



Aboriginal burning promotes fine-scale pyrodiversity and native predators in Australia's Western Desert

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ABSTRACT

Both invasive mesopredators and altered fire regimes impact populations of vulnerable native species. Understanding how these forces interact is critical for designing better conservation measures for endangered species. This study draws on Indigenous ecological knowledge and practice to explore heterogeneity in faunal responses to Indigenously managed landscapes in the Western Desert of Australia. Using track plot surveys and satellite image analysis of fire histories, we find evidence that pyrodiversity increases activity measures of dingoes and monitor lizards. Dingoes were more active in recently burnt patches, while foxes were more active in slightly older burnt patches. These results add to previous work showing significant effects of pyrodiversity on kangaroo populations in the region. Together, the findings suggest that Aboriginal burning not only creates diverse niches for native animals, it helps to facilitate the ecological role of species that are themselves functionally vital. This work adds to a growing body of research suggesting that the loss of Aboriginal burning can cascade through ecosystems by transforming and simplifying ecological networks, thus contributing to the decline and extinction of vulnerable species.

1. Introduction

Fire is a disturbance that shapes ecosystems around the world (Bowman et al., 2009), but its role in promoting biodiversity remains poorly understood (Driscoll et al., 2010). This lack of understanding is concerning given over 1000 animal species are threatened by altered fire regimes (IUCN, 2015), which cover ~60% of the world's terrestrial ecosystems (Shlisky et al., 2009). Drivers of altered fire regimes are manifold, but the displacement of Indigenous people—often in conjunction with subsequent fire suppression and climate change (Enright et al., 2015; Westerling, 2016)—is paramount.

There is increasing evidence that Indigenous burning promotes (or promoted) fire regimes that maintained high levels of 'pyrodiversity' (Bowman et al., 2004; Bliege Bird et al., 2008; Trauernicht et al., 2015). Pyrodiversity refers to the "temporal and spatial heterogeneity of fire" (Martin and Sapsis, 1992)—landscapes with fine-scale patterning of diverse fire histories have high pyrodiversity, while landscapes with broad-scale patterning and more uniform fire histories have low pyrodiversity (Parr and Andersen, 2006). For instance, in grassland

ecosystems in Brazil and Australia, Indigenous burning creates a patchier distribution of fires, preventing fires from burning too frequently and limiting vegetation loss (Vigilante et al., 2004; Welch et al., 2013). It is hypothesized that the loss of pyrodiversity following Indigenous displacement impacts animals by rearranging the distribution of food and shelter resources due to the rescaling of fire mosaics (Keith et al., 2002; Bliege Bird et al., 2008), and in doing so exposes many species to enhanced predation (Doherty et al., 2015; Woinarski et al., 2015).

The impact of shifts in fire regimes on species is further compounded by invasive predators, as fire regime shifts may act synergistically with predator invasion to increase the vulnerability of native animal species (McGregor et al., 2014; Leahy et al., 2016). In Australia, loss of traditional fire regimes has been hypothesized to be an important factor shaping the ability of invasive mesopredators (i.e. feral cats, *Felis catus* and red foxes, *Vulpes vulpes*) to decimate mammal populations (Burbidge et al., 1988; Ziemnicki et al., 2015). Invasive predators may be favored by large, intense fires indicative of modern fire regimes due to increased hunting efficiency in open habitats (McGregor

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et al., 2015; Leahy et al., 2016), resulting in heightened mortality as prey must travel further to access unburnt refugia (Leahy et al., 2016).

Studies of links between indigenous burning, pyrodiversity and biodiversity are challenging because of the enormous scale of indigenous dispossession by European colonialism. One region where traditional fire regimes remain are the spinifex grasslands of Australia's Western Desert, where Indigenous traditional owners (Martu) continue to burn for subsistence purposes in ways that recall historic landscape-scale patterning of fire regimes in some locations (Bliege Bird et al., 2008). In landscapes where Martu hunt more, hunting fires rescale pyrodiversity and buffer against climate-driven shifts in mean fire size (Bliege Bird et al., 2008; Bliege Bird et al., 2012; Bliege Bird et al., 2016). Landscapes that are not utilized by Martu exhibit a shift in fire regime toward much larger fires, with a pronounced seasonal dominance in ignition toward summer fires (Burrows et al., 2006; Bliege Bird et al., 2012). The latter fire regime may favor invasive predators, which prefer to hunt in recently burned areas (McGregor et al., 2014; McGregor et al., 2016; McGregor et al., 2017), driving down native mammal populations. This synergy between altered fire regimes and invasive predators has been offered as an explanation for the local extinction of 21 mammal species and the decline of a further 43 that coincided with a brief (~15 year) Martu exodus from their homelands (Burbidge et al., 1988; Burrows et al., 2006).

In this paper, we examine the response of native and invasive predators and prey to fire history and successional stage diversity in the Martu homelands of the Western Desert (Fig. 1a). Our approach draws on Martu ethnoecological knowledge to classify patches recovering from fire into functionally important stages linked to food and shelter. Martu are uniquely placed to provide such knowledge through their shared history with the region's climates and environments and their attachments to country. Martu recognize at least five distinct successional classes following fire (Fig. 1b), categorized by the food and shelter each stage provides, to people and other animals. We focus on the responses of common invasive and native predators and prey to these stages—the dingo (*Canis dingo*), cat, fox, monitor lizards (sand goanna, *Varanus gouldii*), mulgara (*Dasycercus blythi*) and native mice (including *Notomys alexis* and *Pseudomys hermannsburgensis*). Using track surveys conducted by Martu and researchers they've trained (Fig. 1c), we examine how predator and prey activity varies with the cover, presence and diversity of ethnoecologically-defined successional stages.

