



## Indigenous pyrodiversity promotes plant diversity

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### ABSTRACT

Pyrodiversity (temporally and spatially diverse fire histories) is thought to promote biodiversity by increasing environmental heterogeneity and replicating Indigenous fire regimes, yet studies of pyrodiversity-biodiversity relationships from areas under active Indigenous fire stewardship are rare. Here, we explored whether Indigenous pyrodiversity promoted plant richness and diversity in an arid ecosystem from north-western Australia. We selected landscapes that ranged from highly pyrodiverse and under active Indigenous burning to more coarse-scale and less diverse mosaics under lightning fire regimes. We modelled how the visible (time-since-fire diversity and proportion of post-fire successional stages) and invisible fire mosaic (fire frequency diversity and maximum proportion of landscape burnt) influenced plant richness and diversity, including edible plants. We found evidence that pyrodiversity maintained by Indigenous people increases the richness and diversity of some plant groups: time-since-fire diversity was associated with higher total plant richness and diversity; fire frequency diversity was associated with higher total plant diversity; and total plant diversity decreased with increasing the maximum proportion of a landscape that had burnt. Additionally, we found that some plant groups, including culturally important edible plants, were sensitive to the spatial extent of specific fire ages. By linking our previous work that shows Indigenous burning promotes pyrodiversity and reduces fire size, we find evidence for the notion that Indigenous fire stewardship, through the provision of pyrodiversity, promotes plant richness and diversity. Our work highlights the importance of Indigenous burning for maintaining and promoting plant diversity in fire-prone ecosystems.

### 1. Introduction

Many ecosystems have long evolved with fire (Pausas and Keeley, 2009), yet it remains a challenge for fire managers to identify fire regimes that enhance and maintain biodiversity (McLauchlan et al., 2020). One prominent method proposes the creation of ‘pyrodiverse’ landscapes—a fine scale mosaic of fire histories (Martin and Sapsis, 1992). A diversity of fire histories is thought to enhance biodiversity by increasing the diversity of niches, limiting the likelihood of large, severe fires, and, in some regions, by replicating Indigenous fire regimes (Martin and Sapsis, 1992). Indigenous fire regimes promote pyrodiversity through burning small, frequent, low-intensity fires in regions across the world; in Australia (Bliege Bird et al., 2008), South America (Pivello, 2011), North America (Roos et al., 2021), and Africa (Sheuyange et al.,

2005). The loss of fine-scale fire mosaics following Indigenous displacement and dispossession has been implicated in species declines (Liebmann et al., 2016; Woinarski et al., 2015), supporting the notion that Indigenous fire stewardship promotes biodiversity around the world (Hoffman et al., 2021).

Whether or not pyrodiversity promotes biodiversity appears to be highly contextual (Jones and Tingley, 2021); some show support for the “pyrodiversity begets biodiversity” hypothesis (Ponisio et al., 2016; Sitters et al., 2014), while others do not (Davis et al., 2018; Taylor et al., 2012). In some instances, the spatial extent of particular successional stages—rather than pyrodiversity per se—can be disproportionately important for promoting diversity (Taylor et al., 2012). The vast majority of studies of the pyrodiversity-biodiversity relationship have focussed on animal communities (Jones and Tingley, 2021), but studies

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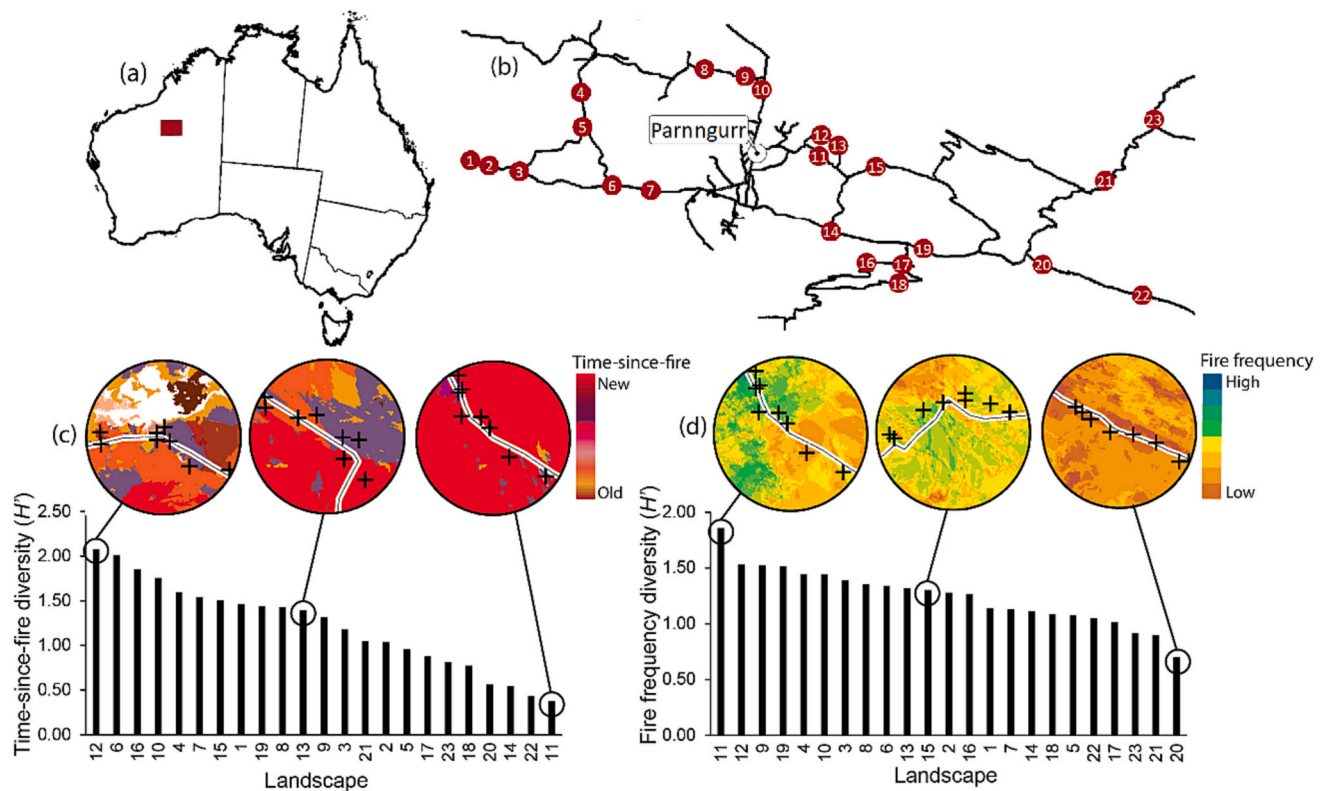
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**Fig. 1.** (a) Study area in Australia highlighted by red rectangle and (b) 23 study landscape (5 km diameters), black lines: roads. Diversity of (c) time-since-fire ages ( $H'$ ) and (d) fire frequency patches ( $H'$ ) for study landscapes, white lines: roads, crosses: sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of plant communities reflect the broader trend (Jones and Tingley, 2021); some show that pyrodiversity promotes plant richness and diversity (Ponisio et al., 2016; Wilkin et al., 2021), whereas others show that plant diversity peaks at moderate levels of pyrodiversity (McGrannan et al., 2018). Gordijn and O'Connor (2021) highlight that different plant groups can respond differently to pyrodiversity, for instance, owing to their life history strategies.

