

People, fire, flora, and fungi in semi-arid Australia

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Certificate of authorship

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Preface and thesis structure

My initial project was to be fully conducted on Martu country in the semi-arid spinifex (*Triodia* spp.) grasslands of north-western Australia. Prior to collecting data, I spent the winters of 2017 and 2018 living in the Martu community of Parnngurr with the intention of forming relationships, learning about what is important to Martu, and formulating research questions. My conversations were primarily with anthropologists Rebecca Bliege Bird and Doug Bird, members of the Parnngurr community, and Kanyirninpa Jukurrpa (KJ). Rebecca and Doug had spent several years living in Parnngurr and undertaken several long-term collaborative projects with Martu exploring the social and ecological dynamics of Martu cultural landscapes. KJ is a Martu organisation that delivers cultural, environmental, and social programs across the Martu estate. Through these conversations, there was interest expressed in understanding the response of plant communities to Martu burning, with a particular interest in edible plants, as Martu had recognised they were declining. Due to my interest in fungi, I also initiated conversations with Martu about the responses of fungal communities to fire, which many people expressed interest in learning more about. As a result, my supervisors and I designed a study to be conducted on Martu country that amalgamated research foci highlighted by Martu (i.e., fire and plants) and my own interests (i.e., fire and fungi), with hope that the project would align with Martu values and benefit both Martu and KJ.

In the winter of 2019, on my third visit to Parnngurr, I arrived in community with a research proposal and an intention to spend several weeks in consultation with community members prior to data collection. I began by holding a community wide meeting to present my research proposal, facilitated by KJ. Following the meeting, I had conversations with community members and elders about the research proposal. Within the first week of consultations, a Martu elder expressed concerns about collecting and taking soil samples off Martu country, which would be necessary to assess soil fungi. Thus, I altered my research proposal and continued with plant surveys, but not soil surveys. As my interests remained in the responses of fungi to fire, my supervisors and I designed an additional field project on Wotjobaluk, Wergaia, Jadawadjali, Jaadwa, and Jupagalk country in the Little Desert National Park, south-eastern Australia. As a result of consultations and project alterations, three of my PhD chapters (**two, three, and four**) were focused on the interactions between people, fire, and plants on Martu country in

the semi-arid spinifex grasslands of north-western Australia. The final data chapter (**chapter five**) focuses on the responses of fungal communities to fire on Wotjobaluk, Wergaia, Jadawadjali, Jaadwa, and Jupagalk country in the semi-arid heathlands of south-eastern Australia.

I have structured this thesis into six chapters: an introductory chapter, four data chapters, and a summary chapter. **Chapter one** provides relevant background information and introduces the main objectives for my thesis, which are addressed in the following chapters. **Chapters two, three, four, and five** are manuscripts that have either been published (**chapter two**) or are in preparation for submission (**chapters three, four, and five**). As a result, there is some unavoidable repetition between chapters. **Chapter six** summarises my data chapters, places my work within a global context, and discusses broader implications. I am the principal contributor on all chapters in this thesis, and they are all co-authored by a minimum of three supervisors.

Approvals and funding

For our study on Martu country we received approval from the Western Desert Lands Aboriginal Corporation (WDLAC), the community executive, Parnngurr community Elders, and Kanyirninpa Jukurrpa (KJ).

Permits to collect plant material on Martu country were issued by Western Australian Department of Biodiversity, Conservation, and Attractions (reference: FT61000111). Permits to collect soil samples on Wotjobaluk, Wergaia, Jadawadjali, Jaadwa, and Jupagalk country were issued by Parks Victoria and the Department of Land, Water, and Planning (reference: 0028904).

This project was supported by a scholarship from Charles Sturt University. Further funding was provided by the Holsworth Wildlife Research Endowment – Equity Trustees Charitable Foundation, Ecological Society of Australia, Australian Research Council Early Career Researcher Award (DECRA), Hermon Slade Foundation, and Australasian Mycological Society.

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Publications resulting from the research

Chapter 2: Indigenous burning shapes the structure of visible and invisible fire mosaics

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Greenwood, L. conceived and developed ideas, collected data, analysed data, created accompanying figures, and contributed to manuscript preparation.

Bliege Bird, R. conceived and developed ideas, and contributed to manuscript preparation.

Nimmo, D. conceived and developed ideas, assisted with data analysis, and contributed to manuscript preparation.

Senior author: Nimmo, D.

Chapter 3: Fire history shapes plant diversity and composition in Australia's western deserts

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Authors: Greenwood, L., Bliege Bird, R., McGuire, C., Jadai, N., Price, J., Skroblin, A., van Leeuwen, S., and Nimmo, D.

Greenwood, L. conceived and developed ideas, collected data, analysed data, created accompanying figures, and contributed to manuscript preparation.

Bliege Bird, R. conceived and developed ideas, and contributed to manuscript preparation.

McGuire, C. aided in data collection, and contributed to manuscript preparation.

Jadai, N. aided in community communication and cultural guidance, and contributed to manuscript preparation.

Price, J. conceived and developed ideas, and contributed to manuscript preparation.

Skroblin, A. contributed to manuscript preparation.

van Leeuwen, S. aided in plant identification and contributed to manuscript preparation.

Nimmo, D. conceived and developed ideas, assisted with data analysis, and contributed to manuscript preparation.

Senior author: Nimmo, D.

Chapter 4: Indigenous pyrodiversity promotes plant richness and diversity in semi-arid Australia

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Authors: Greenwood, L., Bliege Bird, R., McGuire, C., Jadai, N., Price, J., Skroblin, A., van Leeuwen, S., and Nimmo, D.

Greenwood, L. conceived and developed ideas, collected, and analysed data, created accompanying figures, and contributed to manuscript preparation.

Bliege Bird, R. conceived and developed ideas, and contributed to manuscript preparation.

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Skroblin, A. contributed to manuscript preparation.

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Nimmo, D. conceived and developed ideas, assisted with data analysis, and contributed to manuscript preparation.

Senior author: Nimmo, D.

Chapter 5: Fire shapes fungal guild diversity and composition through direct and indirect pathways.

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Greenwood, L. conceived and developed ideas, collected data, analysed data, created accompanying figures, and contributed to manuscript preparation.

Frew, A. conceived and developed ideas, conducted PCR, and contributed to manuscript preparation.

Egidi, E. conducted bioinformatics and contributed to manuscript preparation.

Price, J. contributed to manuscript preparation.

McIntosh, R. established sites, collected data, and contributed to manuscript preparation.

Nimmo, D. conceived and developed ideas, assisted with data analysis, and contributed to manuscript preparation.

Senior author: Nimmo, D.

Abstract

This thesis comprises two parts. In **part one**, encapsulated in **chapters two, three, and four**, I investigated the interaction between fire, people, and flora in the semi-arid spinifex grasslands of Western Australia. Species in fire-prone ecosystems are dependent on the spatiotemporal patterning of fire, or the 'fire regime'. Indigenous people have shaped fire regimes for millennia and continue to in many areas around the world. It is increasingly evident that species are dependent on Indigenous fire regimes, which often create 'pyrodiverse' landscapes with diverse temporal and spatial fire histories. In **part two** encapsulated in **chapter five**, I investigated the response of fungal communities to fire in the semi-arid heathlands of south-eastern Australia. Fire is a key driver of fungal communities, but the response of fungal communities to fire are not well understood.

Chapter one provides a brief introduction to the thesis. In **chapter two**, I examined how Indigenous people shape landscape pyrodiversity by investigating how travel time from Indigenous communities (used as a proxy for land-use intensity) affected aspects of the visible fire mosaic (i.e., time-since-fire diversity and maximum landscape area burnt) and invisible fire mosaic (i.e., number of years burnt, diversity of fire frequency patches, and number of unique fire histories). Indigenous burning creates diverse visible and invisible fire mosaics, which dwarf the pyrodiversity of distant areas, and limits fire size.

In **chapter three**, I examined how time-since-fire and fire frequency affected several plant richness and diversity variables (including edible plants), vegetation structure, and plant composition. Fire was a strong driver of plant communities, with spinifex playing a key role. Patterns in plant richness and diversity largely followed the "initial floristic composition" model. Additionally, burning enhanced the productivity of areas for Indigenous people; edible plant richness peaked shortly after fire and frequent fires enhanced edible plant availability.

In **chapter four**, I explored whether pyrodiversity maintained by Indigenous people promoted plant richness and diversity, by comparing landscapes that ranged from highly pyrodiverse under active Indigenous burning, in both visible and invisible fire diversity, to more coarse-scale and less diverse mosaics under lightning fire regimes. Indigenous created pyrodiversity enhanced several plant richness and diversity variables, but mid-

successional stages were particularly important for enhancing plant diversity. Additionally, plant diversity declined when maximum landscape area burnt increased.

Collectively, results from **chapters two, three, and four** suggest that by increasing the frequency that landscapes are burnt, increasing diversity in the visible and invisible fire mosaic, and reducing fire size, Indigenous people enhance plant diversity and enhance the productivity of landscapes for people. Indigenous-led burning could offer solutions to restoring appropriate fire regimes and conserving global biodiversity.

In **chapter five**, I investigated how time-since-fire and fire frequency influenced the richness and composition of all fungi, ectomycorrhizas, saprotrophs, and pathogens. Saprotrophic richness increased with time-since-fire, but direct and indirect effects had opposing impacts. Distinct fungal communities arose under different post-fire successional stages and fire frequency classes, with substantial differences in ectomycorrhizal species composition. Fire is a key driver of fungal communities in semi-arid heathlands.

Chapter one: Introduction

Fire, people, and flora

Fire has shaped global ecosystems for over 400 million years (Bond and Keeley, 2005, Scott, 2018). Fire destroys, creates, and rearranges habitats and resources (He et al., 2019, Fox et al., 2022, Pausas and Ribeiro, 2017). By evolving with fire, species and ecological communities have become dependent on and adapted to fire and its' patterning, or the 'fire regime' (Gill, 1975). Each attribute of the fire regime, such as fire frequency, interval, season, intensity, shape, severity, and extent—and the interactions between attributes of the fire regime— can affect species and ecological communities differently (Gill, 1975, Martin and Sapsis, 1992). For example, fire plays a critical role in triggering germination cues for plants around the world (Pausas and Keeley, 2014), but the season a fire occurs can dictate whether those seedlings survive to adulthood (Miller et al., 2019). Understanding how to maintain and promote biodiversity in fire-prone ecosystems remains a key challenge for fire ecologists and managers (Driscoll et al., 2010, Kelly et al., 2020).

