Faunal responses to fire in Australian tropical savannas: Insights from field experiments and their lessons for conservation management

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Abstract

Aim: Fire is particularly frequent, complex and contentious in the vast tropical savannas of northern Australia, where declines in many threatened species are associated with fire, and substantial areas are under fire management for greenhouse gas abatement. Controlled field experiments are crucial for understanding biodiversity responses, and here I present key insights into faunal responses to fire that have been revealed by them, along with their lessons for fire management.

Location: Australian monsoonal tropics.

Methods: Results are synthesized from six replicated fire experiments that have been conducted in Australian savannas and include multispecies assessments of fauna. The synthesis also draws on other fire studies and is presented in the form of five key insights into faunal responses.

Results: The key insights are as follows: (a) most faunal groups are extremely resilient to fire, with highly contrasting fire regimes often having little or no detectable impact on species abundances, at least in the medium term; (b) the most important effects of fire are typically indirect through habitat modification, even when there is substantial direct mortality; (c) fire intensity is not as important a factor as is widely thought; rather, fire frequency is particularly important; (d) there will always be winners and losers with any fire; and (e) fire is required for the maintenance of diversity.

Main conclusions: These insights have important implications for conservation management in Australian savannas: management needs to focus on fire-induced changes to habitat suitability, and to consider faunal outcomes at the landscape scale; a combination of frequently (every 2–3 years) and less frequently (every ≥5 years) burned habitat may adequately conserve the great majority of animal species without a need for complex fire mosaics; special management attention is required for frequent-fire losers because of an extremely low representation of longer-unburnt habitat; and fire needs to be actively managed to promote diversity, not excluded. The insights are widely applicable to tropical grassy ecosystems more generally, and some appear to be universal to fire-prone biomes.
1 | INTRODUCTION

Fire is a dominant agent of disturbance in many of the world’s terrestrial ecosystems (Bond et al., 2005; Bowman et al., 2009; Whelan, 1995), where it is a powerful tool for conservation management at the landscape scale (Driscoll et al., 2016; Kelly et al., 2015). However, the effects of fire on fauna are highly context-dependent and therefore difficult to predict (Griffiths & Brook, 2014; Vasconcelos et al., 2017; Woinarski & Recher, 1997), which poses a serious challenge for conservation management in fire-prone ecosystems. Here I present key insights into faunal responses to fire in Australian tropical savannas as revealed by controlled field experiments, discuss their implications for fire management and consider their broader applicability to other fire-prone biomes.

Tropical savannas are the most fire-prone of all biomes (Chuvieco et al., 2008; Lipsett-Moore et al., 2018); each wet season produces high levels of herbaceous biomass that cures over the following dry season to fuel the fires that occur annually in these landscapes (Bourlière, 1983). Such fires are relatively low in intensity compared with those in temperate forests, and at most scorch rather than burn (Bourlière, 1983). Such fires are relatively low in intensity compared with those in temperate forests, and at most scorch rather than burn (Bourlière, 1983; Williams et al., 2003). In mesic (>700 mm mean annual rainfall) regions, these fires maintain the open vegetation structure of tropical savannas, limiting tree cover (Durigan & Ratter, 2016; Sankaran et al., 2005) and ultimately preventing conversion to forest (Bond, 2019; Bowman, 2000). In addition to limiting tree cover and therefore terrestrial carbon stocks, savanna fires also make a significant contribution to global greenhouse gas (GHG) emissions through the release of methane and nitrous oxide in smoke (Beringer et al., 1995; Cook et al., 2010; Lipsett-Moore et al., 2018; van der Werf, 2010).

Fire is a particular conservation concern in the vast tropical savannas that dominate the northern third of the Australian continent, where up to one-quarter of the approximately two million km² is burnt each year overall (Russell-Smith & Yates, 2007). This proportion is far higher in very mesic regions—for example, at least half the lowland savannas of Kakadu National Park (ca. 1,200–1,500 mean annual rainfall) in the Top End of the Northern Territory is usually burnt each year (Gill et al., 2000). Northern Australia has a 60,000-year history of fire management by Aboriginal people who burnt the landscape throughout the year, including extensively during the early and mid-dry season (April–August) (Altman et al., 2020; Braithwaite, 1991; Haynes, 1985; Preece, 2002). However, following the disruption of traditional Aboriginal burning practices due to European settlement a large proportion of savanna fires began occurring as unmanaged wildfires late in the dry season (September–November) when the size and intensity of fire is highest, and there is concern that such changed fire regimes have a detrimental impact on biodiversity (Russell-Smith et al., 2013; Russell-Smith & Yates, 2007). Recent decades have witnessed precipitous declines in populations of small mammals across northern Australia (Fisher et al., 2014; Woinarski et al., 2010; Woinarski et al., 2011), and changed fire regimes have been implicated as an important factor (Burbidge et al., 2009; Lawes et al., 2015; Woinarski et al., 2011). There is also concern that changed fire regimes are threatening granivorous birds through changed seed availability (Franklin, 1999; Fraser et al., 2003; Garnett et al., 2015; Legge et al., 2015; Murphy et al., 2010) and that they are sub-optimal for birds more generally (Reside et al., 2012; Woinarski & Legge, 2013).

