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Prescribed burning benefits threatened mammals in northern Australia

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Abstract

Despite substantial investment in prescribed burning for biodiversity conservation there has been surprisingly little demonstration of its efficacy in achieving intended conservation aims for fauna. In the case of northern Australia’s threatened mammal fauna, most studies have reported negative responses to fire. We used satellite-derived fire scar imagery and small mammal survey data to compare fire regimes and threatened mammal abundance before and after implementation of broad-scale prescribed burning in north-western Australia. Specifically, we tested: (1) whether prescribed burning was effective in changing fire regimes; (2) whether all mammal species and functional groups responded to prescribed burning; and (3) what regional fire and environmental variables explained changes in mammal status. Low-intensity, patchy prescribed burning in the early dry season reduced the extent of high intensity late dry season wildfires. In sandstone habitats the abundance of all mammals, and the large marsupials and specialist rodent functional groups, increased concurrently with early dry season prescribed burning. All mammals and the small dasyurid functional group in woodland habitats also increased during this period. Early dry season prescribed burning extent was the strongest explanatory variable for mammal increases. Early dry season burning was also the strongest explanatory variable for woodland mammal abundance, but these mammals also had a positive association with extent of large patches of old growth vegetation (>4 years since fire). Generalist rodents did not respond to prescribed burning and two other species declined following prescribed burning in one habitat. Generalist rodents and the two declining species had a negative association with extent of late dry season fire and a positive association with old growth vegetation (interacting with patch size). These results suggest an increased application of patchy early dry season prescribed burning of up to ca. 30% of the area will benefit positive fire responder species of threatened mammals including large specialist rock/arboreal rodents and most marsupial species. For mammals such as generalist terrestrial rodents with predominantly negative associations with fire, managers should seek to increase the size and extent of old growth vegetation.

Introduction

Despite considerable investment in conservation programs, there is ongoing global, net decline in biodiversity; on average 52 vertebrate species move one International Union for the Conservation of Nature (IUCN) Red List category closer to extinction annually (Hoffmann et al. 2010). However, conservation successes do occur (Rodrigues 2006; Donald et al. 2007). Global biodiversity trends would be much worse if it were not for these successes (Hoffmann et al. 2010). It is important to report conservation successes, not only so we can continue to justify ongoing investment in biodiversity conservation, but also so that we can inform ongoing threat management programs for optimal biodiversity outcomes.

Considerable conservation investment is made in prescribed burning programs in flammable biomes throughout the world. These include prescribed burning to manage forest biodiversity (Zwolak and Foresman 2007; Fontaine and Kennedy 2012), Mediterranean heathland (Heelemann et al. 2008; Keith and Bradstock 1994), tropical heath, rainforest and conifer (Russell-Smith et al. 1998) as well as savannas (van Wilgen et al. 1990; Russell-Smith et al. 2003). Traditionally, these programs have focused on management of vegetation (Clarke 2008; Fontaine and Kennedy 2012). Until recently, relatively little attention has been given to the effects of prescribed burning programs on fauna (Clarke 2008; Driscoll et al. 2010; Fontaine and Kennedy 2012; Pastro et al. 2014). Despite considerable knowledge of individual fauna fire responses (e.g. to single fire events, fire frequency, time since fire, fire intensity; Griffiths and Brook 2014; Pastro et al. 2014) few studies have demonstrated improvements in the conservation status of fauna resulting from prescribed burning (Clarke 2008; Driscoll et al. 2010; for exceptions see Connor et al. 1995, 2002).

The threatened mammal fauna of northern Australia (i.e. mammals in the critical weight range 35 g – 5000 kg; Burbidge and McKenzie 1989) are adversely affected by high-intensity, frequent, extensive wildfires that occur in the late dry season (from August to December; Andersen et al. 2005; Legge et al. 2008; Woinarski et al. 2010; Lawes et al. 2015; Radford et al. 2015; Legge et al. 2019). The impacts of late dry season wildfire on threatened mammals have led to calls for mitigation of these fires (Russell-Smith et al. 2003; Woinarski et al. 2010; Lawes et al. 2015). While a number of prescribed burning programs report fire regime changes, including reductions in extent and frequency of late dry season fires (Murphy et al. 2015; Russell-Smith et al. 2015) only one northern Australian study has demonstrated direct benefits to threatened mammals resulting from implementation of prescribed burning, albeit only where livestock grazing has been removed (Legge et al. 2019). Indeed, current evidence suggests that threatened mammals continue to decline in many areas (Ziembicki et al. 2015; Ibbett et al. 2018; Stokeld et al. 2018) even after prescribed burning has been implemented (Murphy et al. 2015; Russell-Smith et al. 2015; Corey et al. 2020).

In this study we use the opportunity of shifting fire regimes under prescribed burning in far north-western Australia to test whether threatened mammals benefited from prescribed burning. Using fire regime metrics and mammal surveys both before and after prescribed burning, we ask: (1) how did prescribed burning change fire regimes? (2) did mammal species and functional groups respond to prescribed burning? and (3) what regional fire regime related variables were most strongly associated with mammal changes? This information will be used to address whether prescribed burning has provided a net benefit to threatened species in the region and will highlight which fire regime variables at the regional scale are most important in achieving conservation gains.

Methods

Study region

The study area was located within Wunambal Gaambera Country which includes the Uunguu Indigenous Protected area and West Australian (WA) State Government conservation reserves (WGAC, 2010) in the Northern Kimberley Bioregion of WA (Fig. 1). The study area has a tropical monsoonal climate with most rain falling between November-April. Annual rainfall ranges from 1400 mm on the Mitchell Plateau down to 1200 mm in surrounding areas. This Bioregion is the only mainland area in Australia to retain its entire pre-European mammal fauna (McKenzie et al. 2007). Vegetation is predominantly savanna woodland and open forest with eucalypt trees and tussock/hummock grasses dominating the ground layer (Beard 1979). Geologically, the study area consists of volcanic and laterite hills/plateaus and subdued but rugged sandstone (Beard 1979). Much of the variation in mammal assemblages are partitioned between volcanic/lateritic open woodland/forest habitat (from now on described as woodland) and structurally complex sandstone habitats (i.e. sandstone; Bradley et al. 1987; Radford et al. 2014).

Prescribed burning

Prescribed burning was done by two organisations: (1) a government agency, the Department of Biodiversity, Conservation and Attractions (DBCA) (and predecessors); and (2) the Indigenous land-owning organisation, the Wunambal Gaambera Aboriginal Corporation (WGAC). Prescribed burning in the early dry season, was done for cultural, infrastructure protection and conservation purposes. The main aim of this prescribed burning was to mitigate negative impacts of high intensity late dry season wildfire (WGAC 2010; Moorcroft et al. 2012; Corey and Radford 2017). Given the limited road and track network (Fig. 1), this was mostly undertaken using incendiaries dropped from aircraft. The Department of Biodiversity Conservation and Attractions and Wunambal Gaambera Aboriginal Corporation initially undertook some very localised joint prescribed burning from 2008, then extended to the full project area in 2010, and then from 2015 WGAC undertook operations independently (Vigilante et al. 2017). We refer to the period from 2000 to 2010 as pre-management (lower investment and localised prescribed fire) and 2011 to 2016 as the fire-management period (increased investment, extensive application of broad-scale prescribed fire).

Fire scar mapping and climate variables

Fire scars were obtained from the North Australia and Rangelands Fire Information (NAFI) website (http://www.firenorth.org.au/nafi3/) and clipped by the Wunambal Gaambera Native Title determination area (Fig. 1). Fire scars were attributed by year (2000–2016) and season (early dry season (EDS): January–July; late dry season (LDS): August–December). The following annual metrics were calculated for the study area: (1) proportion of total area burnt; (2) proportion burnt in the early dry season of current year (prior to mammal survey); (3) proportion of late dry season fire in the previous year; (4) number of patches of early dry season and late dry season burnt; (5) total proportion of old growth vegetation >4 years post-fire, and (6) mean size (in hectares) of old growth patches. Justification of these fire attributes is based on current fire ecology literature (Table 1). Unburnt patches were generated by erasing the clipped fire scar polygons from the focus area boundary. All spatial analyses were carried out in ArcMap 10.1 using tools in the Spatial Analyst extension and the burnt and unburnt summary statistics were calculated in MS Access. Wet season rainfall (July–June) was obtained from Bureau of Meteorology stations at Kalumburu Aboriginal community and Theda pastoral station (Fig. 1) and averaged for analyses.

Small mammal surveys

We use data from six separate survey programs with differing methodologies and trap effort (Radford et al. 2014; Corey and Radford 2017; Table S1). Survey sites were all located at the Mitchell Plateau within the Uunguu Indigenous Protected area as this is the only part of the region serviced by existing roads and tracks (Fig. 1). In all surveys, sites were stratified across major geology/vegetation types (i.e. sandstone scree/woodland, volcanic open woodland/laterite open forest) where much of the variation in mammal assemblages is partitioned (Bradley et al. 1987; Start et al. 2007; Radford et al. 2014). Sites were all chosen to be within 300 m of roads to reduce logistical difficulty of access. Within each of the geographic areas accessible by roads, representative sites were chosen for each habitat type. Due to the inaccessibility of some habitat types (e.g. sandstone scree and woodland) from the road network, some survey sites of differing geology/vegetation were a minimum of 100 m apart. However, replicate survey sites within the same habitat were always >3 km apart.

Due to differing methodologies among surveys (e.g. designs included transects (Start et al. 2007), grids (Radford 2012) and quadrats (Radford et al. 2015; Annette Cook unpublished data 2008), differing trap effort and area sampled per site), it was impossible to precisely match survey sampling between years and sites during the entire study period (Table S1). However, a minimum of 720 trap nights from at least three different survey sites per habitat type (sandstone and volcanic/lateritic) were included in each survey year (Table S1). All surveys used metal box (Elliott) traps (large: 17x17x50 cm and medium: 10x10x33 cm) baited with peanut butter and rolled oats. In addition, wire cage traps (*c*. 25x30x73 cm) were used in some surveys.

Only species small enough to be captured reliably in Elliott traps were included in analyses here due to irregular use of cages between surveys prior to 2011 (Table S1). This precludes analysis of trends for the largest mammal species trapped (>2 kg) including possums and rock wallabies (e.g. *Petrogale burbidgei* (monjon rock wallaby), *Wyulda squamicaudata* (scaly-tailed possum)). Trap success (number of individuals caught per 1000 trap nights) was used as a standard measure of abundance.