If Indigenous fire management buffers native species from the impacts of invasive predators in the Western Desert, we predict that: 1) pyrodiversity should be greater and unburned habitat refugia more common in areas close to Martu communities than more remote areas, due to the frequent lighting of small fires by Martu for hunting (Bliege Bird et al., 2008), which reduces the frequency of large fires, thereby protecting unburned refuges (Bliege Bird et al., 2012); 2) invasive predators should be associated with recently burned areas due to their enhanced hunting efficiency in open habitats (McGregor et al., 2015) and should be more common in areas subject to altered fire regimes (i.e. low pyrodiversity areas further from Martu communities); 3) native predators that have co-evolved alongside Martu should be favored by traditional burning regimes and thus pyrodiversity (Bliege Bird et al., 2013); and 4) potential prey species should be associated with traditional fire regimes due to pyrodiversity improving foraging returns and diminishing predation risk.

2. Methods

2.1. Study area

This study is situated within the spinifex dominated sandplains of the Little Sandy Desert bioregion of Western Australia (Fig. 1a). The region includes Martu Native Title lands and Karlamilyi National Park. Climate is hot and semi-arid, with a variable mean annual rainfall of

363 mm, ranging from 108 to 1455 mm (www.bom.gov.au); winter lows are typically well above freezing, 10–12 °C, with summer high temperatures exceeding 40 °C (www.bom.gov.au). Vegetation in the region is mostly spinifex (*Triodia schinzii* and *T. basedowii*) and Acacia (*A. pachycarpa* and *A. ligulata*, among others) on sandplain and dune substrates covering 85.6% of the land area. Current human occupation of the study region is limited to one Martu community, Parnngurr, and limited tourist visitation; a gold mine (Telfer) and two other Aboriginal communities lie to the north of the National Park.

The Western Desert was first occupied in the Late Pleistocene, between 40,000 and 50,000 years ago (Veth et al., 2009; McDonald, 2017), with the last 9000 years witnessing a population growth trend culminating in a rapid population increase during the late Holocene (Williams, 2013; Williams et al., 2013). The region thus likely has a long history of Aboriginal burning, perhaps intensifying with increased climatic variability at the onset of ENSO conditions 4.5–2000 years ago (Zeanah et al., 2017). Martu (including Manyjiljarra, Warnman, and Kartujarra linguistic groups) lived in this region until 1966, when the last nomadic bands left for missions and cattle stations on the desert fringe. Martu returned in 1984 to reoccupy the study area, establishing Parnngurr community as a base for traditional foraging activities and patch mosaic burning (see Bliege Bird et al., 2008; Bliege Bird et al., 2012; Bliege Bird et al., 2013; Bliege Bird et al., 2016). However, hunting and burning activities are heterogeneously distributed across the landscape, concentrated in certain regions along tracks within 40–50 km of the community (Fig. 1a). This heterogeneity provides a unique natural experiment to examine the effects of human-induced pyrodiversity on faunal populations.

2.2. Site selection and survey methods

A total of 76 1 ha plots were randomly chosen from a stratified sample of 5000 sample plots located across a gradient of Martu hunting activity within 75 km of Parnngurr community. Plot map shapefiles were loaded onto GPS-enabled tablets enhanced with more accurate external Bluetooth GPS units (BadElf GPS), which were used to navigate to each plot and establish boundaries. Plots chosen for survey were constrained to be within 2 km of a vehicle track (to facilitate access), to fall on soil types that retain track imprints (were limited to plots with 50% or more spinifex sandplain), and had to be at least 1 km from their nearest neighbor. Plots were sampled during winter months between July 2014 and July 2016. Due to the logistical and financial difficulty of conducting fieldwork in this remote region, and because many plots were 1–2 km away from tracks to diminish their influence on species' occurrence (which can be problematic for predator surveys: Hayward et al., 2015), sites were surveyed on one occasion each. Tracks were readily visible on the smooth sand surfaces between spinifex hummocks (Fig. 1c), and fire is commonly applied to sandplain ecosystems by Martu and therefore most tracking occurs in this ecosystem type.

Percent cover of the five Martu successional categories within each 1 ha plot was evaluated by an experienced Martu-trained observer (RBB and/or DWB) using standard comparison charts (examples at <https://www.for.gov.bc.ca/hts/risc/pubs/teecolo/fmdte/veg.htm>). Martu burn small patches in the winter to create *nyurnma*, recently burned areas that are ideal for locating cold season monitor lizard (sand goanna) burrows (Bliege Bird et al., 2008, 2013; Bird et al., 2009). A few weeks following a fire, shrubs, trees, and some grasses will begin to resprout, and following rain, new seedlings create a flush of vegetation, which is the signal that plant recovery (*waruwaru*) has begun (Fig. 1b). If there is no available soil moisture following a fire, a *nyurnma* can remain dormant and not progress to *waruwaru* for months, even years, until the rains return. Once plants have matured and produced flowers or fruits, the area enters the next stage, *nyukura*, characterized by its high species diversity and the presence of a number of forbs and subshrubs that possess large edible fruits (e.g. bush tomatoes, *Solanum* spp., and the fan flower *Scaevola parvifolia*) and a greater diversity of seed grasses such as

