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The influence of fire mosaics on mammal occurrence in north-western Australia

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Abstract

Background Understanding the relationship between fire and species habitat preferences is critical in an era of rapid environmental change. In northern Australia, large, intense, and frequent fires are thought to be a primary cause of mammal population declines, particularly through their influence on habitat suitability. Here, we used a large species presence database in combination with satellite-derived fire history data to assess the influence of fire attributes, including burn extent, frequency, and pyrodiversity, on the likelihood of occurrence of eight mammal species in north-west Western Australia.

Results The likelihood of occurrence declined for some species with an increasing proportion of recently burnt habitat and increased for most species with an increasing proportion of long unburnt habitat. The occurrence of six species was negatively correlated with increasing fire frequency, while the occurrence of four species was positively correlated with increasing pyrodiversity.

Conclusions Our results indicate that fire likely plays an important role in influencing mammal occurrence in the Pilbara and support previous research indicating that frequent large-scale burns have a mostly negative impact on small to medium-sized mammals in northern Australia. To improve mammal habitat suitability, land managers should aim to reduce the extent of large late dry season burns and increase the availability of mature spinifex grasslands.

Keywords Fire ecology, Spatial modeling, Threatened species

Resumen

Antecedentes El entender las relaciones entre el fuego y las preferencias de hábitats por diferentes especies es crítico en una era de rápidos cambios ambientales. En el norte de Australia, se presume que fuegos frecuentes e intensos puede ser la causa primaria en la declinación de mamíferos, particularmente a través de su influencia en la disponibilidad de hábitats. En este trabajo, usamos una base de datos de presencia de grandes especies en combinación datos de fuegos derivados de satélites para determinar la influencia de los atributos del fuego, incluyendo la extensión de los incendios, su frecuencia, y piro-diversidad, en la probabilidad de ocurrencia de ocho especies de mamíferos en el noroeste de Australia.

Resultados La probabilidad de ocurrencia declinó para algunas especies con un incremento proporcional de hábitats recientemente quemados y se incrementó para la mayoría de las especies con un incremento en la proporción de hábitats no quemados por un largo período. La ocurrencia de seis especies fue negativamente correlacionada con el incremento en la frecuencia de incendios, mientras que cuatro fueron positivamente correlacionados con incrementos en la piro-diversidad.

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Conclusiones Nuestros resultados indican que el fuego puede jugar un rol importante en influenciar la ocurrencia de mamíferos en el Pilbara, y apoya investigaciones previas que indican que fuegos frecuentes de gran escala tienen un impacto más bien negativo sobre mamíferos pequeños y medianos en el norte de Australia. Para mejorar la disponibilidad de hábitats para mamíferos, los manejadores de recursos deberían tartar de reducir los incendios de gran extensión que ocurren al final de la estación de crecimiento, e incrementar la disponibilidad de pastizales espinescentes maduros.

Background

Fire is an inherent feature of many arid (rainfall/evaporation < 0.4) landscapes (van Etten et al. 2022) but plays a particularly pronounced role in the arid ecosystems of Australia's vast interior (Morton et al. 2011; Keith et al. 2022). In these landscapes, fires shape landscape structure across large areas (e.g., > 100,000 ha; Wright et al. 2021). Successive fires create "fire mosaics"—landscapes comprised of areas that differ in their fire history (Parr and Andersen 2006). Fire mosaics can be characterized in terms of their visible properties, such as the extent or diversity of fire-ages (Jones and Tingley 2022), or by their invisible properties, such as the frequency of fires within a landscape (Bradstock et al. 2005). A conservation objective in many fire-prone regions is to identify fire mosaics that enhance habitat suitability for a range of species (Jones and Tingley 2022).

One hypothesis is that diverse fire mosaics can support a broader array of species than those with a more uniform fire history (Law and Dickman 1998; Nimmo et al 2022). This theory is derived from two primary observations. Firstly, Indigenous fire stewardship often yields a patchwork of diverse fire histories, and it is under this spatial and temporal configuration of fire histories that native species have evolved (Hoffman et al. 2021). For instance, in the spinifex hummock grasslands of north-western Australia, patch-mosaic burning by Traditional Owners doubles the "pyrodiversity" of fire mosaics (i.e., diversity of fire histories within a landscape) compared to landscapes that are rarely subject to Indigenous fire (Greenwood et al. 2022). Secondly, diverse fire mosaics should, in theory, offer a broader range of resources to species and communities (Martin and Sapsis 1992). For individual species, a diverse range of resources in close proximity can facilitate landscape complementation (Nimmo et al. 2019; Stillman et al. 2021), thereby improving habitat suitability. However, the empirical evidence is mixed. Notably, Australian studies have often identified specific successional stages as being of disproportionate importance to individual species, especially "long unburnt" vegetation (von Takach et al. 2022). Increases in fire diversity that come at the expense of important successional stages may therefore reduce habitat suitability.