One factor that might explain the context-dependence of the pyrodiversity begets biodiversity relationship is consideration of historical levels of pyrodiversity under which communities evolved (Martin and Sapsis, 1992). In many fire-prone regions, this means understanding how current patterns of pyrodiversity relate to pyrodiversity maintained under Indigenous fire stewardship. However, few pyrodiversity studies occur where Indigenous fire stewardship continues to maintain historic patterns in pyrodiversity (but see Bliege Bird et al., 2018). Given Indigenous fire regimes are highly tailored, both spatially and temporally (Hoffman et al., 2021), contemporary patterns of pyrodiversity in landscapes devoid of Indigenous people are unlikely to bear much resemblance to those of pre-colonial times.

While pyrodiversity can be conceptualised in numerous ways (Jones and Tingley, 2021), there are “visible” and “invisible” components that warrant consideration (Bradstock et al., 2005; Parr and Andersen, 2006). The visible fire mosaic describes the attributes of the most recent and visible fire patterns (Bradstock et al., 2005), such as the diversity of time-since-fire patches (e.g. Bliege Bird et al., 2008; Sitters et al., 2014). Less studied and hidden under the scars of the most recent fires—the invisible mosaic describes the cumulative underlying, long term spatiotemporal patterns of fires (Bradstock et al., 2005), such as the diversity of fire frequency patches (Brown and York, 2017). Consideration of the invisible mosaic is important, as variation in the invisible mosaic can create differences in species composition and vegetation structure (Burgess et al., 2015; Brown and York, 2017).

Over a quarter of arid Australia is dominated by the superior

competitor, spinifex (*Triodia* spp.) (Wright et al., 2021). In spinifex grasslands, fire is thought to be an important driver of plant communities because it removes the competitive pressure of spinifex by killing or reducing spinifex to its' roots (Rice and Westoby, 1999) and cues germination through heat and smoke (Commander et al., 2008; Commander et al., 2017). Reduced competition allows a suite of sub-shrubs, herbs, and grasses, including many of the edible species important to Indigenous Australians, to germinate and reproduce in mid-successional stages (Burrows et al., 2020; Latz, 1995; Wright and Clarke, 2007). When spinifex regains dominance in later-successional stages, many small statured species disappear, and composition shifts to taller shrubs and trees that can persist with mature spinifex hummocks (Burrows et al., 2020; Wright and Clarke, 2007). Distinct plant communities within each successional stage lend itself to the idea that visible diversity (time-since-fire diversity and proportion of post-fire successional stages) could increase landscape-level plant richness and diversity (Burrows et al., 2020; Latz and Griffin, 1978). The effects of fire frequency in spinifex grasslands are less understood, however Wright and Clarke (2007) show that short fire intervals can reduce spinifex seedling abundance. If differing levels of fire frequency create differing levels of competitive pressure, which supports distinct plant communities, landscapes with a diversity of fire frequency patches could increase plant richness and diversity.

Martu, which includes Manyjilyjarra, Kartujarra, Kiyajarra, Putijarra, Nyiyaparli, Warnman, Ngulipartu, Pitjikala, Kurajarra, Jiwaliny, Mangala, and Nangajarra language groups, are the Traditional Owners of a vast number of estates in Western Australia. Martu resisted the colonisation process until the mid-1960s, and thus many elders have traditional fire experience and knowledge that pre-dates European contact. Today Martu concentrate burning along roads (within 5 km) and within 50 km of communities (Bird et al., 2013), creating a gradient of pyrodiversity across the landscape (Bliege Bird et al., 2008; Greenwood et al., 2021). Martu regard landscapes as *ngurra juri* (sweet

country) when they contain a fine mosaic of these successional stages (i.e., are pyrodiverse) (Bird et al., 2016). Areas close to communities are highly pyrodiverse, with the diversity of both visible and invisible properties of fire mosaics decreasing rapidly with increasing distances from communities (Bliege Bird et al., 2008, Greenwood et al., 2021).

Here, we explore whether Indigenous pyrodiversity promotes plant richness and diversity, including edible plants, at the landscape scale (sensu Bennett et al., 2006). We examine how the visible (time-since-fire diversity and proportion of post-fire successional stages) and invisible fire mosaic (diversity of fire frequency patches and the maximum proportion of landscape burnt in any year) influence richness and diversity of all plant species, sub-shrubs, edible species, edible sub-shrubs, and edible shrubs and trees. We hypothesised that: (1) total species and edible richness and diversity would increase with time-since-fire and fire frequency diversity; (2) sub-shrub and edible sub-shrub richness and diversity would increase with extent of mid-successional stages; (3) edible shrub and tree richness and diversity would increase with extent of late-successional stages; and (4) total and edible richness and diversity would decline with maximum area of landscape burnt. We interpret our findings through an Indigenous burning lens by drawing on prior work that shows that Martu increase diversity in the visible and invisible fire mosaic and decrease fire size (Bliege Bird et al., 2012; Bliege Bird et al., 2018; Greenwood et al., 2021).

## 2. Methods

### 2.1. Study system

Our study area was within the Martu Native Title determination and Karlamilyi National Park in Western Australia (Fig. 1). This research is part of a larger, long-term collaborative project with Martu communities on the social and ecological dynamics of Martu cultural landscapes. The area is characterised by high evaporation rates, fluctuating temperatures (10–40 °C), and low, variable rainfall (113–817 mm; annual average 370 mm) (BOM, 2019). The main ecological communities are sandplains and dunes dominated by spinifex (*Triodia schinzii* and *T. basedowii* complex), wattles (including *Acacia pachycarpa* and *A. ligulata*), and desert bloodwoods (*Corymbia chippendalei*); rocky ranges dominated by spinifex grasslands and wattle shrublands; watercourse margins and wash areas sparingly dominated by eucalypts (primarily *Eucalyptus victrix* and *E. camaldulensis*); lateric uplands dominated by mulga (*Acacia aneura*) woodlands; and *Senna* shrublands.

### 2.2. Fire mapping

We used detailed fire maps created by RBB to quantify the fire histories of our study area. RBB has digitised every fire in the study area using a time series of 30 m resolution Landsat 5 TM two image mosaics taken at roughly six month intervals (barring cloud free days) from 1990 to 2019 (see Bliege Bird et al., 2012 for more details).