Australia is the only country to include emissions from savanna fires in its national GHG accounts, and such emissions represent approximately 4% of the annual total (Cook & Meyer, 2009). Registered “savanna burning” projects can earn carbon credits by reducing GHG emissions through changed fire management, which is typically achieved by extensive prescribed burning early during the dry season and a consequent reduction in extent of late-season fire (Heckbert et al., 2012; Russell-Smith et al., 2013). Such projects have created important livelihood opportunities for remote Aboriginal communities, which own a large proportion of Australia’s tropical savannas (Cook et al., 2012; Heckbert et al., 2012; Richards et al., 2012; Russell-Smith et al., 2013), and have also provided significant funding for pastoralists (Skroblin et al., 2014). As of 2019, registered savanna burning projects cover approximately 20% of Australia’s tropical savanna biome (Corey et al., 2020). The switch from a predominance of late- to early-season fires in savanna burning projects has potential co-benefits for biodiversity (Fitzsimmons et al., 2012; Russell-Smith et al., 2015), but it has its own significant biodiversity concerns (Corey et al., 2020; Perry et al., 2016).

Appropriate fire management in Australian savannas is severely limited by an inadequate understanding of responses of biodiversity to different fire regimes, and this limitation is especially acute for fauna. There has been a range of research approaches to understanding responses of fauna to fire in Australian savannas, as is the case for fire-prone biomes more generally (Driscoll et al., 2011). A small number of autecological studies have looked in mechanistic detail at responses of one or a small number of species to particular fire events (e.g. Leahy et al., 2015; Murphy et al., 2010). However, most relevant studies are phenomenological, relating the diversity and abundance of faunal groups to either individual fires or to longer-term fire regimes.

Many of these phenomenological studies are correlative, examining associations between historical fire patterns and contemporary patterns of animal distribution and abundance. However, this has typically led to weak or inconsistent results. For example, in analysing results from long-term monitoring plots in Kakadu National Park, Lawes et al. (2015) found that declines in small-mammal richness and abundance were correlated with a range of fire variables.
**Table 1** Summary of replicated fire experiments in Australian tropical savannas that include a faunal component

| Location                                      | Mean annual rainfall (mm) | Study period | Fire regimes \(a\) | Number of replicates per regime | Size of experimental units | Faunal groups sampled                                      | References                      |
|-----------------------------------------------|---------------------------|--------------|---------------------|---------------------------------|---------------------------|------------------------------------------------------------|---------------------------------|
| Munmarlary, Kakadu National Park, NT          | 1,400                     | 1973–1996    | E1, E2, L1, U       | 3 in each of woodland and open forest | 1 ha                      | Ants                                                       | Russell-Smith, Whitehead, et al. (2003) |
| Kapalga, Kakadu National Park, NT             | 1,300                     | 1989–1995    | E1, L1, P1, U       | 3                               | 10–20 km\(^2\)            | Aquatic macroinvertebrates, terrestrial Insect assemblages, ants, beetles, grasshoppers, frogs, reptiles, birds, mammals | Andersen, Cook, et al. (2003)     |
| Kidman springs, Victoria River Research Station, NT | 650                       | 1993–present | E2, E4, E6, L2, L4, L6, U | 2–4 on each of two soil types   | 2.6 ha                    | Ants, reptiles, birds                                      | Woinarski et al. (1999)          |
| Burdekin catchment, nr. Charters towers, Qld | 700                       | 1999–2004    | Burnt once (Dec 1999), twice (Dec 1999 and 2001) and unburnt | 3                              | 20 ha                     | Birds                                                     | Radford et al. (2008)             |
| Territory Wildlife Park, nr. Darwin, NT       | 1,700                     | 2003–present | E1, E2, E3, E5, L2, U | 6                              | 1 ha                      | Insect assemblages, ants, termites, skinks                 | Parr and Andersen (2008)         |
| Tiwi carbon study, Melville Island, NT        | 1,500–2,000 mm            | 2008–present | E1, E3, U           | 6                              | 50–100 ha                 | Ants, reptiles, birds, small mammals                      | Richards et al. (2012)           |

*Note: All are in the Northern Territory. Modified from Andersen et al. (2012).*

\(a\) E, L and P = fires lit early, late and progressively during the dry season; U = unburnt; numbers refer to years between successive fires.
However, the correlations were all weak, and a substantial proportion of sites with the highest declines in mammal richness and abundance had experienced little or no fire over the study period. None of three fire variables (fire frequency, late-fire frequency, years since burnt) considered in models of factors influencing the abundance of brush-tailed possums *Trichosurus vulpecula* and savanna gliders *Petaurus ariel* in north-western Australia were significant for either species (Stobo-Wilson et al., 2019). In contrast to the negative associations between fire and small mammals in the Kakadu study, the only associations between small mammals and fire over the preceding 5 years on Groote Eylandt were found to be positive (Heiniger et al., 2020). There was also a positive association between fire activity and the abundance of declining small-mammal species revealed by a comprehensive analysis of survey data from the northern half of the Northern Territory (Stobo-Wilson et al., 2020).