Since European invasion, Australia holds the world's worst record for mammal extinction (Woinarski et al. 2015). In total, 34 mammal species, including ~10% of all endemic mammal species, have been driven to extinction since 1788 (Woinarski et al. 2019). The causes of mammal extinctions are manifold and uncertain, but predation by introduced predators (feral cats and foxes) and altered fire regimes following the displacement of Indigenous people (and the interaction between them) are thought to have played a significant role (Woinarski et al. 2015, 2019). In Australia's arid landscapes, the synergy between these two processes has been offered as an explanation for the local extinction of > 20 mammal species and the declines of > 40 others following the (in some instances temporary) loss of Indigenous fire (Burbidge et al. 1988; Burrows et al. 2006). Despite widespread declines and extinctions, Australia's arid zone still hosts a diversity of small and medium-sized mammals, a number of which of which are threatened. Contemporary management of these species focuses on fire and predator management, often in partnerships between government, non-government agencies, and Traditional Owners. More recently, acknowledging the ecological expertise of Indigenous peoples in applying "right way fire"—a traditional method of controlled burning—has gained recognition as a crucial component in the strategy to mitigate further mammal extinctions (Wysong et al. 2022; Ruscalleda-Alvarez et al. 2023).

The effects of fire on many mammal species remain poorly understood, owing to a lack of systematic monitoring (Woinarski et al. 2018). Of particular interest is how mammal species respond to the spatial aspects of fire (Senior et al. 2021). In northern Australia, fire mosaics that are comprised of large amounts of recently burnt vegetation have been associated with lower species abundance and richness (Radford et al. 2015), while the opposite is true for landscapes comprising large proportions of long unburnt habitat (Andersen et al. 2005; Radford et al. 2015; von Takach et al. 2022). Some species of Australian mammal are also thought to be linked to specific combinations of fire ages, for instance sheltering in unburnt areas and foraging in nearby burnt areas (Bolton and Latz 1978; Southgate et al. 2007; Bliege Bird et al. 2018), suggesting a potentially positive influence of pyrodiversity on some individual species vis landscape complementation (Nimmo et al. 2019).

The Pilbara bioregion is located within the arid region of northwest Western Australia, a rugged and fire-prone landscape comprised vast swathes of flammable spinifex hummock grasslands. These landscapes, punctuated by granite-greenstone outcrops and ancient rocky ranges dating back over 3.6 billion years (Buick et al. 1995), are home to a diverse array of mammal species, including several threatened with extinction, such as the northern quoll (*Dasyurus hallucatus*), greater bilby (*Macrotis lagotis*), and brush-tailed mulgara (*Dasycercus blythi*). While fire is thought to play a pivotal role in the ecology of these species, research quantifying the impacts of fire on their habitat suitability is currently limited. Understanding these impacts is critical from a management perspective, particularly for species dependent on fire-prone hummock grasslands for foraging and shelter (Masters et al. 2003; Cramer et al. 2016a, 2016b; Gibson et al. 2023). Our study examines the influence of fire mosaic properties on the habitat suitability of eight native mammals across the Pilbara. Utilizing presence-only models, we explore associations between the habitat suitability of select mammal species and fire mosaic attributes, such as the diversity and extent of fire ages and the frequency of fire events. We hypothesize a negative correlation between mammal occurrence and recently burnt habitat extents owing to the short-term impact of fire on mammal shelter, exposure to predators, and food resources and a positive association with areas of long unburnt vegetation (von Takach et al. 2022).

Methods

Study area

This study was conducted within the Pilbara bioregion, an area spanning 17.8 million hectares in north-west Australia—roughly equivalent in size to the US state of Missouri. Prior to European colonization of Australia, land within the study area was managed by the Ngarluma, Yindjibarndi, Kariyarra, Banjima, Nyamal, Kuruma, Puutu Kunti Kurrama, Pinikura, Thalanyji, Nyiyaparli, Palyku, Ngarla, Yinhawangka, Eastern Guruma, Yaburara, and Mardudhunera peoples. Similar to other parts of Australia before European colonization, Aboriginal fire-management practices significantly shaped the ecosystems of the Pilbara. These practices created fine-scale habitat mosaics and limited large wildfires, which may have benefited native mammals (Bowman 1998). Contemporary burning patterns in the Pilbara are still influenced by people, but the migration of Aboriginal people to towns and communities, at times by force, has removed traditional burning practices from the landscape.

The Pilbara is bordered by the Great and Little Sandy Deserts to the north and east, the Gascoyne region to the south, and the Indian Ocean to the west (see Fig. 1). The climate in the Pilbara is defined as arid. Annual rainfall averages below 450 mm, with most of it occurring between December and March. Daily summer temperatures maximums range from 35 to 45 °C, while winter maximums are typically mild (22–30 °C). The region has distinctive geology, comprising vast expanses of open spinifex hummock grasslands intersected by steep rocky ranges and ancient granitic outcrops dating back over 3 billion years. These geological features provide important habitats for a diverse array of fauna, including endangered mammals such as the northern quoll (Moore et al 2021).

Vegetation

The Pilbara bioregion's vegetation is primarily comprised of extremely flammable spinifex (mostly *Triodia melvillei*, *T. pungens*, *T. wiseana*, *T. lanigera*, *T. epactia)* grasslands under scattered shrubs or trees (*Acacia* spp., *Grevillea* spp., *Eucalyptus* spp.) (Beard 2019) (Fig. 2). Other vegetation types in the region include acacia shrubland, open woodland, sparse shrubby steppes, and annual grasslands (McKenzie et al. 2009).

