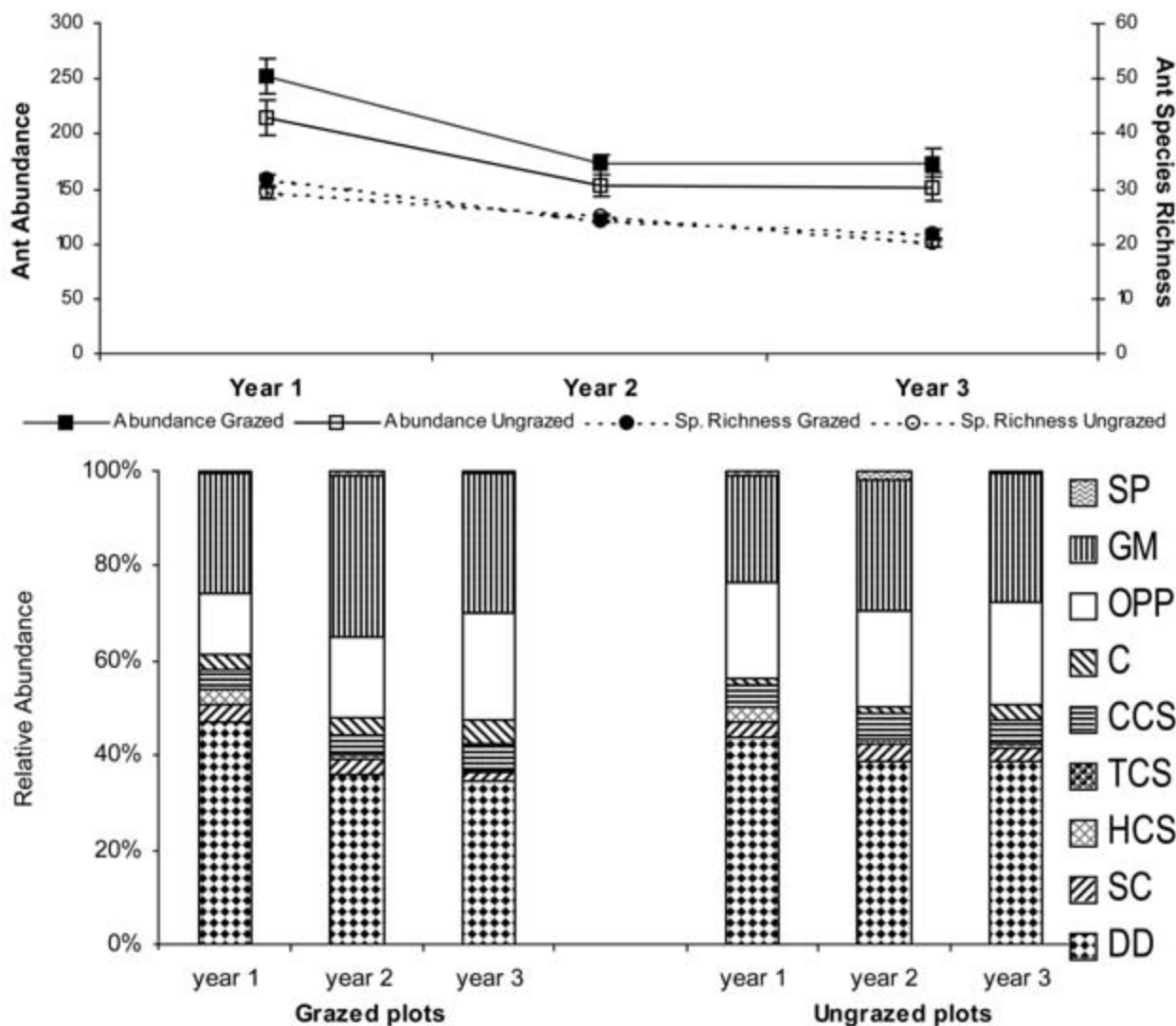
Figure 8. Ant abundance and species richness (a); and relative abundance of ant functional groups (b) at the grazed and grazing protected plots within the annually burned area over a period of three years.

previous study conducted in the region (Vanderwoude *et al.* 1997) and with hypotheses proposed by Greenslade and Thompson (1981) from observations made at the nearby Cooloola National Park. The relative abundance of Dominant Dolichoderines was also lower, but the relative abundance of Opportunists was higher.

