

Burning for biodiversity: highly resilient ant communities respond only to strongly contrasting fire regimes in Australia's seasonal tropics

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Summary

1. According to the pyrodiversity paradigm, a wide range of fire regimes is required to maintain biodiversity in fire-prone landscapes. However, the requisite level of pyrodiversity has seldom been tested and may actually be very low.

2. Here, we examine the sensitivity of tropical savanna ants to variation in fire regimes using results from a long-term fire experiment near Darwin, Australia. Six experimental fire regimes, with varying fire frequency and seasonality, have been applied to 18 one-ha plots in three replicated blocks since 2004, with ants sampled prior to experimental burning and then annually after up to 2009. Our primary focus is on the extent to which different patterns of ant richness and composition are associated with each of the six treatment regimes, or whether there is such high overlap that differences only become apparent when experimental treatments are grouped to provide strongly contrasting fire regimes.

3. When treating each of the six fire treatments separately, we were unable to detect a significant influence of fire on any ant community response variable. We were only able to detect significant ant responses when we grouped the experimental treatments into two contrasting fire frequency classes, low (burnt at most once over the 5 years) vs. high (burnt every 1 or 2 years). Even then, these responses were only evident after 3 years of fire treatment.

4. Our findings demonstrate that ant communities have very high resilience in relation to fire, with differences evident only between strongly contrasting regimes. Such resilience appears to be characteristic of savanna ants throughout the world.

5. *Synthesis and applications.* A large range of finely tuned fire regimes is unlikely to promote regional ant diversity. Rather, only very limited pyrodiversity (a combination of frequently and infrequently burnt areas) would appear to be sufficient for maintaining diversity at a landscape scale. It is important that fire management for biodiversity conservation focuses on the demonstrated requirements of target species, rather than be based on an assumption that 'pyrodiversity begets biodiversity'.

Key-words: fire experiment, functional groups, heterogeneity, landscape diversity, patch mosaic burning, pyrodiversity, tropical savanna

Introduction

It is a self-evident truism that environmental heterogeneity – a product of inherent site variation and variable disturbance regimes – is a key driver of species diversity at the landscape scale (Whittaker 1960; Costanza, Moody & Peet 2011). However, it is unclear how much variability in disturbance regimes is required to maintain landscape-scale heterogeneity

and therefore what management interventions might be required to conserve regional diversity. Although management for heterogeneity is often advocated for biodiversity conservation (Du Toit, Rogers & Biggs 2003; Gossner *et al.* 2013; Müller *et al.* 2013; Pryke, Roets & Samways 2013), the degree to which a diversity of management interventions actually promotes regional diversity has rarely been tested.

Fire is the primary agent of disturbance in many biomes of the world (Chuvieco, Giglio & Justice 2008; Bowman

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et al. 2009), where fire plays a key role in the population dynamics and community assembly of species (Whelan 1995; Bond & van Wilgen 1996; Bradstock, Gill & Williams 2012). Different plant and animal species show a wide variety of responses to fire, which has led to the popular notion that in fire-prone landscapes 'pyrodiversity begets biodiversity' (Martin & Sapsis 1992). This has been translated to ecosystem management in the form of patch mosaic burning (PMB), where landscape diversity is thought to be maximized through the creation of a mosaic of patches of different fire histories (Saxon 1984; Parr & Brockett 1992; Brockett, Biggs & van Wilgen 2001).

The PMB paradigm is based on the assumption that the biotas of fire-prone biomes have finely tuned responses to a wide range of specific fire regimes. This assumption has recently been challenged on the basis that much variation in fire regimes appears to have no ecological significance; indeed, in highly fire-prone ecosystems, the biota is so resilient that differences are often only evident between strongly contrasting regimes (Parr & Andersen 2006; Davies *et al.* 2012). It has been suggested that the level of pyrodiversity required to maintain biodiversity might actually be very low (Andersen *et al.* 2005).