People have occupied most of the planet and fulfilled important ecological roles within ecosystems for hundreds of thousands of years (Ellis et al., 2021a, Hoffman et al., 2021). Over 0.79 million years ago, fire became one of the first and most significant tools used by people to shape their surroundings (Ellis et al., 2021a, Goren-Inbar et al., 2004, Pausas and Keeley, 2009). By evolving with people and their fire regimes, a wide range of species and ecological communities demonstrate dependence on the way that Indigenous people burn (Hoffman et al., 2021), such as birds (Borges, 2007), mammals (Rocha and Silva, 2009), fungi (Wendiro et al., 2019), reptiles (Bliege Bird et al., 2018), and plants (Marks-Block et al., 2021). The importance of Indigenous fire regimes extends to culturally significant edible plants, with burning thought to enhance the productivity of landscapes for people (Gould, 1971, Jones, 1969, Latz, 1995, Marks-Block et al., 2021, Pivello, 2011). The displacement of Indigenous people and subsequent cessation of their fire regimes has been implicated in ecosystem changes and declines in species (Burrows et al., 2006a, Liebmann et al., 2016, Price and Bowman, 1994, Woinarski et al., 2015). For example, following the displacement of Indigenous people in North America, fire frequency substantially increased, which profoundly altered vegetation structure (Liebmann et al., 2016).

Fire continues to be an integral part of Indigenous societies around the world (Marks-Block et al., 2021, Pivello, 2011, Trauernicht et al., 2015). While Indigenous fire regimes are highly tailored and purposeful, they are often characterised by small, frequent, low-intensity fires (Hoffman et al., 2021, Stambaugh et al., 2018, Trauernicht et al., 2015). By burning this way, Indigenous fire regimes can create pyrodiverse landscapes —fine scale mosaics of temporally and spatially diverse fire histories (Martin and Sapsis, 1992)— shown in Australia (Bliege Bird et al., 2008, Trauernicht et al., 2015), South America (Pivello, 2011), North America (Roos et al., 2021), and Africa (Sheuyange et al., 2005). Given species show varying responses to the fire regime, pyrodiverse landscapes are thought to enhance biodiversity by increasing niche diversity and/or quality, and limiting the likelihood of large, severe fires (Martin and Sapsis, 1992). While there is mixed support for the “pyrodiversity begets biodiversity” hypothesis (Jones and Tingley, 2021), few studies have investigated levels of pyrodiversity maintained by Indigenous people (however, see Bliege Bird et al., 2018). Insight into how Indigenous people shape fire patterns and how those fire patterns shape ecological communities is key to increasing recognition and understanding of the role of Indigenous burning in fire management and biodiversity conservation.

Fire is prevalent across Australia’s semi-arid spinifex (*Triodia* spp.) grasslands (Fig. 1.1) (Allan and Southgate, 2002, Marsden-Smedley et al., 2012, Nano et al., 2012). The effect of fire in spinifex grasslands in Australia’s western deserts takes on particular importance for Martu, the region’s Traditional Owners who have occupied and burnt these regions for tens of thousands of years (Bird et al., 2016, Burrows et al., 2006a). Martu, which includes Manyjilyjarra, Kartujarra, Kiyajarra, Putijarra, Nyiyaparli, Warnman, Ngulipartu, Pitjikala, Kurajarra, Jiwaliny, Mangala, and Nangajarra language groups, were among the last Indigenous Australian groups to have contact with Europeans, as late as the 1960s. Many Martu Elders were born prior to European contact and are highly skilled and experienced in burning. Martu continue to harvest edible plants and burn small patches of spinifex, primarily to access small, burrowed reptiles (Bliege Bird et al., 2008, Bliege Bird et al., 2012). Today, Martu mostly burn areas within 50 km of their communities (Bird et al., 2013), which has created a transition of anthropogenic to lightning fire across the landscape. Fires close to communities are mainly set by Martu and fires more than two hours from communities are mainly ignited by lightning (Bliege Bird et al., 2018). By burning small patches, frequently, Martu increase the diversity of time-since-fire patches

(Bliege Bird et al., 2008, Bliege Bird et al., 2012) and limit fire size (Bliege Bird et al., 2012). Burning is recognised to carry longer-term benefits by increasing food plant abundance for people (Commander et al., 2017, Gould, 1971, Jones, 1969) and animals (Bliege Bird et al., 2008, Bliege Bird et al., 2018, Bliege Bird et al., 2013, Codding et al., 2014).



Figure 1.1 Semi-arid spinifex (*Triodia* spp.) grassland sites on Martu country at (top left) 0 years-since-fire, (top right) 4 years-since-fire, (bottom left) 10.5 years-since-fire, and (bottom right) 18.5 years-since-fire.

Fire and fungi

Fungi play integral roles within ecosystems, such as shaping plant productivity and community composition (Tedersoo et al., 2020), decomposing organic material, and nutrient cycling (Frac et al., 2018, Ferris and Tuomisto, 2015). Fire is a key driver of fungal communities, yet our understanding of fungal responses to fire are not well understood because fungi are diverse, hidden, and their responses to fire are inherently linked to ecosystem functions (Fox et al., 2022, McMullan-Fisher et al., 2011). In semi-arid heathlands, fire is a prevalent disturbance (Fig. 1.2) (Cheal, 2010, Clarke et al., 2021, Pausas and Bradstock, 2007). Evidence suggests that semi-arid fungal communities could respond to different attributes of the fire regime (Fultz et al., 2016, Hinojosa et al., 2016, Muñoz-Rojas et al., 2016, O'Dea, 2007). However, there are few studies that investigate the long-term trends post-fire or the effects of fire regime attributes, other than time-since-fire on semi-arid fungal communities. Understanding the response of fungal communities is vital given the important roles fungal communities play in post-fire ecosystems and in overall ecosystem functioning (Dove et al., 2022, Wagg et al., 2014).





Figure 1.2 Semi-arid heathland sites on Wotjobaluk, Wergaia, Jadawadjali, Jaadwa, and Jupagalk country at (a) 0 years-since-fire, (b) 1 year-since-fire, (c) 8 years-since-fire, and (d) 44 years-since-fire.

Thesis objectives

In **chapter two**, entitled *Indigenous burning shapes the structure of visible and invisible fire mosaics*, I explored how travel time from Martu communities (used as a proxy for land-use intensity) influenced the visible fire mosaic, in terms of time-since-fire diversity and maximum fire size, and the invisible fire mosaic, in terms of the number of years a landscape burns, diversity of fire frequency patches, and number of unique fire histories.

In **chapter three**, entitled *fire history shapes plant diversity and composition in Australia's western deserts*, I investigated how travel time from Martu communities, time-since-fire and fire frequency influenced plant richness and diversity, vegetation structure, and plant composition, including several plant groups such as sub-shrubs and edible species. By investigating edible species, I sought to explore the “fire-stick farming” hypothesis, which suggests that Indigenous burning increases the availability of edible plants.

In **chapter four**, entitled *Indigenous pyrodiversity promotes plant richness and diversity in semi-arid Australia*, I examined how the visible fire mosaic, in terms of time-since-fire diversity and proportion of post-fire successional stages, and the invisible fire mosaic, in terms of fire frequency diversity and maximum proportion of landscape burnt, influenced

plant richness and diversity, including several plant groups such as sub-shrubs and edible species.

In **chapter five**, entitled *fire shapes fungal guild diversity and composition through direct and indirect pathways*, I explored how time-since-fire and fire frequency, through direct effects and indirect interactions between fire, soil properties, and substrates, influenced total fungal richness, ectomycorrhizal richness, saprotrophic richness, and pathogenic richness. Additionally, I explored how total fungal community composition and the composition of fungal trophic guilds differed between post-fire successional stages and fire frequency classes.

In **chapter six**, I summarise the findings of each of my four data chapters and briefly discuss broader implications.

Chapter two: Indigenous burning shapes the structure of visible and invisible fire mosaics

Manuscript published

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Abstract

In many regions of the world, Indigenous people continue to shape landscape patterns using fire. Some studies show that Indigenous fire regimes create a diverse “visible mosaic” of time-since-fire ages. Less is known about the underlying, cumulative spatiotemporal patterns of fires that are hidden beneath visible fire scars—termed the “invisible fire mosaic”—despite its role in shaping biota in fire-prone landscapes. We investigated how distance from Indigenous communities affects landscape patterns, focusing on aspects of the visible (i.e., time-since-fire diversity and maximum landscape area burnt) and invisible (i.e., number of years burnt, diversity of fire frequency patches, and number of unique fire histories) fire mosaic. We quantified fire histories for 450 landscapes across Western Australia. We calculated the distance of each landscape to the nearest Indigenous community (a proxy for the intensity of human landscape use) and used regression models to investigate how distance influenced the properties of the visible and invisible fire mosaic. Landscapes near Indigenous communities experienced more frequent fire, had higher time-since-fire diversity, higher diversity of fire frequency patches, and a greater number of unique combinations of fire histories (seasons, interval lengths, and time-since-fire ages). Pyrodiversity was negatively related to the maximum area burnt, supporting the notion that Indigenous burning limits fire size. Indigenous burning creates distinctive visible and invisible fire mosaics which dwarf the pyrodiversity of more distant areas, thereby potentially crafting ecosystem states that profoundly differ from those without human presence.

Introduction

Fire is a potent force that has influenced ecosystems for millennia through its spatiotemporal patterning—the fire regime (Bowman et al., 2009, He et al., 2019). Species are adapted to particular fire regimes, such that alterations in spatiotemporal patterns can lead to species decline and changes in range, with these declines often attributed to the displacement of Indigenous people and their fire regimes (Liebmann et al., 2016, Woinarski et al., 2015). The importance of Indigenous people in shaping fire regimes continues to grow in global recognition (Bliege Bird et al., 2008, Duncan et al., 2021, Roos et al., 2021), and one recurrent finding emerging from this research is that such regimes often enhance biodiversity (Hoffman et al., 2021).

Effective landscape management requires an understanding of the processes through which fire regimes shape biodiversity, and many management goals attempt to mimic Indigenous fire regimes by creating ‘pyrodiverse’ landscapes: those that have a fine scale mosaic of fire histories (McLauchlan et al., 2020). Pyrodiverse landscapes are argued to increase species diversity by increasing niche diversity and/or quality (Martin and Sapsis, 1992). Consequently, fire managers in many regions have sought to maintain high levels of pyrodiversity for biodiversity conservation (Parr and Andersen, 2006), but with mixed results (Jones and Tingley, 2021). This may be due to the differing ways that pyrodiversity can be measured. Fire mosaics can be conceptualised with respect to their visible and invisible properties (Bradstock et al., 2005, Parr and Andersen, 2006). The visible mosaic describes the attributes of the most recent and visible fire patterns, with measures including the age and size of fire patches, and the diversity of time-since-fire patches. In contrast, the invisible mosaic describes the cumulative underlying, long term spatiotemporal patterns of fires that are often hidden below the scars of the most recent fires (Bradstock et al., 2005), such as the diversity of patches defined by fire frequency or interval (Brown and York, 2017). The underlying fire histories and properties of the invisible mosaic can create substantial differences in species composition and vegetation structure (Burgess et al., 2015, Brown and York, 2017, Foster et al., 2017). If Indigenous fire stewardship shapes the properties of invisible fire mosaics, such practices may play a key role in governing the responses of biota to fire events.