The layers of influence determining these overall patterns can be established from the experimental results. The suite of species that made up the total ant community was drawn from the same species pool. Only 23 ant species from a possible 122 species were exclusive to any one area, demonstrating low species turnover at that scale. Ant abundance was governed by site variables, such as vegetation and soil type, and these variables also played an important role in determining which species dominate and which do not. At unburned sites where ground-level insolation is reduced, Opportunist species with widespread biogeographic affiliations (e.g. *Aphaenogaster longiceps, Rhytidoponera 'metallica'*) were dominant. At burned sites, experiencing greatest insolation at ground level, Dominant Dolichoderine ants (predominantly *Iridomyrmex* sp. B (*rufoniger*) were found in greatest abundance.

The different patterns of ant community composition found in the three areas have not been formed as the result of a single fire but have developed from more than 45 years of repeated burning at the annually burned area and over 50 years of fire exclusion at the unburned area. We acknowledge the lack of replication in this experiment but point to similar trends in the replicated fire exclusion experiment as evidence of its validity. These burning frequencies therefore represent extremes of what may be expected in open forests of south-east Queensland and would rarely be normal management practice in Crown-owned or privately owned open forests. The ant community at the typically hot and open annually-burned area therefore represents the arid-adapted extreme of possible community structure while the ant community at the shadier and cooler long-unburned area represents the shade-adapted extreme of ant community structure in these open forests. The ant community at the periodically burned area exhibited species richness, abundance and functional group composition intermediate between these values, suggesting that ant community structure and gross vegetation structure are indeed closely linked.
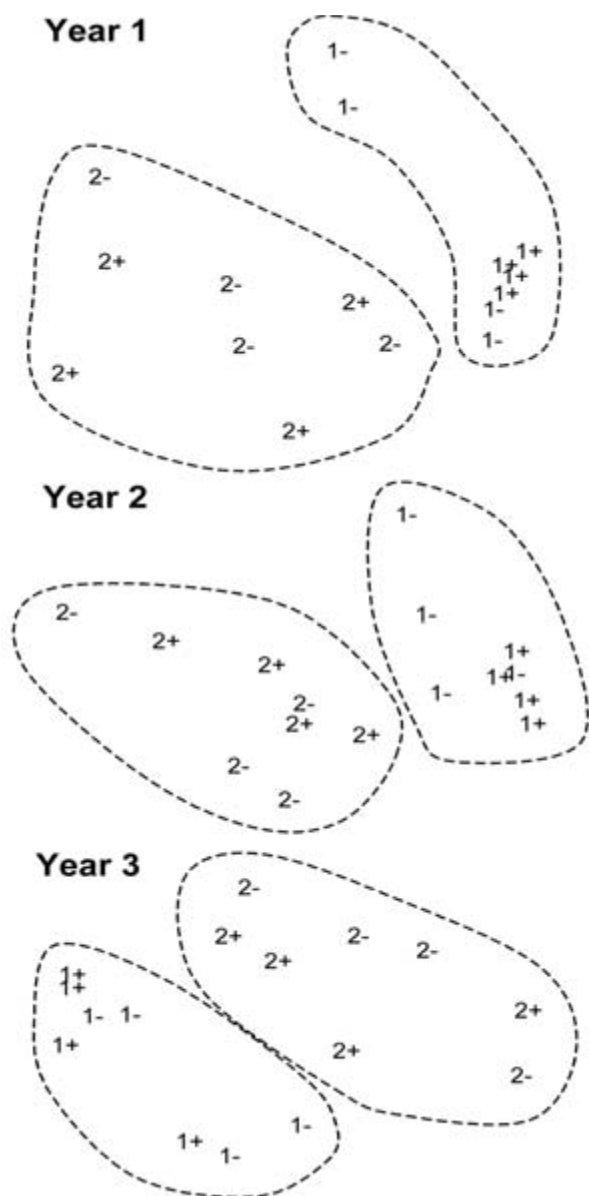
Figure 9. Ordination of ant community data for year one, two and three showing ant community relatedness at grazed and ungrazed plots. Sites ("1" and "2") are enclosed with a stippled line and treatments (where there was an obvious effect, with a solid line). The + symbols represent grazed plots while the − symbol represents ungrazed plots. The ant community at grazed plots was significantly different from that at ungrazed plots in the second year (Global R = 0.193, P<0.05)

