

Savanna burning for biodiversity: fire management for
faunal conservation in Australian tropical savannas

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Abstract Tropical savannas are the world's most fire-prone biome, and savanna biotas are generally well-adapted to frequent fire. However, in northern Australia there are concerns that recent increases in the frequency and extent of high-intensity fire are causing substantial declines in regional biodiversity values. In this paper we use two well-studied and contrasting faunal groups, ants and small mammals, as case studies for reviewing faunal responses to fire in Australian savannas. The Australian savanna ant fauna is dominated by arid-adapted taxa that are highly resilient to fire and are not considered to be threatened by prevailing fire regimes. Direct mortality during fire is largely inconsequential for most species because of their soil-nesting habits, and frequent fire maintains the open habitats that they favour. The impact of fire increases with increasing rainfall, with long-term fire exclusion increasingly seeing a decline in abundance of arid-adapted taxa, an increase in abundance of highly generalised, more shade-tolerant taxa, and an overall reduction in diversity. In contrast, many small mammal species of high conservation value are significantly impacted by fire, and there are widespread concerns that their populations are threatened by current fire management. Many of the species have shown dramatic population declines over recent decades, and, although the causes are poorly understood, there is little doubt that fire is an important contributing factor. It is likely that fire is acting synergistically with other underlying causes of decline, such as predation by feral cats. The overall resilience of the savanna biota in relation to fire suggests that the level of 'pyrodiversity' needed to maintain savanna biodiversity is rather limited, and that most species are secure under all but the most extreme fire regimes. However, it is clear that more fire-sensitive groups such as small mammals need special fire management attention. This needs to involve less frequent and finer-scale burning, along with the protection of some large, infrequently-burnt source areas.

Key words: ants, small mammals, fire regimes, fire resilience, frequent fire

INTRODUCTION

Fire is a routine part of the annual wet-dry cycle of the vast tropical landscapes of northern Australia (Andersen *et al.* 2003), where more than 40 million hectares are burnt each year (Russell-Smith & Yates 2007). Savanna ecosystems are a product of frequent fire, and without it there would be a dramatic biome shift and loss of biodiversity (Bowman 2003; Bond & Parr 2010). On the other hand, savanna biotas can be threatened by overly severe fire regimes. The burning question is: What mix of fire frequency, intensity and spatial extent is required to maintain savanna biodiversity?

Throughout the world, most savanna fires are nowadays lit by people. Savanna burning by people has a particularly long history in northern Australia, where landscape fire management has played an integral role in traditional Aboriginal society for up to 50,000 years (Jones 1969; Nicholson 1981; Bowman 1998). However, the disruption to traditional burning practices following European settlement of northern Australia from the nineteenth century has meant that for decades fire has been subject to little active management over vast areas of northern Australia. As a consequence there has been an increase in the frequency and extent of higher intensity fires occurring late in the dry season, and there are widespread fears that such changed fire regimes have caused substantial declines in regional biodiversity values (Russell-Smith & Yates 2007; Yates *et al.* 2008). There is particular concern that inappropriate fire regimes have contributed to the catastrophic declines in populations of small mammals and granivorous birds that have been

documented over recent decades (Franklin 1999; Woinarski *et al.* 2001; Burbidge *et al.* 2009; Murphy *et al.* 2010).

The role of fire in such biodiversity declines is difficult to resolve because there have been concurrent changes in a range of other ecosystem drivers across northern Australia, including pervasive spread of introduced livestock, predators and weeds, as well as possible vegetation changes associated with increased atmospheric CO₂ (Woinarski *et al.* 2007). This is coupled with an inadequate understanding of the ecological impacts of contemporary fire regimes. The problem is especially acute for fauna: the negative impacts of frequent fire on particular elements of the vegetation, such as rainforests (Russell-Smith & Bowman 1991), the gymnosperm *Callitris intratropica* (Price & Bowman 1994) and obligate seeders (Russell-Smith *et al.* 1998) are highly visible, but this is not so for animals.