Here, we seek to increase our understanding of how Indigenous people shape landscape-level fire regimes by examining the relationship between pyrodiversity and Aboriginal

Australian landscape use, with a particular focus on the invisible fire mosaic. In the western deserts of Australia, Martu, the traditional owners of a vast number of estates in Western Australia, continue to regularly burn small patches of spinifex (*Triodia* spp.) sandplain, primarily to hunt brumating goannas (*Varanus gouldii*) in the winter months (April – September). Burning remains an important practice for Martu to care for country, maintain social ties, and upkeep the obligations of Law established by their ancestors. Contemporary fire regimes on Martu country are associated with a temporal and spatial pattern that is linked to the intensity of landscape use, which follows travel corridors and radiates outward from permanent settlements. At the local scale, close to vehicle tracks and communities, fire regimes today closely mimic those of the pre-settlement past (pre-1960) when Martu were nomadic foragers ranging widely across the landscape: fires are small, typically under five ha, and burn predominantly in the winter months (Bliege Bird et al., 2016, Bliege Bird et al., 2020). At the landscape scale, there are vast areas of the desert that are not visited by Martu, leading to the dominance of a lightning fire regime in those regions, with typically large fires (> 2000 ha) burning mainly in the hot, dry summer months (Bliege Bird et al., 2012).

Human landscape use is predicted well by central place models in which people are tethered to residential sites, using landscapes according to a distance-decay function (Bliege Bird et al., 2008). Travel time by vehicle from central places (the contemporary residential community) should thus predict the intensity of landscape and resource use, in turn affecting the likelihood of fire ignition. Prior work has shown that distance to Indigenous communities predicts changes in pyrodiversity measured as the diversity of time-since-fire patches (Bliege Bird et al., 2008, 2012, 2018) and that fire number and size interacts with rainfall, with higher rainfall associated with more, smaller fires close to communities, but fewer, larger fires far from communities (Bliege Bird et al., 2012). Here, we build on these results by (i) investigating whether the intensity of land use affects other measures of pyrodiversity that relate to the invisible mosaic (number of years a landscape burns, diversity of fire frequency patches, and number of unique fire histories); (ii) using a more precise measure of landscape use intensity that accounts for the cost of travel to and from a central place; (iii) exploring the interaction between rainfall, travel time, and measures of pyrodiversity; and (iv) accounting for spatial variation in vegetation cover.

Methods

Study system

Our 47 000 km² study area was within the 150 000 km² Martu Native Title and Karlamilyi National Park, in the Little Sandy and Great Sandy deserts of Western Australia (Fig. 2.1). This research is part of a larger, long-term collaborative project with Martu communities on the social and ecological dynamics of Martu cultural landscapes. Martu estates are among the most remote and intact arid environments in the world, supporting a number of animal and plant species of international, national, and/or state significance (Department of Conservation and Land Management, 2002). The area is characterised by high evaporation rates, fluctuating temperatures (10 – 40 °C), and low, variable rainfall (113 – 817 mm; annual average 370 mm). South-easterly trade winds determine the weather —cool, dry, and sunny— from May to September, and the Indo-Australian monsoon determines the weather —thunderstorms and tropical storms— from December to April. Most (83 %) rain falls between November and January (BOM, 2019). The main ecological communities are; sandplains and dunes dominated by spinifex (*Triodia schinzii*, *T. basedowii* complex, and *T. birrilibirru*), 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*); lateritic uplands dominated by mulga (*Acacia sen. lat. aneura*) woodlands; and *Senna* shrublands (Bliege Bird et al., 2012). Fire is common, with an average of 9.7 % of the study area burnt each year (Bliege Bird et al., 2012).

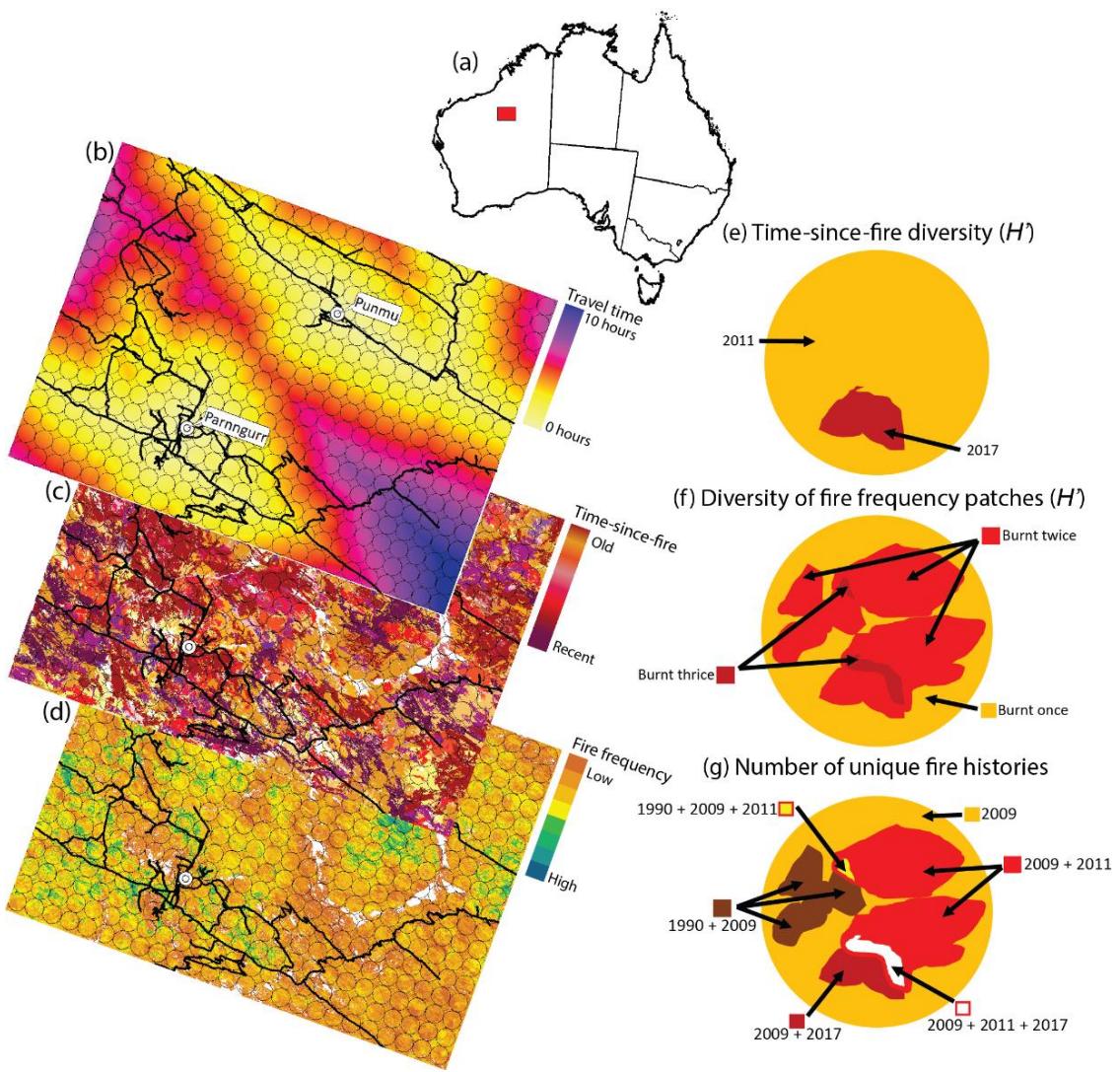


Figure 2.1 (a) Study area (red rectangle) in Australia. Representation of (b) travel time from Martu communities' layer, (c) time-since-fire layer, and (d) fire frequency layer, across 450 study landscapes with 10 km diameters. White circles: Martu communities, black lines: roads. Representation of the methods used to estimate (e) time-since-fire diversity (H'), (f) diversity of fire frequency patches (H'), and (g) the number of unique fire histories (i.e., combinations of seasons, interval lengths, and times-since-fire ages).

Landscape selection

To capture the spatial gradient of fire ignitions, we divided our 47 000 km² study area into a grid of 450 circular landscapes 10 km in diameter placed side by side (i.e., no overlap) (Fig. 2.1). Landscapes spanned from areas near Martu communities to remote areas dominated by lightning fires (Fig. 2.1). We chose 10 km diameters after also exploring 1, 2, and 5 km diameters, as this size demonstrated the strongest effects between our response and predictor variables.

Fire mapping

To quantify the fire histories of each landscape, we used detailed fire maps created by RBB, who 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 – 2016. From each image mosaic we derived the normalised burn ratio (NBR) which is calculated as a ratio between near infrared band and short-wave infrared band values. On Landsat 4 – 7 imagery, $NBR = (\text{Band 4} - \text{Band 7}) / (\text{Band 4} + \text{Band 7})$. In Landsat 8 imagery, $NBR = (\text{Band 5} - \text{Band 7}) / (\text{Band 5} + \text{Band 7})$. Following the calculation of NBR, change detection was employed using the previous image time-step to create $\Delta - NBR$ images. Fire scars were digitised from the Δ -NBR images with the region-growing algorithm implemented in QGIS (2.18). The minimum size of detectable fires was 3600 m² (4 pixels). In May 2011, 50 map pixels were randomly selected and ground truthed; 90 % of the selected pixels were classified correctly relative to their estimated burn age. Detailed methods are described in Bliege Bird et al. (2012).

We quantified the fire history of the 450 landscapes within 13 temporal windows that each spanned 15 years, beginning from 1990 – 2004 and ending in 2002 – 2016. Hence, each of the 450 landscapes were represented 13 times in the dataset. The cut-off of 15 years was chosen because it represents the approximate beginning of the final successional stage recognised by Martu: areas > 15 years post-fire are regarded as long unburned *kunarka*. Splitting the data into multiple temporal windows allowed us to model the influence of antecedent rainfall on fire mosaics, which is known to be an important driver of fire regimes in arid Australia (Allan and Southgate, 2002). We quantified the fire history for each 15-year window for all the 450 landscapes.

Landscape response variables

We prepared maps for analysis by layering 30 seasons over the 15-year window with the most recent observed fires in the top layer. This created a ‘fire history’ map with each polygon corresponding to a time-since-fire designation. We then converted each raster map into a shapefile using ‘intersect’, ‘union’, and ‘spatial join’ in ArcMap to extract information about each patch within each landscape (ESRI. ArcGIS Desktop: Release 10.7.1. Redlands, California: Environmental Systems Research Institute, 2019). For each of the 450 landscapes, across each 15-year temporal window we calculated the (i) number of years where a fire was recorded within the landscape, (ii) diversity of proportional time-since-fire patches, (iii) diversity of patches defined by fire frequency, (iv) number of patches with a unique fire history, and (v) maximum area of landscape burnt (ha) across all years (Fig. 2.1).