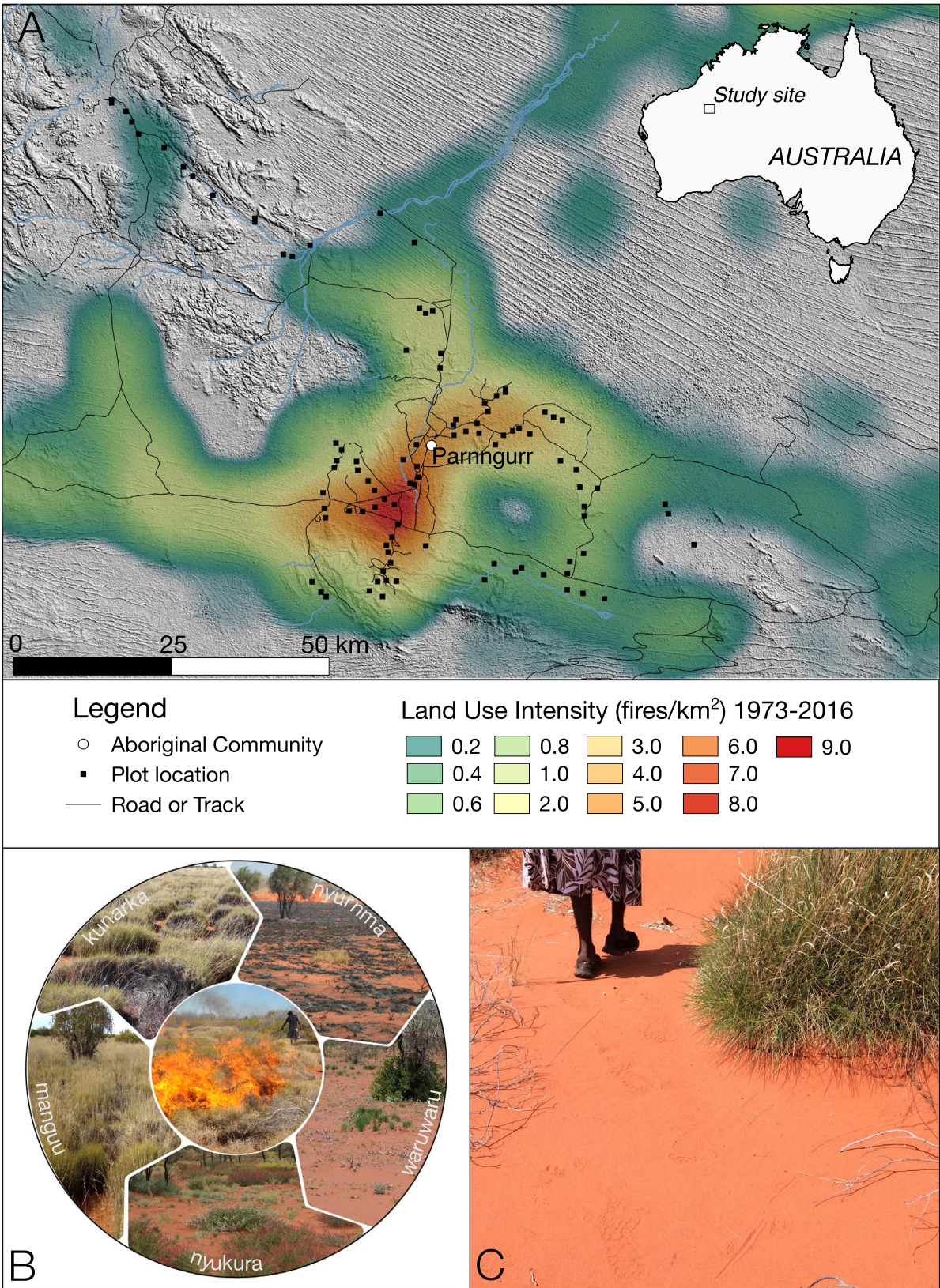


Fig. 1. Panel A) map of the study region showing variation in land use intensity as measured by 43-year fire density along a gradient of distance from community and tracks. Fire densities were derived from density maps (averaged over a 5 km radius) of polygon centroids of fire footprints observed on Landsat imagery from 1973 to 2016. Panel B) depicts the Martu successional classification scheme, based on functional aspects of vegetation structure and time since fire. Panel C) illustrates track visibility in sandy substrates (a goanna track is visible in the bottom quadrant of the photo).

Eragrostis eriopoda and *Yakirra australiensis*. These mid-successional plants produce for a few years, and as *Triodia* (spinifex) grows to dominate the ground layer, *nyukura* transitions into *manguu* anywhere between 4 and 10 years following fire. *Manguu* is a flammable plant community comprised primarily of *Triodia* together with flowering woody shrubs that offers food for a narrower range of species (*Hakea* and *Grevilla* flowers and nectar, *Acacia* seeds, and *Triodia* seed). Tall and dense spinifex hummocks in *manguu* signals that the area is ready to again carry fire. If *manguu* escapes fire it will transition into *kunarka*, a stage in which the spinifex begins to senesce in the center, creating large, donut-shaped hummocks up to 2–3 m in diameter. Our analyses used these definitions to classify patch types within the 1 ha plot into five categories: *nyurnma* (no sprouts present), *waruwaru* (sprouts but no mature plants), *nyukura* (mature plants, highest plant species diversity), *manguu* (mature spinifex able to carry a fire), and *kunarka* (senescent spinifex). No plots were established in *nyurnma* younger than approximately two weeks to allow time for tracks to accumulate.

We calculated two measures of pyrodiversity using Shannon's diversity index for each site (Bliege Bird et al., 2008; Farnsworth et al., 2014). Local pyrodiversity was the Shannon's diversity of the Martu successional stages observed within each 1 ha plot. Landscape pyrodiversity was derived from existing fire history maps based on 30 m resolution Landsat imagery taken at 6 month intervals (see Bliege Bird et al., 2012 for details). Fires observed to burn between 1973 (the date of the earliest image) and 2016 were overlaid to construct a vegetation classification of time since fire for the region. To convert the temporal classes into Martu seral classes we used ground control points identifying Martu seral stage to parameterize a classification scheme that merged patches of similar temporal age: patches at 0 months were classified as *nyurnma*, 6 months as *waruwaru*, 1 year to 4.5 years as *nyukura*, 5 to 10 years as *manguu*, and > 10 years as *kunarka*. Shannon's Index of landscape pyrodiversity was calculated for each 20 ha circular landscape surrounding the plot using Fragstats v 4.2 (McGarigal and Ene, 2015).