The most reliable information on the ecological effects of fire are obtained from controlled field experiments (Whelan 1985), and several such experiments have been conducted in Australian savannas (Williams *et al.* 2003; Table 1). However, most of these have applied experimental fires at small (one or a few hectares) spatial scales, have a limited time frame, and have focussed on vegetation responses. The most important fire experiment from a faunal perspective is the Kapalga study in Kakadu National Park, where the landscape-scale experimental units allowed a comprehensive range of faunal groups to be studied (Andersen *et al.* 2003). However, experimental fires at Kapalga were applied for only five years. Information at larger spatial and temporal scales is more readily available from ‘natural experiments’ (Hargrove & Pickering 1992), involving assessments of sites with well-documented variation in fire history (Williams *et al.* 2003). Unfortunately, this correlative approach has limited power, given the confounding effects of other environmental

variables and the typically chaotic rather than tightly controlled fire regime contrasts between sampling units. In Australian savannas, important natural experiments include the long-term ecological monitoring programs in Kakadu, Litchfield and Nitmiluk National Parks in the Top End of the Northern Territory (Woinarski *et al.* 2001, 2010, 2011; Russell-Smith *et al.* 2009), the long-term fire exclusion site at Solar Village near Darwin (Woinarski *et al.* 2004; Andersen *et al.* 2006), and the Department of Environment and Conservation's fire research programme in the Mitchell Falls area of the Kimberley region of Western Australia (Radford & Andersen, this volume). Finally, there have also been a range of more-detailed autecological studies of particular species (Crowley & Garnett 1999; Fraser & Whitehead 2005; Firth *et al.* 2010; Murphy *et al.* 2010).

The most important effects of fire on fauna are typically indirect, through changes in habitat, resource availability and predation risk, rather than through direct mortality. For example, even high-intensity, late-season fires may cause no direct mortality of red-backed fairy wrens (*Malurus melanocephalus*), but they lead to a shorter breeding season, lower nestling survival, a lack of multiple broods and therefore reduced reproductive output (Murphy *et al.* 2010). Conversely, although high intensity, late-season fire causes substantial mortality of the iconic frilled lizard (*Chlamydosaurus kingii*), lizard densities are higher in late-burnt compared with unburnt habitat, presumably because of increased prey accessibility (Griffiths & Christian 1996). This highlights the importance of focussing on the longer-term effects of fire, and more particularly on responses to fire *regimes* rather than to individual fire events.

Results from Kapalga show that much of the savanna biota is remarkably resilient in relation to fire, remaining unaffected even by extremes of fire regimes

ranging from annual late-season fires to fire exclusion over fire years (Andersen *et al.* 2003). Fire had a limited influence on arthropod assemblages (Andersen & Müller (2000), and a significant effect on only a minority of the frog, lizard and bird species that were common enough for statistical analysis (Corbett *et al.* 2003). However, some taxa at Kapalga were clearly not so resilient, and their persistence under prevailing fire regimes presents a conservation concern (Andersen *et al.* 2005).

In this paper we use two well-studied and contrasting faunal groups, ants and small mammals, as case studies for reviewing faunal responses to fire in Australian savannas. Like many other taxa, ants are highly resilient and are not considered to be threatened by prevailing fire regimes. In contrast, many small mammal species of high conservation value are significantly impacted by fire, as they can be elsewhere in Australia (Kelly *et al.* 2010), and there are widespread concerns that their populations are threatened by current fire management. We then discuss a way forward for improving fire management for the conservation of Australia's savanna fauna.

ANTS

Ants are dominant organisms in terms of biomass and energy flow in savanna ecosystems throughout the world, and they are exceptionally abundant and diverse in Australian savannas (Andersen 2000). The Australian savanna ant fauna is dominated by arid-adapted taxa with close affinities to those characteristic of the central arid zone, featuring behaviourally dominant species of *Iridomyrmex* and numerous thermophilic species of *Melophorus*, *Meranoplus* and *Monomorium* (Andersen 2003). Local communities are among the richest in any biome anywhere in the world, with 100 or more species often occurring within less than a hectare (Andersen 1992, 2000).

This fauna presents a dramatic contrast to that of rainforest patches embedded in the savanna landscapes, which are dominated by forest-adapted taxa with South-East Asian affinities and are far less diverse (Reichel & Andersen 1996; van Ingen *et al.* 2008).