The utility of spinifex grasslands as fauna habitat varies according to the structural complexity of individual spinifex hummocks, as well as the matrix formed by hummock aggregations (Letnic and Dickman 2005). For example, spinifex grasslands comprising densely organized hummocks are preferable for some small vertebrates given they provide a maximum amount of cover which limits the vulnerability of these species to predation from larger terrestrial predators, as well as aerial hunters (Paltridge 2005; von Takach et al. 2022). Similarly, spinifex grasslands comprised of more mature plants have increased capacity to buffer ambient temperatures and thus are used by some species to help thermoregulate. By contrast, spinifex grasslands that are more open and less structurally complex can be preferable foraging habitat for species, given they are easier to navigate though and often comprise higher abundances of important food producing plant such as herbs and shrubs (Haythornthwaite 2005; Southgate et al. 2007). However, vulnerability to predation is likely to be increased here.

Importantly, the level of structural complexity present within a spinifex grassland is primarily determined by its age, which is reset each time it is burnt. Within this study area, this occurs on average once every 12

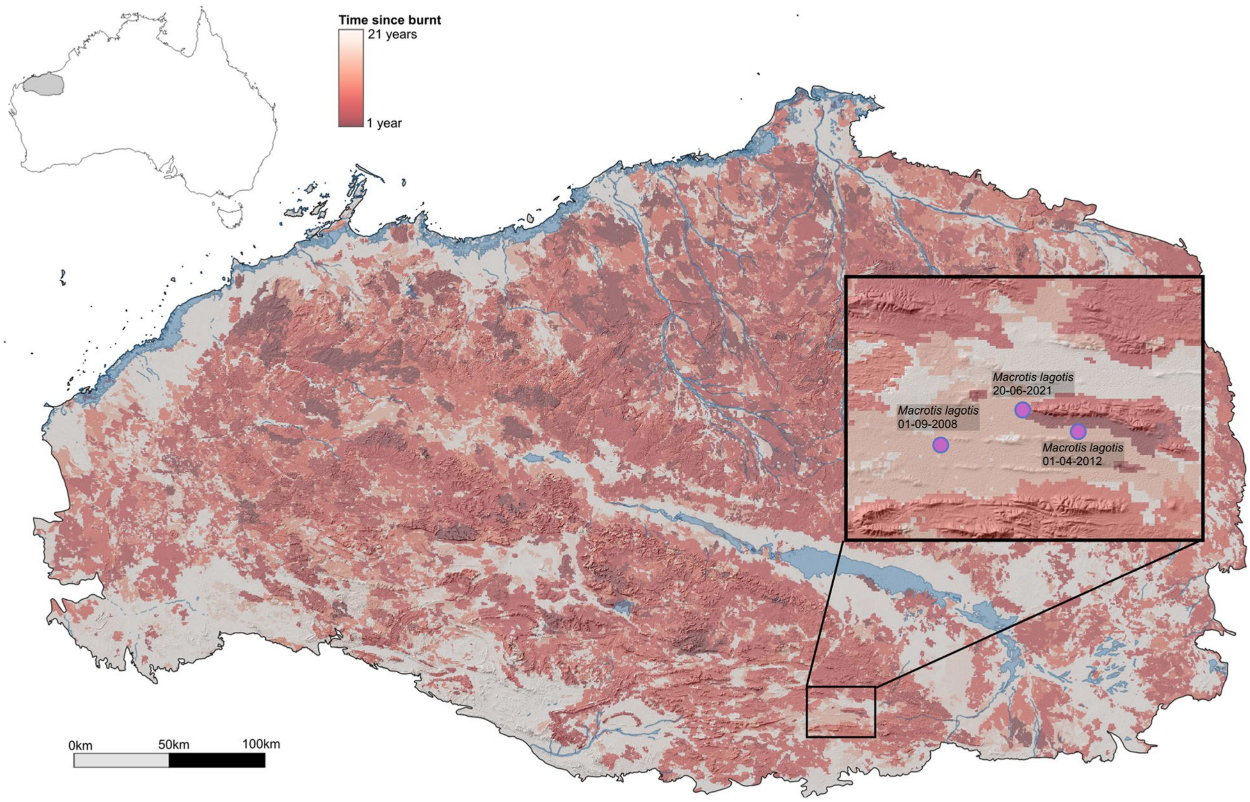

Fig. 1 Fire data illustrating time since the last burn within the Pilbara bioregion. The inset displays an example of species presence data correlated with fire attributes from the corresponding year of observation

Fig. 2 Spinifex (*Triodia spp.*) grasslands in the Pilbara Bioregion of North-West Western Australia

to 13 years (NAFI 2022). While spinifex grassland left unburnt for long periods of time can be subject to some shrub encroachment (Nicholas et al. 2009), the spinifex itself remains, with some clumps living for over 60 years (Kenny et al. 2018). This longevity contributes to the habitat's stability and supports diverse fauna by maintaining critical cover. Burning that occurs too frequently, or occurs at extensive scales, can modify habitat complexity within spinifex grasslands such that its value as habitat may be diminished.

Study species

Our study focused on eight mammal species native to northern Australia, all of which utilize spinifex grasslands for foraging, as refuge, or a combination of both (Menkhorst and Knight 2001) (Fig. 3). Species included the greater bilby (*Macrotis lagotis*) or *kartukarli* (Nyangumarta language), brush-tailed mulgara (*Dasycercus blythi*), spinifex hopping mouse (*Notomys alexis*) or *galunyja* (Yindjibarndi language), northern quoll (*Dasyurus hallucatus*) or *marlarlparra* (Nyamal) or *Yirriwardu* (Yindjibarndi), desert mouse (*Pseudomys desertor*) or *jilyku* (Nyangumarta), Pilbara Ningaui (*Ningaui timealeyi*), kaluta (*Dasykaluta rosamondae*), and sandy inland mouse (*Pseudomys hermannsburgensis*) or *jilyku* (Nyangumarta). Among these, the kaluta and Pilbara ningaui are both endemic to the Pilbara region. The northern quoll and greater bilby are listed as endangered and vulnerable respectively according to the IUCN Red List (IUCN 2024), while the brush-tailed mulgara is listed as Near Threatened under the West Australian Biodiversity Conservation Act (2016). All species are nocturnal, and typically shelter within dense vegetation, underground burrows, or dens during the day.