Here, we test the pyrodiversity paradigm using ant responses to fire in a tropical savanna of northern Australia. Savanna ecosystems are the world's most fire-prone biomes (Chuvieco, Giglio & Justice 2008), and fire frequency is particularly high in northern Australia (Andersen, Cook & Williams 2003). Ants are an ecologically dominant faunal group throughout the tropics (Hölldobler & Wilson 1990; Folgarait 1998; Del Toro, Ribbons & Pelini 2012) and are especially diverse and abundant in Australian savannas (Andersen 2000). Such diversity and abundance are promoted by frequent fire (Andersen, Hertog & Woinarski 2006), and this is particularly the case for arid-adapted functional groups (*sensu* Andersen 1995) such as Dominant Dolichoderinae (especially species of *Iridomyrmex*) and Hot-Climax Specialists (such as species of *Melophorus*), which are favoured by the open habitats maintained by frequent fire (Andersen, Woinarski & Parr 2012). We base our analysis on results from a field experiment where six fire regimes have been applied to replicate experimental plots since 2004. Our primary focus is on the extent to which different patterns of ant richness and composition are associated with each of the six treatment regimes, or whether there is such high overlap that differences only become apparent when experimental treatments are grouped to provide strongly contrasting fire regimes.

The short-term effects of the first experimental fires on ants at the study plots have been previously described, with the local ant fauna shown to be highly resistant to fire (Parr *et al.* 2007; Parr & Andersen 2008). There were declines in abundance of a small number of species that are more typical of forested habitats rather than of open savanna, but there were no effects of fire on overall ant abundance or species richness (Parr & Andersen 2008).

Here, we describe results after 5 years of experimental burning, testing the predictions that (i) the fauna is so highly resilient in relation to fire that differences between plots subject to different fire regimes become evident only after several years of repeated fire treatment; (ii) the effects of fire only become evident when fire treatments are grouped into contrasting low- and high-frequency regimes; and (iii) arid-adapted components of the fauna are the most favoured by fire. We then discuss our findings in the context of pyrodiversity and the PMB paradigm.

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN

The study was conducted as part of a long-term fire experiment at the Territory Wildlife Park (12°42'S 130°59'E), located 40 km south-east of Darwin in the Northern Territory. The experimental site is covered with tropical savanna woodland dominated by *Eucalyptus tetrodonta* and *Eucalyptus miniata*, with *Acacia* spp., *Calytrix exstipulata*, *Exocarpos latifolius* and *Petalostigma pubescens* as common understorey shrubs. The grass layer is dominated by perennial species of *Eriachne* and *Eragrostis* (Scott *et al.* 2009). Mean annual rainfall is approximately 1800 mm (nearest station Darwin airport, Bureau of Meteorology), the majority of which falls in the summer wet season between November and April. Temperatures are high all year-round, with a mean daily maximum of 32.2 °C and minimum 23.4 °C (Bureau of Meteorology for period from 1981 to 2010). The study site supports an extremely rich ant fauna (>150 savanna species) that is dominated numerically and behaviourally by species of *Iridomyrmex* (Andersen, van Ingen & Campos 2007; Parr *et al.* 2007; Andersen & Hoffmann 2011; Arnan, Gaucherel & Andersen 2011), with species of *Monomorium* also highly abundant and diverse (Andersen, Arnan & Sparks 2013).

The fire experiment comprises 18 one-ha plots, each separated by 15 m and arranged in three blocks (A–C) of six plots, with each block including each of six experimental treatments with varying frequency and timing of fire: E1 – burning early during the dry season (May/June) each year; E2 – early burning every 2 years; E3 – early burning every 3 years; E5 – early burning every 5 years; L2 – burning late in the dry season (September/October) every 2 years; and U – unburnt. Experimental burning commenced in June 2004.