The composition of local ant communities is overwhelmingly driven by intrinsic climatic and edaphic factors rather than by variation in fire regimes (Andersen 2000). Ants are generally resilient in relation to fire in Australian savannas for two reasons. First, direct mortality during fire is largely inconsequential for most species because of their soil-nesting habits. A major exception is the leaf-nesting green tree ant (*Oecophylla smaragdina*) from the higher rainfall zone, which can suffer very high rates of mortality during fire (Parr & Andersen 2008). Second, frequent fire maintains an open habitat that favours the arid-adapted taxa that dominate the regional ant fauna (Andersen 1991a; Andersen, Parr *et al.*, 2007; Parr & Andersen 2008). The effect of fire on ant communities is therefore related primarily to its effects on vegetation structure. For example, in Purnululu National Park fire had a far greater impact on ants in spinifex habitat, where there were pronounced differences between burnt and unburnt sites in vegetation composition and structure, than it did in sandplain habitat, where vegetation change was less persistent (Barrow *et al.* 2007).

Such an association with vegetation structure means that fire has an especially limited impact on ant communities in areas of low rainfall, where vegetation structure responds slowly to an absence of fire because of low plant growth rates. For example, at Kidman Springs in the semi-arid Victoria River District of the Northern Territory, there was no clustering of ant communities according to fire frequency or seasonality at experimental sites, and there was little change in ant species richness even after ten

years of fire exclusion (Hoffmann 2003). The resilience of ant communities to variation in long-term fire regimes is even more dramatic in arid savannas of southern Africa (Parr *et al.* 2004).

In high rainfall areas, long-term fire exclusion sees more-rapid change, with a progressive decline in abundance of arid-adapted taxa, an increase in abundance of highly generalised, more shade-tolerant taxa (such as species of *Nylanderia*, *Tetramorium*, *Pheidole* and *Odontomachus*), and an overall reduction in diversity (Andersen *et al.*, 2006; Andersen, Parr *et al.*, 2007). For example, species of *Iridomyrmex* accounted for more than half of total ants collected in pitfall traps in annually burnt plots at Munmarlary (Table 1), compared with <20% in plots with 14 years of fire exclusion (Andersen 1991). Sample richness averaged about 40 species in annually burnt plots compared with <30 in unburnt plots, with particular losses in arid-adapted species of *Melophorus*, *Meranoplus* and *Monomorium*. The shade-tolerant species that increasingly dominate sites in the absence of fire all appear to be well-represented in the regional landscape under prevailing fire regimes, so that there does not appear to be any special ant biodiversity values associated with active management for long-term fire exclusion (Andersen & Hoffmann 2011).

Interestingly, the ant community of one of the biennial plots at Munmarlary closely resembled those at annually burnt plots, whereas the other closely resembled those at unburnt plots. This suggests that fire might mediate the occurrence of two alternative stable states, rather than a gradient in the relative abundance of arid-adapted and shade-tolerant taxa. Results from experimental plots at the Territory Wildlife Park show that there is in fact continuous variation in the relative abundance of arid-adapted *Iridomyrmex* (Fig. 1). However, there is a very rapid switch from high to low abundance of *Iridomyrmex* as the representation of shade-tolerant (forest-

associated) species increases, with *Iridomyrmex* declining markedly once the mean forest association score exceeds 0.5 (Fig. 2).