All larger animal tracks and traces located within the plot—burrows, scat, diggings, and tracks—including those from dingoes, cats, foxes, mulgara, mice and sand goanna, were enumerated by experienced Martu and non-Martut trackers (RBB and DWB) and ranked as fresh (distinct edges), moderately old (blurred edges), or very old (indistinct edges). Unless tracks were clearly of different individuals or from different occasions (based on size or differences in freshness), trackways of similar freshness and size were counted as a single record. All track counts were constrained to be completed within 30 min. These counts were used to establish an abundance scale within the plot where 0 = “absent”, no evidence present; 1 = “rare”, 1 fresh track or other minimal evidence (digging, scat) present; 2 = “moderate” 2 fresh tracks or one track and additional evidence present; 3 = “common”, three or more fresh tracks and/or other evidence of activity throughout the plot. Tracks in *nyurnma* were not enumerated if they were clearly made before the fire (underneath ash or charcoal, had smoke charring on the track surface, or appeared older than the fire itself). The one exception to this was sand goanna burrows: as goannas were brumating in their winter burrows for at least three months prior to the survey, no tracks were visible, so burrow presence was the main measure of their activity. As such, any relationship between *nyurnma* and goannas could not be interpreted as a habitat preference (as they would have chosen their burrows prior to sites being burned and becoming *nyurnma*). Fresh tracks were common for all other species that remain active during winter.

2.3. Analytical methods

We first modeled the relationship between the distance to Parnngurr and 1) local pyrodiversity, and 2) the proportional cover and presence of each Martu successional stages within each of the 1 ha plots. To model the relationship between local pyrodiversity and distance to

community, we used a Generalized Linear Model (GLM) with an identity link function. We focus on local pyrodiversity as the relationship between Martu fire regimes and landscape-level pyrodiversity has been demonstrated previously (Bliege Bird et al., 2008), whereas such a relationship has not been documented at the finer scale of 1 ha plots. As the relationship between distance to Parnngurr and local pyrodiversity appeared non-linear, we used Akaike's Information Criterion (AIC) values to confirm that a log relation provided better fit given the data (linear relationship, AIC = 38.9, log relationship, AIC = 35.2). As rainfall is a driver of fire in the western desert (Bliege Bird et al., 2012), models of the cover and presence of recently burned *nyurnma* also included rainfall from the previous 12 months. The relationship between distance to community and the proportional cover/presence of successional stages was modeled using a GLM with a binomial distribution and a logit link function (Crawley, 2012).

As the response variable for animal activity was ordinal, we used ordinal regression to examine the influence of predictor variables on species' activity. We fit models for each species' activity in relation to: the proportional area of Martu successional stages within the 1 ha plot; local pyrodiversity (i.e. at the 1 ha plot scale); landscape level pyrodiversity (i.e. at the 20 ha scale); the cumulative rainfall from the previous 12 months (obtained from the nearest recording station, Telfer Aero 013030 www.bom.gov.au), given rainfall is important in arid ecosystems (Letnic et al., 2004; Holmgren et al., 2006); the distance of the plot from the closest Martu community (Parnngurr); and, for larger eutherian mammals (dingoes, foxes, cats), a variable measuring the distance of the plot to the nearest permanent water source and the distance to Parnngurr. Water source maps were constructed by RBB and DWB using a combination of available satellite-derived water sources (<http://eos.ga.gov.au/geoserver/web/>), 250 k topographic maps, and site visits to local water sources by DWB and RBB, and were reviewed for location accuracy and permanence by two Martu coauthors of this paper (NT and WT). As the proportional area of Martu successional stages are collinear (i.e. as one increases others must decrease), we included only two successional stages in any species model to reduce multiple collinearity. To decide which successional stages to include, we related each species' activity to each successional stage in univariate models, and then used AIC values to reveal which variables had the best fit. We regarded predictor variables as being influential when the 95% confidence interval did not overlap zero. Two measures of each successional stage were included in this initial stage: one in which the successional stage was measured as proportional cover of the 1 ha plot, and one in which the presence or absence of that successional stage within the plot was measured. The two successional stages in models with the lowest AIC were then included in subsequent multivariate models. No two variables included in the final models shared pairwise collinearity coefficients of > 0.6.

We used an information theoretic approach to examine which variables influenced species' activity levels (Burnham and Anderson, 2003). We again used Akaike's Information Criterion, adjusted for small sample size (AICc), to rank models from most to least supported, given the data. Models with the lowest AICc are the most parsimonious models. Models within 2 AICc values of the best models have substantial support from the data, and a model is regarded as clearly best if it has an Akaike weight > 0.9 (Burnham and Anderson, 2003). Where no models were identified as clearly best, we undertook model averaging to quantify the strength and direction of parameter estimates (Burnham and Anderson, 2003). Arnold (2010) suggests using 85% confidence intervals derived from model averaging for identifying influential variables within an information theoretic framework. Therefore, for this analysis, variables were regarded as being influential when their 85% confidence interval did not overlap zero. Ordinal regression models were fit using the ‘ordinal’ package (Christensen, 2015) and model selection and averaging was undertaken using MuMin (MuMin, 2016) in R version 3.1.