ANT SAMPLING

Ants were sampled in November 2003, May 2004 (immediately before the first experimental fires) and then annually from 2005 to 2009 inclusive. The latter samplings were conducted during May/June (prior to experimental fires), except in 2008 when sampling was conducted during July (1 month after experimental fires). Ants were sampled using a 5 × 3 grid of pitfall traps with permanent locations in the centre of each plot. Traps consisted of 4.5-cm plastic specimen containers, partly filled with ethylene glycol as a preservative, and were operated for 48 h per sampling period (Parr & Andersen 2006). Samples were sorted to species and identified where possible. Unidentified species were given number codes (sp. 1 etc.) that follow and extend those previously published from studies in the region, including

from the fire plots (Parr & Andersen 2006; Arnan, Gaucherel & Andersen 2011; Andersen, Arnan & Sparks 2013). The study site includes many *Monomorium* species of the *nigrius* group that are extremely similar morphologically (Andersen, Arnan & Sparks 2013), and to rationalize the identification process, these were sorted into two composite 'species': *Monomorium* sp. A (larger species: *M. fieldi*, *M. donisthorpei* and *Monomorium* spp. 9, 18, 37 and 50) and *Monomorium* sp. B (smaller species: *Monomorium* spp. 13 and 14). Voucher specimens of all species are held at the CSIRO Tropical Ecosystems Research Centre (TERC) in Darwin.

DATA ANALYSIS

Our analytical strategy was to compare results when all experimental treatments were considered separately (finely tuned responses) with those when treatments were combined into two broad fire frequency classes (strongly contrasting responses): low (U + E5; burnt at most once over the 5 years) and high (E1 + E2 + L2; burnt every 1 or 2 years). Data from E3 were not considered in the latter analyses.

Our data set consisted of the frequency of occurrence in traps (maximum of 15) of each ant species recorded per experimental plot per year. Preliminary analysis indicated that there was no community divergence during the first 2 years of experimental burning (2005–2006), followed by a switch to substantial divergence from 2007 to 2009. All our analyses therefore divided time into three time periods: pre-treatment (2003 and 2004); early (2005 and 2006); and later (2007–2009). A main effect of fire in the absence of significant interaction between fire and time period would mean that there were pre-existing differences between plots subject to different experimental regimes; we therefore used the interaction between fire and time period as our principal explanatory variable of interest.

We examined variation in a range of univariate variables using mixed effects models of repeated measures ANOVA with the three time periods blocked as a fixed factor and spatial blocking as a random factor, using the nlme package (Pinheiro *et al.* 2013) in R (R Core Team 2013). The response variables tested included total ant abundance (the sum of species frequencies), sample species richness and the abundance (frequency of occurrence in traps) of the 13 most common species: *Iridomyrmex* sp. 1 (*anceps* gp.), *I. minor*, *I. pallidus*, *I. reburrus*, *Melophorus* sp. 10, *Monomorium* sp. A (*nigrius* gp.), *Monomorium* sp. B (*nigrius* gp.), *Monomorium* sp. 24 (*laeve* gp.), *Odontomachus* cf. *turneri*, *Oecophylla smaragdina*, *Papyrius* sp., *Rhytidoponera aurata* and *R. borealis*. These species covered a wide range of subfamilies (Dolichoderinae, Ectatomminae, Formicinae, Myrmicinae and Ponerinae) and functional groups (see below).

We used the same ANOVA model to test variation in the abundances of functional groups, and the biogeographical affinities of species, in both cases defined as the sum of the frequency scores of component species. The functional groups used were those described by Andersen (1995, 1997), based on geographical-scale responses of higher taxa to environmental stress and disturbance. Six functional groups were abundant enough for statistical analysis: Dominant Dolichoderinae (primarily species of *Iridomyrmex*), Generalized Myrmicinae (species of *Monomorium*, *Pheidole* and *Crematogaster*), Opportunists (primarily species of *Rhytidoponera*, *Odontomachus*, *Nylanderia*, *Paraparatrechina* and *Tetramorium*), Subordinate Camponotini (species of *Camponotus*, *Polyrhachis*

and *Opisthopsis*), Hot-Climatic Specialists (primarily species of *Melophorus* and *Meranoplus*) and Specialist Predators (species of *Anochetus*, *Bothroponera*, *Cerapachys* and *Leptogenys*). The biogeographical affinities of each species was described as Eyrean (arid), Torresian (tropical), Bassian (cool temperate) or Widespread, following Andersen (2000).