To quantify the visible fire mosaic, we calculated the diversity of time-since-fire patches, we assigned all polygons within a landscape with their most recent fire-age ranging from 0 – 15 + years since fire (Fig. 2.1). Based on the number and proportional extent of fire ages we calculated Shannon's diversity index (H') of each landscape (Fig. 2.1); a widely used approach to quantify pyrodiversity (e.g., Bliege Bird et al., 2008, Sitters et al., 2014).

To quantify the invisible fire mosaic, we calculated the diversity of fire frequency patches, the number of unique fire histories, the number of years in which a fire occurred, and the maximum areas burnt per landscape. To calculate the diversity of fire frequency patches we first assigned polygons according to the number of times they had been burnt over each 15-year period, e.g., burnt once, twice, thrice etc. (Fig. 2.1). We used this to calculate H' of each landscape based on the proportional number and extent of each fire frequency (Fig. 2.1). For unique fire histories, we defined polygons by the year and season they were burnt. We smoothed the fire scar raster images and removed any overlapping areas that were < 3600 m² (4 pixels) to ensure that we did not overestimate the number of unique fire histories due to mapping errors. Removing areas any larger could have resulted in the loss of real fire scars, as 12.5 % of the fires set by Martu during 1990 to 2016 were smaller than 1 ha (Bliege Bird, unpublished data). We manually combed through the data to ensure that there were no duplicate fire histories in the data set that had been identified as unique due to varying chronological order. Next, we counted the number of unique fire history combinations within a landscape (Fig. 2.1). We conceptualised the number of years in which a fire occurred within the landscape by assigning polygons according to year and then calculating the number of years in which a fire was recorded (i.e., maximum 15). Finally, we calculated maximum area burnt per landscape (ha) by identifying the largest polygon across all years, for each landscape.

Predictor variables

We considered several predictor variables as potential drivers of pyrodiversity: (i) travel time from Martu communities (used as a proxy for land-use intensity), (ii) five measures of antecedent rainfall (see below), (iii) percentage of spinifex sandplain, (iv) percentage of clay pan and lake, and (v) the interaction between travel time and rainfall.

Travel time from Martu communities was estimated by developing a cost-distance raster for the region assuming land use patterns are structured primarily by vehicular travel, as they currently are today (Bliege Bird et al., 2008). The cost-distance raster was based on

travel time by vehicle, assigning a velocity per hour of 80 km for major roads (unsealed, usually graded, ~25 m wide), 60 km for minor roads (unsealed, ~15 m wide), 20 – 40 km for minor trails (ungraded trails created by past vehicle use, ~2.5 m wide), 15 km for largely abandoned trails (former vehicle-made trails that have become overgrown), and 10 km cross-country travel (no visible track). We then used ‘cost distance analysis’ in ArcMap to derive the time required to travel from each of the two Martu communities (Parnngurr and Punmu) to any raster cell (1 x 1 m) in the study area. This involved defining a cost raster layer as 1/speed, such that cost (1/speed) multiplied by distance = travel time. Finally, we used ‘zonal statistics as table’ to extract the average travel time from the closest community to each of the 450 landscapes (Fig. 2.1).

We included a measure of antecedent rainfall in the models, as rainfall is a major driver of fire events in arid environments (Allan and Southgate, 2002) and people respond to antecedent rainfall by lighting more fires (Bliege Bird et al., 2012). In this ecosystem, spinifex (predominantly *Triodia schinzii*, *T. basedowii* complex, and *T. birrilibirru*) is the main fuel load component, although ephemeral shrubs and grasses can contribute to fuel loads after heavy rainfall events (Allan and Southgate, 2002). Spinifex is usually killed during fires and takes 3 – 30 years to accumulate enough biomass to once again carry fire, with re-growth highly dependent on rainfall (Allan and Southgate, 2002). Thus, rainfall largely dictates fire activity (Allan and Southgate, 2002, Burrows, 2006, Edwards et al., 2008). Time-since-fire pyrodiversity may be affected primarily by short-term antecedent rainfall, in that large rainfall-driven fires would reduce heterogeneity by sweeping across entire landscapes, without time for a new mosaic to become established (Edwards et al., 2008). Fire frequency diversity and unique fire history diversity measures accumulate over a longer temporal window and thus longer-term rainfall patterns, such as average rainfall over the entire 15-year period, might be more important as each fire season is influenced by the antecedent years of rainfall leading up to it.

To explore how rainfall effects pyrodiversity, we calculated five different rainfall measurements for each landscape. First, we downloaded monthly grids (5 km resolution) from the Bureau of Meteorology (www.bom.gov.au). Next, we used ‘extract multi values at points’ in ArcMap to calculate the monthly rainfall for the centroid of each landscape. For each of the 450 landscapes, for each temporal window, we used this to calculate the (i) cumulative 1-year rainfall prior to the end of the 15-year period (i.e., total rainfall over

the final year of each 15 year window), (ii) cumulative 2-year rainfall prior to the end of the 15-year period (i.e., total rainfall for the two final years for each 15-year window), (iii) cumulative 3-year rainfall prior to the end of the 15-year period (i.e., total rainfall for the three final years for each 15 year window), (iv) average annual rainfall over the 15-year period, and (v) coefficient of variation in annual rainfall (measure of relative variability in rainfall) over the entire 15-year period, which we calculated by: standard deviation (yearly rainfall) / mean (yearly rainfall) x 100.

For many analyses, we conceptualised time-since-fire as successional stages, loosely following Martu classification schemes: recently burnt patches 0 – 1 year post-fire as *nyurnma*; 1 – 5 years post-fire when plants mature and flower as *nyukura*; 5 – 10 years post-fire when spinifex matures and becomes burnable as *manguu*; and 10 + years post-fire when spinifex becomes senescent as *kunarka* (Bliege Bird and Bird, 2020). Martu also recognise *waru waru* (when plants re-sprout after rain), however we chose to omit it as it depends on the timing of rainfall which can cause significant temporal overlap with *nyukura*.

The occurrence, spread, and severity of fires are determined by the type and biomass of vegetation (Marsden-Smedley et al., 2012). As mentioned, spinifex is the major component of the fuel loads because of its highly flammable, persistent, sclerophyllous, and resin laden leaves (Allan and Southgate, 2002). As fire spreads easily in mid- to late-successional spinifex, landscapes with higher proportions of spinifex could have reduced pyrodiversity (Allan and Southgate, 2002). In contrast, claypans and lakes rarely or never carry fire, due to a lack of vegetation (Marsden-Smedley et al., 2012). Claypans and lakes therefore have the potential to influence pyrodiversity by acting as natural fire breaks. To calculate the percentage of spinifex sandplain and claypans and lakes in each landscape, we used vegetation maps created by RBB, who hand-drew major habitat boundaries on high resolution satellite imagery. We calculated the percentage cover of each vegetation community for each 30 m grid cell in Fragstats v4.3 (McGarigal et al., 2012). Next, we converted this to a shapefile, and using ‘intersect’, ‘union’, and ‘spatial join’ in ArcMap we calculated the percentage of spinifex sandplain, and claypans and lakes for each of the 450 landscapes.

Data analysis

First, we explored our data following Zuur et al. (2009): (i) we tested for spatial correlation between variables with a variance inflation factor of > 3 as the threshold, (ii) we investigated the relationships between response and predictor variables, and (iii) we scaled predictor variables to allow for easier comparison and interpretation of model outputs. We log transformed travel time when there was evidence of a non-linear relationship with a landscape response variable. The number of years a landscape experienced fire was proportional and followed a Binomial distribution. The diversity of time-since-fire patches and diversity of fire frequency patches were continuous and followed a Gaussian distribution. The number of unique fire histories was positively skewed and discrete, following a Poisson distribution. For these models we fitted Generalised Linear Mixed Models (GLMMs). The relationship between travel time and maximum landscape area burnt demonstrated increasing variance with travel time. Such relationships can be indicative of a predictor variable affecting the upper limit of a response variable, as opposed to the mean (Cade and Noon, 2003). It can also suggest violation of the homogeneity of variance assumption of many regression models. Thus, we fitted quantile regression mixed models.

For all regression models (except quantile regression 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 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 landscape response variable, we created a model candidate set with all combinations of the predictor variables. Models were deemed parsimonious and retained if they were within 2 AICc of the top model (Burnham and Anderson, 2002). To assess the influence of the predictor variables, we calculated the 95 % confidence intervals around the estimate, deeming variables important if the confidence intervals did not overlap zero. For the quantile regression models, we fitted univariate models that only included the maximum area burnt as the response variable, and travel time as the predictor variable. As we were only interested in the upper limit of maximum area burnt, we investigated the relationship between travel time and the 95th quantile of maximum area burnt. For all models (regression and quantile) we included landscape ID as a random effect to account

for temporal autocorrelation due to repeated measures, as landscape properties were measured for each of the 13 temporal windows.

All analyses were conducted in R version 2.1 (R Core Team, 2018) using glmmTMB (Brooks et al., 2017), lme4 (Bates et al., 2015), and lqmm (Marco, 2014) packages.

Results

Preliminary analyses indicated that cumulative three-year rainfall best explained the data for all landscape variables (Table S2.1).

The proportional number of years a landscape experienced fire ranged between 0 (no years burnt) to 1 (15 years burnt) (mean = 0.4 or 6 years). The top models explained a high amount of variation in the number of years burnt (83 %) and all included travel time from Martu communities, rainfall, percentage of claypans and lakes, and the interaction between travel time and rainfall (Table 2.1, 2.2, and S2.2). The number of years a landscape experienced fire decreased with increasing travel time (Table 2.2, Fig. 2.2 and 2.6). For example, the number of years burnt was 0.67 (10 years) per landscape (CI = 0.7 – 0.7) 20 minutes from Martu communities, sharply reducing to 0.33 (5 years) (CI = 0.2 – 0.3) three hours from communities, and to 0.13 (2 years) (CI = 0.1 – 0.1) eight hours from communities. The interaction between rainfall and travel time indicated the number of years burnt increased sharply with increasing rainfall close to communities (i.e., < 2 hours from communities), whereas far from communities (i.e., > 2 hours from communities) rainfall had a smaller effect (Table 2.2). The proportional number of years a landscape burnt increased with increasing cumulative 3-year rainfall and declined with increasing percentage of claypans and lakes (Table 2.2).

Table 2.1 Model selection for how travel time (hours) from Martu communities (time), rain (antecedent rainfall variable), percentage of spinifex sandplain (spinifex), percentage of claypan and lake (claylake), and the interaction between travel time and rainfall (time*rain) effects landscape response variables. K: number of model parameters, AICc: model rank, ΔAICc : difference between top model and described model, w_i : Akaike weight (i.e., the likelihood of the model being the best in the candidate set), R^2 : model fit. Only models with $\Delta\text{AICc} \leq 2$ are shown.