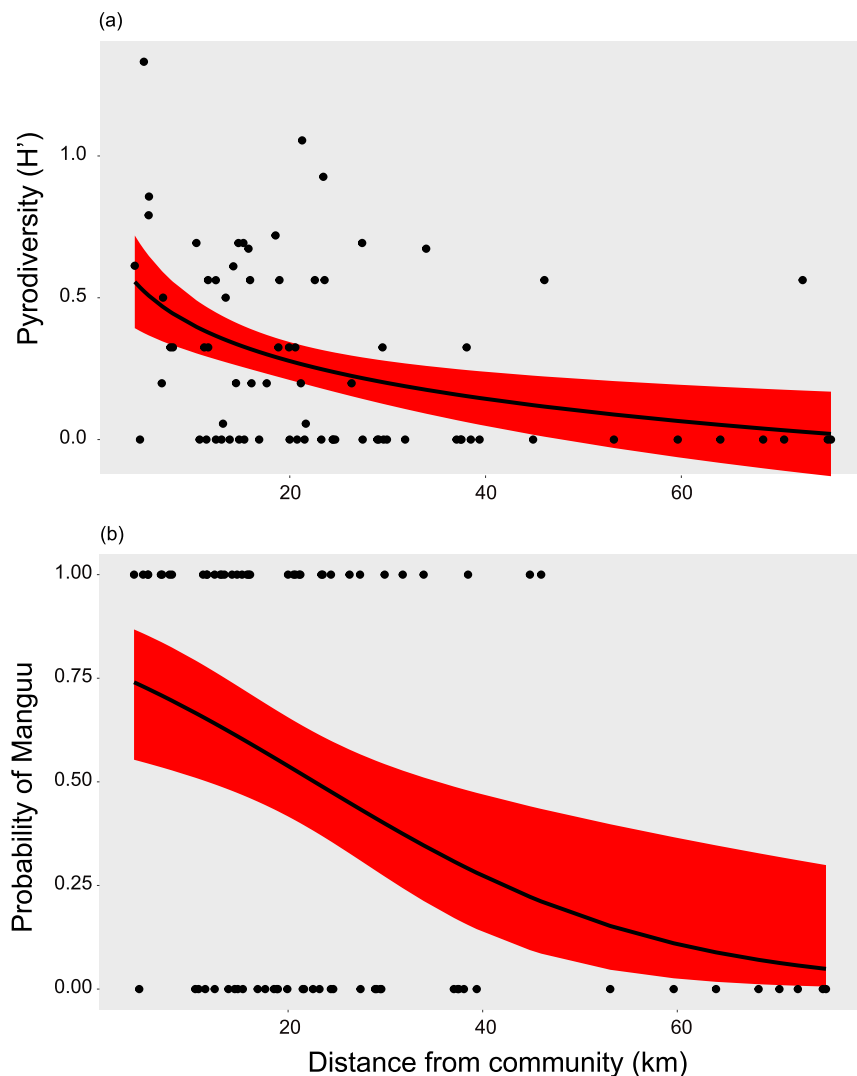


Fig. 2. The relationship between (a) pyrodiversity and (b) the probability of occurrence of the late successional Manguu patches with increasing distance from Parnngurr. Black circles are raw data, black line is the fitted relationship derived from Generalized Linear Models, red shading is the 95% confidence intervals of the predictions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

Across the 76 plots, dingoes were recorded at 21% of sites, cats at 26%, foxes at 12%, sand goannas at 46%, mulgara at 12%, and mice at 75% of sites. The 1 ha plots had an average of 1.6 Martu successional stages within them, ranging from one to four. Shannon's Index ranged from 0 (a single successional stage) to 1.3 (4 evenly distributed successional stages), averaging 0.56. Plots were dominated primarily by nyukura (54% cover on average) and manguu (21%), while kunarka (9%), waruwaru (8%), and nyurnma (7%) were less common.

Consistent with previous work showing strong links between pyrodiversity and community distance at larger spatial scales (Bliege Bird et al., 2008), we found local pyrodiversity (i.e. within 1 ha plots) to be negatively related to distance from the community (Fig. 2, Table 2S), indicating that even at this fine scale, Martu fire-stick farming promotes heterogeneity of fire ages. Consistent with previous work (Bliege Bird et al., 2012); the probability of late successional *manguu* (mature *Triodia*) patches being present within a plot was negatively related to distance to community (but not the presence of other patch types; Table 1).

Several influential relationships were detected between fire history and species' activity (i.e. 85% CIs not overlapping zero). Dingoes were positively related to local pyrodiversity (Fig. 3) and recent fire, being more active in plots with *nyurnma* present (Table 1). Foxes and cats responded to the early successional stage, *waruwaru*, but in opposite

ways—while foxes were more common in plots with *waruwaru* present, cats became less active in sites with more *waruwaru* cover (Table 1). Goannas were associated with two successional stages, the early successional *nyurnma* and late successional *manguu* (Table 1). Goannas were active in plots within landscapes that were more pyrodiverse (Fig. 3, Table 2S). Neither of the small mammals responded any measure of fire history, although mice showed a positive response that failed to reach significance. However, along with the dingo, both were active following years of higher rainfall (Fig. 3, Table 2S).

4. Discussion

Consistent with previous work at coarser spatial scales (Bliege Bird et al., 2008), this study shows that Martu burning promotes pyrodiversity even at very fine spatial scales. Many of the 1 ha plots < 40 km from the community contained three or four successional stages, highlighting the fine-grained nature of the aboriginal mosaic. Also consistent with previous work is the increased likelihood of mature habitat in closer proximity to the Martu community. These findings join the growing evidence that indigenous fire management promote pyrodiversity across diverse ecosystems, ranging from tropical rain forests (Nepstad et al., 2006) to Australian savannahs and deserts (Vigilante et al., 2004; Burrows et al., 2006; Trauernicht et al., 2015) and south American grasslands (Pivello, 2011; Durigan and Ratter, 2016).