Presence data

We sourced species presence data from a dataset maintained by the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA). The presence records within this dataset originated from various contributors, including museums, DBCA staff, private environmental consultants, industry professionals, and the general public. Data was filtered before being included in our analysis. We discarded any records that were obviously erroneous (well outside known distribution), had high uncertainty (> 1000 m), or lacked collection dates. To mitigate the effects of spatial clustering arising from potential sampling biases, we retained only a single record per 250 m × 250 m pixel, for each year and month. Following Moore et al. (2019) and von Takach et al. (2020), we then constructed alpha hulls (a generalization of a convex hull) for each species to delineate their range within the Pilbara and exclude records outside this area. The alpha value (α) determines the tightness of the boundary around records, and we used 0.5 to create a particularly tight boundary to ensure outliers outside a species core Pilbara climatic envelope were excluded.

Fig. 3 Four of the eight species used to investigate the influence of fire attributes on mammal occurrence in the Pilbara bioregion. **a** Brush tailed mulgara (*Dasycercus blythi*), **b** spinifex hopping mouse (*Notomys alexis*), **c** kaluta (*Dasykaluta rosemondae*), and **d** northern quoll (*Dasyurus hallucatus*)

Pseudoabsence data

Given that species absence data was not available, 3000 pseudoabsence records were created for each species to address sampling bias (Kramer-Schadt et al. 2013). The distribution of pseudoabsence records was restricted to within species' alpha hulls. To compensate for spatial sampling bias in the occurrence data for each species, we modified our sampling of pseudoabsence points by incorporating a probability function that corresponded to the bias in previous sampling effort. Sampling effort within each species' alpha hull was estimated using a Gaussian kernel density grid of records of small- and medium-sized (< 5500 g) non-flying native mammals following Moore et al. (2019) and von Takach et al. (2020). The kernel density grid was created using the "kde2d" function from the "MASS" package (Ripley et al. 2013) in R version 4.1.2 (R Core Team 2021), with the default normal reference bandwidth calculation. This method allows for the proportional sampling of background points, with more points being sampled from areas with greater survey effort and fewer points from less well-surveyed regions. It also ensured that pseudoabsence records were not drawn from habitats where species were unlikely to occur based on their climatic niche.

Environmental data

Fire data used in our study was sourced from the MODIS (Moderate Resolution Imaging Spectroradiometer) vector data, available at a 250-m resolution from the North Australia Fire Information service (http://firenorth.org.au). MODIS is a sensor on board the Terra and Aqua satellites that detects and locates fires by sensing the heat and smoke they produce, as well fire scars. The data collected by MODIS is used to monitor and map wildfire activity globally, providing vital information for fire management and research (Lizundia-Loiola et al. 2020; Campagnolo et al. 2021). For our study, we assessed the status of data pixels (either burnt or unburnt) on a monthly basis between 2000 and 2021, giving 21 years of fire data.

For each species presence record, we derived four fire attributes: pyrodiversity, fire frequency, percentage of recently burnt vegetation, and percentage of long unburnt successional vegetation (refer to Table 1). We aligned these attributes with the timing of the species presence records to the year and month, meaning any fires that occurred post-collection were excluded. Post fire successional changes were therefore tracked with monthly accuracy. This alignment was executed using the Raster package (Hijmans et al. 2015) in R. Previous research indicates that the impact of fire attributes on species can differ based on the scale at which they are measured (Wan et al. 2020 ; Jones and Tingley 2022). To ensure that fire metrics were assessed at scales ecologically relevant to each species, we utilized species movement data from the literature to generate "location buffers" of varying radii around each presence record and subsequently clipping the fire data to fit these location buffers. For medium-sized mammals (> 100 g, < 5000 g) (greater bilby, northern quoll), we used a buffer of 1954 m. Evidence from the literature suggest these species can use home ranges of up to ~300 ha in size (although most are typically smaller) (Moseby and O'Donnell 2003 ; Moore et al. 2021a). By assuming this home range is circular, a radius of 977 m was calculated, which was then doubled to account for the possibility that species records may not have occurred at the center of their home range. For small mammals (< 100 g) (brush-tailed mulgara, spinifex hopping mouse, desert mouse, Pilbara ningaui, kaluta, sandy island mouse), we used a buffer of 1392 m. Previous studies have demonstrated that small arid zone mammals use relatively large home ranges and are capable of large nightly movements (Dickman et al. 1995 ; Bos and Carthew 2007 ; Körtner et al. 2019). For example, Letnic et al. (2003) found spinifex hopping mice and sandy inland mice were capable of moving more than 700 m in a single night. Based on this research, we assumed home ranges of up to 150 ha, giving a radius of 691 m, doubled to 1392 m. We excluded species presence records before 2009 to ensure there was at least 10 years of corresponding fire data available for each record, given our fire data set spanned from 2000 to 2021.

