An experimental test of whether pyrodiversity promotes mammal diversity in a northern Australian savanna

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Abstract:

1. The increasing awareness that a fire regime that promotes biodiversity in one system can threaten biodiversity in another has resulted in a shift away from fire management based on vague notions of maximising pyrodiversity, towards determining the optimal fire regime based on the demonstrated requirements of target species.
2. Here, we utilised a long-running, replicated fire experiment on Melville Island, the largest island off the northern Australian coast, to test the importance of pyrodiversity for native mammals in a northern Australian savanna landscape. We first developed statistical models to determine how native mammal abundance has responded to nine years of experimentally-manipulated fire frequency. Next, given each species' modelled response to fire frequency, we identified the level of pyrodiversity and optimal mix of fire frequencies that would be expected to maximise mammal diversity and abundance, and minimise extinction risk, This was done for both the entire mammal assemblage and for the mammal species currently declining on Melville Island.
3. Fire frequency was a significant predictor of abundance of the northern brown bandicoot (*Isoodon macrourus*), black-footed tree-rat (*Mesembriomys gouldii*), brush-tailed rabbit-rat (*Conilurus penicillatus*), grassland melomys (*Melomys burtoni*), pale field-rat (*Rattus tunneyi*), and mice/dunnarts but not of the common brushtail possum (*Trichosurus vulpecula*).
4. The geometric mean abundance (GMA) of the entire mammal assemblage was positively associated with pyrodiversity, but peaked at an intermediate value. Hence, maximising pyrodiversity would reduce native mammal assemblage GMA below its potential maximum. The fire history for an area that maximised the entire native mammal assemblage GMA consisted of 57% long-unburnt, 43% triennially burnt and <1% annually burnt. Pyrodiversity did not reduce the extinction risk, nor increase the GMA of declining mammals above that predicted in areas entirely annually or triennially burnt.
5. *Synthesis and applications:* We demonstrate a useful approach with which to develop fire management strategies based on the demonstrated requirements of target species. By comparing

the optimal fire regime identified for the conservation of threatened species and that identified for the entire mammal assemblage, we demonstrate the flexibility of this approach to tailor fire management to address specific management priorities in other fire-prone environments.

Keywords: extinction risk, fire experiment, Melville Island, northern Australia, pyrodiversity, tropical savanna, native mammal diversity.

Introduction:

Fire is a global ecosystem driver (Bond et al., 2005, Bowman et al., 2009, Kelly and Brotons, 2017), with profound effects on the evolution of biological communities and ecological processes (Gill et al., 1981, Whelan, 1995, Bond and Van Wilgen, 1996). As a result, fire plays an integral part in the functioning of some biomes (Bowman et al., 2011). The clearing of vegetation, livestock grazing, introduction of exotic plants and animals, alteration of ignition sources and patterns, and the active suppression of fires associated with the expansion of human society has disrupted fire regimes on a global scale, causing substantial ecosystem change and biodiversity loss (Bowman et al., 2011). Worryingly, the disruption of fire regimes is likely to become exacerbated by global climate change (Bowman et al., 2009). Fire also represents one of the few tools for conservation management at the landscape scale. In many fire-prone environments, fire management follows the ‘patch mosaic burning’ paradigm, which attempts to establish and maintain a fine-scale, heterogeneous mosaic of varying fire histories (Parr and Andersen, 2006), under the assumption that “pyrodiversity begets biodiversity” (Martin and Sapsis, 1992). However, this approach lacks a solid empirical or theoretical basis, and has also been criticised for lacking clear operational guidelines that specify which aspects of pyrodiversity should be maximised (Parr and Andersen, 2006, Taylor et al., 2012). This uncertainty has recently stimulated critical analyses of the relationship between pyrodiversity and biodiversity (Parr and Andersen, 2006, Taylor et al., 2012, Kelly et al., 2016). For example, while Tingley et al. (2016) demonstrated that pyrodiversity promotes bird diversity in Californian conifer forests, Taylor et al. (2012) found no such pattern in a semi-arid region of south-eastern Australia, and suggested that burning for fire-mediated heterogeneity could actually threaten the avian fauna in this system. The validity of patch-mosaic burning has also been questioned for reptiles (Nimmo et al., 2013) and mammals (Kelly et al., 2012) in semi-arid Australia. These inconsistent results highlight the context-specificity of pyrodiversity requirements, and the risks associated with the blanket application of a management paradigm focused on maximising pyrodiversity. Hence, fire management for biodiversity conservation must be directly underpinned by the demonstrated fire requirements of the target species (Andersen et al., 2014, Swan et al., 2015, Kelly et al., 2016).

Fire has shaped Australian landscapes for millions of years (Kershaw et al., 2002, Crisp et al., 2011), and has been managed by humans for up to 50,000 years of Aboriginal history. The breakdown of traditional burning practices has been implicated in the decline of a range of taxa across northern Australia, including the native cypress pine (*Callitris intratropica*) (Bowman and Panton, 1993), granivorous birds (Franklin, 1999), and more recently the catastrophic collapse of native mammal populations (Firth et al., 2010, Woinarski et al., 2011, Ziembicki et al., 2014). In an attempt to mitigate these declines, prescribed management fires are widely applied across northern Australian savannas (Andersen et al., 2005). Creating a fine-scale fire mosaic and increasing the amount of long-unburnt vegetation are often key objectives of fire management for biodiversity conservation in northern Australia (Woinarski and Winderlich, 2014). However, with limited and sometimes conflicting empirical data relating Australian biota to specific fire patterns, this approach may be ineffective, and even potentially threaten important biodiversity values.