We examined variation in overall species composition using non-metric multidimensional scaling (NMDS), using frequency of occurrence data and based on Bray–Curtis dissimilarity. For each sampling period, analysis of similarities (ANOSIM) was used to test the effects of fire treatment*time period using a mixed effects model. We used similarity percentages (SIMPER) analysis to determine the species contributing >5% of dissimilarity between plots in the final sample of 2009, when treatment effects would be most pronounced. NMDS analyses were conducted in R STATISTICAL program version 12.5.0 using the vegan package (Oksanen *et al.* 2013), and ANOSIM and SIMPER analyses were performed in PRIMER 6 version 6.1.13 & PERMANOVA+ version 1.0.3 extension (Clark & Gorley 2006).

Results

SPECIES ABUNDANCE AND RICHNESS

A total of 106 918 ants comprising 136 species from 40 genera were collected in traps during the study (Andersen *et al.* 2014). The richest genera were *Monomorium* (15 species), *Meranoplus* (12), *Pheidole* (12), *Camponotus* (9), *Melophorus* (8), *Iridomyrmex* (7), *Cerapachys* (6), *Rhytidoponera* (6), *Tetramorium* (6), *Leptogenys* (5) and *Polyrhachis* (5). The most abundant species were *Iridomyrmex* sp. 1 (*anceps* group) (20.1% total ants collected), *I. pallidus* (12.5%), *I. minor* (10.8%), *I. reburrus* (9.9%), *Monomorium* sp. B (7.8%) and *Monomorium* sp. A (6.9%). There was very marked variability between years in the number of ants captured, ranging from 3411 in 2009 to 24 574 in 2008.

When considering each of the six experimental treatments separately, there was no significant effect of fire*time period on either total ant abundance (Fig. 1a) or species richness (Fig. 1b). In both cases, there was always a very high overlap between individual regimes, without any trend for a distinctive response to any particular regime. For example, variation in total ant abundance was almost identical for treatments L2 and E3 and for E1 and E2 (Fig. 1a). Similarly, variation in species richness was almost identical for treatments E1 and E3 and for E5 and U (Fig. 1b). When mean values were quite different, there were very high levels of within-treatment variation so that such differences were not statistically significant (e.g. species richness for E2; Fig. 1b). However, very strong effects were apparent when treatments were combined into contrasting fire frequency classes for both total abundance [Fig. 1c; F (d.f. = 2) = 3.78 P = 0.028] and species richness [Fig. 1d; F (d.f. = 2) = 3.27 P = 0.042]. There were no effects of fire over the first 2 years of experimental burning, but thereafter both abundance and richness increased markedly under high fire frequency.