Mammal data were analysed collectively, by species (which occurred >10 % of surveys) and by previously described functional groups based on their differing life history/environmental responses (Letnic and Dickman 2010; Radford et al. 2014). Functional groups were “large marsupials” (*Dasyurus hallucatus* (northern quoll), *Isoodon auratus* (golden bandicoot), *I. macrourus* (northern brown bandicoot); size 250–2000 g), “specialist rodents” (the arboreal *Conilurus penicillatus* (brush-tailed rabbit-rat) and *Mesembriomys macrurus* (golden-backed tree-rat), and rock adapted *Zyzomys woodwardia* (Kimberley rock rat); 80–400 g), “generalist rodents” (savanna generalists including *Melomys burtoni* (grassland melomys), *Pseudomys delicatulus* (delicate mouse), *P. johnsoni* (central pebble-mound mouse), *P. nanus* (western chestnut mouse), *Rattus tunneyi* (pale field rat) and *Zyzomys argurus* (common rock rat); 5–180 g) and “small dasyurids” (*Pseudantechinus ningbing* (Ningbing false antechinus), *Sminthopsis virginiae* (red-cheeked dunnart); 5–75 g).

Statistical analyses

To test whether climate and fire attributes, as well as mammal trap success, were the same across the region before and after prescribed burning, we used Kruskal-Wallis nonparametric one-way ANOVA. Generalised linear mixed models (GLMM) (R package lme4: Bates et al. 2015) with Poisson distribution and log-link were used to model the effect of climate and fire regime attributes on mammal trap success, with site included as a random effect. Separate analyses were undertaken for mammal species and functional groups in the two savanna habitats (volcanic/lateritic and sandstone). Because a primary objective of our study was to evaluate the relationship between mammal abundance and predictor variables across habitat types, habitat type was included as an interaction term in all models. However, models did not converge due to over-parameterisation. Therefore, we conducted separate analyses for each habitat type. If models were overdispersed, a negative binomial distribution was considered, as zero-inflated models were unnecessary, i.e.10, 000 simulations of Poisson or negative binomial GLMM's predicted a similar percentage of zeros to that of the observed dataset (Zuur et al. 2012). Total burn was subsequently dropped from analyses due to collinearity with fire extent in the late dry season. To avoid over-parameterisation, we carefully justified *a priori* selection of fire and climatic variables (Table 1). We centred and standardised variables (Gelman, 2008) and allowed for non-linear trends by including all variables as cubic or quadratic polynomial terms.

To identify the best model for each species and functional group from each habitat, we took an information-theoretic model selection approach (Grueber et al. 2011) to select a top (95% confidence) model set according to AIC_c (Akaike Information Criterion corrected for small sample size), i.e. the top models with cumulative sum of Akaike weights less than 0.95 (R package MuMIn: Barton 2018). Best models included only highly influential variables derived from the top model set, i.e. with relative variable importance (the sum of Akaike weights for all models containing a given predictor variable) ≥ 0.73, equivalent to an AIC_c difference of <2 (Richards 2005). Trap effort was incorporated as an offset variable to account for total trap nights at each site and survey. All statistical analyses were run using R version 3.5.2 (R Core Team 2018).

Results

Response of fire regimes to prescribed burning

Extent of early dry season fire (prescribed burning) increased more than three-fold in the fire-managed period across the study area (Fig. 2). At the same time, late dry season fire extent halved (Fig. 2a, b). There was no change in total fire extent within the study area. Inter-annual variability in extent of late dry season and total fire extent was much greater in the pre-management period (Fig. 2a, b). Number of early dry season patches more than doubled in the fire-managed period, but there was no increase in number of late dry season burnt patches (Fig. 3). The number of old growth patches increased by 28% (Fig. 3). There was no change in annual wet season rainfall or mean maximum temperature between management periods (Fig. 3).

Response of small mammals to prescribed burning

Total mammal abundance (trap success = mean captures / 1000 trap nights) increased in both sandstone and woodland habitats from pre-managed to the fire managed period (Fig. 4). In sandstone habitats, large marsupials, specialist rodents and combined mammals increased (by 31%, 575% and 26% respectively) during the fire-managed period (Fig. 4). There was no increase in generalist rodents in sandstone habitat (Fig. 4). Insufficient data on small dasyurids in sandstone habitats was available to test for effects of management. Mammal species from sandstone habitats which increased during the fire managed period (i.e. described from now on as increasers) included the large marsupial *Dasyurus hallucatus* and the large specialist rock rodent *Zyzomys woodwardi* (Fig. S1). One species of generalist rodent *Pseudomys delicatulus* declined in abundance (i.e. was a decreaser) following prescribed burning (Fig. S1).

Within woodland habitats, total mammals and small dasyurids increased (by 59% and 36% respectively) during the prescribed burning period (Fig. 4). There was no statistically clear difference among large marsupials, specialist or generalist rodents in woodland habitats following prescribed burning, although trends suggest an increase (Fig. 4). Increaser species under prescribed burning included the specialist arboreal rodent *Conilurus penicillatus*, the large marsupial *Isoodon macrourus,* the generalist rodent *Pseudomys nanus* and the small dasyurid *Sminthopsis virginiae* (Fig. S2). *Dasyurus hallucatus* in woodland habitats was a decreaser under prescribed burning despite being an increaser under prescribed burning in sandstone habitats (Fig. S2).

Response of small mammals to fire regime variables

The most influential explanatory variable for mammal trap success in sandstone habitats was the extent of early dry season burning (Table 2) with increasing early dry season burning associated with increasing mammal abundance (Fig. 5a). Standardised coefficients for global models of the mammal groups and species are presented in Table S2 to account for model uncertainty. This factor explained 38% of variation in mammal abundance (Table 2). The most influential variables for woodland mammals were the extent of early dry season burning and the interaction between old growth and old growth patch size (Table 2).

Woodland mammal numbers increased with increasing early dry season burning extent. Mammals in woodlands also increased in numbers with increasing extent of old growth vegetation, but this effect was seen only when old growth patch size was large (>500 ha) not if mean patch size was medium or small (<300 ha; Fig. 5b). Early dry season burning extent and interacting old growth and old growth patch size explained 58% of mammal abundance in woodlands (Table 2).

Large marsupial, large specialist rodent and insectivorous dasyurid functional groups had different influential fire variables to the generalist rodents both in sandstone and woodland habitats (Table 2). The extent of early dry season burning was the most influential fire variable for large marsupials (Table 2, Fig. 6) and specialist rodents (Table 2, Fig. S3) in sandstone and woodland habitats, and for insectivorous dasyurids in woodlands only (Fig. S4; Table 2). These groups were all increasers following prescribed burning (Fig. 3). Additional influential variables for large marsupials in both habitats were late dry season fire extent and interactions between late dry season fire and patch number (Table 2). Large sandstone marsupials responded negatively to increases in late dry season fire extent when there were few patches, but patchier late dry season fire was associated with greater abundance (Fig. 6). However uniquely among the functional groups, early dry season burning extent was not an influential variable for generalist rodents (Table 2). Rather, generalist rodents in sandstone habitats had late dry season fire extent as the most influential variable (numbers decreased with increasing late dry season fire extent; Fig. 7a), while in woodlands interactions between late dry season fire extent and late dry season patch number, and old growth and patch size, were the most important explanatory variables (numbers decreased with increasing late dry season fire extent, but greatest abundance (at low late dry season extent) was associated with patchier fires; numbers increased with old growth extent when mean old growth patch size was greater than 300 ha; Table 2, Fig. 7b).

Influential explanatory variables were idiosyncratic among increaser species (Table 2, Fig. S5, S6). However, the two decreaser species (*Pseudomys delicatulus* in sandstone and *Dasyurus hallucatus* in woodland habitats) had the same influential fire variables which differed from those of increaser species. In sandstone, old growth vegetation extent was associated with greater abundance of *P. delicatulus*, but only when old growth patch size was large (> 500 ha), while smaller patch size was associated with greater abundance only if old growth extent was high (> 60%; Fig. S5b). In woodland habitats, greatest *D. hallucatus* abundance was associated with high old growth extent and large patch size (Fig. S6a). Highly influential variables for increaser species included extent of early dry season burning (*D. hallucatus* and *Zyzomys woodwardi* on sandstone, and *Conilurus penicillatus* and *Sminthopsis virginiae* on woodlands responded positively to increases in early dry season fire extent), the interaction between late dry season fire extent and number of late dry season burnt patches (*D. hallucatus* on sandstone and *Isoodon macrourus* in woodlands), the interaction in extent of early dry season burning depending on number of early dry season patches (*I. macrourus* in woodlands) and the interaction between old growth extent and old growth patch size (*Z. woodwardi* on sandstone increased with old growth extent when patch size was large; Fig. S5, S6). There was also evidence of a seasonal response to wet season rainfall for a number of the increaser species; with *Z. woodwardi* on sandstone increasing in numbers with increasing wet season rainfall (Fig. S5), while *D. hallucatus*, *Pseudomys nanus* and *C. penicillatus* had their highest abundance at intermediate wet season rainfall (Fig. S6).

Discussion

Similar to other prescribed burning programs (van Wilgen et al. 1990, 2004; Murphy et al. 2015; Russell-Smith et al. 2015; Evans and Russell-Smith 2020), prescribed burning in the north-west Kimberley increased the extent of early dry season (EDS) fire and reduced the extent of late dry season (LDS) wildfires. Total extent of annual fire was not reduced, the latter attribute possibly being pre-determined by geology and rainfall rather than by management (van Wilgen et al. 2004; Vigilante et al. 2004; Murphy et al. 2015). However, in addition to these changes in fire regimes associated with prescribed burning, this study has also reported predominantly positive changes to the threatened mammal fauna. These apparent net benefits to the mammal fauna from prescribed burning have seldom been demonstrated elsewhere, either in Australia (Penn et al. 2003; Clarke 2008; Driscoll et al. 2010; Pastro et al. 2011) or worldwide (Parr and Chown 2003; Converse et al. 2006; Fernandes et al. 2013; Pastro et al. 2014). Changes include substantial increases in mammal abundance. In addition, IUCN listed species including *Conilurus penicillatus* (Vulnerable) and *Dasyurus hallucatus* (Endangered), the Kimberley endemic rodent *Zyzomys woodwardi,* the bandicoot *Isoodon macrourus,* the generalist rodent *Pseudomys nanus* and the insectivorous dasyurid *Sminthopsis* *virginiae* all increased following the implementation of patchy EDS prescribed burning. Large marsupials as a group (in sandstone habitats) and large specialist rodents as a group (in sandstone habitats) increased during the study period. Some decreaser species in particular habitats were identified under the prescribed burning program. For instance, *D. hallucatus* declined under prescribed burning in woodland habitats, although these declines were offset by even greater increases in nearby sandstone habitats. In addition, decline occurred for the small rodent *Pseudomys delicatulus* in sandstone habitats. This may be a competitive offset of net increases among many of the larger rodents and marsupials (see above). However, this is the first study that we know of in northern Australian (or in Australia) to suggest that implementation of a prescribed burning program can lead to a net gain among the threatened critical weight range mammal fauna at a regional scale.