To minimize the impact of interactions between fire history and vegetation type on our investigation of fire's effects on mammals, our study focused only on spinifex grassland vegetation, excluding areas comprised of all other vegetation types. To minimize the impact of interactions between fire history and terrain, data from habitat with high topographical ruggedness were removed prior to analysis. The threshold separating flat and rugged areas was selected using a combination of fine scale topographical ruggedness data (calculated as the difference in elevation between a cell and the eight cells surrounding it (Riley et al. 1999), satellite imagery, and calibrated based on sites that have previously been ground-truthed. Rainfall can be a strong driver of fire history in northern Australia. Given that species presence and pseudo-absence records were restricted to within species' core climatic envelopes, environmental factors related to climate were not included in models. However, to ensure fire history attributes were not confounded with climate, we tested for a correlation between fire history attributes, rainfall, and temperature and found there was no such relationship (Table S1).

Table 1 Fire mosaic attributes used to investigate the effect of fire on mammal occurrence in the Pilbara bioregion

Attribute	Range	Method	Justification
Recently burnt (< 3 years since last burn)	0–100%	Calculated as the % of vegetation within a location buffer that has been burnt within the previous three years	Recently burnt vegetation was defined as vegetation which had burnt within three years. This is a period in which spinifex grassland cover and complexity is at its lowest in the Pilbara bioregion (Burrows et al. 2009)
Long unburnt (> 10 years since last burn)	0–100%	Calculated as the % of vegetation within a location buffer that has been not been burnt for at least 10 years	Long unburnt vegetation was defined as vegetation which had not burnt for at least 10 years, given 10 years post fire is roughly the time at which *Triodia* cover peaks in Pilbara and Western Desert (Burrows et al. 2009). This definition aligns with the Martu definition *kunarka*, when spinifex becomes senescent (Hernandez-Santin et al. 2019; Bliege Bird and Bird 2021). Late successional vegetation may be favored by some small mammals given it provide increased protection from predators in the form of cover and complexity when compared to earlier successional stages (Radford et al. 2021)
Fire frequency (recent)	0–∞	Calculated as the median number of times each cell within a location buffer has been burnt within the previous 10 years. Data was truncated to the previous 10 years to standardize fire history data available across records collected in different years	Fire frequency can impact fauna by altering the availability of food and shelter which they rely on. Studies in Northern Australia have demonstrated that increased fire frequency can lead to declines in small mammal populations (Andersen et al. 2005; Griffiths et al. 2015; von Takach et al. 2020)
Pyrodiversity	0–∞	Calculated using Shannon's diversity index, incorporating the three post fire successional stages: early, mid, and late. The mid-successional stage is characterized by vegetation that has not burnt for 3 to 10 years	Pyrodiversity refers to the diversity of fire regimes within a landscape. This diversity can be beneficial for small mammals by providing an array of habitats which area suited to different needs (shelter, foraging areas)

Statistical analysis

To measure the effect of fire attributes on mammal occurrence, we fit binomial generalized linear models using the "*lme4*" package (Bates et al. 2015) in R. All fire attributes (extent recently burnt, extent long unburnt, pyrodiversity, fire frequency) were included in a global model for each species. These models were then compared using the "dredge" function in the "MuMIn" package (Barton 2022), fitting 16 models for each species. The most parsimonious model was selected based on AICc. This selected model was subsequently refit, and the contributions of the variables were assessed based on model estimates. Variables with $p < 0.05$ were considered to have a significant influence. Response curves were generated for fire attributes with significant effects using the "predict" function. Model performance was assessed using conditional R^2 values, calculated using the "r.squaredGLMM" function. Model predictions were calculated using the "predict" function.

Result

The filtered dataset included 1685 species presence records, with individual species records ranging from 84 to 483 (Table 2). Additionally, there were 24,000 pseudoabsence records. The average proportion of recently burnt habitat across these records was 0.21 (SD = 0.32), and for long unburnt habitat, it was 0.44 (SD = 0.36). Only 6.5% of records were not exposed to any fire in the 10 years prior to their collection.

The proportion of recently burnt habitat had varied impacts on species presence. The greater bilby had the strongest negative response (− 3.2), followed by the brush-tailed mulgara (− 2.07) and sandy inland mouse (− 1.03). Other species showed no significant response. Conversely, most species responded positively to the proportion of long unburnt habitat. The spinifex hopping mouse (1.77) and kaluta (1.26) had the strongest positive correlations, with the sandy desert mouse (1.21) and sandy inland mouse (1.08) also showing positive responses. The Pilbara ningaui (1.04) had a moderate positive correlation. The likelihood of species presence was generally negatively correlated with fire frequency

Table 3 Generalized linear model (GLM) coefficients for the effects of fire attributes on Pilbara mammals. The table presents the coefficient estimates, standard errors (SE), and *p*-values for each species and fire attribute. Significant effects ($p < 0.05$) are highlighted in bold