As predicted, we found a positive relationship between

Table 1

Results from Generalized Linear Models of the relationship between the distance of a 1 ha plot from the Parnngurr aboriginal community and 1) pyrodiversity 2) the proportional cover and presence of Martu successional stages. Model fit is represented by D^2 , the deviance explained by the model relative to a null model. Relationships for which the 95% confidence interval does not overlap zero are shown in bold.

Response variable	Predictor variable	Coef	SE	t value	Lower 95% CI	Upper 95% CI	D^2
Pyro-diversity	Intercept	0.883	0.167	5.279	0.555	1.211	0.16
	log (Dist to Parnngurr)	-0.199	0.053	-3.725	-0.304	-0.094	
Nyurnma cover	Intercept	-4.407	2.413	-1.827	-9.822	0.038	0.19
	Distance to Parnngurr	-0.052	0.056	-0.934	-0.181	0.037	
	Rainfall	0.009	0.006	1.556	-0.002	0.022	
Nyurnma presence	Intercept	-4.527	2.330	-1.943	-9.742	-0.257	0.18
	Distance to Parnngurr	-0.044	0.052	-0.843	-0.163	0.040	
	Rainfall	0.010	0.006	1.783	0.000	0.022	
Waruwaru cover	Intercept	-1.656	0.705	-2.349	-3.065	-0.260	0.03
	Distance to Parnngurr	-0.034	0.032	-1.080	-0.110	0.016	
Waruwaru presence	Intercept	-1.187	0.731	-1.624	-2.621	0.277	0.05
	Distance to Parnngurr	-0.046	0.035	-1.296	-0.130	0.010	
Nyukura cover	Intercept	0.032	0.354	0.091	-0.666	0.728	0.00
	Distance to Parnngurr	0.006	0.012	0.499	-0.017	0.029	
Nyukura presence	Intercept	1.230	0.448	2.746	0.375	2.145	0.01
	Distance to Parnngurr	-0.013	0.014	-0.925	-0.040	0.015	
Manguu cover	Intercept	-1.541	1.150	-1.340	-3.879	0.666	0.00
	Distance to Parnngurr	0.065	0.366	0.178	-0.655	0.790	
Manguu presence	Intercept	1.283	0.494	2.597	0.369	2.327	0.11
	Distance to Parnngurr	-0.056	0.020	-2.875	-0.100	-0.022	
Kunarka cover	Intercept	-4.776	2.063	-2.315	-9.239	-1.041	0.04
	Distance to Parnngurr	0.793	0.612	1.295	-0.377	2.059	
Kunarka presence	Intercept	-1.869	0.501	-3.729	-2.914	-0.931	0.03
	Distance to Parnngurr	0.023	0.015	1.593	-0.006	0.052	

pyrodiversity and a native predator, the dingo, Australia's largest non-human mammalian predator. Such a relationship may be due to the close association and potential co-evolution with Aboriginal Australians and the ecological conditions they create. Prior to European colonization, Aboriginal Australians and dingoes were ubiquitous partners, likely exhibiting a mutualistic relationship (Balme and O'Connor, 2016). Archeological evidence suggests such a relationship emerged soon after the dingo arrived, around 4000 years ago (Balme and O'Connor, 2016). This relationship was strong in the case of Martu, for which the dingo is a totem animal and, prior to European contact, was a fundamental component of Martu life as an animal companion. Assuming that fire mosaics generated by Martu near the community are locally similar to those maintained for thousands of years, then it is possible that Martu fire mosaics have become a preferred habitat. Patterns consistent with kind of co-evolution between fauna and the ecological engineering effects of Aboriginal people has been seen in hill kangaroos (Coddington et al., 2014) and sand goannas (Bliege Bird et al., 2013). It is also possible that dingoes associate with pyrodiverse areas because it increases their encounter rates with hill kangaroo, a relatively scarce but important prey species, as previous work focusing on fire mosaics near rocky ranges has shown that hill kangaroo are advantaged by pyrodiversity (Coddington et al., 2014; Bliege Bird et al., 2013). Pyrodiversity may also influence pursuit success rates: dingoes in some regions hunt along forest edges (Newsome et al., 1983; Vernes et al., 2001), using the visual obstruction of mature vegetation to enhance the probability of a successful pursuit in adjacent burned areas.

Dingoes were more common in plots with recently burned *nyurnma*. Dingoes have been found to prefer recently burned areas in other regions of Australia (Newsome et al., 1983), perhaps because it increases kangaroo hunting pursuit success. Here, because kangaroo are far scarcer (largely restricted to rocky ranges and adjacent areas) and comprise a much smaller proportion of their diet (Paltridge, 2002), the positive relationship between dingoes and *nyurnma* is more likely due to the enhanced ability of dingoes to locate and successfully capture goannas dug from winter burrows. It is well known among Martu—and a source of frustration—that if dingoes locate *nyurnma* prior to Martu they will dig up goannas and eat them before Martu get a chance. Given that people double their pursuit success and more than triple their

foraging returns in burnt areas when hunting goanna (Bliege Bird et al., 2013), it is quite possible dingoes benefit from *nyurnma* in a similar way. As an apex predator, the dingo may have positive effects on some species, possibly through suppression of invasive mesopredators (Letnic et al., 2012). Acting in concert, human burning may increase refuges while dingoes suppress populations of invasive mesopredators, collectively diminishing the impact of invasive predators on native species.