Experimental fire exclusion

Three years of experimental fire exclusion from previously annually burned plots resulted in protected plots acquiring many characteristics typical of those possessed by the periodically burned area. Shrub foliage cover and amount of bare ground changed significantly, and after three years were within the range recorded for the periodically burned area. The ant community in the protected plots also changed and became more like the ant community at the periodically burned area. After three years of fire exclusion, the following observations were made: lower ant abundance and lower ant species richness, significantly different community structure, and a change

from a strongly cyclical pattern of community organisation to one influenced by other factors. These changes, and the speed at which they occurred, all indicate a rapid response by the ant community to changes in vegetation structure and abiotic variables. Ant abundance and species richness at plot-scales is directly influenced by insolation at ground level, which was reduced in protected plots by increased foliage cover at ground level and shrub level. Microclimatic variation would also be less labile at protected plots as foliage and ground cover afford some protection from climatic extremes. Reduced insolation had most impact on *Iridomyrmex* sp. B, a Dominant Dolichoderine with an Eyrean (arid-adapted) biogeographic affiliation. This ant species is typical of open, hot environments and was found in high numbers at the annually burned and at the periodically burned area, but only in very low numbers at the unburned area. One of the few ant species to exhibit an increase in abundance in the protected plots was *Rhytidoponera 'metallica'* which is an Opportunist with a Widespread biogeographic affiliation. *Rhytidoponera 'metallica'* is common in regions that experience a temperate climate where it is locally abundant in disturbed areas.

According to the functional group model of ant community organisation, *Iridomyrmex* are poor competitors in disturbed or stressed environments, where either Generalised Myrmicines or Opportunists often become dominant. In this study, Opportunists increased in abundance at the expense of Dominant Dolichoderines when plots were protected from fire. The same pattern of decreased relative abundance of Opportunists at frequently burned sites was also observed by Andersen (1991) in tropical savannas of northern Australia. In Andersen's study, abundance of Dominant Dolichoderines was greatly increased in response to frequent burning and Opportunists comprised only a small proportion of all ants.

In Australian forest ecosystems, increases in the abundance of Opportunists in relation to Dominant Dolichoderines due to fire are not always observed. In a study of fire management in coastal blackbutt *Eucalyptus pilularis* forests in northern New South Wales (York 1996; 2000), an increase in Opportunist ant species was recorded in frequently burned plots. Although this is apparently a contradictory finding, it is one of the few replicated studies of ant communities in relation to fire. In Victorian coastal forests (Andersen 1988) and Western Australian jarrah-*Banksia* ecosystems (Whelan *et al.* 1980) the abundance of *Rhytidoponera* was also greater in burned areas suggesting that the increase in *Rhytidoponera* at Bauple State Forest may be a local artefact of ant community organisation.

Alternatively, the changing abundance of Opportunists such as *Rhytidoponera* may be a direct response to the abundance of Dominant Dolichoderines. Dominant ant species exhibit a humped pattern of diversity and abundance along environmental gradients (Andersen 1997c) and lower ant abundance and ant species diversity is expected at either end of the gradient. According to the ant functional group model, Opportunists are poor competitors when Dominant Dolichoderines are numerous, suggesting that the abundance of Opportunists will always contrast with that of Dominant Dolichoderines.