Species	*Coefficient*	*Estimate*	*SE*	*p*
Brush-tailed mulgara	Intercept	-2.33	0.38	0
Brush-tailed mulgara	**Recent**	**-2.07**	**0.63**	**< 0.01**
Brush-tailed mulgara	**Frequency**	**-0.7**	**0.28**	**0.01**
Brush-tailed mulgara	Long	0.47	0.32	0.14
Desert mouse	Intercept	-2.03	0.44	< 0.01
Desert mouse	**Frequency**	**-0.68**	**0.32**	**0.03**
Desert mouse	**Long**	**1.21**	**0.37**	**< 0.01**
Desert mouse	**Pyro**	**0.7**	**0.34**	**0.04**
Greater bilby	Intercept	-1.63	0.18	0
Greater bilby	**Recent**	**-3.2**	**0.45**	**< 0.01**
Greater bilby	Long	-0.37	0.25	0.13
Greater bilby	**Pyro**	**0.92**	**0.28**	**< 0.01**
Hopping mouse	Intercept	-1.46	0.45	< 0.01
Hopping mouse	**Frequency**	**-2.54**	**0.29**	**< 0.01**
Hopping mouse	**Long**	**1.77**	**0.42**	**< 0.01**
Kaluta	Intercept	-1.87	0.36	< 0.01
Kaluta	**Frequency**	**-0.54**	**0.25**	**0.03**
Kaluta	**Long**	**1.26**	**0.29**	**< 0.01**
Kaluta	**Pyro**	**0.72**	**0.28**	**0.01**
Northern quoll	Intercept	-0.64	0.21	< 0.01
Northern quoll	**Frequency**	**-0.57**	**0.17**	**< 0.01**
Northern quoll	**Pyro**	**0.56**	**0.19**	**< 0.01**
Pilbara ningaui	Intercept	-3.16	0.3	< 0.01
Pilbara ningaui	**Long**	**1.04**	**0.36**	**< 0.01**
Pilbara ningaui	**Pyro**	**0.55**	**0.36**	**0.13**
Sandy inland mouse	Intercept	-0.42	0.34	0.21
Sandy inland mouse	**Recent**	**-1.03**	**0.44**	**0.02**
Sandy inland mouse	**Frequency**	**-1.56**	**0.25**	**< 0.01**
Sandy inland mouse	**Long**	**1.08**	**0.29**	**< 0.01**

Table 2 Study species records

Common name	Species name	IUCN status	Records
Brush-tailed mulgara	*Dasycercus blythi*	Least concern	122
Desert mouse	*Pseudomys desertor*	Least concern	125
Spinifex hopping mouse	*Notomys alexis*	Least concern	157
Kaluta	*Dasykaluta rosamondae*	Least concern	198
Northern quoll	*Dasyurus hallucatus*	Endangered	483
Greater bilby	*Macrotis lagotis*	Least concern	289
Pilbara ningaui	*Ningaui timealeyi*	Least concern	84
Sandy inland mouse	*Pseudomys hermannsburgensis*	Least concern	227

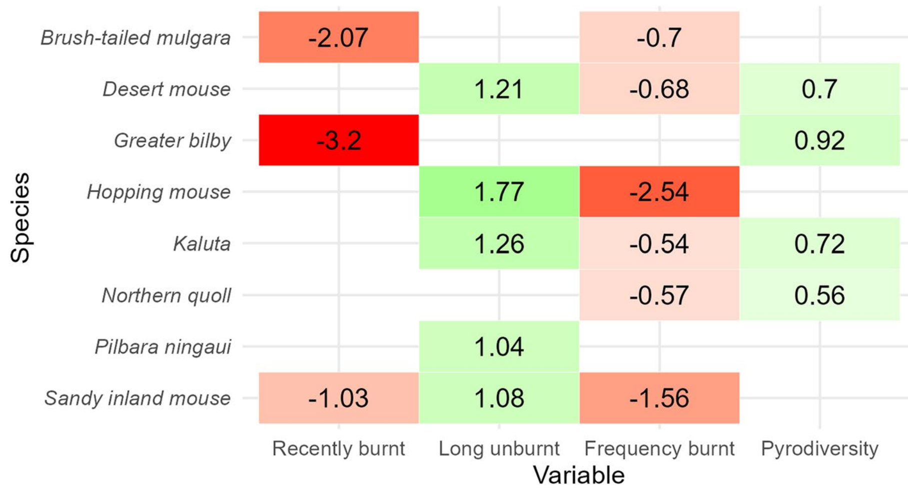

Fig. 4 Generalized linear model (GLM) estimates for significant ($p < 0.05$) fire attribute effects on Pilbara mammals. The color intensity indicates the strength of the effect, with green representing positive effects and red representing negative effects