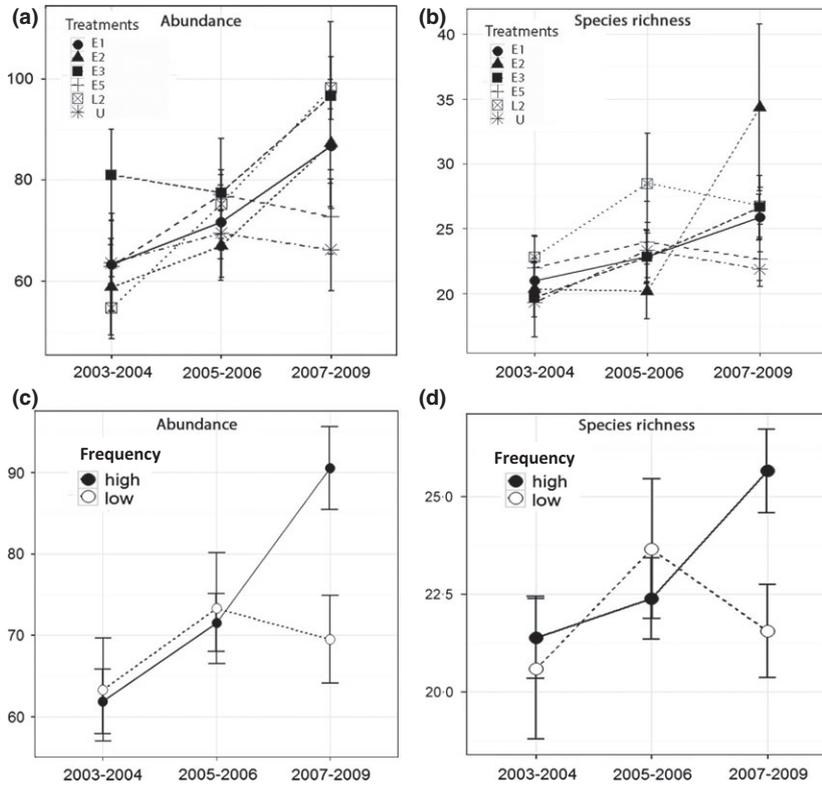


Fig. 1. Mean ($\pm 95\%$ confidence intervals) total abundance and species richness over the three sampling periods with the six experimental treatments (E1 – annual burns, E2 – early burns every 2 years, E3 – early burns every 3 years, E5 – early burns every 5 years, L2 – late burns every 2 years and U – unburnt) considered separately (a,b) and grouped into two frequency classes (high = E1 + E2 + L2; low = c,d). 2003–2004 represent pre-treatment data.

Similarly, there was no variation in abundance in relation to fire*time period for any of the 13 most common species when the six treatments were considered separately. However, fire*time period had a significant effect on three species (*I. reburus*, *I. pallidus* and *Monomorium* sp. A) when they were considered as contrasting frequency classes (Fig. 2). For the two species of *Iridomyrmex*, abundance did not vary with fire frequency for the first two time periods, but was then much higher under high compared with low fire frequency in the last. For *Monomorium* sp. A, abundance was far higher in low compared with high fire frequency plots prior to experimental treatments, but was the same after.

There were no significant effects of fire on the abundance of any functional group or taxa with different biogeographical affinities when the six experimental treatments were considered separately. However, high fire frequency led to significant increases in abundance of Dominant Dolichoderinae and Hot-Climat Specialists (Fig. 3) and Eyrean taxa (Fig. 4). In each of these cases, abundances were very similar at low- and high-frequency plots prior to experimental burning and showed particularly marked divergence between the second and third sampling periods. No significant effects of fire were detected for other functional groups or for taxa with other biogeographical affinities.