Such weak and inconsistent results can be expected when fire is just one of many factors influencing animal distributions. However, correlative studies have a much more fundamental limitation in that any association of faunal patterns with fire cannot be assumed to be causal, as the same variables driving fire mosaics (such as topography, rockiness and proximity to water at local scales, and rainfall at a regional scale) also influence faunal distribution. In other words, patterns of fire and fauna can be correlated because fire is correlated with other environmental factors that actually influence faunal distribution and abundance. For example, the positive correlation between fire activity and occurrence of declining small mammals in the Northern Territory was attributed to the covariance of these factors with annual rainfall, rather than to any preference of small mammals for frequent fire (Stobo-Wilson et al., 2020). Such confounding factors are problematic in a correlative approach to landscape ecology more generally (Ewers & Didham, 2006). They can be reduced through careful site selection, such as standardizing environmental variables known to influence both fire mosaics and animal distribution; however, potentially confounding effects of unknown factors can never be eliminated. Correlative studies play an important role identifying potential causal factors that merit targeted research, but they cannot demonstrate causation.

As is the case more generally in landscape ecology (Hastings, 1989; McGarigal & Cushman, 2002), the most reliable information on causal effects of fire comes from controlled field experiments where fire treatments are applied to replicated plots (Williams et al., 2003). Fire experiments have their own limitations due to logistical constraints, such as the range of fire variables that can be manipulated, the size of experimental plots (treatment size) and the time period over which experiments are conducted (Williams, Woinarski, et al., 2003). However, fire experiments provide particularly robust information on fire impacts in tropical savannas because the intensities of experimental fires are as high as those of wildfires (Williams, Gill, et al., 2003), and fire frequency can be manipulated over relatively short time periods (Driscoll et al., 2011). Field experiments are also often limited by low levels of replication and therefore statistical power, which can mask actual fire responses (Smith et al., 2013). Statistical power can be enhanced through the collection of pre-treatment (baseline) data and by focusing statistical analysis on interactions between treatment and time (Andersen et al., 1998).

Six controlled and replicated fire experiments have been conducted in Australian savannas that include multispecies faunal assessments (Table 1). These are heavily concentrated (four out of six) in the Top End of the Northern Territory, at the high end of the savanna rainfall gradient (Figure 1). The first to be established was at Munmarlary in Kakadu National Park, commencing in 1972 and continuing for 23 years (Russell-Smith, Whitehead, et al., 2003). Three experiments are ongoing: Kidman Springs (commencing in 1993), Territory Wildlife Park (2003) and the Tiwi Carbon Study (2008). The number of fire treatments ranges from three (Burdekin, Tiwi Carbon Study) to seven (Kidman Springs), and each treatment is replicated from two to six times. Three of the experiments (Munmarlary, Kidman Springs and Territory Wildlife Park) have relatively small (<3 ha) plot size, which severely limits their reliability for animals with large home ranges and for highly mobile taxa such as birds, given that occurrences in any plot are potentially influenced by conditions outside. The most extensive faunal data are from Kapalga in Kakadu National Park, where experimental plots were 10–20 km² sub-catchments and the responses of a comprehensive range of faunal taxa were assessed (Andersen et al., 2003).

Here I synthesize the results of these experiments, supplemented by results from other fire studies, in the form of five key insights into the responses of fauna to fire in Australian savannas, as a basis for their conservation management. I consider fauna generally rather than focusing on groups that have attracted most attention, notably small mammals, which do not necessarily reflect broader fire-fauna relationships. The five insights are as follows: (a) most faunal groups are remarkably resilient to fire; (b) the main effects of fire on fauna are indirect through habitat change; (c) fire intensity is not as important as is widely thought; (d) any fire regime will have both winners and losers; and (e) fire is required for maintaining faunal diversity. The insights and their associated lessons for conservation management apply more generally to grassy ecosystems throughout the world, and some are widely applicable to other fire-prone biomes.

2 | KEY INSIGHTS

2.1 | Insight 1. Most faunal groups are extremely resilient to fire

The experiments have consistently shown that most faunal groups are extremely resilient to fire. At Kapalga, fire had relatively little effect on insect communities despite treatments ranging from annual burning late in the dry season to fire exclusion over 5 years. The abundances of most ordinal-level taxa from both the ground and grass layer did not vary significantly among treatments (Andersen & Müller, 2000), and grasshopper species richness was similarly unaffected (Figure 2). The abundance of only one of the 10 most common beetle species in the grass layer was significantly affected by fire treatment (Orgeas & Andersen, 2001). At Kidman Springs, ant species richness
did not vary with fire regime after 5 years (Hoffmann, 2003). Such resilience of insect communities to fire is also evident in savannas of Western Australia’s Kimberley region, where numbers of grass-layer invertebrates were restored to pre-fire levels by the first wet season after fire (Radford & Andersen, 2012).