The fire-mediated dynamic between arid-adapted and shade-tolerant elements of the savanna ant fauna is epitomised by the dynamics between meat ants (*Iridomyrmex sanguineus* and *I. reburrus*; Fig. 3a) and green tree ants (*O. smaragdina*; Fig. 3b). These leading behaviourally dominant ants co-occur throughout Australia's mesic savannas, but have contrasting biogeographic histories and habitat requirements. Whereas the biogeographic origin of meat ants is arid Australia, *Oecophylla* is an Old World tropical genus preferring forest habitats (Hölldobler & Wilson 1990), with *O. smaragdina* distributed from China to subcoastal northern Australia. High-intensity, late-season fires at Kapalga led to marked declines in the abundance of *O. smaragdina*, while promoting the abundance of *I. sanguineus* (Andersen *et al.* 2007). Similarly, the first experimental fires at the Territory Wildlife Park after 20 years of active fire exclusion caused dramatic declines in *O. smaragdina*, and resulted in *I. reburrus* immediately foraging into previously unoccupied burnt plots from nests located in nearby open patches (Parr & Andersen 2008). This relationship between *Iridomyrmex* and *Oecophylla* mirrors the ecosystem-wide, fire-mediated dynamic between eucalypt-dominated savanna and rain forest in tropical Australia, with savannas dominated by fire-resistant elements of Australian origin, and rainforest dominated by fire-sensitive elements of South-East Asian origin (Andersen *et al.* 2007)

Substantial fire-induced changes in ant community composition are likely to result in significant changes in the functional roles played by ants. This has been poorly investigated in Australian savannas (and elsewhere), with the notable exception of the role of ants in seed dispersal (myrmecochory). Globally, plant

species from more than 80 families rely on ants to disperse their seeds, which typically possess a nutrient-rich appendage (elaiosome) for attracting ants and facilitating seed transport (Beattie 1985). A range of plant benefits of myrmecochory have been suggested, including avoidance of seed predation by rodents, dispersal to nutrient-rich nest sites, protection from fire, and reduced parent-seedling competition due to distance dispersal. Many ant species disperse the seeds of myrmecochorous plants in Australian savannas (Andersen & Morrison 1998). Experimental fires at the Territory Wildlife Park had little effect on the rates at which seeds were removed by ants, but markedly altered distance dispersal, more than doubling mean dispersal distance (from 1.6 m to 3.8 m). In particular, fire markedly increased the incidence of longer (>5 m) dispersal events, with dispersal distances reaching nearly 20 m following fire compared with a pre-fire maximum <8 m (Parr *et al.* 2007). These changes were due to longer foraging ranges of ant species, presumably in response to habitat simplification following fire.

SMALL MAMMALS

Australian native mammals have proven to be remarkably sensitive to environmental changes wrought by European settlement. This lack of resilience has been exhibited in the extreme throughout southern and central Australia, through extinction of many species (Johnson 2006). The native mammal fauna in northern Australia has largely retained its full complement of species, but is in a state of crisis, with many species having undergone dramatic population declines and range contractions over recent decades (Woinarski *et al.* 2010, 2011). The cause of these declines is poorly

understood, but the available evidence strongly suggests that an inappropriate fire regime is an important contributing factor.

The sensitivity of small mammals to variation in fire regimes in Australian savannas has been consistently demonstrated. As an extreme contrast, the small mammal assemblage diverged drastically after 26 years of fire exclusion at Solar Village, with northern quoll (*Dasyurus hallucatus*), northern brown bandicoot (*Isoodon macrourus*) and pale field-rat (*Rattus tunneyi*) numerically dominating the assemblage in adjacent, frequently burnt savanna, compared with the regionally declining common brush-tail possum (*Trichosurus vulpecula*) and black-footed tree-rat (*Mesembriomys gouldii*) in the long-unburnt area (Woinarski *et al.* 2004b). This result is consistent with autecological studies showing that the latter two species prefer open forests with taller and denser shrubby understoreys (Friend 1987; Kerle 1985), which are greatly simplified by frequent fire (Williams *et al.* 2003b, Russell-Smith *et al.* 2003, Vigilante & Bowman 2004a,b). Highly frequent fire results in low habitat suitability and food availability for these declining species. Recent archaeological evidence suggests that the availability of fleshy fruits from the woody understorey has declined substantially since European settlement (Atchison *et al.* 2005).