### 2.3. Landscape and site selection

We used a whole of landscape approach to measure the influence of pyrodiversity on landscape-scale plant diversity (sensu Bennett et al., 2006). We used ArcMap to overlay 5 km landscapes that were within 2 km from a road, to ensure ease of access and to reduce the likelihood of entering *ngarlu* (sacred) areas (ESRI, ArcGIS Desktop: Release 10.7.1. Redlands, California: Environmental Systems Research Institute, 2019). Then, we selected 23 study landscapes to capture variation in diversity of time-since-fire patches and the number of fires landscapes experienced over a 29-year period (Fig. 1). Our final 23 landscapes ranged from 3 to 27 in number of fires, 0.38–2.08 in diversity of time-since-fire patches (Shannon's diversity index  $H'$ ), 0.70–1.86 in diversity of fire frequency patches ( $H'$ ) (patches within landscapes burnt 3–9 times), and 0.66–7 h from Martu communities (Fig. 1).

We selected eight sites within each landscape to capture variation in time-since-fire ages, while also being mindful to capture as much variation as possible in post-fire successional stages and variation in fire frequencies within landscapes. Each site was at least 500 m from the nearest site to enhance independence and at least 200 m from roads. Additionally, all sites were in spinifex sandplain (i.e., sandy substrate and dominated by *Triodia* spp. with minimal trees) because it is the most common vegetation type of our study area (85.6 %) and it is where Martu conduct the majority of their burning (Bliege Bird et al., 2008; Bliege Bird et al., 2012).

### 2.4. Vegetation surveys

We sampled sites between June and August 2019. At each site, we established three 10 × 10 m quadrats and LG estimated the cover of each plant species. Both live species and those that had died from causes other than fire (i.e., that were not obviously burnt) were recorded. Specimens of new species were collected for identification using plant identification keys (Department of Biodiversity Conservation and Attractions, 2021). Unknown species were identified by expert botanist SvL.

### 2.5. Response variables

First, we created lists of species and their proportions for each landscape by summing the number of species and their proportion across all eight sites within each landscape. We created plant groups by defining herbs as plants that did not develop woody stems, sub-shrubs as plants that developed multiple woody stems that did not grow higher than 2 m, shrubs as plants that developed multiple woody stems that grew higher than 2 m, and trees as plants with a single main stem or trunk. We identified edible species by collating ethnographic sources (Crabtree et al., 2019; Walsh, 1988; Walsh and Douglas, 2011; Department of Biodiversity Conservation and Attractions, 2021; Veth and Walsh, 1988; Zeanah et al., 2015).

We used these species lists to calculate: (i) species richness (total number of species in each landscape) (227 species), (ii) species diversity (species abundance in each landscape and evenness of their proportion using Shannon's diversity index  $H'$ ), (iii) sub-shrub richness (97 species), (iv) sub-shrub diversity ( $H'$ ), (v) edible species richness (29 species), (vi) edible species diversity ( $H'$ ), (vii) edible sub-shrub richness (7 species), (viii) edible sub-shrub diversity ( $H'$ ), (ix) edible shrub and tree richness (19 species), (x) edible shrub and tree diversity ( $H'$ ) for each landscape. We investigated sub-shrubs and shrub and trees separately because we assumed that fire would have the largest effects on sub-shrubs (Burrows et al., 2020) and the groups would show different responses due to different life histories (i.e., short/long lived) and responses to fire (i.e., regenerate from seed/re-sprout following fire) (Nano and Clarke, 2011). We grouped shrubs and trees together, as our sites had minimal trees. We were unable to explore short/long lived and regenerate from seed/re-sprouting categories due to a lack of information.

### 2.6. Predictor variables

We considered eight predictor variables as potential drivers of our plant species richness and diversity variables at the landscape scale: (i) time-since-fire diversity ( $H'$ ), (ii) diversity of fire frequency patches ( $H'$ ), (iii) maximum landscape area burnt in any year (ha), (iv) proportion of recently burnt, (v) proportion of mid-succession, (vi) proportion of long unburnt, (vii) proportion of spinifex sandplain, and (viii) several measures of antecedent rainfall.

To calculate the diversity of time-since-fire patches, we assigned all polygons within a landscape with their most recent fire-age (Fig. 1). Then, we calculated  $H'$  of each landscape based on the number and proportional extent of fire ages; a widely used approach to quantify pyrodiversity (e.g., Bliege Bird et al., 2008; Sitters et al., 2014). To calculate the diversity of fire frequency patches, we first assigned

polygons according to the number of times they had been burnt over the 29-year period (Fig. 1). We then calculated  $H'$  of each landscape based on the proportional number and extent of each fire frequency class. Additionally, we calculated the maximum area (in hectares) that burnt each year within each landscape across the 29-year fire history.

We used fire maps to group time-since-fire ages into post-fire successional stages. Martu recognise five post-fire successional stages; *nyurnma*: recently burnt patches, *waru waru*: plants re-sprout following rain, *nyukura*: plants mature and produce flowers/fruit, *manguu*: spinifex dominates and can carry fire, and woody shrubs produce nectar, and *kunarka*: spinifex hummocks senesce in the centre (Bliege Bird et al., 2008). We defined our successional stages based loosely on these definitions, as well as ethnographic experience that compared sites where Martu hunters defined successional stages against time-since-fire ages derived from satellite imagery (Bliege Bird et al., 2008; Bliege Bird et al., 2018). We do not use the Martu terms for the successional stages given the relatively crude approach. Each Martu successional stage is defined by the life history stage of its corresponding plant community, which can vary with rainfall, and hence the actual time-since-fire that any successional stage appears is more variable than our scheme (Bliege Bird et al., 2008). Nevertheless, our successional stage classification broadly corresponds with Martu functional definitions; recently burnt: 0–6 months post-fire (roughly equivalent to *nyurnma*), mid-succession: 6 months – 5 years post-fire (*nyukura*), late-succession: 5–10 years post-fire (*manguu*), and long unburnt: 10 + years post-fire (*kunarka*). We have no rough equivalent for *waru waru* as its timing is highly variable, brief, and most dependent on rainfall (which was scarce prior to surveys).

In this ecosystem, spinifex (predominantly *Triodia schinzii* and *T. basedowii* complex) is the main fuel load component (Burrows et al., 2006a) because of its highly flammable, persistent, sclerophyllous leaves (Wright and Clarke, 2008). Other plants can also contribute to fuel, but mostly after large rainfall events (Allan and Southgate, 2002). To calculate the percentage of spinifex sandplain, we used vegetation maps created by RBB, who derived major habitat boundaries from high resolution satellite imagery and calculated the percent cover for each landscape in Fragstats v4.3 (McGarigal et al., 2012).