Most vertebrates also appear to be highly resilient to fire. Of the eleven frog species common enough for statistical analysis at Kapalga, the abundance of only one varied significantly among treatments, and these figures were five from 16 for reptiles and four from 25 for birds (Corbett et al., 2003). At Kidman Springs, species richness of neither birds nor reptiles varied significantly among the seven fire regimes after 4 years, and the abundances of only four of the 49 bird species and none of the 18 reptile species varied significantly (Woinarski et al., 1999). In the Burdekin experiment, a single fire had no effect on bird species richness in riparian habitat; in non-riparian habitat, the single fire caused a decline in bird species richness, but there were no further declines under the twice-burnt treatment (Valentine et al., 2012). A high-intensity late-dry-season fire in the central Kimberley region of Western Australia had no detectable effect on bird abundance or species richness (Legge et al., 2008). Such generally high resilience indicates that most faunal taxa are secure under all but the most extreme fire regimes.

Of all faunal groups in Australian savannas, small mammals appear to be most sensitive to variation in fire regimes (Andersen et al., 2012). Total abundance and species richness of small mammals, and the captures of six of the seven most common species, were all significantly affected by fire treatment at Kapalga (Corbett et al., 2003). Of the seven species that were sufficiently abundant
for statistical analysis, three (northern quoll, *Dasyurus hallucatus*; fawn antechinus, *Antechinus bellus*; and northern brown bandicoot, *Isoodon macrourus*) were clearly most abundant in unburnt sub-catchments, and two (northern brush-tail possum, *Trichosurus vulpecula*; and grassland melomys, *Melomys burtoni*) were more variable but tended to be most abundant in unburnt catchments, such that overall abundance of small mammals was highest by far in unburnt catchments. Modelling of mark–recapture data from Kapalga indicated that an increase in fire frequency above once every 5 years increased extinction risk for all four species (northern quoll, northern brushtail possum, northern brown bandicoot and grassland melomys) that were abundant enough for analysis (Griffiths et al., 2015).

2.2 | Insight 2. The main effects of fire on fauna are indirect through habitat change

Fire can have a direct impact on animal populations by injuring or killing individuals, including through smoke inhalation (Jordaan et al., 2020). However, such impacts appear to be relatively limited in Australian savannas, especially when fire occurs at lower intensity. For example, sampling immediately before and after the first early-season fires at the Territory Wildlife Park revealed no change in the abundance or composition of skink species (Figure 3), and early-season fires caused no direct mortality of frill-necked lizards (*Chlamydosaurus kingii*) at Kapalga (Griffiths & Christian, 1996). Even high-intensity fires may cause no direct mortality, such is the case for red-backed fairy wrens (*Malurus melanocephalus*) (Murphy et al., 2010; Sommer et al., 2018) and small rodents (Leahy et al., 2015) in the Kimberley. However, late-season fires at Kapalga caused 30% mortality in frill-necked lizards (Griffiths & Christian, 1996), and my unpublished observations of insects climbing up trees in response to smoke from experimental fires at the Territory Wildlife Park (cf. Dell et al., 2017) indicate an evolutionary response to direct fire-induced mortality.

![Figure 3](image-url) Changes in captures of skink species immediately after experimental fires at the Territory Wildlife Park (data from Nicholson et al., 2006)

The most important effects of savanna fires on fauna are typically indirect, through changes in habitat, resource availability and predation risk, rather than through direct mortality (Andersen et al., 2012). Such effects can occur after individual fires due to loss of ground-layer vegetation and associated resources. For example, although fire causes no direct mortality of red-backed fairy wrens, it leads to changes in habitat use (Sommer et al., 2018) and reproductive success (Murphy et al., 2010). Experimental fires at the Territory Wildlife Park led to higher rates of myrmecochorous seed collection and dispersal by ants in the months after burning due to increased foraging distances following simplification of ground-layer habitat (Parr et al., 2007). Fire-induced declines in bird species richness during the Burdekin experiment were attributed to declines in a native shrub that produces fleshy fruits (Valentine et al., 2012).

A particularly important indirect effect of individual fires in Australian savannas is an increase in predation risk due to the removal of shelter. Feral cats (*Felis catus*) are voracious predators of small mammals throughout Australia (Murphy et al., 2019; Woolley et al., 2019), and such predation appears to be the primary driver of the catastrophic declines in small-mammal populations across northern Australia (Davies, McCarthy, Firth, et al., 2018; Frank et al., 2014; Legge et al., 2019). Fire increases the hunting efficiency of cats by removing shelter (McGregor, et al., 2015; McGregor et al., 2017), and the association of fire with small-mammal declines appears to be due primarily to increased predation risk rather than to effects on food or other non-shelter resources (Leahy et al., 2015; Whitehead et al., 2018). For example, the brush-tailed rabbit-rat (*Coniluris penicillatus*) has suffered dramatic declines to near extinction in the Northern Territory mainland, with fire shown to be a contributing factor (Firth et al., 2010). However, in the Tiwi Carbon Study on Melville Island where feral cat abundance appears to be relatively low (Davies, McCarthy, Firth, et al., 2018), it was most common under annual fires, and least common at unburnt sites (Figure 4b); this suggests that its fire-related near extinction on the mainland was due to...
increased predation risk rather than through impacts on non-shelter resources. The widespread declines in small-mammal populations with frequent fire at Kapalga were also likely influenced by predation by feral cats, as small-mammal species showed much more variable responses to experimental fires in the Tiwi Carbon Study (Figure 4). As at Kapalga, grassland melomys was most common in unburnt habitat (Figure 4c); however, bandicoots were most common at triennially burnt sites (Figure 4d), and possums showed no fire preference (Figure 4a). Similarly, the association between fire and the occupancy of small mammals is highly variable among species on Groote Eylandt, where cat densities are also low (Heiniger et al., 2020).