Landscape response variable	Model	K	AICc	ΔAICc	w_i	R^2
Number of years burnt	time + rain + claylake + time*rain	5	20983.97	0.00	0.69	0.71377
	time + rain + spinifex + claylake + time*rain	6	20985.60	1.63	0.31	0.71378
Diversity of time-since-fire patches	time + rain + spinifex + claylake	5	-623.10	0.00	0.31	0.68842
	time + rain + claylake	4	-623.10	0.06	0.30	0.68201
	time + rain + spinifex + claylake + time*rain	6	-621.40	1.73	0.13	0.68066
	time + rain + claylake + time*rain	5	-621.40	1.77	0.13	0.68002
Diversity of fire frequency patches	time + rain + claylake	4	-1712.20	0.00	0.44	0.63433
	time + rain + claylake + time*rain	5	-1711.20	0.99	0.27	0.63211
	time + rain + spinifex + claylake	5	-1710.40	1.80	0.18	0.63019
Number of unique fire histories	time + rain + spinifex + claylake	5	46713.89	0.00	0.39	0.94479
	time + rain + claylake	4	46714.38	0.48	0.30	0.94481
	time + rain + spinifex + claylake + time*rain	6	46715.59	1.70	0.17	0.94477
Maximum area burnt	time + rain + spinifex + claylake + time*rain	6	92386.90	0.00	0.44	0.69431
	time + rain + spinifex + time*rain	5	92387.20	0.37	0.37	0.69020%

Table 2.2 Influential (i.e., confidence intervals do not overlap 0) estimated model coefficients from the top models (i.e., lowest AICc) for each landscape response variable. SE: standard error, CI: 95% confidence intervals, travel time: travel time (hours) from Martu communities, spinifex: percentage of spinifex sandplain, claypan and lake: percentage of claypan and lake, travel time*rain: interaction between travel time and rainfall.

Landscape response variable	Model	Predictor variable	Est	SE	CI
Number of years burnt	time + rain + claylake + time*rain	Log (travel time)	-0.60	0.03	-0.66 – -0.55
		Cumulative 3-year rain	0.13	0.01	0.11 – 0.14
		Claypan and lake	-0.11	0.03	-0.16 – -0.06
		Travel time*rain	-0.03	0.01	-0.05 – -0.02
Diversity of time-since-fire patches	time + rain + spinifex + claylake	Log (travel time)	-0.18	0.01	-0.21 – -0.15
		Cumulative 3-year rain	0.04	0.00	0.04 – 0.05
		Claypan and lake	-0.04	0.01	-0.07 – -0.01
Diversity of fire frequency patches	time + rain + claylake	Log (travel time)	-0.16	0.01	-0.18 – -0.14
		Cumulative 3-year rain	0.05	0.00	0.04 – 0.05
		Claypan and lake	-0.06	0.01	-0.08 – -0.04
Number of unique fire histories	time + rain + spinifex + claylake	Log (travel time)	-0.55	0.03	-0.60 – -0.50
		Cumulative 3-year rain	0.11	0.02	0.10 – 0.11
		Claypan and lake	-0.14	0.03	-0.19 – -0.09
Maximum area burnt	time + rain + spinifex + claylake + time*rain	Log (travel time)	424.73	44.38	337.54 – 511.92
		Cumulative 3-year rain	64.04	7.75	48.84 – 79.23
		Spinifex sandplain	94.47	44.83	6.42 – 182.52
		Travel time * rain	62.74	7.94	47.17 – 78.30

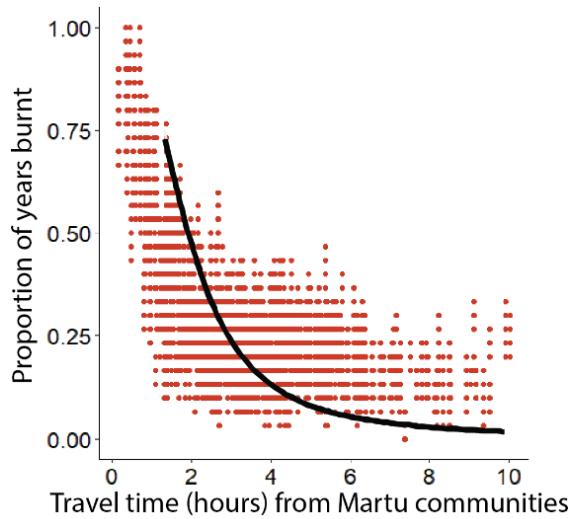


Figure 2.2 The effect of travel time (hours) from Martu communities on the proportion of years burnt (15-year total). Red dots: raw data, black lines: fitted relationships derived from regression models, grey shading: 95 % confidence intervals.

Visible fire diversity, in terms of Shannon's diversity index (H') of time-since-fire patches, ranged between 0.0 to 2.4 per landscape (mean = 1.2). The top models explained a substantial amount of variation in the diversity of time-since-fire patches (68 %) and all included travel time, rainfall, and percentage of claypans and lakes (Table 2.1, 2.2, and S2.2). The diversity of time-since-fire patches decreased with increasing travel time (Table 2.2, Fig. 2.3 and 2.6). For example, time-since-fire diversity was 1.8 (CI = 1.7 – 1.9) 20 minutes from Martu communities per landscape, dropping to 1.2 (CI = 1.1 – 1.2) three hours from communities, and to 0.9 (CI = 0.8 – 0.9) eight hours from communities. While the interaction between travel time and rainfall was included in the best models for time-since-fire diversity, it was not influential (Table 2.1 and S2.2). Visible time-since-fire diversity increased with increasing cumulative 3-year rainfall and declined with increasing percentage of clay pans and lakes (Table 2.2).

Modelling the successional stages separately showed that high time-since-fire diversity close to communities was associated with low cover of recently burnt patches 0 – 1 years post-fire, patches 1– 5 years post-fire, and patches 10 + years post-fire, with high cover of patches 5 – 10 years post-fire (Table S2.3 – S2.5, Fig. 2.4 and S2.1).

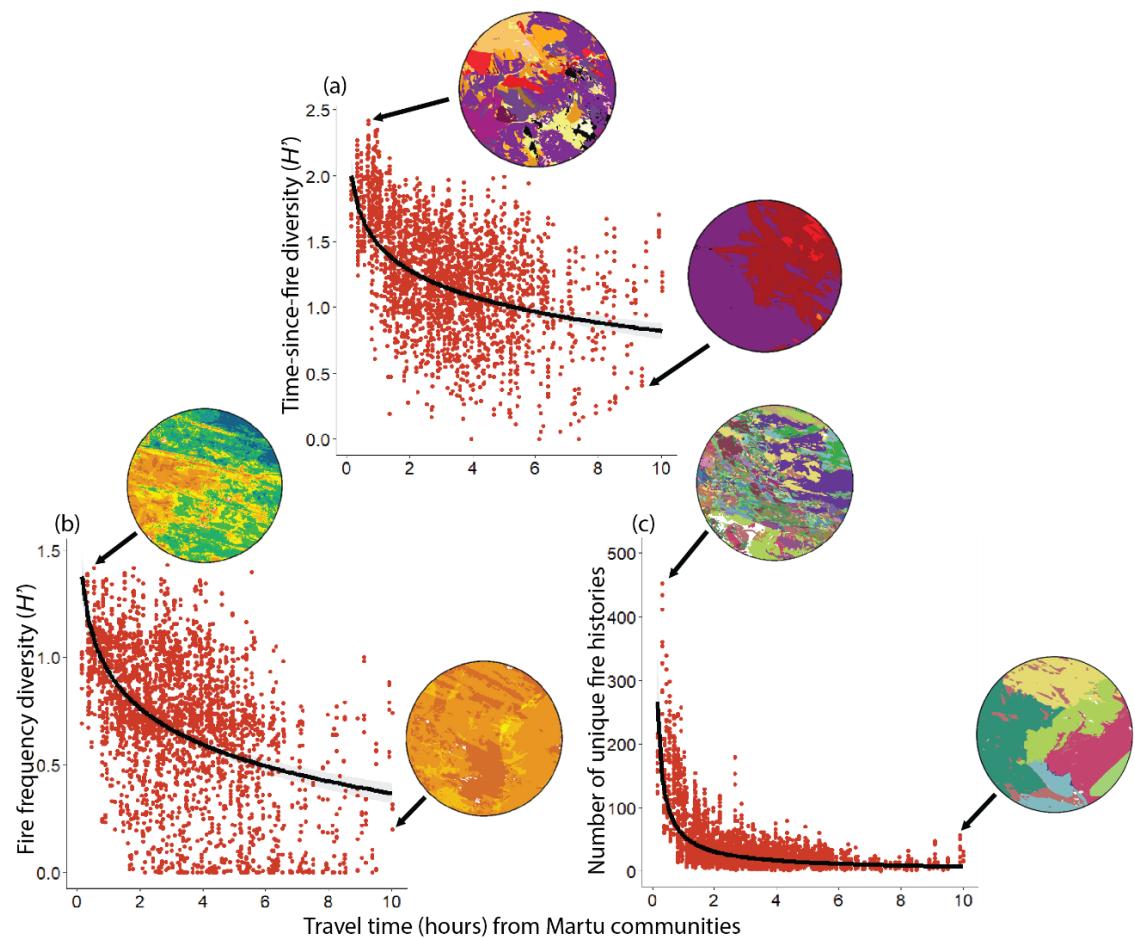


Figure 2.3 The effect of travel time (hours) from Martu communities on (a) diversity of time-since-fire patches (H') with inserts of landscapes of high and low time-since-fire diversity (one colour per time-since age), (b) diversity of fire frequency patches (H') with inserts of landscapes of high and low diversity of fire frequency patches (one colour per number of times burnt), and (c) the number of unique fire histories with inserts of landscapes of high and low numbers of unique fire histories (one colour per unique fire history), at the 10 km landscape scale. Red dots: raw data, black lines: fitted relationships derived from regression models, grey shading: 95 % confidence intervals.