Here, we utilise a long-running (9-year) fire experiment on Melville Island (Richards et al., 2012) to evaluate the relationship between pyrodiversity and native mammal diversity in a northern Australian savanna. We first examine the relationship between experimental fire treatments and mammal diversity and abundance. We then use specific estimates of species abundances in each fire treatment to investigate the relationship between simulated pyrodiversity and mammal diversity and extinction risk. In doing so, we identify the specific proportions of different fire treatments within a simulated landscape that maximises native mammal diversity and minimises extinction risk.

Materials and methods:

Study site:

Melville Island is Australia's second largest island (5788 km^2), and the larger of the two main Tiwi Islands, located 20 km off the coast of Australia's Northern Territory (Fig. 1). The islands experience a tropical monsoonal climate, with a wet season (November–April) in which over 90% of the annual rainfall occurs (Australian Bureau of Meteorology, 2015). There is a substantial annual rainfall gradient on Melville Island, from 1400 mm in the east, to 2000 mm in the northwest. The major vegetation types are savanna woodlands and open forests dominated by *Eucalyptus miniata, E. tetrodonta* and *Corymbia nesophila*, with a predominantly grassy understorey. Shrub density is highly variable, and studies on the mainland have shown that it is negatively affected by frequent, high-intensity fires (Russell-Smith et al., 2003, Woinarski et al., 2004).

Fire mapping of the Tiwi Islands from 2000–2013 has shown that an average of 54% of the savannas were burnt each year, with 65% of this area burning in the late dry season when fire intensity tends to be highest (Richards et al., 2015).

Despite no evidence of recent changes in fire intensity or frequency, feral animal densities or invasive weeds on the Tiwi Islands, native mammal populations appear to have declined significantly over the past 15 years, especially the brush-tailed rabbit-rat (*Conilurus penicillatus*), black-footed tree-rat (*Mesembriomys gouldii*) and northern brown bandicoot (*Isoodon macrourus*) (Davies et al., 2016, H. Davies, *unpublished data*).

Data collection:

In 2008, 18 experimental fire plots (each 50–100 ha) were established at four locations across the western half of Melville Island as part of the Tiwi Carbon Study (see Richards et al. 2012 for details) (Fig. 1). The experiment tests three contrasting fire regimes: (1) annual burning in the early dry season; (2) triennial burning in the early dry season; and (3) no burning (henceforth referred to as long-unburnt).

Each treatment is replicated six times, with one replicate of each treatment at Imalu, Taracumbi, and Pickertaramoor, and three replicates of each treatment at Shark Bay (Fig. 1). Prior to the experiment, all plots were burnt at intervals of 1–3 years (Richards et al., 2012). The mean Byram fire-line intensities of the annual and triennial experimental burns were 650 and 1850 kW m^{-1} respectively (A. Richards, *unpublished data*).

In December 2013, four vertically downward-facing motion-sensor camera traps were established in each of the 18 fire plots (72 cameras in total) to monitor native mammals. These cameras were left operating continuously for two years, being removed during this period only when plots were burnt, with cameras re-deployed as soon as possible after burning. All cameras were Reconyx^{TM} PC800 Hyperfire Professional cameras, with infra-red flash (Reconyx Inc., Holmen, USA). Cameras were deactivated between 8:00 and 18:00 daily, and were programmed to take ten image bursts per trigger. The sensitivity of each camera was set to high, with cameras re-arming five minutes after being triggered.

Data analysis:

To investigate changes in native mammal populations in response to the experimental manipulation of fire frequency, we first derived response variables from camera images to characterise native mammal diversity and abundance in each of the 18 fire plots. Diversity was expressed as the mean number of species recorded per 100 trap nights, and abundance of each native mammal species was calculated as the proportion of total camera trap-nights the species was recorded. There is a positive relationship between the number of individuals of a species recorded at a site in live-traps and the proportion of nights the species was recorded on cameras traps on Melville Island (See Fig. S1 in supplementary material). We calculated this abundance metric for: the northern brown bandicoot, black-footed tree-rat, common brushtail possum (*Trichosurus vulpecula*), brush-tailed rabbit-rat, grassland melomys (*Melomys burtoni*) and pale field-rat (*Rattus tunneyi*). Species smaller than 50 g (native mice [*Pseudomys* spp.] and dunnarts [*Sminthopsis* spp.]) could not be reliably identified, and were combined as a single group referred to as 'mice/dunnarts'. We note that this group could comprise of up to four individual species: delicate mouse (*Pseudomys delicatulus*), western-chestnut mouse (*Pseudomys nanus*), red-cheeked dunnart (*Sminthopsis virginiae*), Butler's dunnart (*Sminthopsis butleri*). The northern brush-tailed phascogale (*Phascogale pirata*) and northern sugar glider (*Petaurus breviceps*) were also recorded, but too infrequently for meaningful analysis of abundance.

We used generalised linear models (GLMs) to investigate how native mammal diversity and abundance, as well as the abundance of each species, was related to fire frequency. To do this we compared four models: a null model, two separate models containing the single main effects of 'fire treatment' and 'site', and a model containing both 'fire treatment' and 'site'. While time since fire inevitably fluctuated over the period of data collection, we consider our focus on fire frequency as warranted as it characterises a fire regime, not a single fire event. We included the 'site' variable to account for spatial autocorrelation. Given the small sample size (n=18), site-specific variation in fire response could not be assessed. Model selection was based on a robust form of Akaike's Information Criterion, AIC_c, an index that favours both model fit and model simplicity (Burnham and Anderson, 2002). Models with lower values of AIC_c are considered to have greater support relative to other models in the candidate set.