Despite these observations, we were unable to demonstrate causation between fire regime change and mammal fauna response due to the absence of appropriate non-managed "control" areas in the Kimberley. However, mammal improvements demonstrated here in association with prescribed burning are almost unprecedented in northern Australia in recent decades (but see Legge et al. 2019). These increases contrast starkly with declining trends or highly depauperate assemblages elsewhere across the region during the same time period (Ziembicki et al. 2015; Ibbett et al. 2018; Stokeld et al. 2018; Kutt et al. 2012; Perry et al. 2016). Declines have occurred despite prescribed burning programs being undertaken across much of northern Australia in recent decades, including some with explicit biodiversity/conservation foci (Murphy et al. 2015; Russell-Smith et al. 2015; Perry et al. 2016; Russell-Smith et al. 2017; Corey et al. 2020).

Divergent mammal outcomes between the study region and prescribed burning programs elsewhere represents a conundrum for land managers. Why would prescribed burning programs differ so much in their biodiversity outcomes despite similarities in fire regime outcomes? Part of the explanation for lesser responses outside the Norther Kimberley to changed fire regimes might be that there are more threatening processes operating and that other regions no longer have a full complement of their mammal fauna (McKenzie et al. 2007; Radford et al. 2014; Ziembicki et al. 2015). For instance, major mammal declines have already occurred in the Northern Territory in northern Australia (Woinarski et al. 2010) and putative indirect impacts of the invasion by toxic anuran *Rhinella marina* has not yet occurred in the Northern Kimberley (Radford et al. 2020). However, another possible explanatory factor for differences in mammal abundance in different savanna contexts, but not considered in this study, may be differences in cattle and large herbivore density/impacts. A number of recent studies in northern Australia have demonstrated negative impacts of both managed (Legge et al. 2011) and feral (unmanaged) cattle (Radford et al. 2015) on mammals, while another study revealed that improved fire regimes benefited generalist rodents only when cattle were also removed (Legge et al. 2019). However, there is currently no comprehensive data on the relative abundance/impacts of cattle/large herbivores across northern Australia. Culling of feral cattle was undertaken in some parts of the study region during the study period, and feral cattle impacts were assessed at survey plots during the second part of the study period (2011–2016) in conjunction with prescribed burning (Corey and Radford 2017). However, we have only one survey of feral cattle density pre-prescribed burning (i.e. in 2008) and no formal assessment of cattle vegetation site level impacts to link with mammal numbers prior to 2011. So even though feral cattle culling, and resulting improved vegetation condition, may have contributed to mammal increases during the second half of this study, we cannot quantify this contribution.

Recent work within the study area has documented cattle densities and the effect of grazing and fire on fine fuels biomass (Reid et al. 2020a), how fine fuel biomass changes across seasons (Reid et al. 2020b) and how these changes have affected macropods, but not critical weight range mammals. Future studies will need to use site-specific fire and cattle density/impact metrics to test directly for the relative importance of these factors in driving mammal dynamics. However, even in the absence of cattle impact assessment in this study, we can still test here for direct functional mammal responses to prescribed burning and fire regime attributes. Such tests are invaluable for highlighting potential benefits and specific features of prescribed burning for threatened iconic north Australian savanna species (Corey et al. 2020) even with the caveat that cattle management may also contribute to mammal improvements observed in this study (Legge et al. 2019).

The extent of EDS burning was the strongest predictor of increases among mammals during the study period, as well as for the observed habitat linked increases among the mammal groups. These results support the notion that habitat changes associated with patchy prescribed burning were directly beneficial to many mammals in the study region. Across the globe there is no generalised fire response among small and medium sized mammals (equivalent to Australia's critical weight range mammals; Burbidge and McKenzie 1989; Fontaine and Kennedy 2012; Pastro et al. 2014). Instead, both positive and negative responses have been observed internationally depending on the species (Zwolak and Foresman 2007; Fontaine and Kennedy 2012; Pastro et al. 2014; Griffiths and Brook 2014). For instance, some species are apparently early succession specialists and increase soon after fire events, while others are old growth or late succession specialists and benefit from long unburnt habitat (Fox 1982; Lunney et al. 1987; Masters 1996; Fontaine and Kennedy 2012). Relatively few Australian studies have reported positive fire ecological responses among small and medium sized mammals (Pastro et al. 2014). Instead, where fire responses have been detected, native mammal responses have generally been negative (e.g. Lunney et al. 1987; Lindenmayer et al. 2008; Letnic and Dickman 2010; Kelly et al. 2011; Pastro et al. 2014) including those from savannas (Andersen et al. 2005; Legge et al. 2008; Woinarski et al. 2010; Radford et al. 2015; Lawes et al. 2015; Ziembicki et al. 2015). Pastro et al. (2014) interpreted these generally negative responses in Australia as due to predation impacts by exotic predators in burnt areas. For instance, increased hunting activity and high cat predation related mammal mortality has been documented for feral cats (*Felis catus*) in recently burnt savannas (McGregor et al. 2014, 2016; Leahy et al. 2016). Despite this, the negative influence of cat predation after burning is apparently not universal across savannas. For instance, fire and cat predation related mammal mortality is much lower after lower intensity, patchy burns that after more extensive fires (McGregor et al. 2014).

Evidence has emerged among several savanna studies, including this one, that fire impacts and responses among mammal assemblages may be context dependent across northern Australia (Corey et al. 2020). For instance, frequent fires promoted persistence of the IUCN listed *Dasyurus hallucatus* in the context of there being long unburnt habitat nearby (Woinarski et al. 2004) but not in extensively burnt savannas (Oakwood 2002). In this study, the same species increased in sandstone habitats but decreased in open savanna woodlands under prescribed burning. Similarly, other species known to respond negatively to fire in some instances, for instance the IUCN listed tree rat *Conilurus penicillatus* (Firth et al. 2010), and also other mammals from the mainland Northern Territory (Woinarski et al. 2010; Lawes et al. 2015) showed no evidence of negative fire responses on nearby Melville Island (Davies et al. 2017, 2018) despite the presence of cats. Another study by Legge et al. (2019) showed that positive responses to prescribed burning were only realised when large introduced herbivores (e.g. cattle) were excluded by fencing. Data presented across these studies suggests that higher rainfall, higher productivity sites (Davies et al. 2017, 2018; this study), or ungrazed sites (Legge et al. 2019), presumably with higher and more continuous vegetation cover (Johnson 2006) were more likely to retain a greater suite of mammal species (McKenzie et al. 2007; Radford et al. 2014) than drier, grazed, extensively burnt or less productive savannas (Lawes et al. 2015; Radford et al. 2015). It is likely that, given the putative role of cats in northern Australian mammal declines (Frank et al. 2014; Ziembicki et al. 2015), more productive savannas such as the study region, facilitate mammal persistence by retaining greater habitat cover, which helps to mitigate cat predation (McGregor et al 2014, 2015). In such habitat, sufficient vegetation cover under patchy fire regimes may be retained for mammals to benefit from enhanced resource availability after low intensity burning.

While it is not clear from our regional scale analyses exactly what mechanisms (as per Sutherland and Dickman 1999; Williams et al. 2003) underlie positive mammal fire responses, a number of studies provide clues. *Dasyurus hallucatus* and *Isoodon auratus* can benefit from burnt areas through intake of larger vertebrate prey (Radford 2012). Conversely, small scale fires lead to increased availability of ground layer invertebrates and small vertebrates (Radford and Fairman 2015) which would benefit predatory/insectivorous mammals. Patchy EDS burning can promote increased temporal and spatial availability and diversity of fruiting and denning resources in savannas (Vigilante and Bowman 2004; Hohnen et al. 2015, 2016; Woolley et al. 2018) which could benefit arboreal species including *Mesembriomys macrurus* and *Conilurus penicillatus*. Early dry season dominated regimes can also lead to increased savanna tree canopy cover (Corey and Radford 2017), thereby increasing the total available arboreal habitat. Internationally, other studies have also revealed benefits to small mammals from fire through the provision of food resources (e.g. insects and plants seeds) and dispersal/habitat opportunities (Zwolak and Foresman 2007; Fontaine and Kennedy 2012).

Interestingly, generalist terrestrial rodents were one of the few groups which failed to benefit from EDS prescribed burning. Instead the strongest (negative) fire related predictor for this group was the regional extent of LDS wildfires. Severe, high intensity fires are known internationally to be associated with greater impacts or effects on fauna than moderate or low intensity fires (Zwolak and Foresman 2007; Fontaine and Kennedy 2012). Previous studies in northern Australia have also indicated that high intensity LDS fires have the greatest negative impacts on mammals (Andersen et al. 2005; Legge et al. 2008; Radford et al. 2015; Lawes et al. 2015). Native rodent species in southern Australia also generally exhibit negative responses to high intensity extensive wildfires (Lunney et al. 1987; Penn et al. 2003; Lindenmayer et al. 2008). Positive responses of rodents in the Northern Kimberley, and elsewhere, to long unburnt (old growth) vegetation patches (i.e. patch number and extent), is consistent with this groups' high susceptibility to cat predation (McGregor et al. 2014; 2016; Leahy et al. 2016). Despite the ability of generalist rodents (e.g. *Rattus tunneyi, Pseudomys nanus*) to respond rapidly under good conditions (Morton and Baynes 1985; Letnic and Dickman 2010; Radford et al. 2014) it is perhaps their susceptibility to elevated predation rates by cats and other predators after extensive fires (McGregor et al. 2016; Leahy et al. 2016) and local extinction/recolonization dynamics (Shaw et al. 2020), that has led to attrition and declines among some of these species in northern Australia (Braithwaite and Griffiths 1996; Corey and Radford 2017). Such high ground cover requiring species may equate to late post-fire succession specialists in terms of generalised international mammal fire responses (Zwolak and Foresman 2007; Fontaine and Kennedy 2012). This contrasts with the other mammal groups detailed in this study which responded more positively to recent patchy EDS burning and which may be considered functionally as early post-fire succession specialists.

Our results have a number of implications for land managers wanting to promote threatened mammal fauna in northern Australia. Firstly, they reinforce previous research indicating that extensive LDS burning has a predominantly negative impact on threatened mammals, and that prescribed burning should aim to reduce the extent and frequency of large LDS fires (Andersen et al. 2005; Woinarski et al. 2010; Radford et al. 2015; Lawes et al. 2015; Russell-Smith et al. 2017; Legge et al. 2019; Corey et al. 2020). Our study is the first to suggest an inherent benefit from increased extent of patchy EDS burning, in addition to its effect in reducing the extent of LDS fires. Early dry season burning operations can be recommended for the Northern

Kimberley region. While this study showed that burning up to ca. 30% of the total area in the EDS achieved positive mammal responses it is likely that this quantum will vary between habitat types. It also needs to be recognised that the patchiness of EDS fires is also a significant factor, particularly if the benefits of EDS fire are to be distributed across the landscape. The results from this study do not indicate what the upper limit of extent of EDS prescribed burning might be for benefits to continue for threatened mammals. This is because we were unable to test for effects of >30 % early burning in this study because they did not occur. Nor do we know from this study what appropriate levels of EDS burning are for mammals in other savanna regions, particularly drier areas, or areas with differing habitat profiles (e.g. extensive high productivity floodplains). The context specific nature of many fire ecology responses (e.g. negative fire impacts for mammals observed in some areas; Andersen et al. 2005; Legge et al. 2008; Woinarski et al. 2010; compared to positive/neutral impacts among mammals elsewhere; Radford 2012; Radford et al. 2015; Davies et al. 2018) suggests that any application of extensive EDS burning should be monitored for its local impacts on target biodiversity (Corey et al. 2020).