Rainfall is a major driver of fire events in arid environments as the growth of spinifex is dictated largely by rainfall (Allan and Southgate, 2002; Burrows, 2006; Ruscalleda-Alvarez et al., 2023). To explore how rainfall affected response variables we downloaded monthly grids (5 km resolution) from the Bureau of Meteorology ([www.bom.gov.au](http://www.bom.gov.au)) and extracted monthly rainfall for the centre of each landscape. We used this to calculate: (i) cumulative 1-year rainfall prior to vegetation surveys, (ii) cumulative 2-year rainfall, (iii) cumulative 3-year rainfall, and (iv) average annual rainfall over the entire 29-year period.

## 2.7. Data analysis

We used generalised linear models to explore the relationship between our predictor and response variables. Diversity variables were continuous and followed a Gaussian distribution, and count data followed a Poisson distribution. If count data was over dispersed (i.e., when dispersion parameters were > 1.5) we fit negative binomial models.

We first investigated which rainfall variable was most appropriate to retain in the models by creating a global model that included all predictor variables (including all successional stages) and only one of the rainfall variables. We then used Akaike Information Criterion adjusted for smaller sample sizes (AICc) to assess which rainfall variable best explained variance in the data, retaining the variable with the lowest AICc for further analysis (Burnham and Anderson, 2002). Then, for each response variable, we created three global models containing time-since-fire diversity, diversity of fire frequency patches, maximum area of landscape burnt, proportion of spinifex sandplain, the retained rainfall variable, and the proportional cover of one of successional stages (i.e., either recently burnt, mid-succession, or long unburnt). Fitting

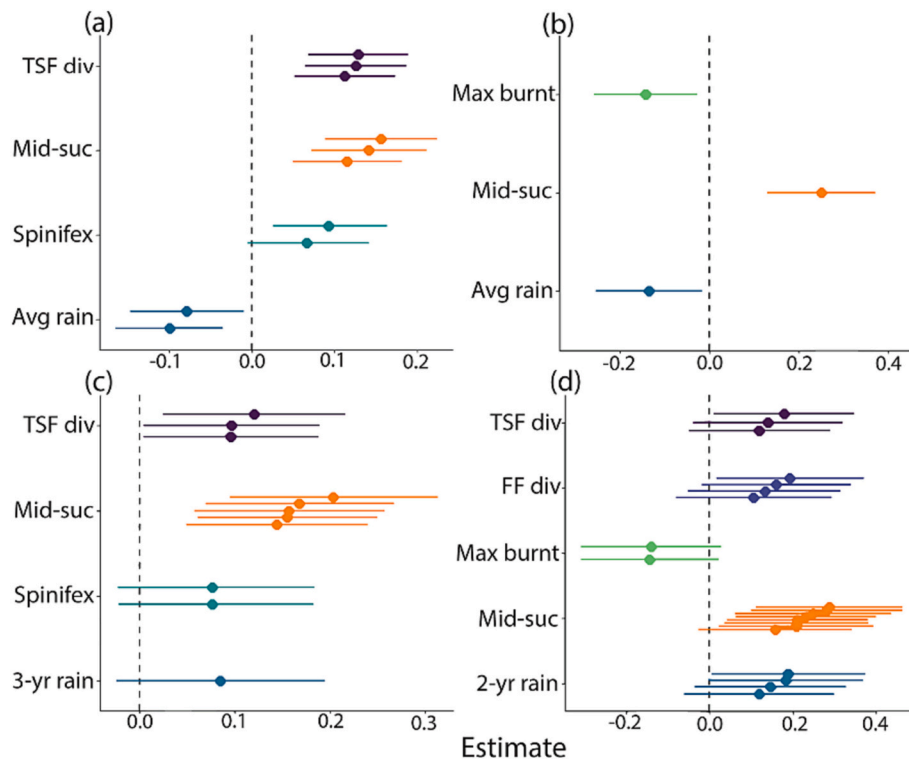
**Table 1**

Model selection for how time-since-fire diversity ( $H'$ ) (TSFDiv), diversity of fire frequency patches ( $H'$ ) (FFDiv), maximum landscape burnt (MaxBurnt), proportion of recently burnt (recent), proportion of mid-succession (mid-suc), proportion of long unburnt (unburnt), proportion of spinifex sandplain, and an antecedent rainfall variable affects plant response variables. AICc: model rank,  $\Delta$ AICc: difference between top model and described model,  $w_i$ : likelihood of the model being the best in the candidate set,  $R^2$ : model fit. Only models within 2  $\Delta$ AICc are shown.

Response variable	Model	AICc	$\Delta$ AICc	$w_i$	$R^2$
Total species richness	TSFDiv + mid-suc + spinifex + rain	164.97	0.00	0.29	0.82
	TSFDiv + mid-suc + rain	165.01	0.04	0.28	0.79
	TSFDiv + mid-suc + spinifex	166.67	1.70	0.12	0.78
Total species diversity	MaxBurnt + mid-suc + rain	11.77	0.00	0.33	0.56
	TSFDiv + mid-suc	143.78	0.00	0.14	0.47
	TSFDiv + mid-suc + rain	144.41	0.64	0.10	0.52
	TSFDiv + mid-suc + spinifex	144.47	0.69	0.10	0.52
	Mid-suc	145.35	1.58	0.06	0.37
Sub-shrub richness	Mid-suc + spinifex	145.74	1.97	0.05	0.43
	TSFDiv + mid-suc + rain	26.30	0.00	0.11	0.44
	MaxBurnt + mid-suc	26.90	0.60	0.08	0.33
	Mid-suc	27.12	0.81	0.07	0.23
	FFDiv + mid-suc	27.61	1.30	0.06	0.31
	TSFDiv + mid-suc	27.69	1.38	0.05	0.31
	FFDiv + mid-suc + rain	27.73	1.42	0.05	0.40
	MaxBurnt + mid-suc + rain	28.00	1.69	0.05	0.39
	FFDiv	28.12	1.81	0.04	0.20
	TSFDiv + FFDiv + mid-suc + rain	28.24	1.93	0.04	0.48
Sub-shrub diversity	Spinifex + rain	157.91	0.00	0.11	0.26
	Mid-suc	158.54	0.63	0.07	0.13
	Unburnt + spinifex + rain	158.65	0.74	0.07	0.33
	Spinifex	158.73	0.82	0.08	0.12
	Mid-suc + spinifex	158.84	0.93	0.06	0.22
	Recent + rain	158.87	0.96	0.07	0.22
	Recent	159.23	1.16	0.06	0.10
	Unburnt + spinifex	159.35	1.33	0.06	0.21
	TSFDiv + Unburnt + spinifex	159.37	1.44	0.05	0.31
	Mid-suc + spinifex + rain	159.41	1.47	0.05	0.31
Edible species richness	TSFDiv + mid-suc	159.56	1.50	0.05	0.20
	Recent	4.33	0.00	0.17	0.21
	Recent + rain	4.92	0.59	0.13	0.28
Edible species diversity	MaxBurnt + recent + rain	6.09	1.76	0.07	0.25
	Unburnt	122.04	0.00	0.28	0.28
Edible sub-shrub richness	Unburnt	23.86	0.06	0.10	0.11
	MaxBurnt	23.93	0.14	0.11	0.10
	Rain	24.04	0.25	0.14	0.10
	Unburnt + rain	24.23	0.44	0.08	0.20
	TSFDiv + rain	25.47	1.68	0.07	0.16
	MaxBurnt + unburnt	25.63	1.84	0.04	0.15
	Spinifex	141.64	0.00	0.16	0.07
	Recent	141.72	0.97	0.10	0.07
	Spinifex	27.21	0.00	0.24	0.21
	FFDiv + spinifex	28.85	1.64	0.10	0.25