Using the respective best model based on AIC_c, we predicted the abundance of each species in each of the three fire treatments. Obtaining species-specific estimates of abundance in each fire treatment allowed us to explore the relationship between mammal diversity and simulated pyrodiversity. To do this, we generated 5000 hypothetical, spatially-dimensionless sites with varying levels of pyrodiversity. We randomly varied the proportion of each fire treatment (annually burnt, triennially burnt and long-unburnt) at each of these sites, such that the sum of the proportions of the three fire treatments was equal to 1. Following studies of birds, mammals and reptiles in semi-arid southern Australia (Taylor et al., 2012, Kelly et al., 2012, Nimmo et al., 2013, Farnsworth et al., 2014), we calculated pyrodiversity using the Shannon's diversity index, scaled such that the maximum (i.e. a site with equal proportions of annually burnt, triennially burnt and long-unburnt vegetation) was equal to 1. As used here, Shannon's diversity (pyrodiversity) is maximised when fire treatments are equally represented at the simulated site, and this would hypothetically lead to a maximisation of overall biodiversity values only if each treatment had equal biodiversity value and we acknowledge here that this is a much simplified way in which to quantify pyrodiversity. We used the species-specific estimates of abundance (derived from GLMs) in each fire treatment to obtain an abundance estimate for each species at each simulated site and then calculated the geometric mean abundance (GMA) for each site as equation 1:

$$\text{GMA} = \sqrt[n]{Pj_1 \times Pj_2 \times Pj_3 \times \dots Pj_n}, \qquad \text{eqn 1}$$

where *n* is the number of species, and *Pj* is the predicted abundance for each species given the simulated fire history. GMA is an appropriate biodiversity index, having heuristic properties that capture a range of desirable criteria with which to assess biodiversity (Buckland et al., 2011, Van Strien et al., 2012, McCarthy et al., 2014). We scaled predicted GMA so the maximum value was equal to 1, and related it to each site's pyrodiversity index.

A useful property of GMA is that it tends to be correlated with the proportion of species within an area that are likely to become extinct (McCarthy et al., 2014). Following Giljohann et al. (2015), we utilised this relationship and quantified the change in extinction risk (ER) resulting from different levels of pyrodiversity at each site as equation 2:

$$\text{ER} = 1 - \frac{\left(\frac{1}{\ln{(GMA)}}\right)}{\left(\frac{1}{\ln{(GMA_{max})}}\right)} \qquad \text{eqn 2}$$

We then plotted the values of both GMA and ER against each site's pyrodiversity index. This was done separately for both the entire assemblage of mammals (seven species) and then for only the three species in significant decline on Melville Island (northern brown bandicoot, black-footed tree-rat, brush-tailed rabbit-rat) (H. Davies, *unpublished data*). By doing so, we identified the specific proportions of the different fire treatments that maximised native mammal diversity and minimised the extinction risk.

We conducted a sensitivity analysis to investigate how the identified optimal fire regime was influenced by the variability surrounding each species' abundance estimate. This was done by randomly selecting values from the distribution surrounding each species' predicted abundance and identifying the level of pyrodiversity that maximised the GMA of the entire native mammal assemblage. This was replicated 10,000 times.

Results:

The best model of diversity contained the term ‘fire treatment’, but this model was not significantly better (<2 AIC$_c$ units) than the similar model without this term (Table 1). Therefore, fire treatment had no clear effect on native mammal diversity. However, species composition clearly varied between fire treatments. For all seven species, the best model included the term ‘fire treatment’, and for all except the brushtail possum, this model was significantly better (≥2 AIC$_c$ units) than a similar model without the term ‘fire treatment’ (Table 1)(for a comparison between the effect size of fire treatment and site on the predicted abundance of each species, see Fig. S2 in supplementary material).

Species varied in their preferred fire treatment: the abundances of the black-footed tree-rat, brush-tailed rabbit-rat and ‘mice/dunnarts’ were highest in annually burnt plots; the abundance of the northern brown bandicoot and pale field-rat was highest in triennially burnt plots; and the abundance of the grassland melomys was highest in long-unburnt plots (Fig. 2). Importantly, due to the logistical constraints of conducting a highly-replicated fire experiment, some of these estimates were uncertain.

The geometric mean abundance (GMA) of the entire mammal assemblage was positively associated with pyrodiversity, but peaked at intermediate pyrodiversity (63% of maximum possible pyrodiversity) (Fig. 3a). The fire history of an area that maximised native mammal GMA (i.e. GMA of 100%) consisted of 57% long-unburnt, 43% triennially burnt and <1% annually burnt vegetation. GMA was 94% for sites composed of entirely long-unburnt vegetation, 83% for entirely triennially burnt sites and 67% for entirely annually burnt sites (Fig. 3a). Mammal GMA at the highest possible simulated pyrodiversity (i.e. equal proportions annually, triennially and long-unburnt) was 95%. Having sites consisting of entirely long-unburnt, triennially burnt or annually burnt vegetation (i.e. those with the lowest possible level of pyrodiversity) increased the average extinction risk by 1.5, 4.0 and 8.0%, respectively (Fig. 3a). Maximum pyrodiversity was associated with a 1.0% increase in extinction risk.

Given species-specific fire preferences (Fig. 2), each simulated fire management scenario represented a trade-off between the abundance of species. The predicted abundance of each species resulting from different approaches to fire management are summarised in Table 2.

In marked contrast, when considering only those mammals which are currently declining on Melville Island, there was little evidence of a positive association between pyrodiversity and GMA (Fig. 3b). GMA again peaked at 63% of the maximum possible value of pyrodiversity. However, the optimal balance of fire histories was markedly different compared with that for all mammals. The optimal regime consisted of no unburnt vegetation, and near equal parts annually burnt (51%) and triennially burnt (49%) (Fig. 3b). Native mammal GMA was 99% for sites composed of entirely triennially burnt vegetation, 98% for entirely annually burnt sites and 77% for entirely long-unburnt sites (Fig. 3b). Having a site consisting of entirely triennially burnt or annually burnt vegetation would increase the average extinction risk of the three declining species by less than 1%, while a site consisting of entirely long-unburnt would increase their average extinction risk by 7% (Fig. 3b). Maximum pyrodiversity was associated with a 2.0% increase in the extinction risk for those species currently declining on Melville Island.