The indirect effects of individual fires are often short-lived because of limited tree mortality, persisting only up to the following wet season when the ground-layer habitat is restored. However, far more persistent indirect effects occur when there is substantial habitat structural change due to variation in longer-term fire regimes (Gill, 1975). In particular, an absence of fire in Australian mesic savannas leads to a rapid growth of mid-storey shrubs and trees, as shown at both Munmarlary (Russell-Smith et al., 2003) and the Territory Wildlife Park (Levick et al., 2019), as well as elsewhere (Woinarski et al., 2003). Such changes in vegetation structure have profound implications for fauna. This has been extensively documented for ants, where different species are characteristic of different levels of fire-mediated habitat openness (Andersen et al., 2012). Fire-induced variation in shrub cover is of particular importance to the many passerine birds that nest and forage in the mid-storey (Corbett et al., 2003), and also has important implications for longer-term rates of predation by feral cats (Davies, McCarthy, Firth et al., 2018). Similarly, different fire regimes can affect grass composition, with important impacts on seed resources for granivorous savanna birds (Crowley & Garnett, 1999; Legge et al., 2015; Weier et al., 2018).

Frill-necked lizards at Kapalga provide a graphic illustration of the primacy of habitat change over the direct effects of fire. Although high-intensity, late-season fire caused substantial mortality, lizard densities were highest in late-burnt sub-catchments (Table 2). This is likely due to increased prey accessibility following the simplification of ground-layer habitat by frequent, high-intensity fire (Griffiths & Christian, 1996). This highlights the importance of focusing attention on the longer-term effects of different fire regimes (Gill, 1975) rather than on individual fire events.

2.3 Insight 3. Fire intensity is not as important as is widely thought

Despite widespread conservation concern over high-intensity, late-season fires, the high resilience of the fauna outlined above indicates that there is not a pervasive negative impact of such fires on Australia’s savanna fauna. Moreover, results from Kapalga show
TABLE 2 Rates of mortality and densities of frilled-necked lizards (Chlamydosaurus kingii) in sub-catchments subject to experimental fire regimes at Kapalga in Kakadu National Park

| Fire regime | Mean fire intensity (MWM\(^{-1}\)) | Mortality (%) | Lizard density (ha\(^{-1}\)) |
|-------------|------------------------------------|---------------|-----------------------------|
| Unburnt     | N/A                                | N/A           | 0.13                        |
| Early       | 2.1                                | 0             | 0.65                        |
| Late        | 7.7                                | 30            | 0.78                        |

Note: Lizard data are from Griffith and Christian (1996), and fire intensity data are from Williams, Woinarski, et al. (2003).

that when fire did have an impact, this was often between burnt and unburnt treatments, with no effect of fire season (and therefore intensity). For example, there was clear differentiation in species composition of grass-layer beetle assemblages between burnt and unburnt sites, but no differentiation according to season of burn (Figure 5). This pattern was also shown by total beetle abundance, species richness and family richness (Orgeas & Andersen, 2001).

There are of course clear examples where some faunal taxa are especially sensitive to high-intensity fires occurring late in the dry season. For example, late but not early fires at Kapalga significantly reduced the number of ground-active beetle individuals, species and families over the following wet season (Blanche et al., 2001). The skink Carlia amax and lemon-bellied flycatcher (Microeca flavigaster) both declined in abundance under the regime of late fires, which likely reflects impacts on their respectively preferred litter and mid-storey habitats (Corbett et al., 2003).

An important caveat with the Kapalga experiment is that the effects on fauna of very-low-intensity (<1,000 kWm\(^{-1}\)) fire was not examined; such fires are typical of management burns very early (April/May) in the dry season and are often highly patchy at small spatial scales. A study of the pale field rat (Rattus tunneyi) in riparian habitat of the central Kimberley showed that declines in trap success following fire increased systematically with the proportion of the immediate (20 m radius) area burnt (Shaw, 2018). This demonstrates a clear effect of intensity at the lower end of the scale, at least in the short term. In all cases, trap success returned to pre-fire levels within 12 months (Shaw, 2018), and so in this case the effects of fire intensity were not persistent.

A primary contrast between frequently burnt versus unburnt, rather than between early- and late-season burning, points to fire frequency having a particularly important influence on fauna in Australian savannas (Andersen et al., 2005). Fire frequency was a more important factor than intensity in explaining changes in small-mammal abundance following changed fire management in the Kimberley (Legge et al., 2019). The Tiwi Carbon Study has shown fire frequency to be a significant predictor of the abundances of most small mammals on Melville Island (Davies, McCarthy, Rioli, et al., 2018).