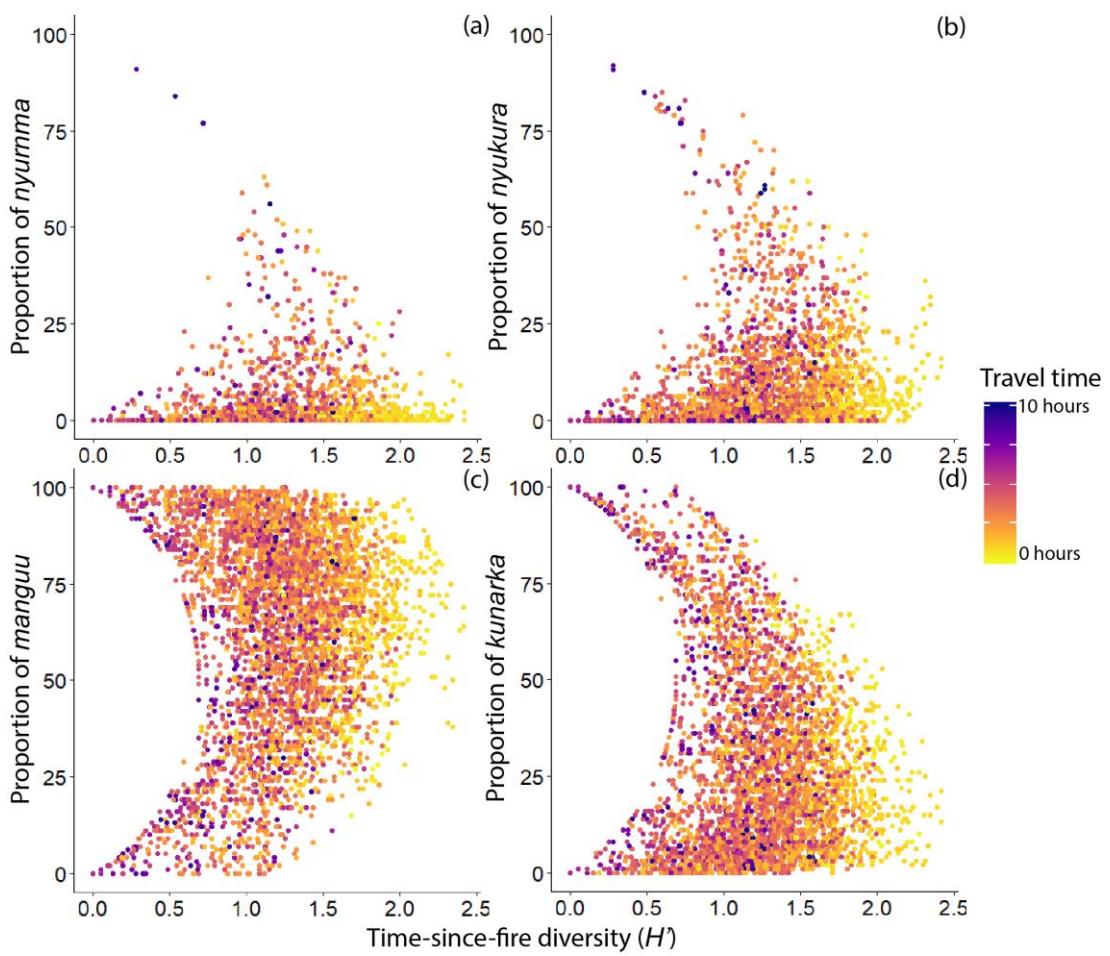


Figure 2.4 The effect of time-since-fire diversity (H') on the proportion of (a) *nyurnma* (0–1 years post-fire), (b) *nyukura* (1–5 years post-fire), (c) *manguu* (5–10 years post-fire), and (d) *kunarka* (10+ years post-fire). Dots: raw data coloured by travel time (hours) from Martu communities.

The number of times a patch burnt ranged from 1 to 7 over the 15-year period. Invisible fire diversity, in terms of the diversity of fire frequency patches (H'), ranged between 0.0 to 1.4 per landscape (mean = 0.7). The top models explained a high amount of variation in the diversity of fire frequency patches (63 %) and all included travel time, rainfall, and percentage of claypans and lakes (Table 2.1, 2.2, and S2.2). The diversity of fire frequency patches decreased with increasing travel time (Table 2.2, Fig. 2.3 and 2.6). For example, the predicted diversity of fire frequency patches was 1.2 (CI = 1.1 – 1.3) 20 minutes from Martu communities per landscape, reducing to 0.7 (CI = 0.6 – 0.7) three hours from communities, and to 0.4 (CI = 0.4 – 0.5) eight hours from communities. While the interaction between travel time and rainfall was included in the best models for the diversity of fire frequency patches, it was not influential (Table 2.1 and S2.2). Diversity of fire frequency patches increased with increasing cumulative 3-year rainfall and declined with increasing percentage of claypans and lakes (Table 2.2).

The number of unique fire histories ranged from 1 to 452 per landscape (mean = 31). The top models explained a moderate amount of variation in the number of unique fire histories (55 %) and all included travel time, rainfall, and percentage of claypans and lakes (Table 2.1, 2.2, and S2.2). The number of unique fire histories decreased dramatically with increasing travel time (Table 2.2, Fig. 2.3, and 2.6). For example, 20 minutes from Martu communities, the number of unique fire histories was 147 (CI = 124 – 177) per landscape, which dropped to 22 (CI = 21 – 23) three hours from communities, and to 9 (CI = 9 – 10) eight hours from communities. While the interaction between travel time and rainfall was included in the best models for the number of unique fire histories, it was not influential (Table 2.1 and S2.2). The number of unique fire histories increased with increasing cumulative 3-year rainfall and declined with increasing percentage of claypans and lakes (Table 2.2).

The maximum area burnt (upper limit of ~7853 ha as that was the area of each sample landscape) ranged from 0 to 6937 ha per landscape (mean = 1902 ha). The top models all included travel time, rainfall, percentage of claypans and lakes, and the interaction between travel time and rainfall (Table 2.1, 2.2, and S2.2). Maximum area burnt increased with increasing travel time (Table 2.3, Fig. 2.5 and 2.6). For example, 20 minutes from Martu communities the maximum area burnt was 676 ha (CI = 579 – 791) per landscape, increasing to 1660 ha (CI = 1591 – 1732) three hours from communities, and 2474 ha (CI = 2287 – 2676) eight hours from communities. The maximum area burnt increased both with increasing cumulative 3-year rainfall and increasing percentage of spinifex sandplain (Table 2.2). Areas with high pyrodiversity tended to experience far fewer large fires (Fig. 2.7).

Table 2.3 Quantile regression coefficient for 95th upper quantile of travel time (hours) from Martu communities in relation to the maximum area burnt (ha). SE: standard errors, CI: 95 % confidence intervals (influence indicated by no overlap with 0).

Quantile	Value	SE	CI
95th	508.18	45.05	417.64 – 598.71

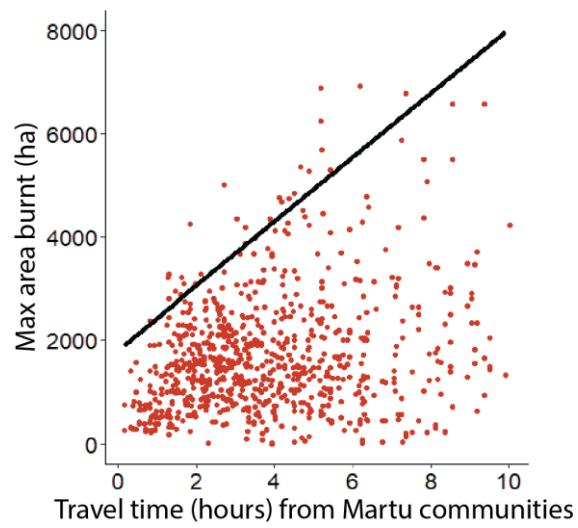


Figure 2.5 Relationship between travel time (hours) from Martu communities and the 95th quantile of maximum area burnt (ha) at the 10 km landscape scale. Red dots: raw data, black line: upper (95th) quantile.

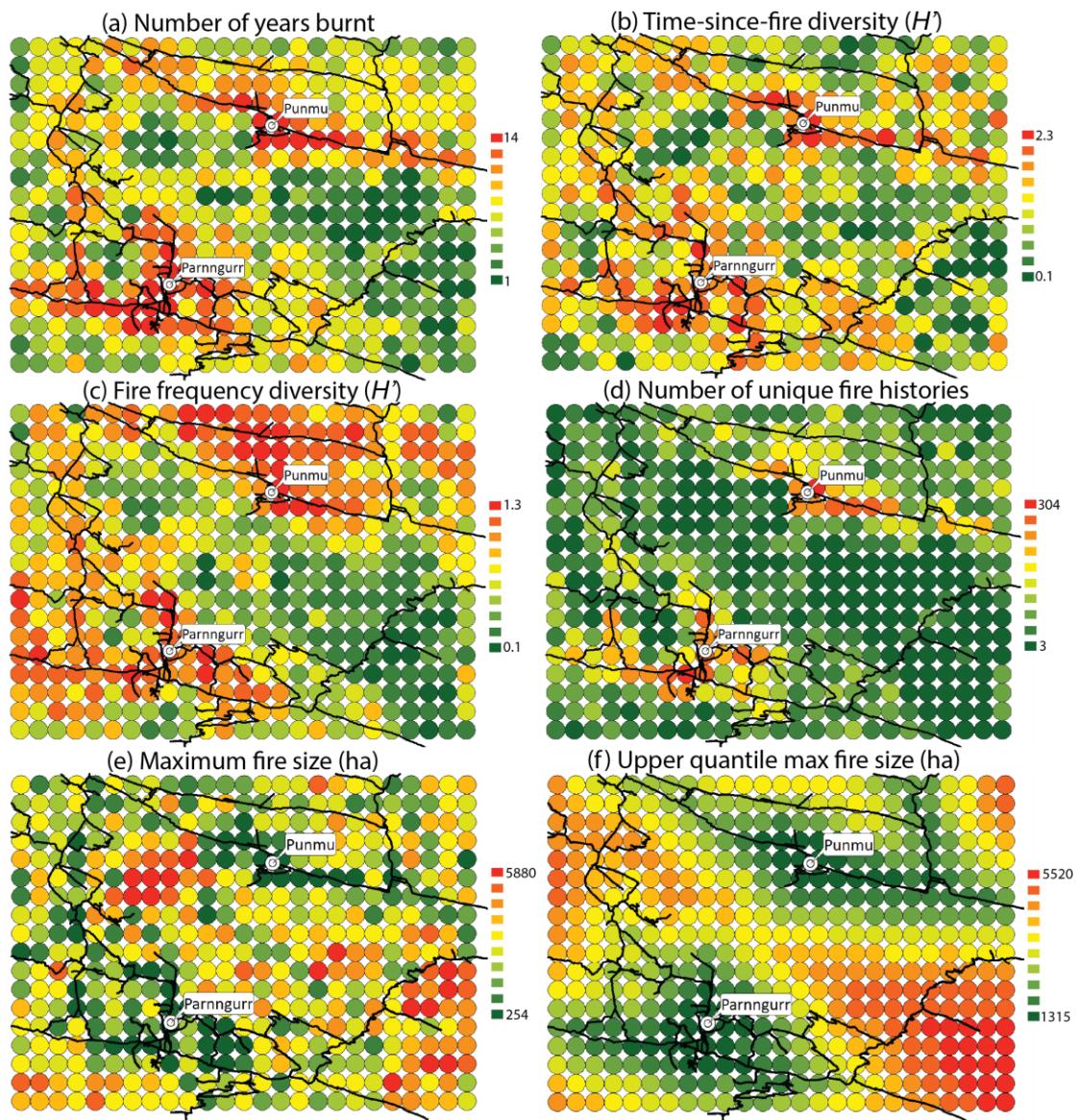


Figure 2.6 Aerial representation of the influence of travel time (hours) from Martu communities on (a) the number of years burnt, (b) time-since-fire diversity (H'), (c) diversity of fire frequency patches (H'), (d) number of unique fire histories, (e) maximum area burnt (ha), and (f) the 95th quantile of maximum area burnt (ha), for each of the 450 study landscapes at the 10 km landscape scale. White circles: Martu communities, black lines: roads.