Fires may also directly affect the abundance of seeds, stems and leaves of grasses and forbs, a critical resource for many rodent species, including the declining pale field-rat and brush-tailed rabbit-rat (*Conilurus penicillatus*; Firth *et al.* 2005). Unlike many species in other continents, the native rodents of northern Australia do not cache food, and hence are forced to rely upon the environment providing a continuous availability of food resources. This can be a challenge in recently burnt landscapes. Changed fire regimes may also force longer-term changes in grass species

composition, and therefore the availability of preferred seeds. The perennial grass *Alloteropsis semialata* is particularly important for some native mammal species, partly because it produces seed early in the wet season when there is little other seed available, and partly because its stems and underground parts are highly nutritious and succulent (Braithwaite & Griffiths 1996; Crowley & Garnett 2001; Crowley 2008). Its abundance is significantly affected by fire and grazing (Crowley 2008). The fate of *Alloteropsis* provides a cautionary tale about interpretation of results from short-term experimental studies: although significant responses to fire may occur for a small minority of plant species, if these provide keystone resources then the ecological consequences may be profound.

Shelter sites, such as hollow logs, tree hollows and dense tussocks of grass represent other critical resources affected by fire. Severe fire regimes reduce the abundance of large trees containing large hollows (Williams *et al.* 1999) and producing hollow logs, thereby reducing habitat suitability for species such as the brush-tailed rabbit-rat (Firth *et al.* 2006a). With fewer refuges or shelter sites available in areas intensively burnt, predation rates are likely to increase (Oakwood 2000).

Several studies have assessed the short- and medium-term responses of mammals to individual fires. One recent study sampled burnt and unburnt patches of otherwise comparable habitat, five weeks after an extensive fire in the central Kimberley (Legge *et al.* 2008), and reported that mammal abundance in unburnt areas was four times that in burnt areas, with particularly marked effects for the declining pale field-rat and western chestnut mouse (*Pseudomys nanus*). Another study (Begg *et al.* 1981), in a sandstone outlier within the tropical savanna, compared the abundance and reproductive success of four mammal species (common rock-rat

Zyzomys argurus, Arnhem rock-rat *Z. maini*, northern quoll, and sandstone antechinus (*Pseudantechinus bilarni*) before and after a single high intensity fire, reporting reductions in reproductive output and/or reduced abundance for all species following the fire.

The most extensive assessment of small mammals in relation to natural variation in fire regimes is the sampling of 136 sites in Kakadu National Park, first in the period 2001-04 and again during 2007-09 (Woinarski *et al.* 2010). Changes in mammal populations between the two sampling events were then related to fire frequency over the same period. There was a marked decline in mammal populations across all sites, but the extent of decline was far greater at sites with higher fire frequency. This reflects a longer-term pattern of small mammal decline in Kakadu (Fig. 4). A study on the Tiwi Islands north of Darwin gave similar results, showing that fire history was significantly correlated with the abundance, diversity and composition of mammal assemblages, typically with fewer mammals at sites that have had a recent history of more frequent or intense fires (Firth *et al.* 2006b).

Demographic information from longer-term autecological studies have been used to model the population dynamics of mammal species under contrasting fire regimes. Pardon *et al.* (2003) used this approach for the northern brown bandicoot at Kapalga, with their models predicting decline under all four of the imposed fire regimes, but steepest with annual late-season fire. A broadly similar result was found for the brush-tailed rabbit-rat at Cobourg Peninsula in northwestern Arnhem Land, from repeat sampling of two populations over a two-year period (Firth *et al.* 2010). Population models predicted rapid local extinction under a regime of annual late-season fires, and a substantially less rapid, but still inexorable, decline to local

extinction in the absence of fire (the only other fire regime that occurred in their study).

All these studies, across a range of methodological approaches, locations and species, tell a consistent story: native mammals in northern Australia are highly responsive to fire, and are particularly disadvantaged by severe fire regimes.

Woinarski *et al.* (2005) presented a source-sink framework for synthesising the fire-mediated dynamics of small mammals at the landscape scale, hypothesising that severely-burnt areas act as population sinks, requiring re-population from unburnt source areas. Such a dynamic may be stable in landscapes where the sinks are of relatively low incidence and closely approximated to sources, but leads to inexorable decline when burnt areas occupy a large proportion of the landscape and each burnt area is extensive.