2.4 | Insight 4. Any fire regime will have both winners and losers

Unsurprisingly, responses to fire vary markedly among faunal species, as illustrated by small-mammal responses to experimental fire revealed by the Tiwi Carbon Study (Figure 4). Any fire will have both “winners” (positively affected) and “losers” (negatively affected). Among lizards at Kapalga, late fires promoted the abundance of frill-necked lizards (Table 2) while having the negative impact on Carla amax. The loss of mid-storey habitat under late fires disadvantaged the lemon-bellied flycatcher, but it promoted the abundance of avian predators such as brown goshawk (Accipiter fasciatus) and red-backed kingfisher (Todiramphus pyrrhopogia), presumably through increased hunting efficiency (Corbett et al., 2003). In the Burdekin experiment, avian frugivores, nectarivores and insectivores were fire losers but this was not the case for granivores or carnivores (Valentine et al., 2012). Late fires at Kapalga disadvantaged some common wet-adapted beetles, while favouring others that were dry-adapted (Blanche et al., 2001).

Such variable responses mean that there is no single fire regime that can maximize all components of faunal diversity in a single place. This highlights the importance of considering fire patterns and biodiversity outcomes at the landscape scale. There are always fire mosaics in a landscape even if they are not obvious (Gill et al., 2003), and the conservation challenge is to identify taxa that might require management intervention, rather than to implement fire mosaics that might not be needed (Parr & Andersen, 2006). Optimal distributions of post-fire vegetation age-classes for faunal conservation have been modelled in temperate forests where fire-return intervals can be very long (Chick et al., 2019; Stefano et al., 2013). However, given the very high fire frequencies and general resilience to fire shown by most faunal groups in tropical savannas, a high degree of “pyrodiversity” might not be needed in these...
systems (Parr & Andersen, 2006). A combination of frequently and less frequently burned habitat may adequately conserve the great majority of species in Australian savanna landscapes without a need for complex fire mosaics.

One group of animals demanding fire management attention in Australian savannas has been identified—those species that require relatively long-unburnt (five or more years) habitat (Andersen et al., 2005). The representation of these taxa varies widely among faunal groups. For example, all ant species occurring in long-unburnt areas of the Territory Wildlife Park are common and widespread throughout the savanna landscapes of the broader region and so do not require management intervention (Andersen & Hoffmann, 2011). However, significant numbers of bird and mammal species strongly prefer longer-unburnt habitat (Woinarski et al., 2003). These frequent-fire “losers” are losing at the landscape scale because of a very low (typically <5% in mesic regions) representation of longer-unburnt habitat, and fire-refuge microhabitats that can cater for relatively fire-sensitive insects are not sufficient for birds and mammals. Increasing the representation of longer-unburnt habitat in Australian savannas is widely recognized as a conservation priority, and it could be achieved by either reducing the total area burnt each year, or by setting prescribed fires more strategically (Andersen et al., 2005). A coordinated fire management programme across the central Kimberley region of Western Australia has been highly successful in increasing the representation of longer-unburnt habitat (Legge et al., 2011). Extensive prescribed burning over several years has also led to an increased representation of longer-unburnt habitat in the northern Kimberley, and this was associated with increases in abundance of a range of small-mammal species (Radford et al., 2020).

2.5 Insight 5. Fire is required for maintaining faunal diversity

Tropical savannas and grasslands are exceptionally diverse ecosystems (Murphy et al., 2016), and in mesic regions, this diversity is a product of frequent fire maintaining an open habitat (Bond, 2019; Parr et al., 2014). The experiments reviewed here provide many examples where the maintenance of faunal diversity in Australian savannas requires fire. Ants—the dominant faunal group in terms of biomass and nutrient flow (Andersen, 2000), are one of the most striking examples (Andersen et al., 2012). At Munmarlary, mean ant richness in annually burnt plots was 40, compared with 24.5 in long-unburnt plots (Andersen, 1991). At Kidman Springs, overall ant abundance and species richness were negatively related to time-since-fire, and the abundance of seven of the eight species that varied significantly among fire regimes was reduced in the absence of fire (Hoffmann, 2003). At the Territory Wildlife Park, frequent burning following decades of fire exclusion led to marked increases in ant abundance and richness (Andersen et al., 2014). Similar results were shown at Solar Village near Darwin where fire had been actively excluded for 23 years—a total of 72 ant species were recorded in burnt habitat, compared with only 45 in unburnt (Andersen et al., 2006). Ants are a particularly striking example because Australia’s savanna ant fauna is strongly arid-adapted, such that the great majority of species favour open rather than shady habitats (Andersen, 2019). Such a requirement of fire for maintaining species richness is also evident in other insect groups; for example, at Kapalga the total abundance, species richness and family richness of grass-layer beetles were all substantially reduced in the absence of fire (Orange & Andersen, 2001).