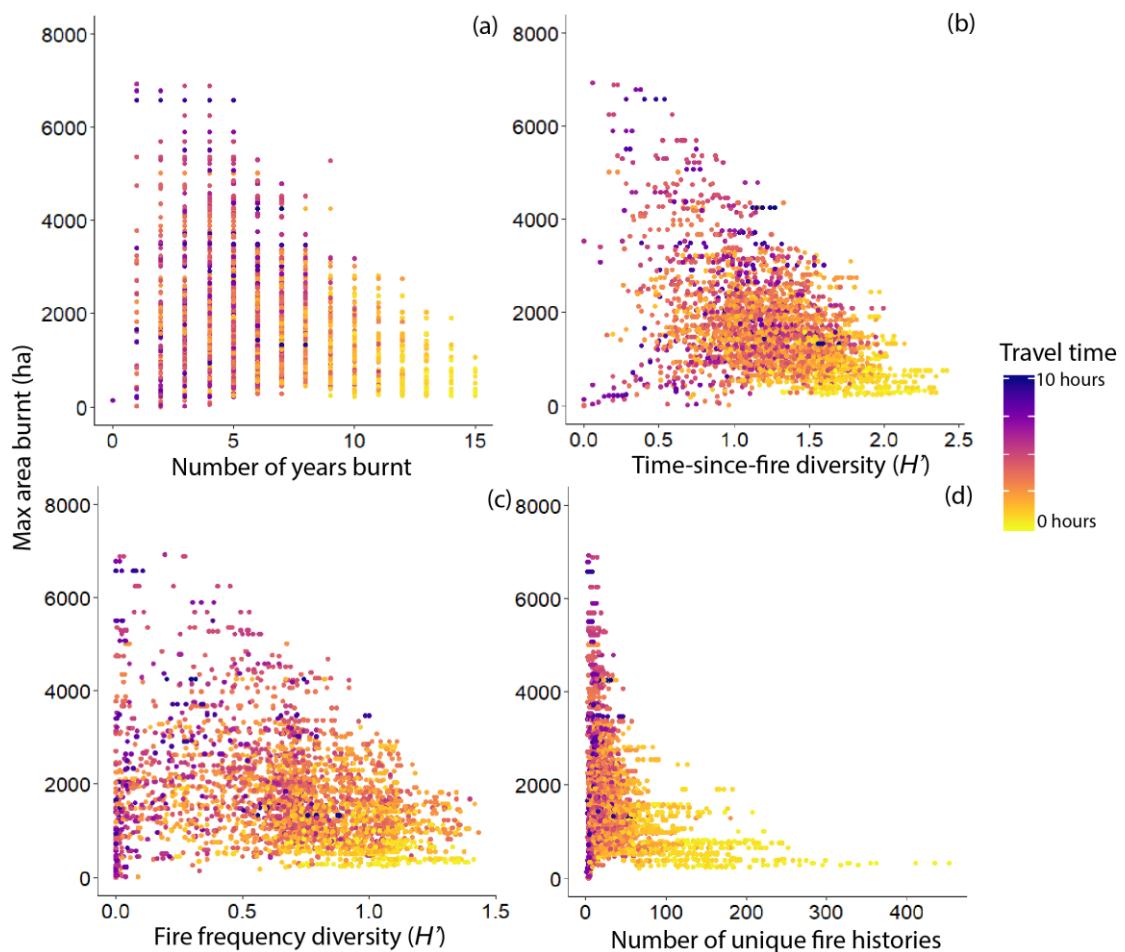


Figure 2.7 The relationship between maximum area burnt (ha) and (a) number of years burnt, (b) time-since-fire diversity (H'), (c) diversity of fire frequency patches (H'), and (d) number of unique fire histories. Dots: raw data coloured by travel time (hours) from Martu communities.

Discussion

Across a 26-year history of landscape use, the cost of travel from Martu communities shapes the fire regimes of local landscapes, creating distinctive visible and invisible fire mosaics which dwarf the pyrodiversity of more distant areas. Within this period, landscapes 20 minutes from Martu communities experienced almost four times the amount of fire, had twice the diversity of time-since-fire ages, almost three times the diversity of fire frequency patches, and over sixteen times the number of unique combinations of fire histories (seasons, interval lengths, and time-since-fire ages), compared to landscapes eight hours from communities. The creation of a pyrodiverse mosaic appears to place an upper limit on the size of fires that can burn in any given year—close to communities, the largest burnt area remained well below 4000 ha (half the landscape), while beyond two hours, burnt areas increased to nearly 7000 ha (almost the entire landscape).

Previous work has explored the mechanisms that underpin spatial patterning in the visible mosaic in the western desert (Bliege Bird et al., 2008, 2012, 2018). Increased diversity of successional stages is a result of the Indigenous application of fire at a landscape scale, which is driven in a large part through the use of burning in the winter months to expose the active burrows of brumating goannas (*Varanus gouldii*), as well as to target other small animals such as desert pythons (*Aspidites ramsayi*) and blue-tongued skinks (*Tiliqua scincoides*) or to attract larger animals (e.g., bustards *Ardeotis australis* and kangaroos *Macropus robustus*) to feed in the burnt patch. Landscape fire is used to expose target animals that are hiding within or burrowed below mature spinifex hummocks, drastically increasing foraging returns (Bliege Bird et al., 2008, Codding et al., 2014). Hunting fires are typically much smaller than lightning fires in both summer and winter (Bliege Bird et al., 2012). Most hunting trips, and thus most fire application by community members, occurs within two hours one-way travel time (Bliege Bird et al., 2008). We show that this pattern in hunting creates an obvious transition in human influence of landscape-scale fire regimes. Places near Martu communities are under an anthropogenic fire regime characterised by diverse fire mosaics, which likely mimics past fire mosaics (Bliege Bird et al., 2016) that extended over the entire landscape (Bliege Bird et al., 2020). As the distance from Martu communities' increases, the anthropogenic control over fire regimes gradually diminishes, and eventually switches to landscapes largely devoid of people, where ignitions occur only from lightning. The two ends of this spectrum are likely to represent alternative ecological states.

This study is the first to shed light on how Indigenous burning shapes not only the visible pattern of the most recent fires, but also the underlying spatiotemporal patterns of historic fires: the ‘invisible mosaic’. Patterns in diversity of the invisible mosaic largely mirror patterns of the visible mosaic, showing sharp declines with distance to communities. However, these patterns likely emerge not by a simple overlaying of multiple ‘visible’ mosaics over time, but by complex social-ecological interactions between Martu, their land, and its productivity (Bird et al., 2016). Using aerial photographs from the 1950s—during which period many Martu remained as nomadic foragers—Bliege Bird et al. (2020) showed that Martu purposefully returned to burnt landscapes that had been subject to regular anthropogenic fire in the past, likely because it increased the predictability and availability of culturally important species. This landscape use produces a positive feedback loop; fire increases hunting success and

foraging efficiency, which provides incentives for people to return, further increasing fire history diversity. While we emphasize here the hunting purpose of the majority of landscape fires, the meaning of fire in the ritual belief system known as the Dreaming (*Tjukurr* for Martu) emerges from the way that hunting creates the pyrodiverse landscapes that support both people and the plants and animals they rely on (see Bird et al., 2016 for more details).

While the pyrodiversity hypothesis has tended to focus on diversity of the visible mosaic, it is widely recognised that the properties of invisible fire mosaics are of ecological importance (Smit et al., 2010, Foster et al., 2017). Like time-since-fire, fire frequency is a driver of vegetation structure and composition (Nano and Clarke, 2011), and this has flow-on effects for animal populations (Lindenmayer et al., 2016). Variability in fire frequency across the landscape could support a more diverse range of species, by initiating different post-fire responses (Burgess et al., 2015, Ponisio et al., 2016, Foster et al., 2017). For example, areas with high fire frequency can promote re-growth of shrubs and small trees, whereas areas with low fire frequency can promote re-growth of canopy species post-fire (Foster et al., 2017). In spinifex grasslands, differing fire frequencies may have minimal effects on woody species, possibly due to fast re-sprouting and germination abilities, short juvenile periods, and rapid seed production; however, increased fire frequency can cause declines in spinifex cover (Wright and Clarke, 2007), which may lead to increases in species diversity (Burrows et al., 2020). One of the few studies of the impact of the invisible mosaic on animal communities found a positive relationship between the diversity of fire frequency patches and the richness of flies and wasps in a heathy woodland (Brown and York, 2017). Studies of the relationship between diversity of the visible mosaic and biodiversity have had mixed results (Jones and Tingley, 2021), but few have measured responses in relation to pyrodiversity maintained by Indigenous land management (but see Bliege Bird et al., 2018). An important next step will be to examine how biodiversity responds to this heightened pyrodiversity of the invisible mosaic under Indigenous stewardship.

The influence of Martu communities on the invisible mosaic was most apparent when viewing pyrodiversity in terms of the unique combinations of burn histories that fires bring about. This measure reflects differences between patches in terms of fire year, season, frequency, and interval. While there are hypotheses for how various attributes

of the fire regime could interact to shape plant and animal communities—for instance differing post-fire successional trajectories due to variation in fire frequency, interval, or season (Haslem et al., 2016)—there are few empirical studies that have assessed such interactions. Consequently, the ecological ramifications of increases in the unique combinations of fire histories are largely unknown. What is becoming clear is that plant species often have quite specific requirements in terms of their regeneration niche as it relates to fire (Smith et al., 2016, Miller et al., 2019), and so having a diverse suite of fire histories across landscapes could increase landscape-scale plant diversity by providing an array of regeneration niches. Landscapes near Martu communities were also far more likely to experience fire in any given year, creating a more continuous provision of early successional habitat and, therefore, opportunities for early successional species.