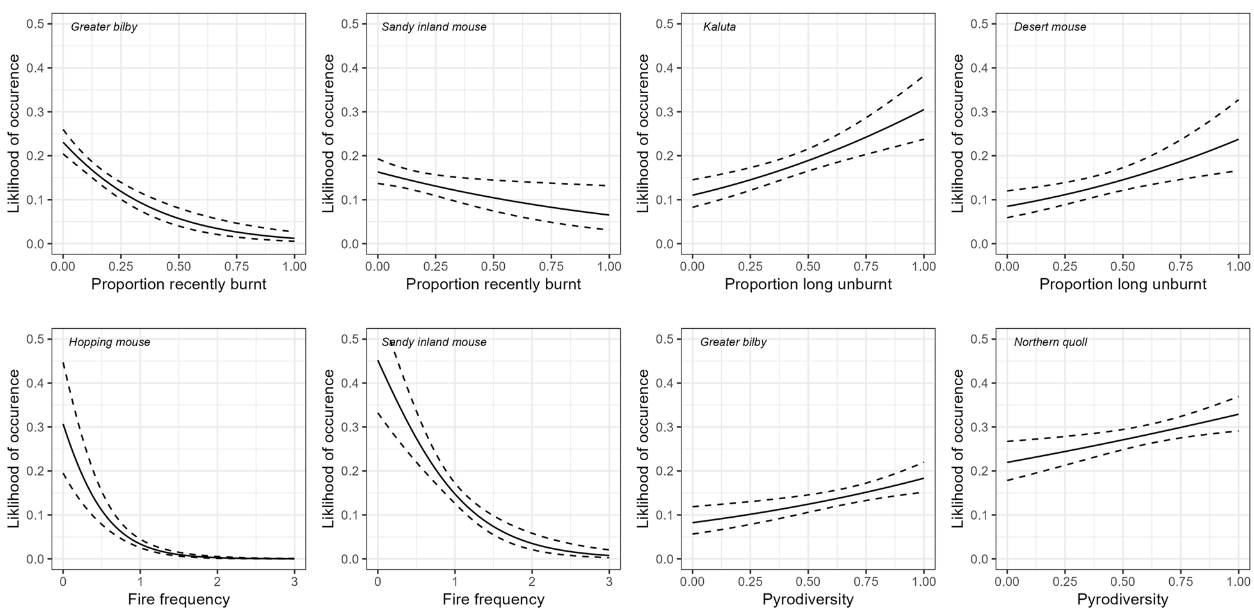

Fig. 5 Predicted likelihood of occurrence for Pilbara mammal species in relation to different fire attributes. The solid lines represent the model predictions, and the dashed lines indicate the confidence 95% intervals

(Table 3, Fig. 4). The hopping mouse (− 2.54) and sandy inland mouse (− 1.56) showed the strongest negative responses, followed by the brush-tailed mulgara (− 0.7), and desert mouse (− 0.54). Half of study species showed positive correlations with pyrodiversity. The greater bilby (0.92), kaluta (0.72), and desert mouse (0.7) had the highest positive responses, with the northern quoll (0.56) also showing positive but moderate correlation.

The likelihood of greater bilby occurrence declined by 22% from areas with no recently burnt habitat to those entirely composed of recently burnt habitat, while the sandy inland mouse showed a 10% decline under the same conditions (Fig. 5). Conversely, the likelihood of kaluta occurrence increased by 19% and desert mouse by 15% in areas with a high proportion of long unburnt habitat compared to those with none. Fire frequency had a strong negative impact on the hopping mouse and sandy inland mouse, with declines of 31% and 44%, respectively, from sites with low to high fire frequencies. The greater bilby and northern quoll showed increases of 10% and 11%, respectively, from areas with low to high levels of pyrodiversity.

Discussion

We found fire mosaic properties were strongly correlated with the occurrence of eight Pilbara mammal species. As predicted, increasing proportions of long unburnt habitat were positively correlated with occurrence for the majority of species within the study area. We also found increasing proportions of recently burnt vegetation in the surrounding landscape were negatively correlated with the likelihood of occurrence for some species. The responses of species to pyrodiversity were generally positive, while the responses of species to fire frequency were mostly negative. Overall, our results indicate that a strategic fire management approach aimed at preventing large-scale wildfires is likely the most effective way to enhance habitat suitability for the eight Pilbara mammal species targeted in this study.

The spatial extent of fire ages has been shown to play a crucial role in shaping the occurrence of mammal species in arid Australia (Kelly et al. 2012; Senior et al. 2021). Here, we found the extent of recently burnt habitat was an important fire mosaic property affecting occurrence of the greater bilby, brush tailed mulgara, and the sandy inland mouse. This result is consistent with previous research in similar ecosystems which suggest smaller dasyurids (e.g., southern ningaui, *Ningaui yvonneae*, crested-tail mulgara, *Dasycercus cristicauda*) (Masters 1993, 1998; Letnic 2003; Kelly et al. 2010, 2011) and some rodents (desert mice, sandy inland mouse) (Southgate and Masters 1996) are less common in recently burnt areas (Griffiths and Brook 2014). For example, How and Cooper (2002) found fewer small mammal species in *Triodia* dominated habitats following fire than in habitats that remained unburnt, and Hayes (2018) found Kaluta were absent in habitat burnt within 5 years. Research focused from more temperate systems have also produced similar findings. For instance, Puig-Gironés et al. (2018) found woodmice (*Apodemus sylvaticus*) abundance declined in the first 18 months following fire at sites located across Catalonia, a Mediterranean section of the Iberian Peninsula. The reduced occurrence of mammals in recently burnt areas could be due to a combination of mortality during fire (Jolly et al. 2022), the loss of specific habitat components that are consumed by fire (e.g *Triodia*; Kelly et al. 2011), and a related increase in predation risk (Doherty et al. 2022). For example, mulgaras (Koertner et al. 2007) and northern quolls (Oakwood 2000) have been shown to be predated on more often in burnt rather than unburnt areas. Similarly, Conner et al. (2011) found hispid cotton rat (*Sigmodon hispidus*) survival declines followed fire, with half of the animals monitored being depredated within a month.