Non-metric multi-dimensional scaling of the community data also revealed a difference between burned and protected plots by the third year, indicating that the changes were community-wide and not restricted to only a few ant species. When fire was removed, the strong cyclical pattern exhibited by the ant community at burned plots ceased after the summer 1996/97 (see Figure 6). This demonstrated the extent to which vegetation structure (shrub cover, bare ground etc) is shaped by fire, and it also demonstrated the strong links between vegetation and insolation, as well as the effects of these factors on the ant community, including the short time-scales in which the ant community changed in response to protection from fire.

It is important to note that this study included a limited manipulation of fire frequency (or fire period), which is only a single aspect of fire regime (Fox and Fox 1987). Other properties such as season, scale, intensity and heterogeneity (Whelan and Muston 1991) have not been investigated here and may also affect ant community structure and dynamics. For example, 'hot' fires such as those studied by Andersen (1988) and Neumann (1992) resulted in very large post-fire increases in ant activity that were not recorded here. Patchy fires result in some burned and some unburned habitat, which is likely to alter foraging by invertebrates in both habitats (Whelan and Main 1979; Whelan et al. 1980). Burning season (Whelan 1995) also affects responses by both plants and animals and therefore is an important consideration, which was not examined here.

Protection from grazing

No differences in ant community structure or other environmental variables were observed between grazed plots and plots released from grazing pressure. Grazing has been permitted in Bauple State Forest for at least 40 years. The cumulative impact of grazing over this period may have been considerable but in the absence of pre-grazing data, and without any measured changes attributable to release from grazing pressure, its actual impact is unknown. There were two possible methodological aspects that may have clouded the results. (1) Plot size may have been too small to adequately measure the effects of grazing on the ecosystem. Although the plot size of 0.25 ha used in this study should be sufficient for assessing ant community composition, it may have been too small to assess changes to the vegetation and to the soil (Whelan 1995 p141). (2) The impact of de-stocking the forest during the latter half of 1997 and early 1998 may also have been sufficient to allow recovery of plots designated as 'grazed' thereby misrepresenting ant community dynamics in grazed plots.

Increased grazing activity by other herbivores, such as marsupials and rodents, within the grazing exclosures may have compensated for reduced grazing pressure from cattle. Increased grazing by large marsupials was evident from the presence of their faecal pellets and browsing damage. Heavy grazing by large marsupials is known to reduce the cover of palatable grasses such as kangaroo grass *Themeda triandra* and twining Glycene *Glycene clandestina* (Neave and Tanton 1989), which were common at all plots. Even though the effects of grazing by marsupials may be different from those of cattle, the net effect on the vegetation and the ant community may well have been similar. These findings agree with those of Abensperg-Traun *et al.* (1996) who found ant communities were not different in ungrazed, moderately grazed and heavily grazed forest remnants in Western Australia.

Finally, the initial impacts of grazing may not have been reversible by exclusion of grazing animals over the period of time in which the measurements were taken. Factors, such as soil compaction, which may affect plant growth and soil water dynamics, are not easily or quickly reversible and this grazing impact may alter ant community structure. Therefore, no definite conclusions can be reached regarding the impact of grazing by cattle in open eucalypt forests from the data presented here. More rigid manipulation of this treatment, rather than utilising existing conditions, may have led to a more definitive conclusion. Another approach may have been to compare ecosystems where grazing had historically been absent to ecosystems where grazing was the norm; or to establish trends by examining gradients of grazing intensity.

Conclusions

Fire management is plainly an equally important determinant of ant community structure as plant community structure. Not all invertebrates will respond to changes in fire management or grazing pressure in the same way, and some of these groups may easily fall victim to even small changes in the way a forest is managed. Forest managers therefore need to consider not only how fire and grazing may influence vegetation, but also what impacts fire management decisions will have on the invertebrate fauna. The dearth of information on how many important invertebrate groups cope (or do not cope) with fire, signals a pressing need for further research in this area. While many invertebrates are inconspicuous in forest ecosystems, they are vitally important to many ecosystem processes and food webs. Changes in invertebrate communities may well have substantial consequences for the entire forest ecosystem.

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