Finally, and most critically, our work highlights the importance of retention of areas of old growth vegetation for mammals, particularly in woodland habitats where this habitat feature has greater importance than it does in rocky habitats which have permanent structural features for mammals. These habitat features are particularly important for generalist rodents which appear to be late succession post-fire specialists. Future prescribed burning in savanna woodlands should have retention and/or increases in older-aged vegetation as an explicit target for savanna mammals (Andersen et al. 2012). The number and distribution of these patches also need to be considered if the benefit of these patches is to be spread across the landscape. Given that the Norther Kimberley has a very high incidence of lightning storms during the LDS (Bowman 2002), larger old growth patches are more fire prone than smaller patches introducing a trade-off between patch size and security from wildfire. In this context fire managers need to try and achieve a high degree of patchiness of EDS fires and patches of other fuel ages. One way to achieve these kinds of specific fire objectives is through setting measurable targets against which fire outcomes can be periodically assessed (e.g. Russell-Smith et al. 2017; Corey and Radford 2017).

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References

Andersen AN, Woinarski JCZ, Parr CL (2012) Savanna burning for biodiversity: fire management for fauna conservation in Australian tropical savannas. Austral Ecology 37: 658-667.

Andersen AN, Cook GD, Corbett LK, Douglas MM, Eager RW, Russell-Smith J, Setterfield SA, Williams RJ, Woinarski JCZ (2005) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. Austral Ecology 30: 155-167.

Barton K (2018) MuMIn: Multi-Model Inference. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 48.

Beard JS (1979) Vegetation mapping in Western Australia. Journal of the Royal Society of Western Australia. 62: 75-82.

Bowman DM (2002) The Australian summer monsoon: a biogeographic perspective. Australian Geographical Studies 40: 261-77.

Bradley AJ, Kemper CM, Kitchener DJ, Humphreys WF, How RA (1987) Small mammals of the Mitchell Plateau region, Kimberley, Western Australia. Wildlife Research. 14: 397-413.

Braithwaite RW, Griffiths AD (1996) The paradox of *Rattus tunneyi*: endangerment of a native pest. Wildlife Research 23: 1-21.

Burbidge AA, McKenzie NL (1989) Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biological Conservation 50: 143-98.

Clarke M (2008) Catering for the needs of fauna in fire management: science or wishful thinking. Wildlife Research 35: 385-394.

Conner RN, Shackelford CE, Schaefer RR, Saenz D, Rudolph DC (2002) Avian community response to southern pine ecosystem restoration for red-cockaded woodpeckers. Wilson Bulletin 114: 324-332.

Conner RN, Rudolph DC, Bonner LH (1995) Red-cockaded woodpecker population trends and management on Texas national forests. Journal of Field Ornithology 66: 140-151.

Converse SJ, Block WM, White GC (2006) Small mammal population and habitat responses to forest thinning and prescribed fire. Forest Ecology and Management 228: 263-73.

Corey B, Radford IJ (2017) Northern Kimberley Landscape Conservation Initiative: 2015–16 Monitoring, Evaluation, Research & Improvement Report. WA Department of Parks and Wildlife, Kununurra.

Corey B, Andersen AN, Legge S, Woinarski JCZ, Radford IJ, Perry JJ (2020) Better biodiversity accounting is needed to prevent bio-perversity and maximise co-benefits from savanna burning. Conservation Letters, 13: e12685.

Davies HF, McCarthy MA, Rioli W, Puruntatameri J, Roberts W, Kerinaiua C, Kerinauia V, Womatakimi KB, Andersen AN, Murphy BP (2018) An experimental test of whether pyrodiversity promotes mammal diversity in a northern Australian savanna. Journal of Applied Ecology 55: 2124-2134.

Davies HF, McCarthy MA, Firth RS, Woinarski JC, Gillespie GR, Andersen AN, Geyle HM, Nicholson E, Murphy BP (2017) Top-down control of species distributions: feral cats driving the regional extinction of a threatened rodent in northern Australia. Diversity and Distributions 23: 272-283.

Donald PF, Sanderson FJ, Burfield IJ, Bierman SM, Gregory RD, Waliczky Z (2007) International conservation policy delivers benefits for birds in Europe. Science 317: 810-813.

Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF, Dexter N, Fensham R, Friend G, Gill M (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. Biological Conservation 143: 1928-1939.

Evans J, Russell-Smith J (2020) Delivering effective fire management for defined biodiversity outcomes: An Arnhem Land case study. International Journal of Wildland Fire 29: 386-400.

Fernandes PM, Davies GM, Ascoli D, Fernández C, Moreira F, Rigolot E, Stoof CR, Vega JA, Molina D (2013) Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Frontiers in Ecology and the Environment 11: e4-14.

Firth RS, Brook BW, Woinarski JC, Fordham DA (2010) Decline and likely extinction of a northern Australian native rodent, the brush-tailed rabbit-rat *Conilurus penicillatus*. Biological Conservation 143: 1193-1201.

Fontaine JB, Kennedy PL (2012) Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22: 1547-1561.

Fox BJ (1982) Fire and mammalian secondary succession in an Australian coastal heath. Ecology 63: 1332-1341.

Frank AS, Johnson CN, Potts JM, Fisher A, Lawes MJ, Woinarski JC, Tuft K, Radford IJ, Gordon IJ, Collis MA, Legge S (2014) Experimental evidence that feral cats cause local extirpation of small mammals in Australia's tropical savannas. Journal of Applied Ecology 51: 1486-1493.

Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27: 2865-2873.

Griffiths AD, Brook BW (2014) Effect of fire on small mammals: a systematic review. International Journal of Wildland Fire 23: 1034-1043.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24: 699-711.

Heelemann S, Proches Ş, Rebelo AG, van Wilgen BW, Porembski S, Cowling RM (2008) Fire season effects on the recruitment of non-sprouting serotinous Proteaceae in the eastern (bimodal rainfall) fynbos biome, South Africa. Austral Ecology 33: 119-127.

Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SH, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WR (2010) The impact of conservation on the status of the world's vertebrates. Science 330: 1503-1509.

Hohnen R, Tuft K, Legge S, Walters N, Johnson L, Carver S, Radford IJ, Johnson CN (2016) The significance of topographic complexity in habitat selection and persistence of a declining marsupial in the Kimberley region of Western Australia. Australian Journal of Zoology 64: 198-216.

Hohnen R, Johnson C, Legge S, Radford IJ, Tuft K., Burridge C, Carver S (2015) Foraging ecology and habitat selection of the golden-backed tree-rat (*Mesembriomys macrurus*), in the North Kimberley, Western Australia. Austral Ecology 40: 941-952.

Ibbett M. Woinarski JCZ, Oakwood M (2018) Declines in the mammal assemblage of a rugged sandstone environment in Kakadu National Park, Northern Territory, Australia. Australian Mammalogy 40: 181-187.

Johnston C (2006) Australia's Mammal Extinctions: A 50 Thousand Year History. Cambridge University Press: Melbourne.

Keith DA, Bradstock RA (1994) Fire and competition in Australian heath: a conceptual model and field investigations. Journal of Vegetation Science 5: 347-354.

Kelly LT, Nimmo DG, Spence-Bailey LM, Haslem A, Watson SJ, Clarke MF, Bennett AF (2011) Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. Diversity and Distributions 17: 462-473.

Kutt AS, Vanderduys EP, Perry JJ, Perkins GC, Kemp JE, Bateman BL, Kanowski J, Jensen R (2012) Signals of change in tropical savanna woodland vertebrate fauna 5 years after cessation of livestock grazing. Wildlife Research 39: 386-396.

Lawes MJ, Murphy BP, Fisher A, Woinarski JC, Edwards AC, Russell-Smith J (2015) Small mammals decline with increasing fire extent in northern Australia: evidence from long-term monitoring in Kakadu National Park. International Journal of Wildland Fire 24: 712-722.

Leahy L, Legge SM, Tuft K, McGregor HW, Barmuta LA, Jones ME, Johnson CN (2016) Amplified predation after fire suppresses rodent populations in Australia’s tropical savannas. Wildlife Research 42: 705-716.

Legge S, Smith JG, James A, Tuft KD, Webb T, Woinarski JCZ (2019) Interactions among threats affect conservation management outcomes: livestock grazing removes the benefits of fire management for small mammals in Australian tropical savannas. Conservation Science and Practice 1 (7): e52.

Legge S, Kennedy MS, Lloyd RA, Murphy SA, Fisher A (2011) Rapid recovery of mammal fauna in the central Kimberley, northern Australia, following the removal of introduced herbivores. Austral Ecology 36: 791-9.

Legge S, Murphy S, Heathcote J, Flaxman E, Augusteyne J, Crossman M (2008) The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. Wildlife Research 35: 33-43.

Letnic M, Dickman CR (2010) Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. Biological Reviews 85: 501-521.

Lindenmayer DB, MacGregor C, Welsh A, Donnelly C, Crane M, Michael D, Montague-Drake R, Cunningham RB, Brown D, Fortescue M, Dexter N (2008) Contrasting mammal responses to vegetation type and fire. Wildlife Research 35: 395-408.

Lunney D, Cullis B, Eby P (1987) Effects of logging and fire on small mammals in Mumbulla State Forest, near Bega, New South Wales. Wildlife Research 14: 163-81.

Masters P (1996) The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. Wildlife Research 23: 39-47.

McGregor HW, Legge S, Jones ME, Johnson CN (2016) Extraterritorial hunting expeditions to intense fire scars by feral cats. Scientific Reports 6: 22559.

McGregor HW, Legge S, Jones ME, Johnson CN (2015) Feral cats are better killers in open habitats, revealed by animal-borne video. PLoS ONE:10: e0133915.

McGregor HW, Legge S, Jones ME, Johnson CN (2014) Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. PLoS ONE 9: e109097.

McKenzie NL, Burbidge AA, Baynes A, Brereton RN, Dickman CR, Gordon G, Gibson LA, Menkhorst PW, Robinson AC, Williams MR, Woinarski JCZ (2007) Analysis of factors implicated in the recent decline of Australia's mammal fauna. Journal of Biogeography 34: 597-611.

Moorcroft H, Ignjic E, Cowell S, Goonack C, Mangolamara S, Oobagooma J, Karadada R, Williams D, Waina N (2012) Conservation planning in a cross-cultural context: the Wunambal Gaambera Healthy Country Project in the Kimberley, Western Australia. Ecological Management & Restoration 13: 16-25.

Morton SR, Baynes A (1985) Small mammal assemblages in arid Australia: a reappraisal. Australian Mammalogy 8: 159-169.