It is increasingly recognised that fire is contributing to small mammal declines across northern Australia that are already occurring because of other factors (Woinarski *et al.* 2010). For example, there were dramatic declines in small mammal populations at Kapalga prior to the fire experiment that were not related to fire (Braithwaite & Müller 1997), with experimental fires acting to accentuate these declines, rather than to drive them (Corbett *et al.* 2003). It is therefore possible that particular fire regimes might not have been a threat historically, but are a conservation problem now that they are acting synergistically with new threatening processes. Small mammal declines at Kapalga and elsewhere in Kakadu National Park have occurred in the absence of weed invasion, grazing by livestock or any other obvious environmental change. There is increasing attention being paid to the role of predation by feral cats, given the dominant role of predation in Australia's history of mammal

extinctions (Johnson 2006). It is plausible that fire contributes to small mammal declines across northern Australia by increasing the risk of predation.

DISCUSSION: FIRE MANAGEMENT FOR FAUNAL CONSERVATION

Tropical savannas are the world's most fire-prone biome, and they support a biota with a high degree of resilience in relation to fire. The level of 'pyrodiversity' needed to maintain savanna biodiversity appears to be rather limited, and most species are secure under all but the most extreme fire regimes (Parr & Andersen 2006). This is good news for conservation managers because it buffers against widespread ecological damage following isolated management 'mistakes'. However, not all species are so resilient. In northern Australia there is strong evidence that an increased incidence of large, high-intensity fires is contributing to the broad-scale decline of at least one important component of the savanna fauna (small mammals), a component that history has shown to be especially at risk of extinction.

Periodic large fires are a feature of extensive, fire-prone landscapes, and such landscapes are not only highly resilient to them but the fires can be important in promoting diversity (Bradstock 2008; Keane *et al.* 2008). Contrary to popular perception, large, intense fires are usually highly heterogeneous and do not create homogeneous landscapes (Bradstock 2008; Schoennagel *et al.* 2008). However, the problem in Australian savannas is that large (>1,000 km²) and intense fires have such short recurrence times, often every 2-3 years (Yates *et al.* 2008), that opportunities for recovery by fire-affected fauna are severely limited.

More effective management can reduce this pressure through less frequent and finer-scale burning, along with the protection of some large, infrequently-burnt source

areas. It is particularly concerning that such an overwhelming majority of the landscape is burnt at least once every three years, with just a fraction remaining unburnt for five years or more (Woinarski 2004). It is common for half of the landscape to be burnt each year, which means that only about 3% remains unburnt for longer than five years given random fires (Andersen *et al.* 2005). If the proportion of the landscape burnt annually were reduced to 40%, then the proportion of land remaining unburnt for at least five years would more than double, and this proportion increases exponentially as the total area burnt declines from 40% (Andersen *et al.* 2005). An increase in the area of relatively long-unburnt habitat can also be achieved by locating fires more strategically by deliberately avoiding previously unburnt habitat. For example, assuming that half of the landscape is still burnt annually, if 25% is re-burnt annually (and the other 25% burnt at random), then the area remaining unburnt for at least five years increases from about 3% to 10% (Andersen *et al.* 2005).

Beyond this broad-brush approach, more tightly focused fire management should be undertaken for particular threatened species at particular locations. Many of the small mammals that have suffered severe declines across northern Australia are still abundant in localised areas, and fire management of these refugia demands special attention. We have focussed on the plight of small mammals, but it is likely that these act as ‘umbrella’ taxa for other more fire-sensitive animal species. However, there remains an ongoing challenge to identify other animal species that require special fire management attention. This requires more than simply showing that fire has a negative effect, or that a particular fire regime is preferred, as all species are routinely subject to limiting factors such as fire. The green tree ant is an example of a species that is severely affected by fire, but remains highly abundant

throughout northern Australia and is of no conservation risk under prevailing regimes of high-frequency fire. The challenge is to identify taxa that are under threat by prevailing fire regimes at the landscape scale, and to tailor management solutions for them.

Given that fire has important interactions with other threatening processes, effective management means that fire cannot be viewed in isolation. The exotic gamba grass (*Andropogon gayanus*), which has invaded extensive areas of the Top End of the Northern Territory, represents a particularly good example. This species has markedly higher fuel loads than do native species, cures later in the dry season, and leads to fires of unprecedented intensity (Setterfield *et al.* 2010). Extensive, high-intensity fires would be inevitable in any landscape that gamba grass dominates. Similarly, if promoting predation risk is a key mechanism by which fire contributes to small mammal declines, then changed fire management would be more effective if it is accompanied by a programme to control feral cats.