Multiple combinations of the three fire treatments resulted in the same level of pyrodiversity, but varied in their predicted GMA and extinction risk i.e. those sites along the dotted black lines (Fig. 3). For example, for the entire mammal assemblage, sites with a pyrodiversity value of 63% varied in their predicted GMA by 19% (representing a 4% range in extinction risk). This variability stemmed from the relative dominance of the three fire treatments at each simulated site, with an increasing proportion of annually burnt resulting in lower GMA and higher extinction risk. For those species currently declining on Melville Island, an increasing proportion of long-unburnt resulted in lower GMA and higher extinction risk.

From 10,000 replications of our sensitivity analysis, the level of pyrodiversity that corresponded to maximum native mammal GMA averaged 60%, with a 95% confidence interval of 13–98%.

Discussion:

Globally, there is a pressing need to identify fire regimes that maximise biodiversity. However, a fire regime that maximises biodiversity in one system may not necessarily do so in another (Farnsworth et al., 2014). As a result, fire management applied without context-specific empirical evidence may not only be a waste of resources but potentially threaten biodiversity (Taylor et al., 2012). In northern Australian savannas, determining the fire regime that most strongly promotes native mammal diversity is a focus of much research, as fire management is widely advocated as a key tool to prevent further population declines (Woinarski and Winderlich, 2014, Davies et al., 2017). By first demonstrating the varied response of individual mammal species to experimentally-manipulated fire frequency, we have provided the first empirical evidence for the relationship between pyrodiversity and both native mammal gamma diversity, and extinction risk, in a northern Australian savanna.

We found that predicted mammal diversity (based on geometric mean abundance; GMA) peaked at an intermediate level of pyrodiversity. Hence, maximising pyrodiversity would actually reduce native mammal GMA (albeit slightly) below its potential maximum. This is a similar result to that found for a range of bird and mammal species in the semi-arid Mallee region of south-eastern Australia (Kelly et al., 2012, Taylor et al., 2012, Farnsworth et al., 2014), which have particular requirements for long-unburnt vegetation, rather than heterogeneous fire. Our results suggest that the optimal fire regime for the entire mammal assemblage would be dominated (>50%) by long-unburnt habitat, highlighting the importance of long-unburnt vegetation to maintain mammal diversity in northern Australian savannas. We demonstrate that the predicted mammal diversity and extinction risk at a particular pyrodiversity value depends on the relative dominance of each of the three fire treatments, suggesting that the initial fire state of an area dictates the potential benefits of applying fire management. Importantly, maximum pyrodiversity was associated with a higher predicted diversity of mammals (and lower extinction risk) than the lowest pyrodiversity (i.e. those sites entirely annually, triennially or unburnt). Hence, while pyrodiversity is clearly an important element of a fire regime that can help maintain high diversity, other components of the fire regime may be particularly important e.g. the proportion of the landscape in a particular desired (or undesired) state.

Despite the majority of species exhibiting the highest abundance in the annually burnt fire plots, we identified the optimal fire regime for total native mammal diversity as an area composed of mostly long-unburnt and triennially burnt vegetation. While seemingly counter-intuitive, this reflects the mathematical properties of the index we used to quantify native mammal diversity: the geometric mean abundance (GMA). GMA is a useful measure of biodiversity and reflects both evenness and abundance; however, as it works on the multiplicative scale, GMA is most sensitive to changes in the rarest species (Buckland et al., 2011). As the pale field-rat and grassland melomys were infrequently detected compared to the other species, their habitat preferences for triennially burnt and long-unburnt vegetation were particularly influential, thus explaining the importance of these fire regimes for maintaining overall mammal assemblage diversity Investigating the relationship between pyrodiversity and the diversity and extinction risk of the entire mammal assemblage allowed us to test the relevance of the pyrodiversity hypothesis for northern Australian mammals. However, conservation efforts are often focused on a small subset of species, which are either threatened or locally declining (Drummond et al., 2010).

For any given area, there will be an optimal fire regime that maximises diversity and minimises overall biodiversity loss (Richards et al., 1999). However, even if the optimal fire regime is known, it will often not be feasible to implement due to resource constraints. As such, managers must balance alternative management strategies, each associated with different costs and benefits. As a result, management objectives targeted towards the conservation of threatened species are often prioritised over more common species. For example, the optimal fire regime identified here for the entire mammal assemblage suggested the optimal fire regime would be dominated (>50%) by long-unburnt habitat. Not only was this relationship primarily driven by the habitat requirements of two relatively stable mammal species (grassland melomys and pale field-rat) (IUCN, 1996, Woinarski et al., 2014), but it represents an impracticable target to achieve in the highly fire-prone mesic savannas of northern Australia, where on average over 50% of the landscape burns each year. As such, from a manager's perspective, this approach would be undesirable as it would involve a significant investment of resources for minimal benefit to species of conservation concern. The optimal fire regime identified for declining mammal species was markedly different, and more feasible, to that which would maximise the diversity of the entire mammal assemblage. Increasing pyrodiversity did not drastically reduce the extinction risk, nor increase the GMA of declining mammals above that predicted in areas entirely annually or triennially burnt. However, increasing pyrodiversity in suboptimal areas for these declining mammals (i.e. areas dominated by unburnt habitat) could result in a 7% reduction in extinction risk. Targeting certain areas in the landscape with an empirically based objective highlights how this method might be utilised by managers in the spatial prioritisation of prescribed fire. We acknowledge the limitation that our fire experiment lacked a spatial component. As such, these results may only be relevant for prescribed fire applied at a similar spatial scale i.e. patches 50–100 ha. Importantly, these results demonstrate that once the species-specific fire requirements in any particular area are established, this approach can be utilised to optimise fire management to achieve explicit management priorities, such as the conservation of threatened species.