Murphy BP, Cochrane MA, Russell-Smith J (2015) Prescribed burning protects endangered tropical heathlands of the Arnhem Plateau, northern Australia. Journal of Applied Ecology 52: 980-991.

Oakwood M (2002) Spatial and social organization of a carnivorous marsupial *Dasyurus hallucatus* (Marsupialia: Dasyuridae). Journal of Zoology 257: 237-48.

Parr CL, Chown SL (2006) Burning issues for conservation: a critique of faunal fire research in southern Africa. Austral Ecology 28: 384-95.

Pastro LA, Dickman CR, Letnic M (2014) Fire type and hemisphere determine the effects of fire on the alpha and beta diversity of vertebrates: a global meta-analysis. Global Ecology and Biogeography 23: 1146-1156.

Pastro LA, Dickman CR, Letnic M (2011) Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. Ecological Applications 21: 3238-53.

Perry J, Vanderduys EP, Kutt AS (2016) Shifting fire regimes from late to early dry-season fires to abate greenhouse emissions does not completely equate with terrestrial vertebrate biodiversity co-benefits on Cape York Peninsula, Australia. International Journal of Wildland Fire 25: 742-752.

Penn AM, Sherwin WB, Lunney D, Banks PB (2003) The effects of a low-intensity fire on small mammals and lizards in a logged, burnt forest. Wildlife Research 30: 477-86.

Radford IJ (2012) Threatened mammals become more predatory after small-scale prescribed fires in a high-rainfall rocky savanna. Austral Ecology 37: 926-935.

Radford IJ, Fairman R (2015) Fauna and vegetation responses to fire and invasion by toxic cane toads (*Rhinella marina*) in an obligate seeder-dominated tropical savanna in the Kimberley, northern Australia. Wildlife Research 42: 302-14.

Radford IJ, Woolley LA, Dickman CR, Corey B, Trembath D, Fairman R (2020) Invasive anuran-driven trophic cascades: An alternative hypothesis for recent critical weight range mammal collapses across northern Australia. Biological Invasions 22: 1967-1982.

Radford IJ, Gibson LA, Corey B, Carnes K, Fairman R (2015) Influence of fire mosaics, habitat characteristics and cattle disturbance on mammals in fire-prone savanna landscapes of the northern Kimberley. PLoS ONE 10: e0130721.

Radford IJ, Dickman CR, Start AN, Palmer C, Carnes K, Everitt C, Fairman R, Graham G, Partridge T, Thomson A (2014) Mammals of Australia's tropical savannas: a conceptual model of assemblage structure and regulatory factors in the Kimberley region. PLoS ONE 9: e92341.

Reid AM, Murphy BP, Vigilante T, Wunambal Gaambera Aboriginal Corporation, Barry LA, Bowman DMJS (2020b) Carbon isotope analysis shows introduced bovines have broader dietary range than the largest native herbivores in an Australian tropical savanna. Austral Ecology 45: 109-21.

Reid AM, Murphy BP, Vigilante T, Wunambal Gaambera Aboriginal Corporation, Bowman DMJS (2020a) Distribution and abundance of large herbivores in a northern Australian tropical savanna: a multi-scale approach. Austral Ecology doi:10.1111/aec.12860

Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86: 2805–2814.

Rodrigues AS (2006) Are global conservation efforts successful? Science 313: 1051-1052.

Russell-Smith J, Evans J, Edwards A, Simms A (2017) Assessing ecological performance thresholds in fire-prone Kakadu National Park, northern Australia. Ecosphere 8: e01856.

Russell-Smith J, Yates CP, Edwards AC, Whitehead PJ, Murphy BP, Lawes MJ (2015) Deriving multiple benefits from carbon market-based savanna fire management: an Australian example. PLoS ONE 10: e0143426.

Russell-Smith J, Yates C, Edwards A, Allan GE, Cook GD, Cooke P, Craig R, Heath B, Smith R (2003) Contemporary fire regimes of northern Australia, 1997–2001: change since Aboriginal occupancy, challenges for sustainable management. International Journal of Wildland Fire 12: 283–297.

Russell-Smith J, Ryan PG, Klessa D, Waight G, Harwood R (1998) Fire regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia. Journal of Applied Ecology 35: 829-846.

Shaw RE, James AI, Tuft K, Legge S, Cary GJ, Peakall R, Banks SC (submitted) Fire patchiness is critical for *in situ* persistence of native rodents in Australian savannas. Ecological Applications.

Start AN, Burbidge AA, McKenzie NL, Palmer C (2007) The status of mammals in the north Kimberley. Australian Mammalogy 29: 1-16.

Stokeld D, Fisher A, Gentles T, Hill B, Triggs B, Woinarski JCZ, Gillespie GR (2018) What do predator diets tell us about mammal declines in Kakadu National Park? Wildlife Research 45: 92-101.

Sutherland EF, Dickman CR (1999) Mechanisms of recovery after fire by rodents in the Australian environment: a review. Wildlife Research 26: 405-19.

Van Wilgen BW, Govender N, Biggs HC, Ntsala D, Funda XN (2004) Response of savanna fire regimes to changing fire-management policies in a large African national park. Conservation Biology 18: 1533-1540.

Van Wilgen BW, Everson CS, Trollope WSW (1990) Fire management in Southern Africa: some examples of current objectives, practices, and problems. In: Fire in the tropical biota (pp:179-215). Springer, Berlin, Heidelberg.

Vigilante T, Ondei S, Goonack C, Williams D, Young P, Bowman DM (2017) Collaborative research on the ecology and management of the ‘Wulo’ monsoon rainforest in Wunambal Gaambera Country, North Kimberley, Australia. Land 6: 68.

Vigilante T, Bowman DMJS, Fisher R, Russell-Smith J, Yates C (2004) Contemporary landscape burning patterns in the far North Kimberley region of north-west Australia: human influence and environmental determinants. Journal of Biogeography 31: 1317-1333.

Vigilante T, Bowman DMJS (2004) Effects of individual fire events on the flower production of fruit-bearing tree species, with reference to Aboriginal people's management and use, at Kalumburu, North Kimberley, Australia. Australian Journal of Botany 52: 405-416.

Williams RJ, Woinarski JC, Andersen AN (2003) Fire experiments in northern Australia: contributions to ecological understanding and biodiversity conservation in tropical savannas. International Journal of Wildland Fire 12: 391-402.

Woinarski JCZ, Armstrong M, Brennan K, Fisher A, Griffiths AD, Hill B, Milne D, Ward S, Watson M, Winderlich S, Young S (2010) Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. Wildlife Research 37: 116-126.

Woinarski JCZ, Risler J, Kean, L (2004) Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. Austral Ecology 29: 156-176.

Woolley LA, Murphy BP, Radford IJ, Westaway J, Woinarski JC (2018) Cyclones, fire, and termites: the drivers of tree hollow abundance in northern Australia’s mesic tropical savanna. Forest Ecology and Management 419: 146-59.

Wunambal Gaambera Aboriginal Corporation (2010) Wunambal Gaambera Healthy Country Plan – Looking after Wunambal Gaambera Country 2010-2020.

Zeimbicki M, Woinarski JCZ, Webb J, Vanderduys E, Tuft K, Smith J, Ritchie E, Reardon TE, Radford IJ, Preece N, Perry J, Murphy B, McGregor H, Legge S, Leahy L, Lawes MJ, Kanowski J, Johnson CN, James A, Griffiths T, Gillespie G, Frank A, Fisher A, Burbidge AA (2015) Stemming the tide: progress towards resolving the causes of decline and implementing management responses for the disappearing mammal fauna of northern Australia. Therya 6: 169-225.

Zuur AF, Saveliev AA, Ieno EN (2012) Zero inflated models and generalized linear mixed models with R. Highland Statistics Ltd, Newburgh.

Zwolak R, Foresman KR, (2007) Effects of a stand-replacing fire on small-mammal communities in montane forest. Canadian Journal of Zoology 85: 815-822.

Table 1. Description of variables considered and justification for inclusion in GLMM's assessing the effect of annual climate and fire regime attributes on mammal species and functional group abundance.

Variable	**Description**	**Justification for inclusion in GLMM**
Late dry season (LDS) fire	Proportion of region burnt in late dry season of previous year	Mammal abundance in the north Kimberley declined with spatial extent of recently burnt habitat and frequency of LDS fire (Radford et al. 2015). Fire extent was the best predictor of mammal declines in Kakadu National Park, Northern Territory (NT; Lawes et al. 2015).
Early dry season (EDS) fire	Proportion of region burnt in early dry season of current year	The effect of the spatial extent of habitat burnt in the EDS on mammal abundance is unknown in the north Kimberley (Radford et al. 2015). Fire extent was the best predictor of mammal declines in Kakadu National Park, NT (Lawes et al. 2015).
Patchiness	Number of patches of early or late dry season fire	Fire extent was the best predictor of mammal declines in Kakadu National Park, NT and patchiness was not important unless incorporated as an interaction with fire extent (Lawes et al. 2015). The impact of the extent of EDS or LDS burnt on mammal abundance is highly dependent on patchiness of burn, an indicator of fire size and intensity (Lawes et al. 2015, Leahy et al. 2016). In the current study, patchiness was not considered alone but always included as an interaction term with EDS or LDS fire extent, as this was considered essential to biological interpretation.
Old growth vegetation	Proportion of unburnt vegetation (more than 4 years post-fire)	The retention of old growth (>4 years unburnt) patches within fire mosaics benefits savanna mammals in the north Kimberley (Radford et al. 2015). The proportion of old growth vegetation was also considered as an interaction with mean patch size of old growth vegetation.
Old growth mean patch size	Mean size of patches of old growth vegetation (ha)	The mean size (ha) of old growth (>4 years unburnt) patches within fire mosaics benefits savanna mammals in the north Kimberley (Radford et al. 2015). Mammals may be affected by the extent of old growth within a fire mosaic and the size of these old growth patches (Radford et al. 2015). In the current study, the size of old growth patches was not considered alone but always included as an interaction term with proportion of old growth vegetation, as this was considered essential to biological interpretation.
Wet season rainfall	Wet season rainfall in previous year (mm)	Mammal populations can fluctuate with rainfall (Radford et al. 2015). Inclusion of previous wet season's rainfall as a main effect accounts for these short-term fluctuations due to rainfall.
Trap effort	Total trap nights per site	Included in all models as an offset term to account for difference in trap effort at each site.
Site	Location of trapping surveys in each habitat type	Included in all models as a random effect to account for repeated measures from each site.

Table 2. The relative importance of fire attribute and rainfall variables derived from General Linear Mixed Models (GLMM) modelling the effect of these variables on mammal species/functional group abundance. Relative variable importance values (w+) and the number of models containing the variable (N, in brackets), from the 95% confidence model set generated from model-averaging are shown. Highly influential variables (w+ ≥ 0.73) are indicated in bold. Marginal (M) and conditional (C) R2 are given as an indication of goodness-of-fit of the optimal model containing only highly influential variables, with marginal R2 describing the proportion of variance explained by the fixed factors alone and conditional R2 describing the proportion of variance explained by both the fixed and random factors. See Table 1 for variable definitions. LM denotes large marsupials, SR specialist rodents, GR generalist rodents and ID insectivorous dasyurids (see Methods for functional group mammal species composition). EDS is early dry season, LDS is late dry season, OG is old growth, OGPS is old growth patch size and WSRain is wet season rainfall.