Mature *Triodia* is believed to be a crucial resource for arid vertebrates, offering protection against extreme temperatures and predators (Masters 1993; Kelly et al. 2011; McDonald et al. 2016; Moseby et al. 2016). Consistent with this, we found that the extent of long unburnt vegetation increased likelihood of occurrence for five of the eight study species. Previous research focusing on arid small mammal species has found similar results (Masters 1993; Kelly et al. 2011; Griffiths and Brook 2014). For instance, Letnic et al. (2005), Letnic (2003), Masters (1993), and Mcdonald et al. (2016) found desert mice were more likely to occur in habitat that had not burnt for 5–25 years when compared to recently burnt habitat. Similarly, Hayes et al. (2018) found kaluta were strongly associated with spinifex that had not been burnt for at least 10 years. Kelly et al. (2011) found that the probability of Mallee Ningaui (*Ningaui yvonneae*)—a closely related species to the Pilbara ningaui—occurrence within spinifex grasslands increased dramatically in the first 30 years since being burnt but did not peak until 100 years post fire. Our results, combined with those of previous studies in arid landscapes, highlight that mature patches of *Triodia* provide critical habitat for a range a small to medium sized marsupials, and thus preserving them should be a focus for fire management in these areas (Fisher and Wilkinson 2005; Moseby et al. 2016; von Takach et al. 2020).

Our study found that the likelihood of occurrence for six of the eight mammal species targeted in our analysis was strongly negatively correlated with fire frequency. Despite being one of the least studied fire regime attributes impacting Australian fauna, existing literature provides strong evidence that increasing fire frequency generally has negative effects on native mammals, particularly in northern Australia (Woinarski et al. 2010; Griffiths et al. 2015; Radford et al. 2015). For example, in a recent synthesis of fire driven declines of Australian mammals, Santos et al. (2022) found frequent fires were a primary cause of population declines by reducing survival rates, disrupting reproduction, and altering habitats. Similarly, in the tropical Kimberley region, Radford et al. (2015) found that the abundance and richness of mammals tended to be higher in areas where there were fewer late dry season fires. In a more arid landscape, Senior et al. (2021) found the occurrence of seven species of microbat was negatively correlated with increasing fire frequency. The mechanisms by which fire frequency impacts species is likely related to the provision of resources; high fire frequency, or low fire intervals, limit the time available for important resources to recover post-fire, such as logs and hollows (Woolley et al. 2018). High fire frequency can also change plant composition, removing species that may be important in terms of food or shelter (Knuckey et al. 2016).

We found increasing pyrodiversity was positively correlated with likelihood of occurrence for half of the study species included in this study. A recent review revealed that most studies investigating how pyrodiversity affects biodiversity found minimal impact, particularly in the case of mammals (Jones and Tingley 2022). The positive associations observed here may reflect the use of fire mosaics by individual species via landscape complementation (Nimmo et al. 2019), whereby animals use different fire history patches for different purposes. For example, similar to our results, Southgate et al. (2007) found bilby occurrence was associated with high fire-age heterogeneity. They suggest that bilbies use more recently burnt habitat for foraging, while longer unburnt areas provide shelter. Studies of pyrodiversity in the nearby Western Deserts have also found positive associations between pyrodiversity and individual species (Bliege Bird et al. 2018). The modest strength of the relationships we observed may relate to differences in the drivers of pyrodiversity across our study region compared to parts of the Western Deserts studied by Bliege-Bird et al. (2018), the latter being under more active Indigenous fire stewardship where regular hunting burns maintain a fine-scaled mosaic of fire histories (Burrows et al. 2006; Hernandez-Santin et al. 2019). By contrast, in the Pilbara, the influence of pastoralists as well as government land managers (DBCA) on the fire regime is more pronounced, leading to more coarse fire mosaics (Stretch 1996).

It is important to note that the number of fire metrics we could include in this study was limited by the available fire data in such a remote location. For example, fire data were only available for a relatively short period (2000 onward), and as such, fire histories beyond 10 years were not available for many of the species records used, and thus were not considered here. Likewise, metrics related to fire severity were also not available and thus were not considered. However, the four variables that we have chosen to focus on are among those most frequently reported in the literature as being important in determining mammal habitat suitability (Griffiths and Brook 2014; Senior et al. 2021; Santos et al. 2022). Temporal elements of these variables (time since burnt) have been adapted to capture key post-fire successional stages in spinifex grasslands and therefore are likely to capture the most important changes in resource availability relevant to predicting habitat utility (Burrows et al. 2009). As such, we feel these variables are sufficiently relevant for the purposes of this work. We also acknowledge that they may not capture all the nuances of species responses to fire in such a unique environment, and therefore future research using more detailed fire mapping data is recommended.

Our results reinforce previous research that has demonstrated the negative impact of frequent large-scale fire on a range of small-to-medium sized mammals in arid Australia (Letnic and Dickman 2005; Andersen et al. 2012; Radford et al. 2015; Shaw et al. 2021). Given this, fire management strategies that minimize the likelihood of large wildfires, such as those employed by Indigenous fire stewardship prior to the arrival of Europeans in the Pilbara (Bliege Bird et al. 2012), are strongly encouraged.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00317-4.

Additional file 1: Table S1. Correlation matrix of model variables showing pairwise correlations. Table S2. Model selection table for generalized linear models assessing the effects of fire on mammal occurrence in the Pilbara.

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Authors' contributions

H.M. contributed to the conception, analysis, writing, and editing of the manuscript. D.N. contributed to the conception, writing, and editing of the manuscript. L.G. was involved in editing the manuscript.

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Availability of data and materials

The data that support the findings of this study are available from the Western Australian Department of Biodiversity, Conservation and Attractions, but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Some data may be available from the authors upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests
The authors declare that they have no competing interests.

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