Experimental results for vertebrates are not as striking as for insects. A major contributing factor is that fewer data are available. Vertebrates have not been as extensively assessed as have insects due to the relatively small size of most experimental plots (Table 1). Vertebrates are longer-lived than are insects, and longer experimental time frames are likely to be required to detect fire effects. Finally, the frequently low diversity of vertebrate taxa in samples (as is particularly the case for mammals) often precludes meaningful analysis of diversity. At Kidman Springs, mammals were too infrequently recorded to be analysed, and only four reptile species were sampled (Woinarski et al., 1999). Bird species richness was highest for plots burnt most recently and for plots with the longest period since fire, but sampling occurred after only 5 years of experimental burning, and the reliability of bird data is open to question due to small (2.6 ha) plot size. Although extensive vertebrate data are available at Kapalga, comparisons of species richness are limited by the low numbers of species whose abundances varied among fire treatments. Experimental burning at Kapalga was conducted for only 5 years, and greater divergence among regimes would be expected over a longer period (Andersen et al., 2005). In the Tiwi Carbon Study, fire treatment had a significant effect on the composition of small-mammal assemblages, but not on species richness; however, fewer than ten species were recorded in total. Finally, relationships between fire and vertebrate diversity are highly confounded by the abundance of feral cats, as illustrated by contrasting results from the mainland (high cat densities) on one hand, and off-shore islands (Tiwi Islands, Groote Eylandt; low cat densities) on the other.

An important consideration in any analysis of the effects of fire on species richness is beta diversity. Different treatments might have similar plot-scale richness, but the same species might keep recurring under one treatment, whereas another treatment might have high species turnover. Analysis of plot-scale richness might therefore mask important effects of different fire regimes at the landscape scale, especially for taxa with relatively low diversity at the plot scale. One way of taking a landscape-scale approach is to classify all savanna species occurring in a region according to whether they prefer open habitats, and therefore frequent fire, or shady habitats, and therefore infrequent fire. This would be highly informative in terms of quantifying the extent to which fire is required for maintaining faunal diversity, but I am unaware of any such analysis for any faunal group other than ants.
3 | DISCUSSION

Controlled field experiments have revealed important insights into faunal responses to fire in Australian tropical savannas, and these provide valuable lessons for fire management in these landscapes (Figure 6). Most faunal groups are extremely resilient to fire, with highly contrasting fire regimes often having little or no detectable impact on species richness or abundances. This suggests that most faunal taxa do not require fire management intervention. Even when there is substantial direct mortality, the most important effects of fire are typically indirect through modification of habitat, both in the short term after individual fires, and in the long term through different fire regimes. Management should therefore focus on fire-mediated habitat change rather than on the direct effects of fire itself. Fire intensity is not as important a factor as is widely thought; rather, fire frequency is a particularly influential component of fire regimes. There will always be winners and losers with any fire, and frequent-fire losers require management intervention due to a very low representation of longer-unburnt habitat. Finally, the maintenance of diversity requires fire at relevant spatio-temporal scales, such that the requirement is for appropriate fire management rather than widespread fire exclusion.

Despite these insights, the experiments suffer from a major weakness in that most data from them are purely phenomenological—the experiments have provided extensive information on how different faunal groups respond to fire, but not on why. A mechanistic understanding is a key feature of "robust fire science" (McGranahan & Wonkka, 2018), and the lack of it severely limits predictive capacity (Resetarits & Bernardo, 1998). In particular, there is a lack of understanding of fire effects on population processes such as demography and spatial movement (Banks et al., 2017; Nimmo et al., 2019), which is fundamental for scaling-up experimental results over space and time, and for understanding the importance of fire size. Fire size is logistically difficult to address experimentally but is clearly an important factor when there is high mortality during or soon after fire and population persistence requires recolonization from unburnt areas (Banks et al., 2017). However, the extent to which these factors hold for savanna fires remains unclear. The high resilience shown by most faunal groups at Kapalga—where fire sizes were 10–20 km², shows that, for most species, population persistence does not require recolonization from outside areas even following high-intensity fire. This is presumably because of limited fire-induced mortality and/or rapid recolonization from unburnt patches within the fire area. Modelling of mark-recapture data for small mammals at Kapalga indicated that fire frequency was more important than fire size (Griffiths et al., 2015). There is also a lack of mechanistic understanding relating to post-fire behavioural adaptation that might contribute to resilience, such as increased torpor for energy conservation and reduced predation risk (Stawski et al., 2015).

The insights from Australian experiments and their lessons for conservation management appear to be widely applicable to tropical savannas and to fire-prone grassy ecosystems more generally. The longest running and most comprehensive savanna fire experiment in terms of burning treatments has been conducted in Kruger National Park, where 12 experimental fire regimes have been maintained in replicated plots across multiple locations since 1954 (Biggs et al., 2003). The experimental fire regimes include combinations of fire frequency and season, as well as total fire exclusion. Ant assemblages show remarkably little differentiation among experimental regimes even after more than 50 years (Parr et al., 2004). This is especially the case at the most-arid location (Mopane, 450 mm mean annual rainfall), where there was no statistically significant differentiation whatsoever in assemblage composition between the seven burning treatments studied, including fire exclusion. There was some differentiation at higher-rainfall locations, likely due to the greater changes in vegetation structure caused by fire in areas of higher productivity; however, the differentiation was primarily between unburnt sites and all others, rather than among different fire