Species/group	***w*+ (N)**						**R^2**	
	LDS	**LDS : Patchiness**	**EDS**	**EDS : Patchiness**	**OG : OGPS**	**WSRain**	**M**	**C**
Sandstone								
Dasyurus hallucatus^{LM}	**0.88 (11)**	**0.82 (7)**	**1.00 (16)**	0.42 (6)	0.28 (6)	0.16 (7)	0.16	0.26
Isoodon auratus^{LM}	0.61 (12)	0.32 (5)	0.37 (11)	0.18 (5)	0.31 (8)	**0.84 (14)**	0.12	0.18
Isoodon macrourus^{LM}	0.36 (12)	0.16 (7)	0.30 (11)	0.06 (4)	0.26 (9)	**0.93 (16)**	0.05	0.16
Pseudomys delicatulus^{GR}	0.36 (14)	0.17 (7)	0.41 (12)	0.21 (5)	**0.84 (15)**	0.49 (10)	0.04	0.20
Pseudomys nanus^{GR}	**1.00 (20)**	0.25 (8)	**0.81 (14)**	**0.73 (10)**	0.26 (8)	**0.75 (11)**	0.12	0.16
Zyzomys argurus^{GR}	**0.73 (14)**	0.15 (5)	0.33 (12)	0.08 (5)	**0.80 (14)**	0.36 (12)	0.13	0.26
Zyzomys woodwardi^{SR}	0.20 (1)	0.19 (1)	**1.00 (3)**	0.17 (1)	**1.00 (3)**	**1.00 (3)**	0.21	0.97
Generalist rodents	**0.92 (19)**	0.23 (8)	0.34 (12)	0.13 (5)	0.71 (12)	0.17 (8)	0.14	0.24
Specialist rodents	0.53 (6)	0.21 (3)	**1.00 (13)**	0.34 (5)	0.47 (6)	0.55 (7)	0.33	0.51
Large marsupials	**0.95 (12)**	**0.86 (7)**	**1.00 (15)**	0.63 (7)	0.25 (6)	0.20 (8)	0.25	0.44
All sandstone mammals	0.55 (11)	0.39 (5)	**1.00 (19)**	0.24 (9)	0.35 (8)	0.20 (7)	0.10	0.38
Woodland								
Conilurus penicillatus^{SR}	0.18 (1)	0.16 (1)	**1.00 (3)**	0.24 (1)	0.35 (1)	**1.00 (3)**	0.21	0.99
Dasyurus hallucatus^{LM}	0.33 (11)	0.09 (4)	0.32 (11)	0.10 (4)	**0.73 (12)**	**0.81 (15)**	0.11	0.16
Isoodon macrourus^{LM}	**0.81 (8)**	**0.73 (7)**	**1.00 (11)**	**1.00 (11)**	0.33 (5)	0.24 (5)	0.18	0.38
Mesembriomys macrurus^{SR}	0.59 (11)	0.20 (6)	**0.88 (13)**	0.17 (5)	**0.73 (7)**	0.53 (8)	0.42	0.50
Pseudomys nanus^{GR}	0.28 (5)	0.07 (2)	0.66 (5)	0.21 (5)	0.21 (3)	**1.00 (9)**	0.19	0.34
Rattus tunneyi^{GR}	**0.73 (10)**	0.49 (5)	0.36 (6)	0.15 (3)	**0.95 (12)**	0.50 (7)	0.18	0.57
Sminthopsis virginiae^{ID}	0.62 (8)	0.21 (3)	**1.00 (13)**	0.35(6)	0.38 (6)	0.29 (5)	0.14	0.27
Insectivorous dasyurids	0.53 (6)	0.32 (5)	**1.00 (13)**	0.34 (5)	0.47 (6)	0.55 (7)	0.12	0.24
Generalist rodents	**0.93 (14)**	**0.73 (12)**	0.59 (10)	0.15 (4)	**0.98 (15)**	0.11 (7)	0.12	0.42
Specialist rodents	0.36 (10)	0.12 (4)	**1.00 (18)**	0.27 (7)	0.32 (8)	0.33 (8)	0.08	0.33
Large marsupials	**0.80 (11)**	**0.76 (8)**	**0.96 (13)**	**0.95 (12)**	0.57 (7)	0.18 (6)	0.12	0.40
All woodland mammals	0.46 (10)	0.29 (7)	**0.93 (13)**	0.50 (6)	**0.90 (11)**	0.12 (5)	0.21	0.58

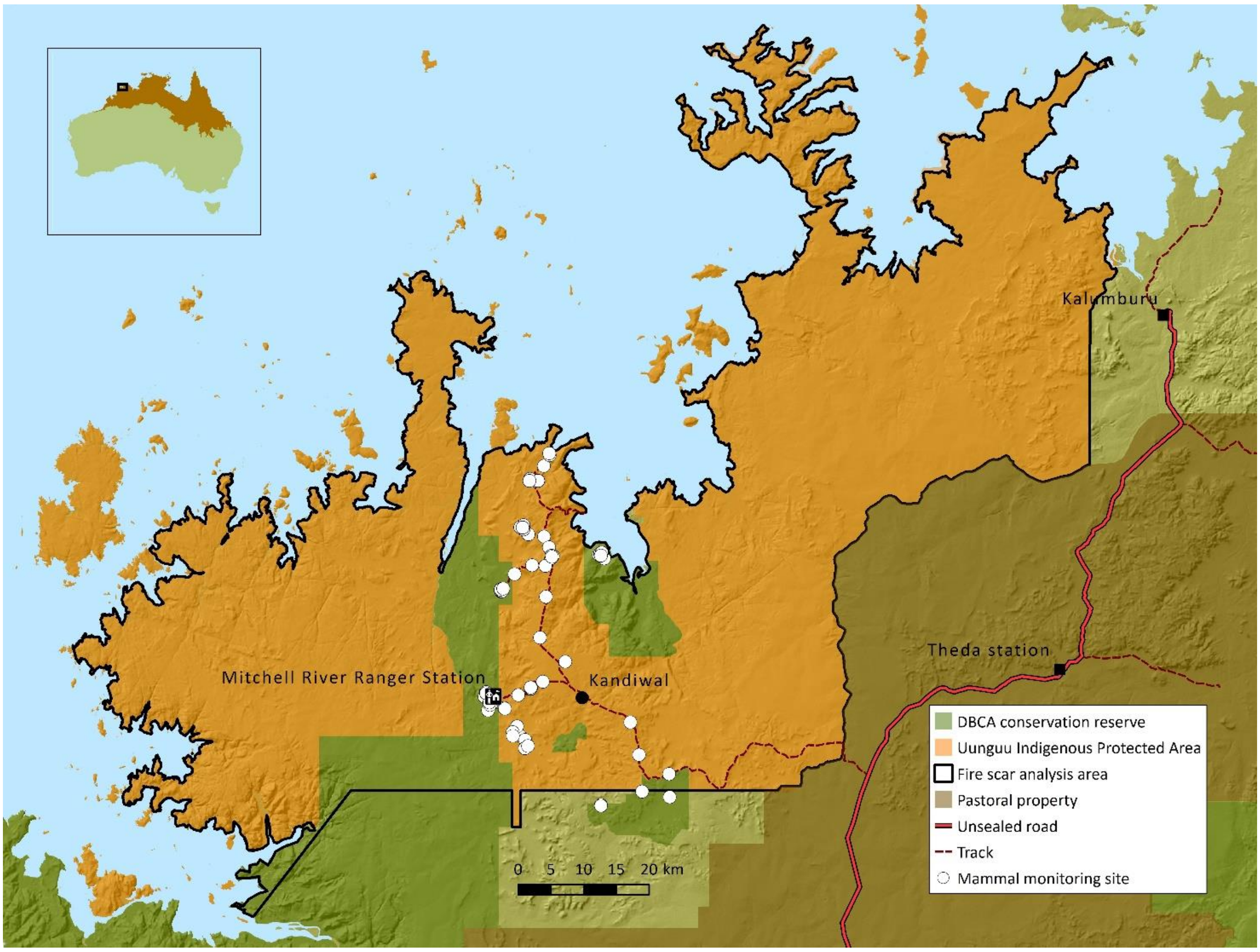


Fig. 1. Location of the study area relevant to northern Australia's tropical savanna (inset), the Mitchell Plateau study area, and small mammal monitoring sites (main figure).