separate models for each of the successional stages reduced the number of predictor variables in each model and avoided collinear variables being included in the same model. We assessed which model combinations, combining all three global models, were most parsimonious (i.e., lowest AICc and within 2  $\Delta$ AICc of the top model) (Burnham and Anderson, 2002). We deemed predictor variables important if 95 %





**Fig. 2.** Estimated model coefficients (dots) and 95 % confidence intervals (lines) from models with substantial support (i.e.,  $w_i < 2$ ) for (a) total species richness, (b) total species diversity ( $H'$ ), (c) sub-shrub richness, and (d) sub-shrub diversity ( $H'$ ).

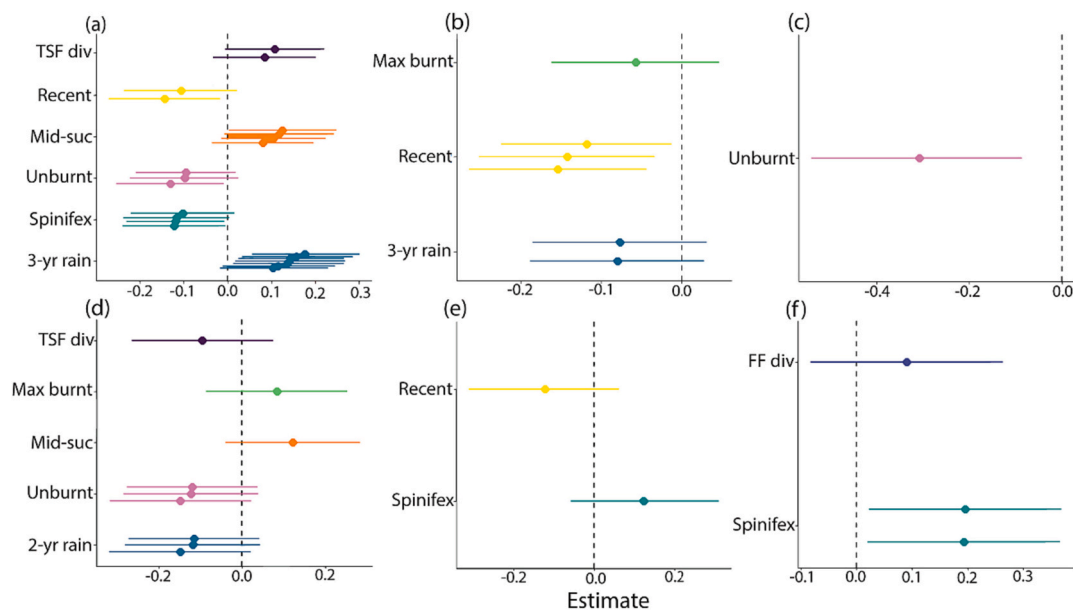
confidence intervals did not overlap 0.

We tested the residuals of each of our models for spatial autocorrelation using correlograms, with Moran's  $I$  as our estimate of covariance, to plot the covariance between landscapes against landscapes, with values near zero indicating a random spatial pattern. We set the number distance classes to 'NULL' to allow an optimal number of neighbours to be chosen. Additionally, we used bubble plots to visually investigate spatial autocorrelation (Schägner et al., 2016). All analyses were

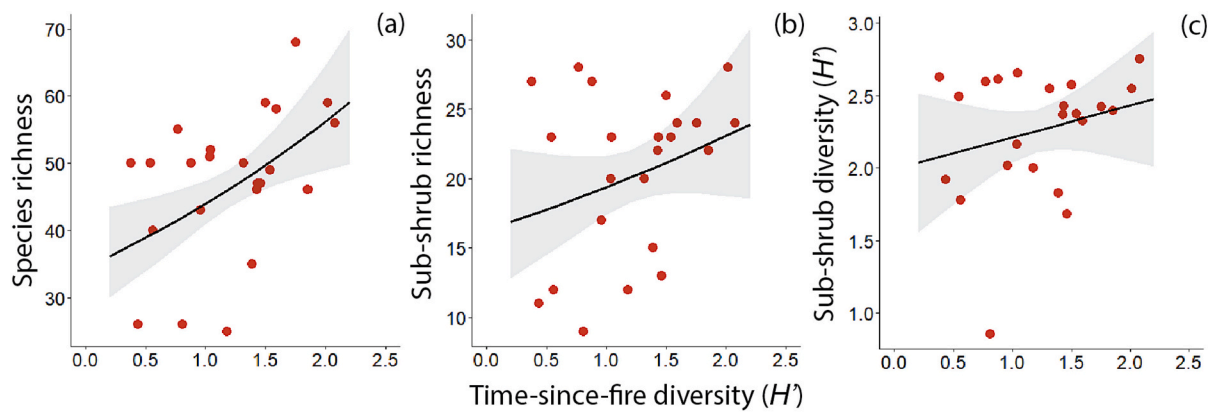
conducted in R version 2.1 (R Core Team, 2018) using lme4 (Bates et al., 2015) and vegan (Dixon, 2003) packages.

### 3. Results

The best rainfall variables to retain were: (i) 1-year cumulative rainfall for edible sub-shrub richness and edible shrub and tree diversity, (ii) 2-year cumulative rainfall for sub-shrub diversity and edible sub-



**Fig. 3.** Estimated model coefficients (dots) and 95 % confidence intervals (lines) from models with substantial support (i.e.,  $w_i < 2$ ) for (a) edible species richness, (b) edible species diversity ( $H'$ ), (c) edible sub-shrub richness, (d) edible sub-shrub diversity ( $H'$ ), (e) edible shrub and tree richness, and (f) edible shrub and tree diversity ( $H'$ ).