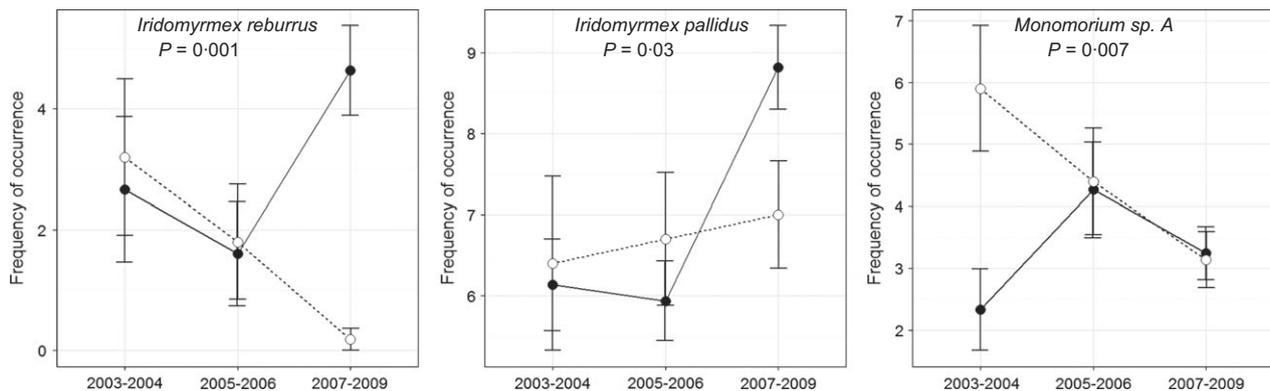


Fig. 2. Variation in mean ($\pm 95\%$ confidence intervals) abundance of *Iridomyrmex reburus*, *Iridomyrmex pallidus* and *Monomorium* sp. A in relation to fire frequency class (closed circles – high; open circles – low). *P*-values relate to the interaction between fire frequency and time period. 2003–2004 represent pre-treatment data.

Fig. 3. Mean ($\pm 95\%$ confidence intervals) abundance of Dominant Dolichoderinae and Hot-Climature Specialists under high (closed circles) and low (open circles) fire frequency. P -values relate to the interaction between fire frequency and time period. 2003–2004 represent pre-treatment data.

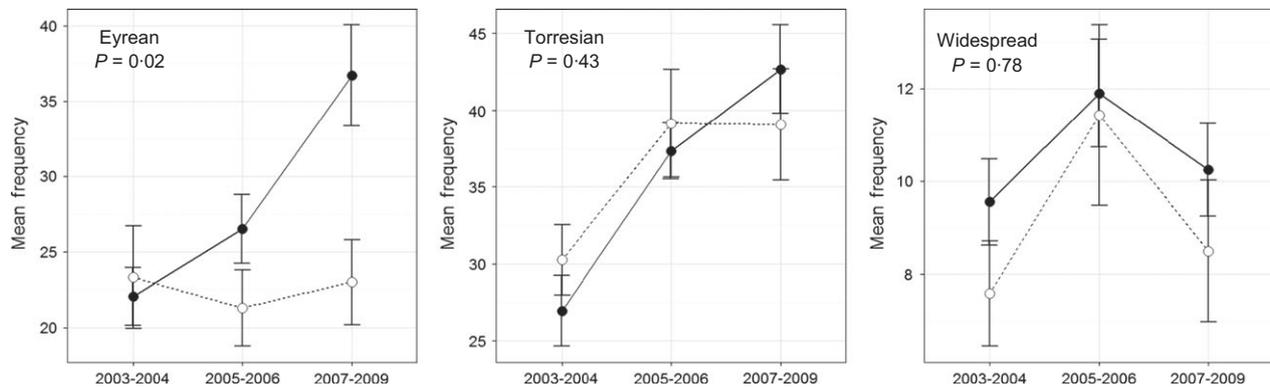
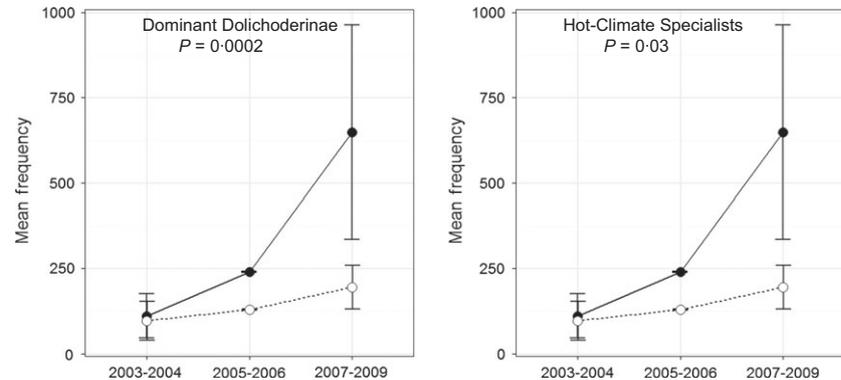


Fig. 4. Mean ($\pm 95\%$ confidence intervals) combined abundances of Eyrean, Torresian and Widespread under high (closed circles) and low (open circles) fire frequency. Bassian taxa were not sufficiently abundant for analysis. P -values relate to the interaction between fire frequency and time period. 2003–2004 represent pre-treatment data.