Goanna responded positively to pyrodiversity at the landscape scale, consistent with previous work suggesting that lizards were more abundant near habitat edges (Bliege Bird et al., 2013). Goanna are generalist and opportunistic predators (Losos and Greene, 1988), and as such, access to fine-grained habitat mosaics will tend to reduce foraging costs and increase foraging returns if alternative high ranked prey occur in different patch types (Ritchie, 1998). We found a preference for late successional *manguu*, which corroborates previous work showing increased monitor lizard abundance in late successional patches near early or mid successional (*nyurnma* or *nyukura*) patches. Goanna may prefer *manguu* for winter denning because it may reduce the predation risk by human and nonhuman predators (Bliege Bird et al., 2013). Although we found a positive relationship between goanna activity and *nyurnma*, this is probably an artifact of how goannas were surveyed, rather than a habitat preference. As the track surveys occurred during winter, the only goanna signs were their burrows (unlike all other species that remain active throughout winter). The *nyurnma* patches surveyed during this study were likely to have burned during autumn or winter, after the goannas had chosen sites for their winter burrows for brumation, and indeed, cross-checking with satellite imagery showed that all *nyurnma* sites were *manguu* or *kunarka* when sand goanna entered the brumation period in April. Thus, goannas chose these sites when they were unburnt, and remained underground in their winter burrows after they burned to become *nyurnma*.

Invasive mesopredators have compounded the impact of fire on native wildlife in Australia (McGregor et al., 2014; Leahy et al., 2016; Hradsky et al., 2017). In some ecosystems, feral cats seek out recently burned sites, making long, direct, extraterritorial movements to hunt exposed wildlife in open habitats (McGregor et al., 2016; McGregor et al., 2017). While we found little evidence of foxes and cats seeking out the most recently burned areas, *nyurnma*, we did find foxes were

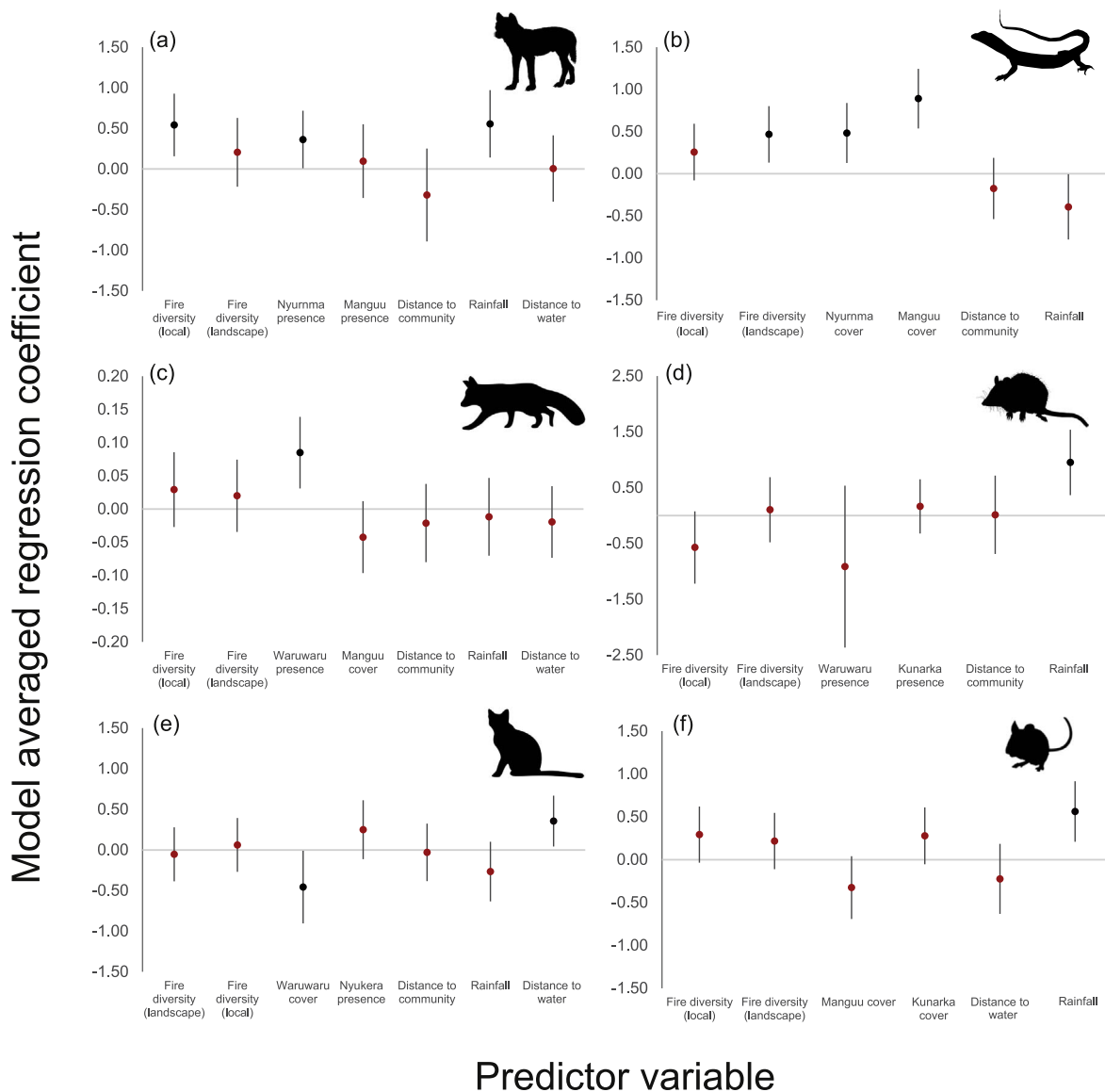


Fig. 3. Model averaged coefficients (circles) and 85% confidence intervals (lines) of ordinal regression model of the response of animal species to predictor variables in the Martu homelands of Australia's western desert. Black circles = variables for which the 85% confidence intervals do not overlap zero. Species included (common name/Martu name) are (a) dingo/wanapari, *Canis dingo*, (b) sand goanna/parnajarlpa, *varanus gouldi*, (c) red fox/waltaki, *Vulpes vulpes*, (d) mulgara/langamarlu, *Dasycercus blythi* (e) feral cat/pujikatu, *Felis catus*, (f) other rodents, primarily spinifex hopping mouse/kilu, *Notomys alexis*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