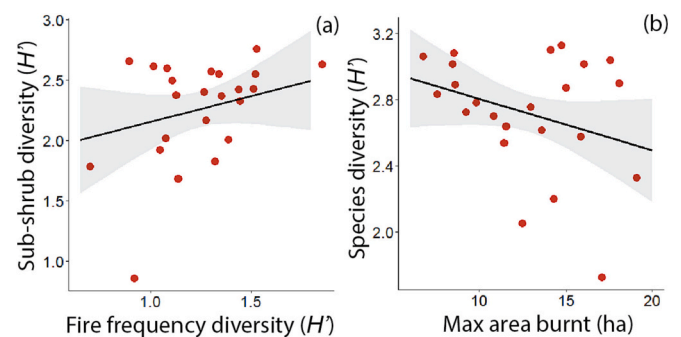
**Fig. 4.** Relationship between time-since-fire diversity ( $H$ ) and (a) total species richness, (b) sub-shrub richness, and (c) sub-shrub diversity ( $H$ ). Points: raw data, black lines: model trendline, grey shading: 95 % confidence intervals.

shrub diversity, (iii) cumulative 3-year rainfall for edible species richness and edible species diversity, and (iv) average annual rainfall for total species richness, total species diversity, sub-shrub richness, and edible shrub and tree richness (Table S1). We found little evidence of spatial autocorrelation: < 3 % of distances showed spatial autocorrelation and there was no clear trend in residuals in correlograms and bubble plots for any response variable (Figs. S1–S2).

The top models for total species richness explained a high amount of variation (78–82 %) and all included time-since-fire diversity and proportion of mid-succession (Tables 1 and S2, and Fig. 2). Total species richness was higher in landscapes with high time-since-fire diversity and high proportions of mid-succession (Figs. 4 and 6). The top model for total species diversity explained a high amount of variation (56 %) and included maximum proportion of landscape burnt, proportion of mid-succession, and average rainfall (Tables 1 and S2, and Fig. 2). Total species diversity was lower where the maximum proportion of a landscape burnt was higher, and higher with high proportions of mid-succession (Figs. 5–6).

For sub-shrub richness, there was considerable model uncertainty, top models explained a moderate amount of variation (37–52 %), and all included the proportion of mid-succession (Tables 1, S2, and Fig. 2). Sub-shrub richness was higher in landscapes with high time-since-fire diversity and high proportions of mid-succession (Figs. 4 and 6). There was also model uncertainty for sub-shrub diversity, the top models explained a low to moderate amount of variation (20–48 %) and did not share any common predictor variables (although mid-succession was in almost all the top models) (Tables 1 and S2, and Fig. 2). Sub-shrub diversity was higher in landscapes with high time-since-fire diversity, high diversity of fire frequency patches, and high proportions of mid-succession (Figs. 4–6).

For edible species richness, there was considerable model uncertainty, top models only explained a modest amount of variation (20–33 %), and there were no common predictors across the models (Tables 1 and S2, and Fig. 3). Edible species richness was higher in landscapes with high proportions of mid-succession, and lower with high proportions of recently burnt and long unburnt (Fig. 6). The top models for edible species diversity explained a small amount of variation (21–28 %) and all included proportion of recently burnt (Tables 1 and S2, and Fig. 3). Edible species diversity was higher in landscapes with high proportions of recently burnt (Fig. 6). For edible sub-shrub richness, the top model explained a modest amount of variation (28 %) and only included proportion of long unburnt (Tables 1 and S2, and Fig. 3). Edible sub-shrub richness was higher in landscapes with high proportions of long unburnt (Fig. 6). The top models for edible sub-shrub diversity and edible shrub and tree richness explained a low amount of variation (10–16 % and 7 %, respectively), shared no common predictor variables, and had no significant fire predictor variables (Tables 1 and S2, and



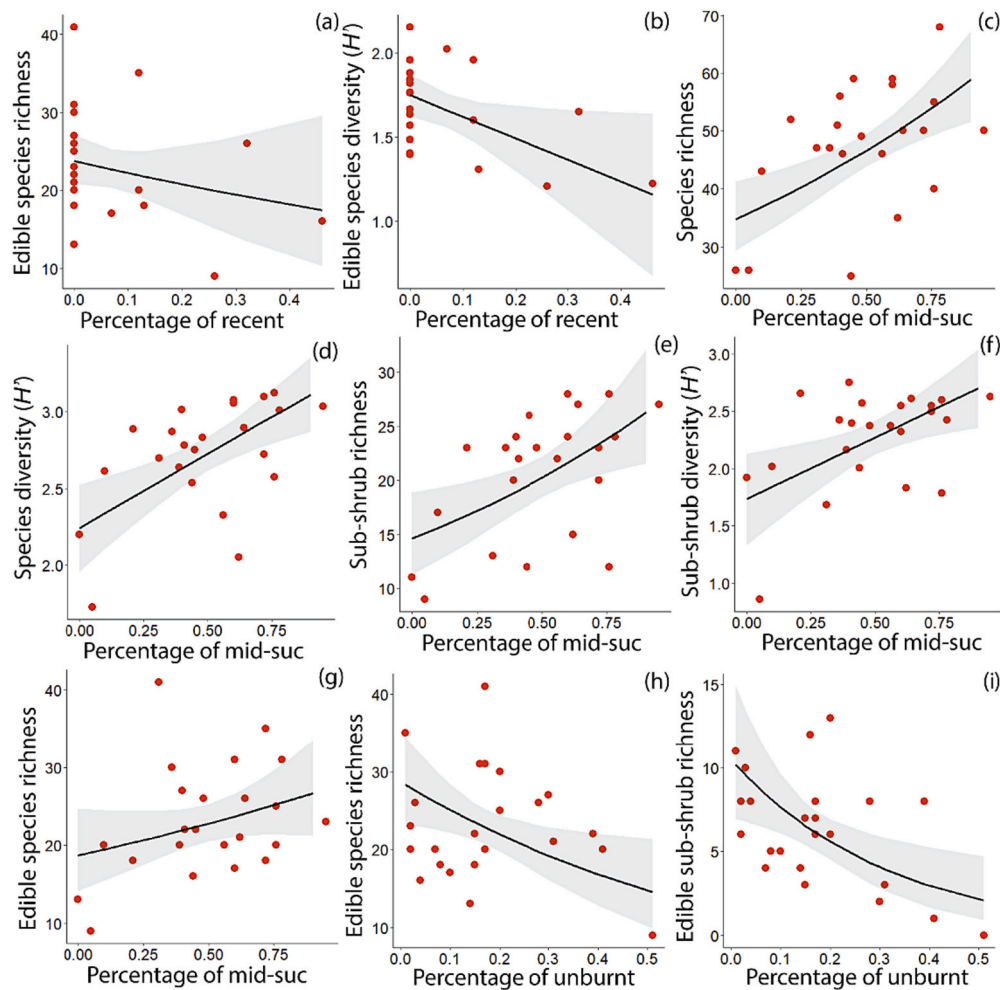
**Fig. 5.** Relationship between (a) diversity of fire frequency patches ( $H$ ) and sub-shrub diversity ( $H$ ), and relationship between (b) maximum landscape area burnt (ha) and total species diversity ( $H$ ). Points: raw data, black lines: model trendline, grey shading: 95 % confidence intervals.