Finally, although anthropogenic climate change is unlikely to have a direct impact on savanna fire regimes (Williams *et al.*, this volume), it might have an important indirect impact through the increasing interest in savanna burning in the context of greenhouse gas abatement (Heckbert *et al.*, this volume). Carbon is emerging as a nationally important value of Australian savannas that could potentially compete with biodiversity values. To date, carbon and biodiversity values have been viewed as being closely aligned – reducing the severity of prevailing fire regimes can have highly significant carbon benefits, and this can provide important funding opportunities for improved fire management for biodiversity conservation (Russell-Smith *et al.* 2009). However, there is not a simple relationship between carbon stocks and biodiversity (Midgely *et al.* 2010; Hatanaka *et al.* 2011). If there is pressure from

the emerging carbon economy to manage fire for maximum carbon sequestration through extensive increases in the density of woody vegetation, then this would have serious implications for savanna biodiversity.

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Table 1. Summary of manipulative fire experiments designed to examine the ecological effects of different fire regimes in Australian savannas, and including a faunal component. All are in the Northern Territory.

Location	Mean Annual Rainfall (mm)	Study period	Fire regimes*	Size of experimental units	Faunal groups sampled	Reference
Kapalga, Kakadu National Park	1300	1989 – 1995	E1, L1, P1, U	10-20 km ²	Insect assemblages, ants, beetles, grasshoppers, frogs, reptiles, birds, mammals	Andersen <i>et al.</i> (2003)
Territory Wildlife Park, Berry Springs	1700	2003 -	E1, E2, E3, E5, L2, U	1 ha	Insect assemblages, ants, termites, lizards	Parr & Andersen (2008)
Munmarlary, Kakadu National Park	1400	1972 – 1996	E1, E2, L1, U	1 ha	Ants	Russell-Smith <i>et al.</i> (2003)
Victoria River Research Station, Kidman Springs	650	1993 -	E2, E3, L2, L3, U	2.6 ha	Ants	Hoffmann (2003)

*E, L and P = fires lit early, late and progressively during the dry season; U = unburnt; numbers refer to years between successive fires.

Fig. 1. Experimental plots at the Territory Wildlife Park ordered according to the percentage contribution of *Iridomyrmex* species to total ants collected in pitfall traps after five years of fire treatments (A. Andersen, unpublished data).