Compared with invertebrates, there has been limited research relating savanna mammal diversity to pyrodiversity (Briani et al., 2004, Griffiths et al., 2015). While our results concur with those of Maravalhas and Vasconcelos (2014), who demonstrated the importance of pyrodiversity for ant diversity in Brazilian cerrado (savanna), they contrast with research of Australian and African savanna invertebrates, which exhibited a high-level of resilience to fire (Parr et al., 2004, Andersen et al., 2014). Again, while our results concur with some studies linking pyrodiversity to the diversity of faunal groups in biomes other than savanna (Tingley et al., 2016, Ponisio et al., 2016), they contrast with others (Taylor et al., 2012, Farnsworth et al., 2014). The inconsistent support for the pyrodiversity hypothesis between biomes and faunal groups emphasises the proposition of Kelly and Brotons (2017) of the need for fire management to be tailored to local conditions.

While much of the biota in fire-prone environments has evolved to be remarkably resilient to fire, fire-sensitive elements often persist within the same landscapes (Kelly and Brotons, 2017). The native mammal fauna of northern Australia is a group widely reported to be highly responsive to fire; several studies have demonstrated strong, but marked variation in the response of different mammal species to both experimentally manipulated and naturally varying fire regimes (Corbett et al., 2003, Woinarski et al., 2004, Andersen et al., 2005). For example, Woinarski et al. (2004) demonstrated significant differences in the abundance of native mammal species between an annually burnt area and an area where fire had been excluded for 23 years. They showed that the black-footed tree-rat and common brushtail possum were more abundant in the long-unburnt area, while the northern quoll (*Dasyurus hallucatus*), northern brown bandicoot and pale field-rat were more abundant in the annually burnt area. However, the large-scale, replicated Kapalga fire experiment demonstrated a preference for unburnt areas for five out of seven mammal species, including the northern quoll, fawn antechinus (*Antechinus bellus*), northern brown bandicoot, common brushtail possum and grassland melomys (Andersen et al., 2005). Given the variable requirements of northern Australian native mammal species in relation to fire, any area subject to a spatially homogeneous fire history will inevitably disadvantage some species, thus explaining the positive association between pyrodiversity and native mammal diversity demonstrated here. This is consistent with the predictions of the original pyrodiversity model proposed by Martin and Sapsis (1992). That is, when species have different preferences in relation to fire history, pyrodiversity is required to maximise the persistence of all species. However, in order to develop clear and effective fire management, and avoid the often vague operational guidelines based on pyrodiversity rhetoric, it is vital to determine the optimal level of pyrodiversity to achieve specific management objectives (Parr and Andersen, 2006).

While we have suggested fire regimes that may support biodiversity on Melville Island, for a number of reasons this may not necessarily be the case for other areas of northern Australia's savannas. Fire is a stochastic, spatially complex form of disturbance and the fire experiment reported here manipulated only one aspect of the fire regime: fire frequency. As a result we were unable to account for many aspects of the fire regime including the intensity and spatial patterning of fires. As such, our results are based on a much simplified application of fire, and future research should focus on incorporating other aspects of the fire regime into a similar analysis. It is also important to note that our burning treatments did not include high-intensity fires that typically occur late in the dry-season. For example, the intensity of experimental annual fires on Melville Island averaged just 650 kW m^{-1}. By comparison, at Kapalga in Kakadu National Park, the Byram fire-line intensity of experimental annual early dry season fires averaged 2100 kW m^{-1} (Williams et al., 1998). High-intensity fires have been shown to have both direct (Firth et al., 2010) and indirect negative impacts (Legge et al., 2008, Leahy et al., 2016) on the survival of multiple species in northern Australian savannas. While Andersen et al. (2005) suggested that fires of very low-intensity (occurring in April/early May) could benefit ground-active native mammals, they pointed out that early dry season management fires are typically of higher intensity. As our results are based on small, low-intensity experimental fires, the suggested optimal fire regime may only be applicable in areas where such low-intensity fire regimes are achievable.

The effect of fire regimes on biodiversity can act synergistically with other threatening processes (Driscoll et al., 2010, Andersen et al., 2012). In northern Australian savannas, these include the density of exotic mega-herbivores (Legge et al., 2011), invasive grasses (Rossiter et al., 2003), as well as the density of mammalian predators including the dingo (*Canis dingo*) and feral cat (*Felis catus*) (Leahy et al., 2016). As these other threatening processes vary across the landscape, so too will the optimal fire regime for biodiversity conservation. For example, in areas with high predator densities, it may be that species that would otherwise inhabit more open areas, are forced to shelter in long-unburnt vegetation due to its mitigating effect on predation pressure (McGregor et al., 2015, McGregor et al., 2016, Leahy et al., 2016). The presence and density of the threatened native species for which management is commonly aimed at conserving, also vary across the landscape. Here we have identified the optimal fire regime for the ground-active native mammals of Melville Island. Again, given that a different suite of mammal species occurs in the savannas of mainland northern Australia, the optimal fire management for species conservation will likely differ to some extent. While our study investigated how different fire patterns influence native mammal diversity, future work should also incorporate the fire response of other non-mammal species, especially those thought to be declining and sensitive to fire regimes (e.g. partridge pigeon, *Geophaps smithii*; (Fraser et al., 2003)). Our results were sensitive to the variability in species' specific abundance estimates (due to both the limited replication of our fire experiment and the sensitivity of GMA to rare species). As such, future work utilising this method should include a sensitivity analysis. Furthermore, the approach outlined in this manuscript may be strengthened by the incorporation of diversity metrics other than Shannon's diversity index and GMA.