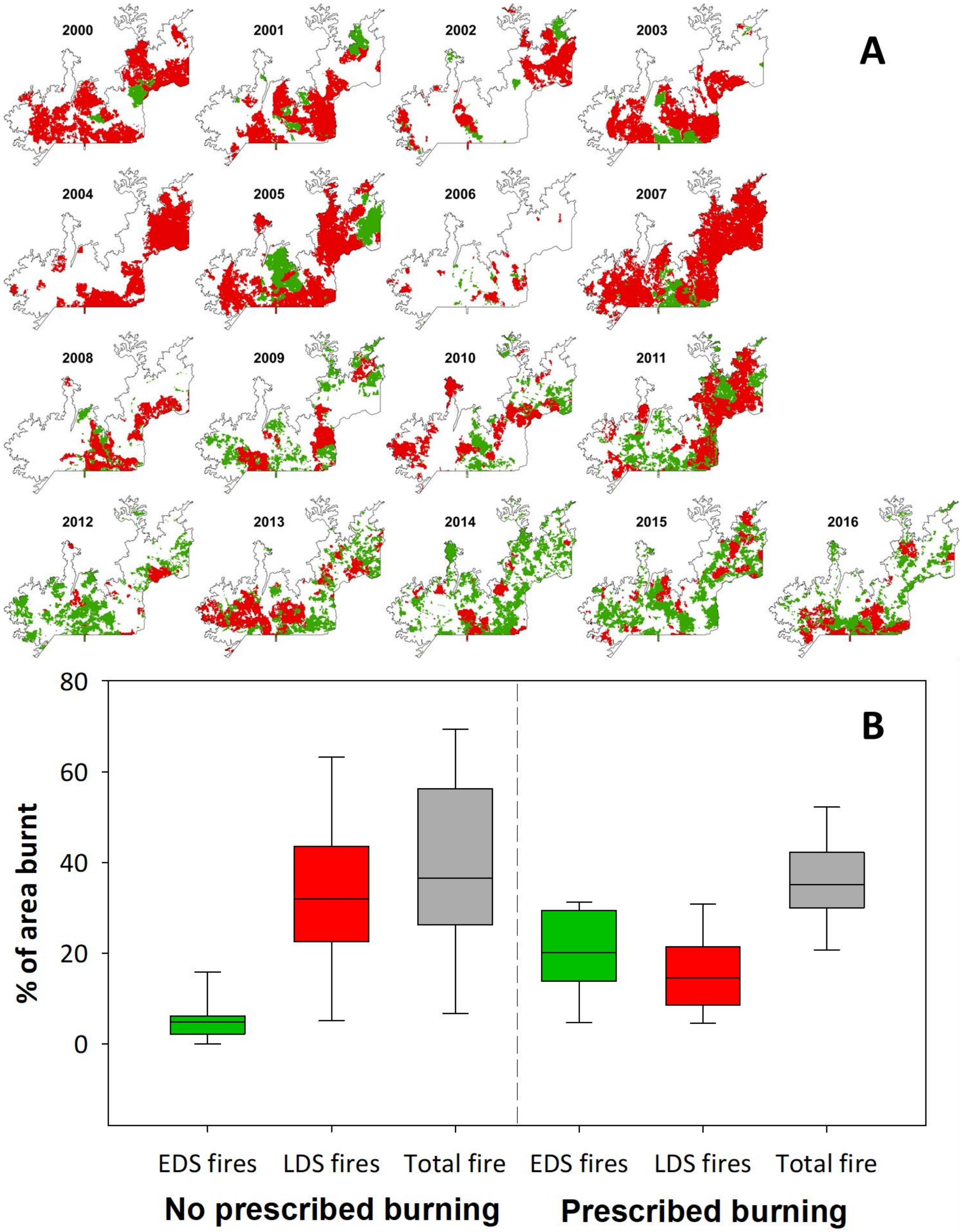


Fig. 2. Annual early (green) (EDS) and late (red) dry season fires (LDS) in the Uunguu Indigenous Protected Area from 2000–2016 **(a)**, and box plots of early and late dry season fires, and total fire extent before (2000–2010) and after (2011–2016) prescribed burning **(b)**. P-values from Kruskal-Wallis nonparametric one-way ANOVA testing for difference between management types are shown top centre of fire management plot, with significance codes: 0.01, *** 0.001.

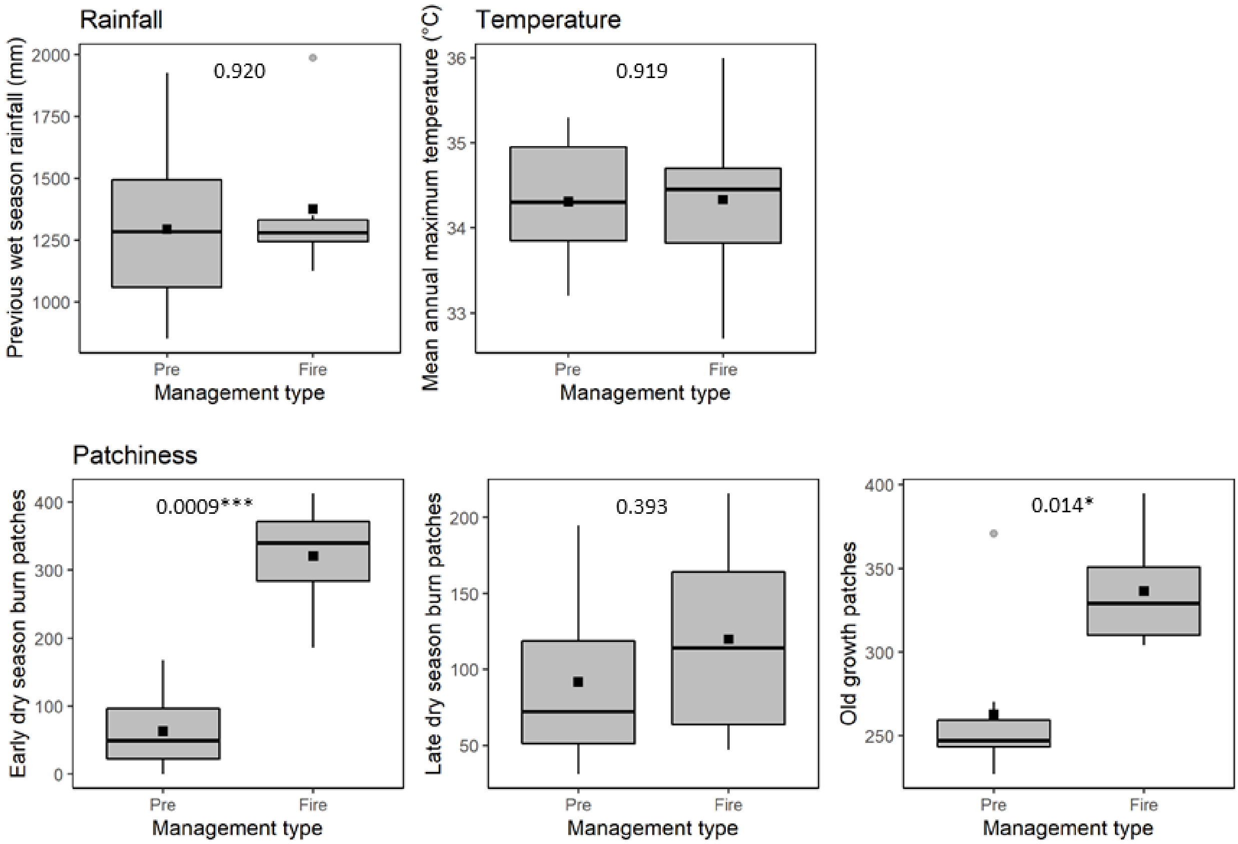
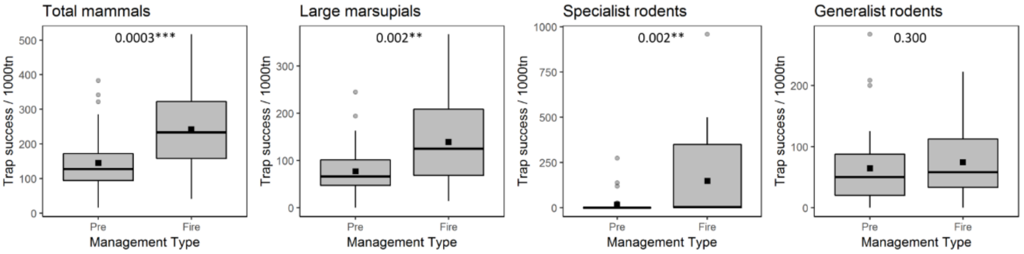


Fig. 3. Regional climate, as well as patchiness of early dry season and late dry season burns and old growth (> 4 years) vegetation under pre-management and fire-management periods. Box plots display the mean (black square), median (thick black line), upper and lower quartiles (box), minimum and maximum values (whiskers) and outliers (grey circles). *P*-values from Kruskal-Wallis nonparametric one-way ANOVA testing for difference between management types are shown top centre of each plot, with significance codes * 0.05, and *** 0.001.

(a) SANDSTONE



(b) VOLCANIC/LATERITIC

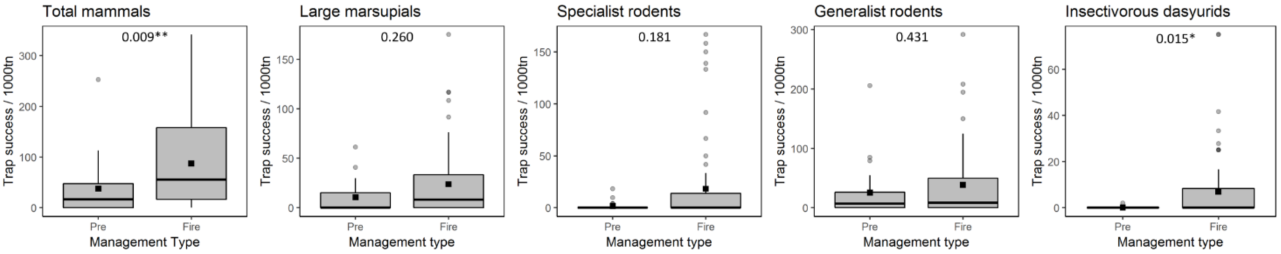


Fig. 4. Mammal functional group trap success per 1000 trap nights (tn) in (a) sandstone and (b) volcanic/lateritic woodland habitats under pre-management and fire-management periods. Box plots display the mean (black square), median (thick black line), upper and lower quartiles (box), minimum and maximum values (whiskers) and outliers (grey circles). *P*-values from Kruskal-Wallis nonparametric one-way ANOVA testing for difference between management types are shown top centre of each plot, with significance codes * 0.05, ** 0.01 and *** 0.001. Species included in functional groupings: Sandstone – large marsupials: *Dasyurus hallucatus*, *Isoodon auratus*, *I. macrourus*; specialist rodents: *Mesembriomys macrurus*, *Z.woodwardi*; generalist rodents: *Melomys burtoni*, *Pseudomys delicatulus*, *P. johnsoni*, *P.nanus*, *Rattus tunneyi*, *Zyzomys argurus*; Volcanic/Laterite woodlands – large marsupials: *D. hallucatus*, *I. macrourus*; specialist rodents: *Conilurus penicillatus*, *Mesembriomys macrurus*; generalist rodents: *Melomys burtoni*, *P. delicatulus*, *P. nanus*, *R. tunneyi*, *Z. argurus*; insectivorous dasyurids: *Pseudantechinus ningbing*, *Sminthopsis virginiae*.