Fig. 3). For edible shrub and tree diversity the top models explained a moderate amount of variation (21–25 %) and all included proportion of spinifex sandplain, but again showed no significant relationships with our fire predictor variables (Tables 1 and S2, and Fig. 3).

#### 4. Discussion

We found strong evidence that pyrodiversity increases the richness and diversity of plants and some plant (e.g., sub-shrubs) groups in the Western Deserts. The mechanism by which pyrodiversity maintains plant diversity appears to include aspects of the visible and invisible mosaic, although properties of the visible mosaic were more often associated with measures of plant diversity. The maximum extent of large wildfires appeared to reduce plant richness, while the extent of mid successional vegetation tended to enhance the diversity of several plant groups, including edible species richness. Given that we have shown that Martu burning increases the diversity of visible and invisible fire mosaics, and that such pyrodiversity is negatively associated with fire size (Bliege Bird et al., 2012; Greenwood et al., 2021), our findings underscore the importance of Indigenous fire regimes for promoting plant diversity in this fire-prone ecosystems.

Our findings offer broad support for the ‘pyrodiversity begets biodiversity’ hypothesis. Landscape level studies that investigate the relationship between plants and pyrodiversity are few, but they suggest that plant communities can be more diverse with higher pyrodiversity, but relationships can be inconsistent and non-linear (Cohn et al., 2015; McGranahan et al., 2018; Ponisio et al., 2016). For example, Cohn et al. (2015) found that plant diversity increased with pyrodiversity, but the response differed along the productivity gradient. McGranahan et al.



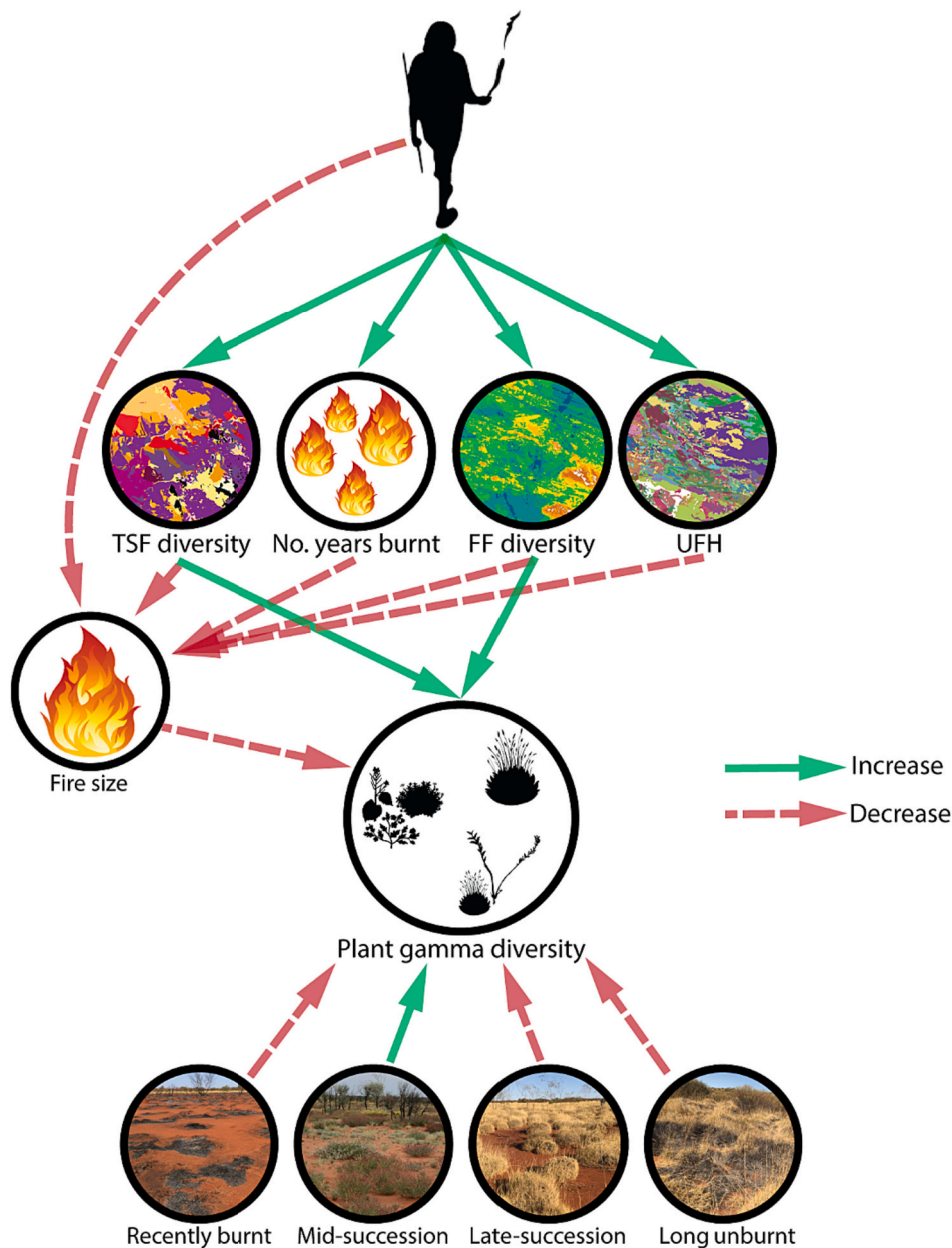
**Fig. 6.** Relationship between percentage of recently burnt (recent) and edible species (a) richness, and (b) diversity ( $H'$ ). Relationship between percentage of mid-succession (mid-suc) and total species (c) richness and (d) diversity ( $H'$ ), sub-shrub (e) richness and (f) diversity ( $H'$ ), and (g) edible species richness. Relationship between percentage of long unburnt (unburnt) and (h) edible species richness and (i) edible sub-shrub richness. Points: raw data, black lines: model trendline, grey shading: 95 % confidence intervals.

(2018) found that moderate levels of pyrodiversity promoted highest plant diversity, and Ponisio et al. (2016) found that plant richness increased with pyrodiversity, except following severe fires. Thus, although we found that plant species richness and diversity increased linearly with pyrodiversity, simply maximising pyrodiversity, without consideration of historical levels of pyrodiversity (e.g., the pyrodiverse landscapes that Indigenous people maintain), may not equate to appropriate fire management.