more active in the second earliest successional stage, *waruwuru*. *Waruwuru* is still a simplified ecosystem compared to mature spinifex sites, with large open spaces and few refuges for small vertebrates. Foxes may be capitalizing on this simplified ecosystem, while avoiding *nyumma* due to the increased likelihood of encountering dingoes, which are known to suppress fox activity and abundance (Letnic et al., 2012). The negative relationship between cat activity and *waruwuru* is difficult to explain. There is evidence that foxes suppress cat populations through interference competition (Risbey et al., 2000; Marlow et al., 2015). Using a fox-removal experiment, Molsher et al. (2017) showed that cats changed their diets and made greater use of open habitats in the absence of foxes. It is therefore possible that cats are avoiding *waruwuru* to avoid competition for food with the similarly sized but competitively superior fox.

Both small mammals, as well as dingoes, responded positively to antecedent rainfall. Arid ecosystems around the world are driven by rainfall (Lima et al., 1999; Letnic et al., 2004; Holmgren et al., 2006; Greenville et al., 2009), with population 'booms' (i.e. rapid increases in

population size) following periods of deluge, and busts (i.e. rapid population declines) following periods of drought. Population dynamics of small mammals and predators in arid Australia are tightly linked to rainfall (Dickman et al., 2001; Letnic et al., 2005; Letnic and Dickman, 2010). Consistent with our findings, Dickman et al. (2001) showed that mulgara abundance increased in relation to rainfall in the previous 7–9 months, while Dickman et al. (1999) and (Southgate and Masters, 1996) found spinifex hopping mice increase in abundance following above average rainfall. Predators respond to increased abundances of small mammals as a food source in turn (Letnic and Dickman, 2006; Greenville et al., 2014), driving down small mammal populations through predation. Thus, the positive relationship between dingoes and antecedent rainfall may well be linked to the increased activity of small mammals during those periods.

Although we did not observe significant relationships between the two small mammals (mulgara and mice) and fire history, we interpret this cautiously for two reasons. First, recent research has shown that faunal responses to fire history can be difficult to detect, because they

can be variable across space (Watson et al., 2012) and time (Hale et al., 2016), due to interactions between fire, vegetation and climate (Greenville et al., 2017). Using a long-term dataset, Hale et al. (2016) showed that some small mammal species in southern Australia showed significant relationships with fire history during some climatic conditions (e.g. drought) but not others. Our study was undertaken over a shorter time period and we were not in a position to model interactions between climate and fire history due to sample size. Thus, it is possible that mice and mulgara do respond to fire history, but only under particular conditions that were not present during our study. Indeed, Martu hold that hopping mice do have a relationship with fire history, albeit a complex one:

Some animals such as the kilu (hopping mice) like it both ways. They move into the burnt area to feed and then return to safety in the large unburnt spinifex hummocks where they have their burrows (Desmond Taylor).

In support of this, Letnic (2001) showed that *N. alexis* can travel up to 2 km a night, utilizing a mix of burned and unburned habitat. Thus, hopping mice may be utilizing complementary resources from burned and unburned areas across much greater distances than those captured by our measures of fire history or pyrodiversity. Further research is underway that will explore this hypothesis.

The integration of Indigenous ecological knowledge into research and conservation has been promoted as a way to boost our understanding of complex ecosystems, while at the same time promoting Indigenous concerns and values (Huntington, 2000; Yibarbuk et al., 2001; Ens et al., 2015). Here, our use of Martu ethnoecological classifications of successional stages to characterize fire history and diversity provides a way to incorporate traditional ecological knowledge into ecological research without compromising analytical and methodological rigor, or treating the ethnographic only as a source of rich environmental description. That several species responded to these classifications suggests that it was successful in capturing a meaningful measure of fire history and pyrodiversity. Further, that these responses occurred at a 1 and 20 ha scale emphasizes the multi-scalar nature of species' responses to fire history and the ecological relevance of fine-scale pyrodiversity for individual species (Parr and Andersen, 2006).

5. Conclusions

We have shown that fire-stick farming by Martu increases pyrodiversity at finer scales than recognized, and ensures the provision of older successional stages of vegetation. In doing so, Martu create preferred habitats for two species of native predator: the dingo, which was most active in pyrodiverse plots, and the sand goanna, which was most active in plots with late successional *manguu* patches. Taken together with previous work (Bliege Bird et al., 2008; Bliege Bird et al., 2013; Coddling et al., 2014), our study shows the substantial role that Aboriginal Australians play in their ecosystems when living remotely and burning in a traditional way. Of particular note are the species that Martu burning is now known to favor: the dingo, the sand goanna, and the hill kangaroo. Each of these species has played an important role in Martu livelihoods, as a source of food (goanna and hill kangaroo) or, prior to European contact, as a companion animal (the dingo). Each of these species is likely to be important to their ecosystems through predation (Letnic et al., 2009; Sutherland et al., 2011) and grazing (Foster et al., 2014). Thus, Martu burning not only creates niches for native biodiversity, it helps to facilitate the ecological role of species' that are themselves functionally vital. This work adds to a growing body of research suggesting that the loss of Aboriginal burning can cascade through ecosystems by transforming and simplifying ecological networks, thus contributing to the decline and extinction of vulnerable species.

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Conflicts of interest

The authors declare no conflicts of interest.

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