Specific targets that go beyond pyrodiversity rhetoric are necessary for fire management for biodiversity conservation to be operationally effective (Andersen et al., 2005). However, these targets are highly context specific and depend on a range of factors including management priorities, the fire requirements of the species present in a particular area, as well as the presence and severity of other threatening processes. The realisation that a fire regime that promotes biodiversity in one system is often not applicable to another, has resulted in a more concerted effort to develop fire management that is supported by ecological theory, but tailored to local conditions (Farnsworth et al., 2014, Kelly and Brotons, 2017). By utilising a long-running fire experiment we have demonstrated not only the utility of first determining species-specific responses to fire with which to develop fire management, but the flexibility that this approach affords to develop and tailor fire management based on specific and changing management priorities in other fire-prone environments, i.e. conserving threatened species vs. conserving an entire mammal assemblage. While the feasibility of implementing replicated fire experiments is low, conducting correlative pilot studies that are specifically designed to relate biodiversity to fire regimes will greatly improve our ability to develop effective fire management strategies.

Authors' contributions:

HD, MM, AA, BM, W. Rioli, JP, W. Roberts, CK, VK and KBM conceived the ideas and designed the methodology; HD, WR, JP, WR, CK, VK and KBM collected the data; HD and BM analysed the data; HD, MM, AA and BM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements:

We would first like to thank the Tiwi Land Council and the Tiwi traditional owners for their ongoing support of biodiversity research on their land. We also acknowledge the amazing field assistance provided by Michael Davies, Chris Davies, John Davies, Casey Visintin, Karl Sobott, Fin Roberts, John van Osta, Phoebe Burns, Hayley Geyle and Tiwi College staff and students. This work was supported by the Australian Research Council (DE130100434), Hermon Slade Foundation, the Tiwi Land Council, CSIRO, the National Environmental Science Programme's Threatened Species Recovery Hub, Paddy Pallin Foundation and Holsworth Wildlife Research Endowment. We wish to thank Anna Richards and Jon Schatz for their help in the field, and for supplying the data on fire intensities.

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Figures and Tables:

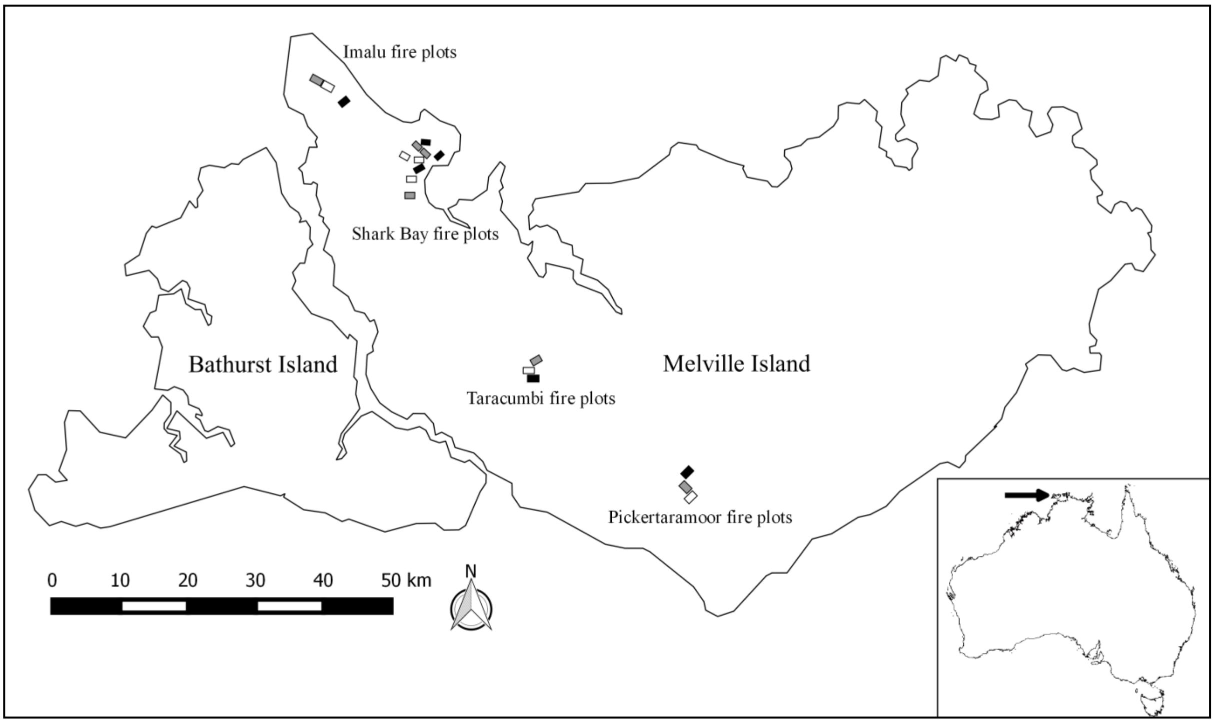
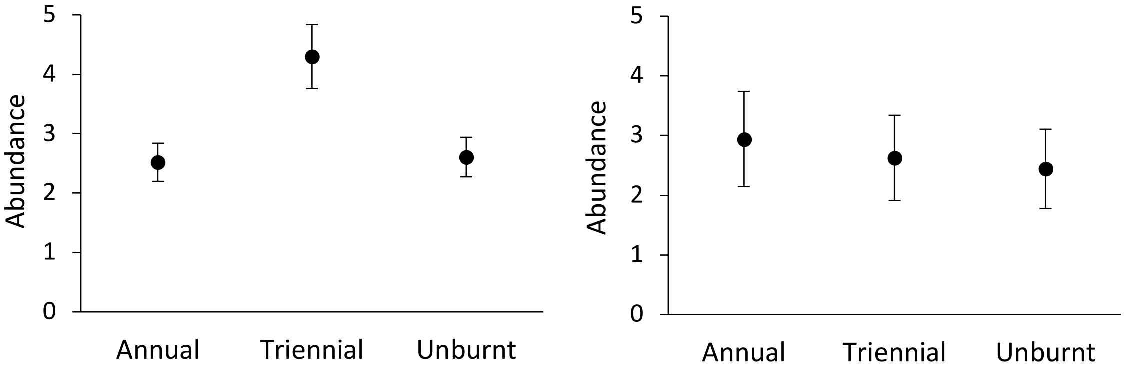


Figure 1: Locations of the 18 experimental fire plots on Melville Island, northern Australia. The black, grey and white rectangles represent the six annually burnt, triennially burnt and long-unburnt plots, respectively. The location of Melville Island relative to mainland Australia is shown in the inset.