1. Generally high resilience

Most species secure under all but most extreme regimes

2. Indirect effects most important

Focus on changes in habitat suitability

3. Fire frequency rather than intensity particularly important

Increase area of relatively long-unburnt habitat

4. Always winners and losers

Focus on outcomes at landscape scale

5. Fire needed to maintain diversity

Fire management, not exclusion

FIGURE 6 Summary of the implications for fire management from five key insights into responses of fauna to fire in Australian tropical savannas as revealed by replicated field experiments
frequencies and seasons (Parr et al., 2004). Similarly, a study of termites at the Kruger fire plots showed little effects of fire season and intensity (Davies et al., 2012). A study of bird responses to a large fire elsewhere in Kruger found that species richness and composition did not vary with fire intensity, and it was concluded that bird communities are likely to be robust to all but the most extreme fire regimes (Mills, 2004). The Brazilian savanna fauna is likewise highly resilient to fire (Durigan et al., 2020).

A high degree of resilience is also shown by fauna in other fire-prone grassy ecosystems, such as invertebrate assemblages in buttongrass moorlands of Tasmania (Driessen & Kilpatrick, 2017). This is also the case for many faunal taxa in highly fire-prone shrubby ecosystems. For example, fire often appears to have little long-term effect on ordinal-level abundance of arthropods in temperate woodlands and open forests of southern Australia (Abbott et al., 1984; Friend & Williams, 1996; Neumann & Tolhurst, 1991). Different fire-interval sequences over 30 years had minimal effects on ants, beetles, frogs, reptiles and mammals in open forest and shrubland of south-western Western Australia (Wittkuhn et al., 2011). A study of birds in this region found no effect of heterogeneity in post-fire age on species richness at either local or landscape scales (Wills et al., 2020). An analysis of fire frequency and post-fire age in Greek pine forests showed no effects on the richness of flower-visiting bees, beetles, flies, sawflies and wasps (Lazarina, 2017). In mallee woodlands of south-eastern Australia, patterns of fire age-classes had little influence on the frequency of occurrence of termite species (Avitabile et al., 2015) or on the diversity at any spatial scale of reptile assemblages (Farnsworth et al., 2014). Lizard diversity was not affected by fire in arid grasslands and shrublands of central Australia (Pastro et al., 2013). A large wildfire had no impact on species composition or local richness of amphibians in a Mediterranean environment (Muñoz et al., 2019). Fire treatments in different seasons had little impact on bird communities in Californian chaparral (Newman et al., 2018), common bird species were resilient to prescribed burning in ponderosa pine forests of the south-western United States (Dickson et al., 2009), and prescribed burning did not affect bird species richness in pine stands of northern Portugal (Moreira et al., 2003). Prescribed burning had little effect on species richness of small mammals in scrubland of southern Spain (Moreno & Rouco, 2013).

Fire has a greater impact on fauna in forested ecosystems that burn less frequently, at decadal or century scales. In these systems, fire can also cause surprisingly limited direct mortality (Banks et al., 2011; Nowack et al., 2016; Stawski et al., 2015). However, severe fire causes major habitat transformation, initiating a long-term series of habitat changes that successively favour different animal species (Fox, 1990; Gosper et al., 2019; Lindenmayer et al., 2016, 2019). A feature of such forests is the occurrence of old-growth specialists that are often under conservation threat because of habitat fragmentation and inappropriate burning or logging (Chalmandrier et al., 2013; Dixon et al., 2018, 2019; Lindenmayer et al., 2017; Taylor et al., 2012). However, in some cases inappropriate fire exclusion has placed early-successional species most at risk (Reilly et al., 2018).

The key insights from fire experiments and their lessons for conservation management of fauna in Australian savannas have wide applicability to flammable biomes, but three in particular appear to be universal. First, the primary effects of fire are indirect through habitat change, which is caused by both individual fires and by different fire regimes. This has been shown for many biomes for a wide range of animal taxa, including ants (Andersen, 2019), reptiles (Costa et al., 2020; Dixon et al., 2018), birds (Gosper et al., 2019; Woinarski & Recher, 1997) and small mammals (Griffiths & Brook, 2014). In particular, fire has a pervasive effect on fauna through its impact on habitat openness (Andersen, 2019). Longer-unburnt habitat is often most at risk due to anthropogenic increases in fire frequency, often in association with land clearing or logging (Andersen et al., 2005; Dixon et al., 2018, 2019; Lindenmayer et al., 2017; Woinarski & Recher, 1997). Second, different faunal taxa show a wide range of responses to fire such that there will always be winners and losers with any individual fire or fire regime. Such winner/loser trade-offs mean that fire management needs to be considered at the landscape scale rather than attempting to maximize diversity in all places (Reilly et al., 2018). Finally, as to be expected with evolutionary histories in association with it, fire at some spatio-temporal scale is required for the maintenance of faunal diversity in flammable ecosystems. In grassy and shrubby systems where fire is highly frequent, fire-promoted diversity occurs at the individual site level. In forests that experience fire less frequently, it is expressed at the landscape scale through variation in post-fire ages (Burrows, 2008; Lindenmayer et al., 2016; Reilly et al., 2018). These insights can help guide fire management in flammable biomes throughout the world.

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**BIOSKETCH**

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