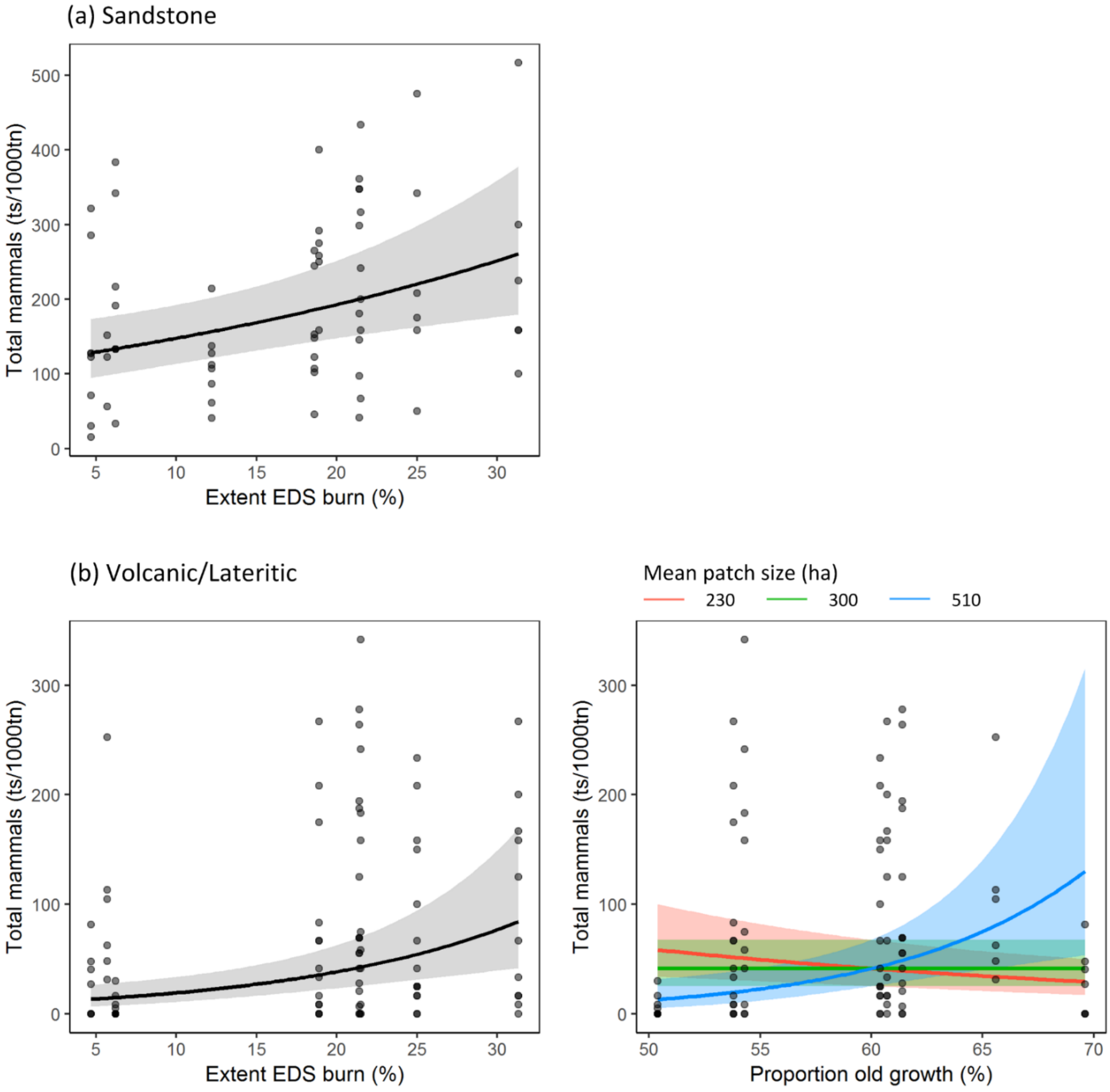


Fig. 5. Total mammal abundance (trap success per 1000 trap nights (ts/1000tn)) in (a) sandstone and (b) volcanic/lateritic habitats shown only for highly influential predictor variables (see Table 3). Model fit for extent of early dry season (EDS) burn is shown by a black line and the grey band represents the 95% confidence interval. The relationship between abundance and proportion of old growth vegetation is given as an interaction with mean old growth patch size, where red and blue lines (and bands) are model fit (and 95% confidence intervals) at first and third quartile levels of patch size respectively, and the green line (and band) is model fit (and 95% confidence intervals) at median patch size. Grey circles indicate observed data values and these circles become darker with repeated observations at the same point.

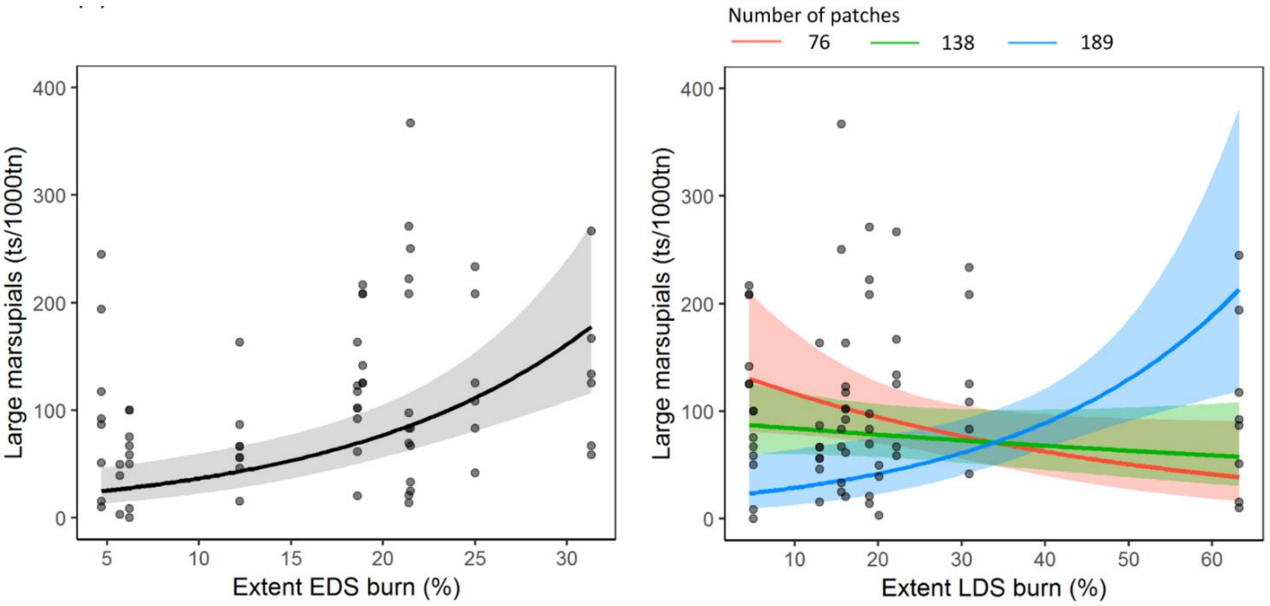
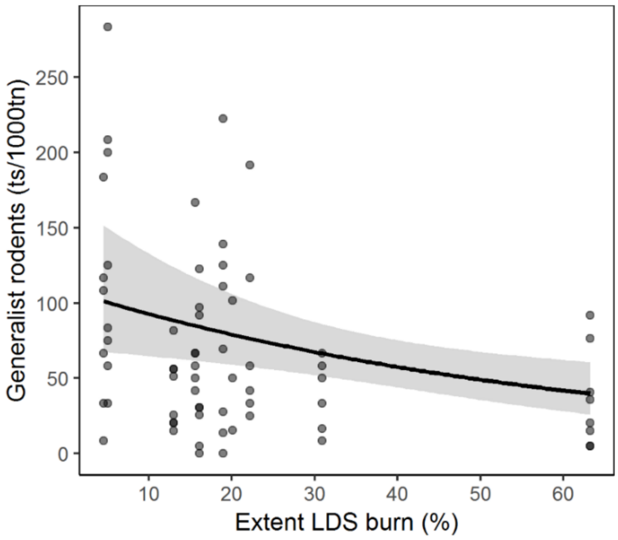


Fig. 6. Modelled relationships between large marsupial abundance (trap success per 1000 trap nights (ts/1000tn)) in sandstone habitats with the most highly influential predictor variables (see Table 3). Relationships between abundance and extent of early dry season (EDS) and late dry season (LDS) burn are given as interactions with number of patches, where red and blue lines (and bands) are model fit (and 95% confidence intervals) at first and third quartile levels of patchiness respectively, and green lines (and bands) are model fit (and 95% confidence intervals) at median levels of patchiness. The black line is model fit for extent of early dry season burn (main effect) and the grey band is the 95% confidence interval. Grey circles indicate observed data values and these circles become darker with repeated observations at the same point. Species included within the large marsupial functional group on sandstone are *Dasyurus hallucatus*, *Isoodon auratus* and *I. macrourus*.

(a) Sandstone



(b) Volcanic/Lateritic

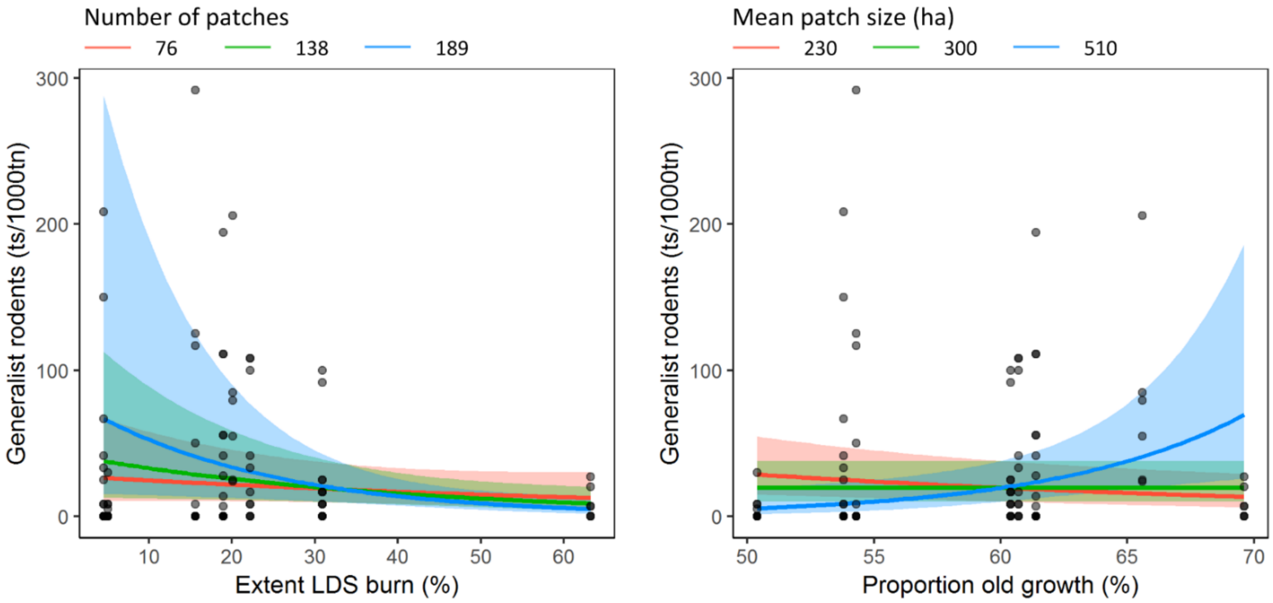


Fig. 7. Generalist rodent abundance (trap success per 1000 trap nights (ts/1000tn)) in (a) sandstone and (b) volcanic/lateritic habitats shown only for highly influential predictor variables (see Table 3). The black line is model fit for extent of late dry season (LDS) burn main effect for sandstone and the grey band represents the 95% confidence interval. Volcanic/lateritic relationships between abundance and extent late dry season burn and proportion of old growth vegetation are given as interactions with number of patches and mean patch size respectively, where red and blue lines (and bands) are model fit (and 95% confidence intervals) at first and third quartile levels of patchiness and patch size respectively, and green lines (and bands) are model fit (and 95% confidence intervals) at median levels of patchiness and patch size. Grey circles indicate observed data values and these circles become darker with repeated observations at the same point. Species included in generalist rodent functional group: Sandstone – *Melomys burtoni*, *Pseudomys delicatulus*, *P.nanus*, *P. johnsoni*, *Rattus tunneyi*, *Zyzomys argurus*; Volcanic/Lateritic – *M.burtoni*, *P.delicatulus*, *P.nanus*, *R.tunneyi*, *Z. argurus*.