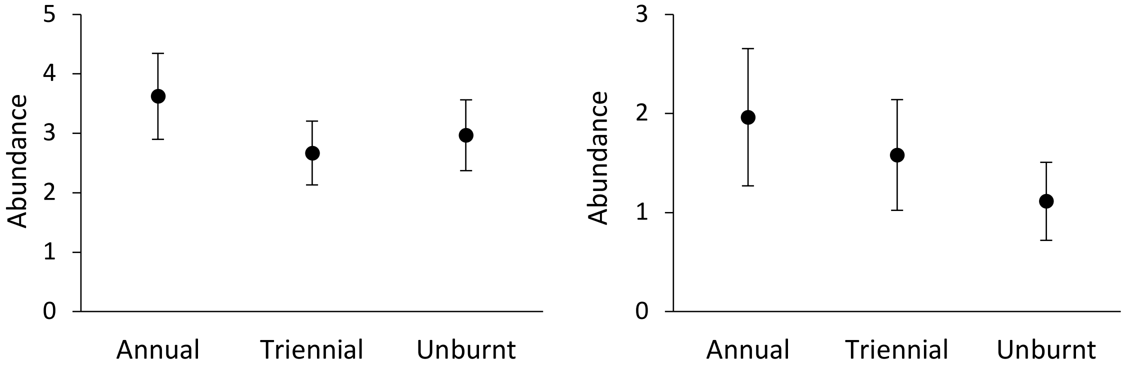
Northern brown bandicoot:

Common brushtail possum:



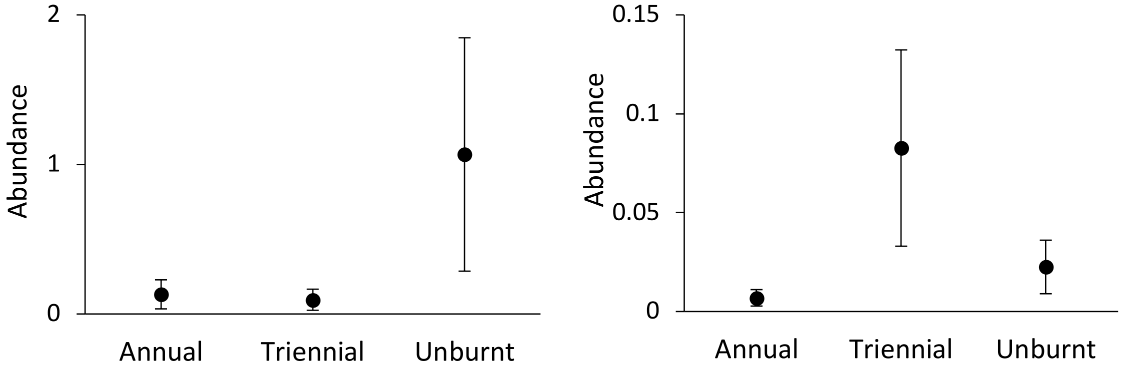
Black-footed tree-rat:

Brush-tailed rabbit-rat:



Grassland melomys:

Pale field-rat:



Mice/dunnarts:

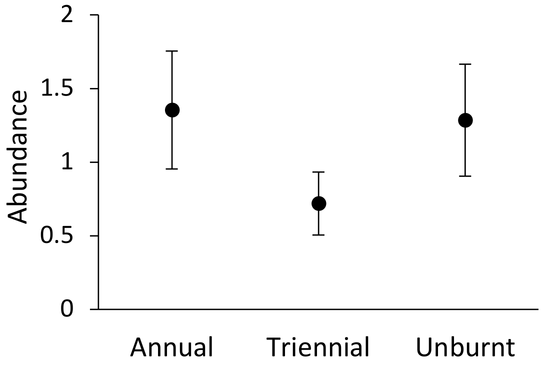


Figure 2: The predicted index of abundance (±SE) of native mammals for each experimental fire treatment.

a)