Diversity in time-since-fire ages was the most influential measure of pyrodiversity. Time-since-fire can overshadow the effects of underlying fire histories in determining plant community composition because fire breaks seed dormancy and triggers germination through heat and smoke cues (Commander et al., 2008; Commander et al., 2017) and different aged patches provide varied resources (e.g., light, space) (Davis et al., 2018; Martin and Sapsis, 1992; Pastro et al., 2011). For instance, immediately following fire, nutrients and water are more available due to volatilisation of nutrients and competitive pressure release when fire kills or reduces spinifex to its roots (Burrows et al., 2020; Wright and Clarke, 2007). Different successional stages support different plant communities, and it is the combination of these different plant communities within pyrodiverse landscapes that contributes to landscape-scale richness and diversity (Fig. 7). The strength of the relationships we observed could be due to the functional importance of the successional stages that we used to measure pyrodiversity. Bird et al. (2016)

note that for Martu, the patchwork of successional stages present in a landscape can be viewed as “an index of devotion to one's estate”. Martu burning drastically increases the diversity of fire histories within the landscape to create *ngurra juri* (sweet country), and this study confirms that such landscapes are more diverse than landscapes without Martu. Given that the configuration and composition of fire mosaics crafted by Martu are highly scale-dependent (Bliege Bird et al., 2008), further research could explore the spatial scales at which the pyrodiversity-biodiversity relationship is maximised for plants, and other taxa (e.g., animal groups), in this ecosystem (Jones and Tingley, 2021).

Mid-successional patches were disproportionately important for promoting species richness and diversity. Martu recognise that mid-successional stages are important for people and animals alike, with abundant edible plants such as staple bush tomatoes (e.g., *Solanum diversiflorum*) and edible grasses (e.g., *Eragrostis eriopoda*) (Bird et al., 2016; Coddling et al., 2014; Walsh, 2008). However, burning is a practice designed around hunting burrowed animals, and is rooted in social obligations and Law; it is not perceived as a conservation practice (Bird et al., 2016). Rather, increased plant diversity and abundance is viewed as an emergent outcome (Bird et al., 2016). Nevertheless, these findings suggest that Indigenous fire regimes promote culturally significant plant and animal species (Bliege Bird et al., 2008; Gould, 1971; Jones, 1969). It also highlights that sound consideration of the configuration and extent of different aged patches within landscapes is important (Taylor



**Fig. 7.** Conceptual model linking our previous work that shows that Martu increase visible (i.e., time-since-fire diversity  $H'$ ) and invisible (i.e., number of years burnt, diversity of fire frequency patches  $H'$ , and the number of unique fire histories) pyrodiversity, and reduce fire size (Greenwood et al., 2021). Our current results indicate that pyrodiversity increases the richness and diversity of some plant groups and fire size reduces plant diversity, at the landscape scale. Thus, we conceptualise that through increasing pyrodiversity and reducing fire size, Martu increase plant diversity at the landscape scale.

et al., 2012).

Fire frequency is an important driver of plant communities (Nano and Clarke, 2011), with studies indicating different plant composition in landscapes with varying fire frequencies (Burgess et al., 2015; Ponisio et al., 2016). Therefore, we assumed that increased diversity of fire frequency patches would lead to increased diversity in resources and niches, and thus increased plant richness and diversity. However, of all the plant groups that we investigated, only sub-shrub diversity responded positively to increased diversity in fire frequency patches (i.e., invisible fire diversity), and this relationship was weak and inconsistent across models. In a similar arid ecosystem dominated by spinifex, Wright and Clarke (2007) found that fire frequency had minimal effects on woody species (both that re-sprout and regenerate through the seed bank), which they suggest could be due to fast re-sprouting and germination abilities, short juvenile periods, and rapid seed production.

However, more frequent fires did lead to reduced spinifex seedlings (Wright and Clarke, 2007), suggesting that increased diversity in fire frequency patches could influence plant diversity and richness.

Sub-shrubs showed several significant relationships with pyrodiversity and post-fire successional stages. This was expected, as many of these species are fire ephemerals (i.e., short-lived plants that primarily germinate after a fire) (Clarke et al., 2015; Nano and Clarke, 2011) and rely on fire for germination (Commander et al., 2008; Commander et al., 2017). An increase in sub-shrubs following fire is a pervasive pattern in spinifex dominated ecosystems (Burrows et al., 2020; Marsden-Smedley et al., 2012; Wright and Clarke, 2007). This response is likely linked to patterns in spinifex, with fire killing or reducing spinifex to its roots, reducing competition (Burrows et al., 2006b; Nano and Clarke, 2010), while simultaneously increasing soil organic matter, nutrients and moisture (Muñoz-Rojas et al., 2016).



We find support for the notion that large fires can cause declines in species diversity at the landscape scale. Large fires could work to reduce species diversity by homogenising landscapes and burning at higher severities than smaller fires (Williams et al., 2015), reducing soil seed bank viability, and altering soil conditions (Day et al., 2019; Moya et al., 2019). For example, in mixed conifer forests, Ponisio et al. (2016) found that flowering plant richness increased with pyrodiversity, except after high severity fires, when richness declined with pyrodiversity. Large fires also can create large, homogenous areas of vegetation of the same seral stage (Cassell et al., 2019), which may reduce species richness and diversity between sites (i.e., beta diversity) within landscapes as entire landscapes are reduced to the same time-since-fire age (Farnsworth et al., 2014). Previous work indicates that Indigenous pyrodiversity can reduce the spread of wildfires (Greenwood et al., 2021), even under fluctuating rainfall (Bliege Bird et al., 2012). Therefore, by limiting the occurrence of large fires, Martu pyrodiversity confers an additional benefit to species diversity.

This work builds on an emerging narrative of the importance of Indigenous fire regimes in maintenance of fire-prone ecological communities (Hoffman et al., 2021). Species are dependent on the fire regimes that they evolved under (Pausas and Keeley, 2009) and people have been burning across global ecosystems for millennia (Ellis et al., 2021). It also suggests that the displacement of Indigenous people and their fire regimes can lead to local species decline (Burrows et al., 2006a; Liebmann et al., 2016; Burbidge et al., 1988). Identifying and restoring fire regimes that enhance and maintain biodiversity remains a challenge for fire management around the world (McLauchlan et al., 2020). Evidence suggests that supporting Indigenous-led burning could offer some solutions to these challenges, with co-benefits for biodiversity and community wellbeing (Ansell and Evans, 2019; Bliege Bird et al., 2018; Hoffman et al., 2021; Ruscalleda-Alvarez et al., 2023).

#### CRedit authorship contribution statement

**L. Greenwood:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **R. Bliege Bird:** Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **C. McGuire:** Investigation, Methodology, Resources, Writing – review & editing. **N. Jadai:** Conceptualization, Data curation, Investigation, Project administration, Resources, Supervision, Writing – review & editing. **J. Price:** Conceptualization, Methodology, Supervision, Writing – review & editing. **A. Skroblin:** Methodology, Supervision, Writing – review & editing. **S. van Leeuwen:** Data curation, Resources, Supervision, Writing – review & editing. **D. Nimmo:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing.

#### Declaration of competing interest

The authors state that there are no known competing financial interests or personal relationships that could have seemed to influence the work reported in this paper.

#### Data availability

The authors do not have permission to share data.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110479>.

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