SPECIES COMPOSITION

Non-metric multidimensional scaling analyses showed that prior to the imposition of experimental treatments in 2004, there was no clustering according to treatment. This was the case whether individual treatments were considered separately or grouped into two frequency classes, with ANOSIM P -values of approximately 0.6 in both cases. When individual treatments were considered separately, there was still no significant clustering after 5 years of treatments, with the ANOSIM P -value for Global R remaining very high (0.67). Even after 5 years of treatment (2009), no pairwise comparison of treatments in ANOSIM even approached statistical significance (P -values always >0.10 , and usually >0.4). When treatments were grouped into two frequency classes, ANOSIM P -values also remained high during the early treatment period. However, it declined markedly to near significance ($P = 0.06$) in 2007 and remained at similar levels for the remainder of the later treatment period (Fig. 5).

Similarity percentages analysis identified six species contributing $>5\%$ of dissimilarity between high- and low-frequency plots in the final sample of 2009 (Table 1). Three of these [*Iridomyrmex* sp. 1 (*anceps* group), *I. reburrus* and *R. aurata*] were more abundant in high-frequency plots, and three [*Monomorium* sp. 24 (*laeve* group), *Monomorium* sp. B (*nigrius* gp.) and *Monomorium* sp. 8

(*carinatum* gp.)] were more abundant in low-frequency plots (Table 1).

Discussion

We found no detectable effects of experimental fires on any variable measured – total ant abundance, species richness, species composition or abundance of any common species – after 2 years of treatment. This was the case even when treatments were grouped into contrasting fire frequency classes. It is clear that the ant communities in our study are highly resilient in relation to fire, in line with our first prediction. Such resilience appears to be typical for savanna ants. For example, there was no detectable variation in ant species composition among most experimental fire regimes at Kruger National Park in South Africa, even after 50 years (Parr *et al.* 2004). Ants are also highly resilient in relation to fire in neotropical savannas (Frizzo, Campos & Vasconcelos 2012).

When each of the treatments remained ungrouped, we found no effects on any variable even after 5 years. This was because results from any particular treatment showed very strong overlap with those from other treatments, and so no distinctive response was evident for any of the six treatments. Consistent with our second prediction, the effects of fire only became evident when treatments were grouped into contrasting low and high fire frequency clas-

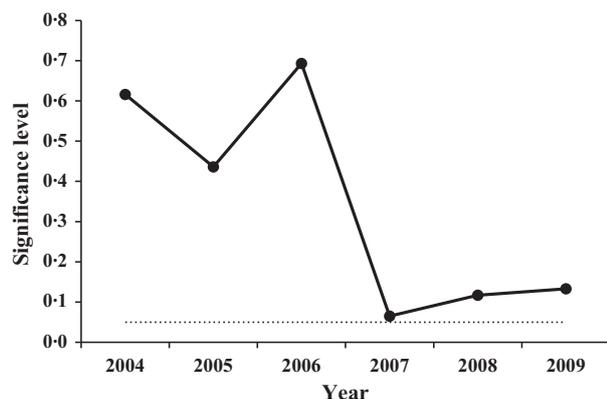


Fig. 5. Analysis of similarities (ANOSIM) Global R P -values for each study year when treatments were grouped into high- and low-frequency classes. Dotted line indicates $P = 0.05$. The Global R -values for 2004–2009 are -0.041 , -0.006 , -0.061 , 0.179 , 0.124 and 0.12 , respectively.