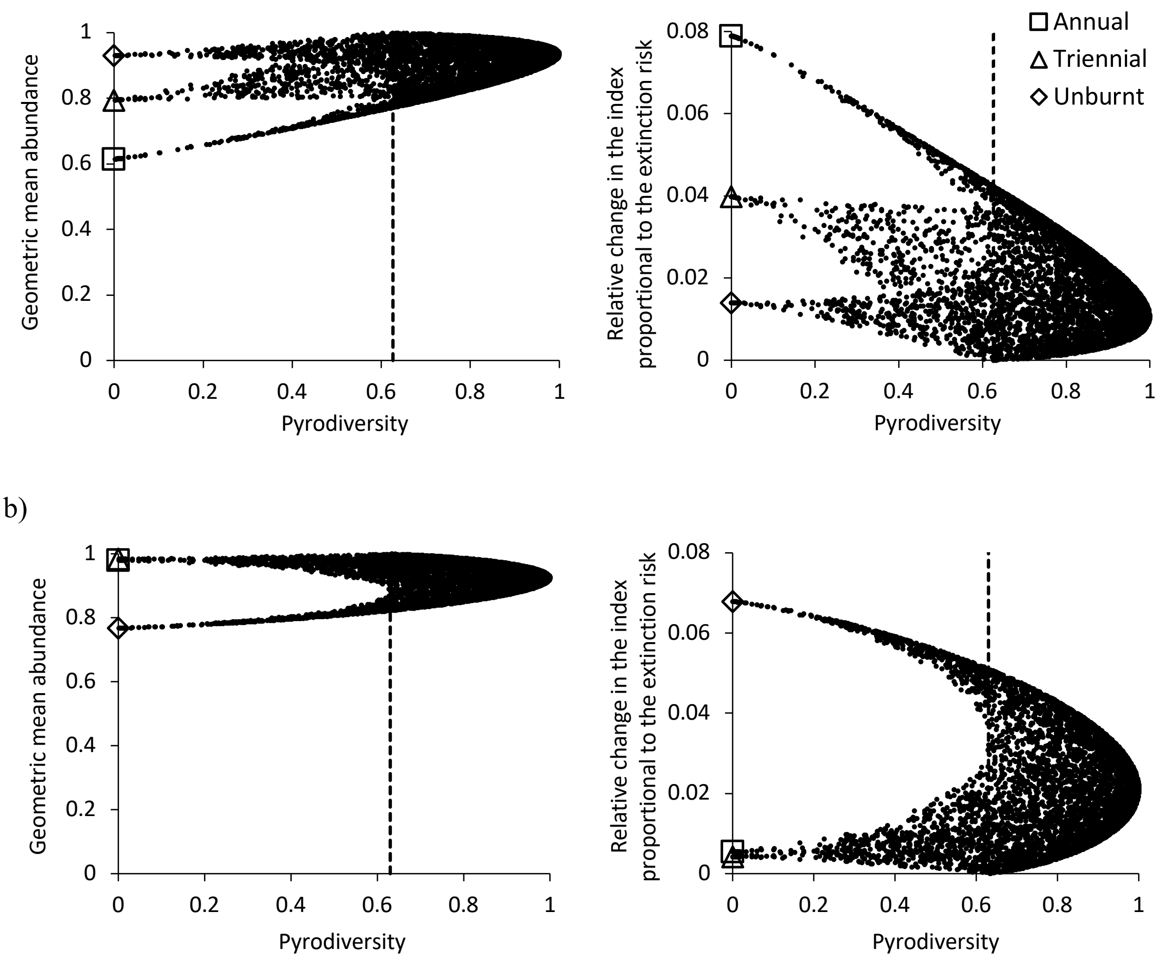


Figure 3: The relationship between pyrodiversity and the geometric mean abundance (GMA) and the relative change in the index proportional to the extinction risk for (a) all ground-active native mammal species; (b) the three declining native mammal species, at 5000 simulated sites. The square, triangle and diamond intercept markers indicate the predicted mammal diversity and extinction risk at sites composed of entirely annually burnt, triennially burnt and long-unburnt vegetation, respectively. The dotted vertical lines indicate the level of pyrodiversity with the maximum predicted mammal GMA and minimum change in extinction risk.

Table 1: Summarises the model selection process for native mammal alpha diversity and species-specific abundance in 18 experimental fire plots across Melville Island, Northern Territory. K indicates the number of parameters; $\Delta \mathrm{AIC}_c$ is the difference between the model's AIC_c value and the minimum AIC_c value in the candidate set; w_i is the Akaike weight (the likelihood of the model being the best in the candidate set). Bold text indicates significant effect of fire treatment ($\Delta \mathrm{AIC}_c \leq 2$, relative to other models in the candidate set). Models with essentially no empirical support ($\Delta \mathrm{AIC}_c > 10$) are not included in the table.

Response	Model	K	ΔAICc	w_i
Native mammal alpha diversity	~ Fire treatment + Site	8	0.0	0.60
	~ Site	6	1.0	0.36
	~ Null model	1	6.0	0.03
	~ Fire treatment	3	8.5	0.01
Native mammal abundance	~ Fire treatment + Site	8	0.0	0.57
	~ Site	6	0.6	0.43
Northern brown bandicoot abundance	**~ Fire treatment + Site**	**8**	**0.0**	**1.00**
Common brushtail possum abundance	~ Fire treatment + Site	8	0.0	0.67
	~ Site	6	1.5	0.33
Black-footed tree-rat abundance	**~ Fire treatment + Site**	**8**	**0.0**	**1.00**
Brush-tailed rabbit-rat abundance	**~ Fire treatment + Site**	**8**	**0.0**	**1.00**
Grassland melomys abundance	**~ Fire treatment + Site**	**8**	**0.0**	**1.00**
Pale field-rat abundance	**~ Fire treatment + Site**	**8**	**0.0**	**0.97**
	~ Site	6	7.1	0.03
Mice/dunnart abundance	**~ Fire treatment + Site**	**8**	**0.0**	**1.00**

Table 2: Predicted abundance of each native mammal species resulting from different approaches to fire management.

Approach to fire management	Northern brown bandicoot	Common brushtail possum	Black-footed tree-rat	Brush-tailed rabbit-rat	Grassland melomys	Pale field-rat	Mice/ dunnarts
Entirely annually burnt	2.52	2.94	3.62	1.96	0.13	0.01	1.35
Entirely triennially burnt	4.30	2.63	2.67	1.58	0.10	0.08	0.72
Entirely unburnt	2.61	2.44	2.97	1.11	1.01	0.02	1.29
Maximum pyrodiversity	3.15	2.67	3.09	1.55	0.43	0.04	1.12
Maximum GMA/ Minimum extinction risk	3.33	2.52	2.84	1.31	0.65	0.05	1.04