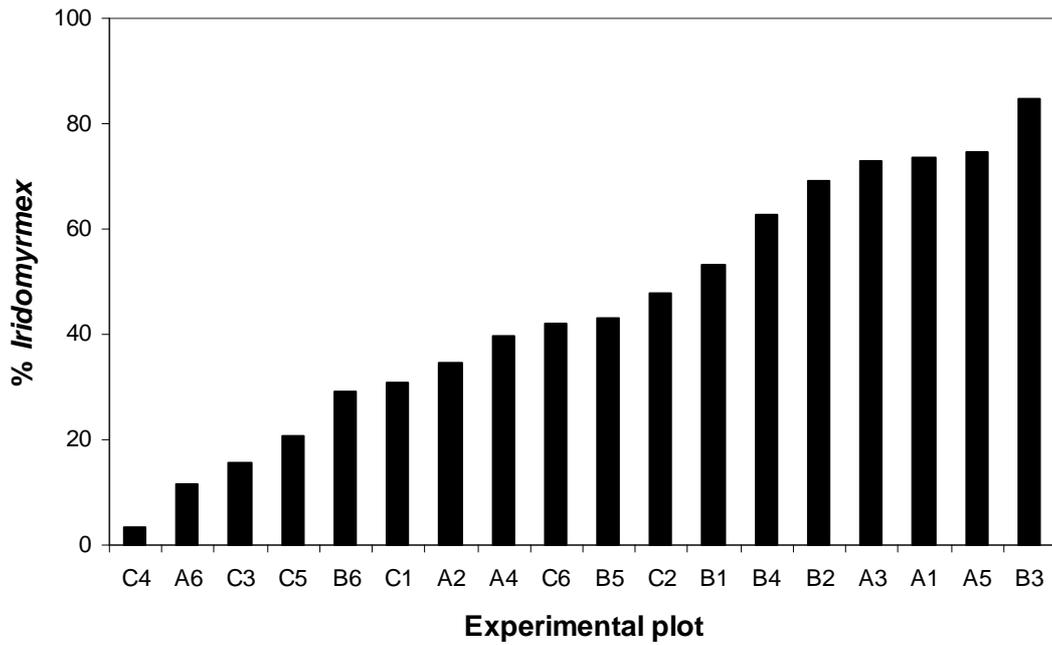


Fig. 2. Relationship between the relative abundance of species of *Iridomyrmex* and mean forest association score at sites representing a gradient in severity of fire regime (see Fig. 1). Mean forest association scores are from Andersen *et al.* (2006), and data for the relative abundance of *Iridomyrmex* are from Andersen (1991), Andersen & Reichel (1994) and Andersen *et al.* (2006).

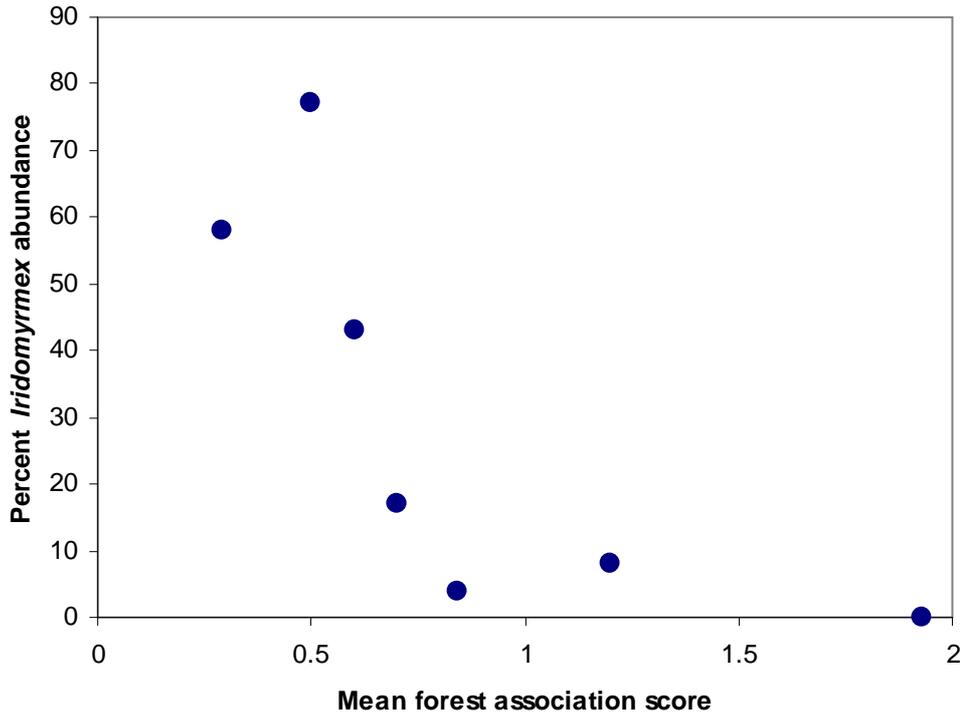


Fig. 3. The northern meat ant *Iridomyrmex sanguineus* (a) and green tree ant *Oecophylla smaragdina* (b) are behaviourally dominant ants throughout Australia's mesic savannas, and have contrasting responses to fire. Soil-nesting *Iridomyrmex* is an arid-adapted genus that is favoured by frequent fire, whereas leaf-nesting *Oecophylla* is a forest-adapted genus that is highly sensitive to frequent fire. Photos: Alan Andersen

(a)



(b)



Fig. 4 Dramatic recent declines in the abundance of small mammals at long-term monitoring plots (n = 15) in Kakadu National Park (data from Woinarski *et al.* 2010)