Table 1. Mean plot abundances of ant species identified by similarity percentages (SIMPER) as contributing $>5\%$ of overall compositional dissimilarity between low and high fire frequency treatments in 2009

	Contribution (%)	Mean abundance	
		High frequency	Low frequency
<i>Iridomyrmex</i> sp. 1 (<i>anceps</i> gp.) (12.0%)	12.0	9.8	5.5
<i>Iridomyrmex reburrus</i> (7.0%)	7.0	4.2	0.0
<i>Monomorium</i> sp. 24 (<i>laeve</i> gp.) (6.8%)	6.8	6.7	9.0
<i>Monomorium</i> composite B (<i>nigrius</i> gp.) (6.3%)	6.3	5.2	6.2
<i>Rhytidoponera aurata</i> (5.9%)	5.9	4.9	3.3
<i>Monomorium</i> sp. 8 (<i>carinatum</i> gp.) (5.9%)	5.0	1.7	3.5

ses. Such a grouping revealed substantial differences in total ant abundance, species richness, species composition and the abundance of three common species, with ant abundance and richness higher under high fire frequency.

Our final prediction was that arid-adapted components of the fauna are the most favoured by fire, and this was also borne out. The two arid-adapted functional groups Dominant Dolichoderinae and Hot-Climade Specialists were the only ones of the six tested showing significant variation in overall abundance in relation to fire, and in both cases, they were more abundant under high- compared with low-frequency treatments. Similarly, the overall abundance of Eyrean (arid) taxa was higher under high compared with low fire frequency, whereas the abundances of Torresian (tropical) and Widespread taxa did not vary with fire.

Our results show that ants in our study system do not have finely tuned responses to a wide range of specific fire regimes. Rather, they respond only to strongly contrasting

regimes. Indeed, there is evidence that savanna ant communities in the region occur in one of two alternative stable states, associated with frequent and infrequent burning, with the former characterized by high abundances of Dominant Dolichoderinae and Hot-Climade Specialists (Andersen 1991). There is no evidence that any savanna species requires long-term fire exclusion (Andersen & Hoffmann 2011). This suggests that the occurrence of just two broad fire regimes – high and low frequency – is sufficient to maintain ant diversity at the landscape scale, as has been suggested for the savanna biota more generally (Andersen *et al.* 2005). In other words, ‘duogeneity’ rather than heterogeneity would appear to be sufficient pyrodiversity for maintaining ant diversity.

Our findings are consistent with those emerging from other taxa in other fire-prone biomes. For example, a study of landscape-scale pyrodiversity in mallee woodlands of semi-arid south-eastern Australia found little evidence that either species richness or capture rates of small mammals were influenced by the diversity of fire age classes (Kelly *et al.* 2012). Another component of this study concluded that management aimed at creating diverse mosaics is ‘unlikely to enhance the status of reptiles in the region’ (Farnsworth *et al.* 2014). Much of pyrodiversity can therefore be ecologically meaningless for highly resilient biotas. Moreover, the deliberate creation of pyrodiversity can have a negative impact. For example, many mallee birds show a strong preference for older vegetation (Taylor *et al.* 2012), such that management aimed at creating a high diversity of post-fire age classes would actually disadvantage more bird species than they would promote (Taylor *et al.* 2013). The negative impacts of prescribed burning that reduces the area of favoured post-fire ages, especially long-unburnt habitat, is a widespread concern (Taylor *et al.* 2012; Lindenmayer *et al.* 2013; Nimmo *et al.* 2013; Smith, Michael Bull & Driscoll 2013).

In conclusion, there appears to be no basis for automatically assuming that a complex patchwork of different fire regimes is required for maintaining biodiversity in highly fire-prone biomes. It is important that fire management for biodiversity conservation focuses on the demonstrated requirements of target species, rather than be based on an assumption that ‘pyrodiversity begets biodiversity’.

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Data accessibility

Ant species abundances in each experimental plot for each sampling year are available in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.41vh5> (Andersen *et al.* 2014).

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