The arrangement of vegetation elements within fire mosaics is important for biodiversity, as some elements can be disproportionately crucial for different species to meet their needs at different life stages (Kelly et al., 2017). Close to Martu communities, landscapes had high time-since-fire diversity with low covers of newly burnt and old vegetation, and high cover of mid-succession vegetation. This suggests that Indigenous fire regimes work to protect mid-succession vegetation patches within pyrodiverse landscapes (Bliege Bird et al., 2008, Trauernicht et al., 2015). Lower cover of successional stages within these landscapes close to communities is likely because each successional stage is represented, whereas distant landscapes would have higher cover, but fewer successional stages. In arid environments, recently burnt vegetation can be important for competitive release for plants, allowing a suite of plants to germinate (Burrows et al., 2020), which in turn provides food for animals (Coddington et al., 2014, Murphy and Bowman, 2007). The structural complexity of older spinifex patches is important for meeting species shelter, nesting, and thermoregulation requirements (Coddington et al., 2014, Letnic, 2003). Thus, simply maximising pyrodiversity, without sound consideration of species resources needs and historical levels of pyrodiversity under which communities evolved (Martin and Sapsis, 1992, Parr and Andersen, 2006), may not be the most effective way to promote biodiversity (Kelly et al., 2017). Understanding how current patterns of pyrodiversity relate to pyrodiversity maintained under Indigenous fire stewardship is key.

Our findings support the notion that fire spread and size is reduced by pyrodiverse landscapes that are created by Indigenous burning. Pyrodiverse landscapes probably limit

fire spread and size by reducing fuel loads through increased burning (i.e., increased fire frequency) and by creating fire breaks of early successional stages (i.e., increased time-since-fire diversity) (Loehle, 2004, Boer et al., 2009, Price et al., 2015). The effect of the number of unique fire histories on maximum area burnt seem especially evident: high diversity of unique fire histories and larger fires simply do not co-occur in these landscapes. Decreased fire size under Indigenous pyrodiversity has been demonstrated by Bliege Bird et al. (2012): in a ten-year period from 2000 – 2010, fires remained consistently small close to Indigenous communities (i.e., 326 ha in the wet season and 109 ha in the dry season) regardless of rainfall, whereas under lightning regimes fire size was much larger and fluctuated more dramatically dependent on rainfall (i.e., 1910 ha in the wet season increasing to 6255 ha in the dry season). Our results suggest that the continued application of fire over successive years to build up a mosaic that varies in both recent and, importantly, long-term fire histories may drive the reduction in large fires near Martu communities. The regular application of fire likely results in more constant barriers to fire spread in the form of very recently burned vegetation but may also result in reductions in flammable vegetation. Spinifex seedlings, for example, can be less abundant where fires are frequent and intervals between fires are short (Wright and Clarke, 2007).

Limiting fire size and spread is important because large summer wildfires (i.e., characteristic of lightning regimes) often burn at high intensities (Williams et al., 2015) and create large, homogenous areas of vegetation of the same growth stage (Cassell et al., 2019). This can reduce the likelihood of long unburnt patches persisting (Trauernicht et al., 2012), increase the likelihood of fire entering ecosystems that are sensitive to fire (Cochrane, 2003), and further promote large fires through regrowth of continuous fuel (Loepfe et al., 2010). Increasing fire size and severity is often attributed in part to the displacement of Indigenous people and their fire regimes (Holz and Veblen, 2011, Liebmann et al., 2016). Previous work in the western deserts showed Indigenous burning decouples relationships between climate and fire size, such that areas near Indigenous communities' experience smaller fires even when climatic conditions favour large fires (Bliege Bird et al. 2012). Our findings also support the hypothesis that Indigenous burning suppresses large fires, given that maximum area burnt was positively related to travel time. Emerging evidence from Northern tropical Australia suggests that the re-establishment of Indigenous burning can reduce wildfire spread through the re-establishment of fine

scale fire mosaics, reduced ground layer fuel, and creation of fire breaks (Ansell and Evans, 2019).

This research sheds new light on the magnitude of impacts of Indigenous people on fire regimes, underscoring the radical changes in fire regimes that can emerge when Indigenous people are displaced from their land. In doing so, we contribute to a building global narrative of the importance of Indigenous fire around the world, e.g., in South America (Durigan et al., 2016, Nepstad et al., 2006, Pivello, 2011), North America (Liebmann et al., 2016), Mali (Laris, 2002), and Australia (Bliege Bird et al., 2008, Trauernicht et al., 2015, Bliege Bird et al., 2018). We highlight that Indigenous fire regimes work to craft ecosystems into states that are profoundly different from the ecosystems without their presence (Bliege Bird and Nimmo, 2018), separating a transition from fine scale fire mosaics to landscapes with homogenised fire histories.

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Chapter three: Fire history shapes plant diversity and composition in Australia's western deserts

Manuscript is preparation for submission

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Abstract

Fire has shaped plant communities since plants first colonised land over 400 million years ago. In semi-arid spinifex (*Triodia* spp.) grasslands of Australia, many plants, including culturally significant edible plants, are thought to rely on fire for competitive release and fire-cued germination. Here, we explored how time-since-fire and fire frequency influenced the richness and diversity of several plant groups (including edible plants), vegetation structure, and plant composition. Consistent with the “initial floristic composition” model, several plant richness and diversity variables were highest shortly after fire, before undergoing a reduction coincident with increases in spinifex cover. Edible plants peaked shortly post-fire and edible sub-shrub presence was highest in areas that were burnt frequently, consistent with the “fire-stick farming” hypothesis. We also found that distinct plant communities arose under each post-fire successional stage and fire frequency class. Our results contribute to the importance of fire in promoting and maintaining diverse plant communities in semi-arid spinifex grasslands and in increasing the productivity of landscapes for Indigenous people. By linking our previous work that shows Indigenous people increase time-since-fire landscape heterogeneity and the frequency that landscapes are burnt, we highlight the significant role of Indigenous burning in the maintenance of plant diversity in these regions.

Introduction

Fire has shaped plant communities since plants first colonised land over 400 million years ago (Bond and Keeley, 2005, Pausas and Ribeiro, 2017, Scott, 2018). Fire consumes plant biomass, killing or reducing plants to their roots, stems, or trunks, while also acting on seed dormancy through heat and smoke cues (Pausas and Lamont, 2022). By creating vegetation gaps, fire affects resources (e.g., space, light) and competitive interactions, setting in motion successional processes that shape plant composition for extended periods (Eales et al., 2018, Joner et al., 2021, Swanson et al., 2011). The sequence of changes that occur following fire and other disturbances have been the focus of ecologists for over a century (Clements, 1916).

Plant communities can be affected by all aspects of the fire regime (Gill, 1975). Two attributes that have received particular attention are time-since-fire (i.e., the amount of time that has elapsed since the last fire) and fire frequency (i.e., the number of times burnt over a given period). Several theories predict plant succession with time-since-fire (Pulsford et al., 2016), with broad support for the “initial floristic composition” model (Egler, 1954, Eales et al., 2018, Swanson et al., 2011). Under this model, most present species germinate shortly after fire, creating a peak in plant richness and diversity soon after fire, which then declines with increasing time-since-fire due to different plant life histories (e.g., short-lived, quick maturing plants disappear), competitive abilities (strong competitors outcompete weaker competitors), and increased vegetation structural complexity (fewer vegetation gaps to exploit) (Egler, 1954, Gosper et al., 2012a, He et al., 2019).

Fire frequency can alter plant composition and structure by affecting whether species reach maturity to produce propagules (Vigilante et al., 2004), the vigour of resprouting species (Noble and Slatyer, 1980, Pausas and Keeley, 2014), and the viability of propagules (Cury et al., 2020). High fire frequencies typically select for short-lived quick-maturing plants (e.g., herbs and sub-shrubs), and low fire frequencies for long-lived slow-maturing plants (e.g., shrubs and trees) (Pausas and Keeley, 2014). Thus, fire frequency can dramatically change vegetation structure (Ratajczak et al., 2014). As different fire frequencies can select for different plant species, the richness and diversity of plant groups within ecosystems can respond differently to fire frequencies (Peterson and Reich, 2008, Kayes et al., 2010). For example, increased fire frequency can promote

understorey plant richness, but decrease over-storey tree richness (Peterson and Reich, 2008). Hence, mixed responses of overall plant richness and diversity to fire frequency can occur (Palmquist et al., 2014, Guidoni-Martins et al., 2021).

The pattern of post-fire plant succession has received particular attention in Australia's vast arid and semi-arid spinifex (*Triodia* spp.) grasslands, which cover over a quarter of Australia (Wright et al., 2021). Spinifex is a diverse genus of highly flammable perennial grasses that form distinctive hummocks (Allan and Southgate, 2002, Marsden-Smedley et al., 2012, Nano et al., 2012). Mature spinifex hummocks are strong competitors and many plants that coexist with spinifex are thought to rely on fire for competitive release (Allan and Baker, 1990, Burrows et al., 2020, Wright and Clarke, 2007). During fire, spinifex is either killed (e.g., *T. basedowii*) or reduced to its roots (e.g., *T. schinzii*) (Rice and Westoby, 1999), which is thought to provide an opportunity for less competitive, smaller statured species (e.g., herbs, grasses, and sub-shrubs) to germinate and reproduce (Wright et al., 2021). Along with changes in plant composition, predictions consistent with the “initial floristic composition” model suggest that plant diversity peaks shortly after fire and declines as spinifex regains dominance (Egler, 1954). Fire frequency has been given less consideration; however, spinifex could be sensitive to short fire intervals as it is relatively slow to mature and requires sufficient time between fires to reach reproductive maturity and mast (Wright and Clarke, 2007, Wright and Fensham, 2018). Therefore, higher fire frequencies could favour less competitive species by reducing spinifex recruitment.

The successional dynamics of arid Australia take on particular importance to Indigenous people that have occupied and applied fire in these regions for tens of thousands of years (Burrows et al., 2006a, Bird et al., 2016). Fire is an indispensable component of human economies and cultural landscapes in Australia's western deserts (Bird et al., 2016). Over half a century ago, Gould (1971) hypothesised that fire could “free areas of relatively useless spinifex for the growth of more productive food plants”. Like other plants in spinifex grasslands, many of the edible plants that are important to Indigenous Australians are thought to rely on fire for competitive release from spinifex and for fire-cued germination (Commander et al., 2017, Gould, 1971, Jones, 1969). For example, 70 % of edible plants in central Australia are thought to be reliant on fire, and several edible sub-shrubs, herbs, and grasses have been shown to increase in abundance in mid-

succession (1.5 years post-fire) (Latz, 1995, Parker, 2015). Frequent fire could favour edible species by disadvantaging spinifex recruitment and growth (Wright and Clarke, 2007, Wright and Fensham, 2018).

Martu are the Traditional Owners of a large portion of Australia's western deserts, and includes Manyjilyjarra, Kartujarra, Kiyajarra, Putijarra, Nyiyaparli, Warnman, Ngulipartu, Pitjikala, Kurajarra, Jiwaliny, Mangala, and Nangajarra language groups. Martu were among the last Australian Indigenous groups to have contact with Europeans, and thus, many elders in the community have traditional burning experience that pre-dates European contact. Martu continue to regularly harvest traditional foods and burn small patches of spinifex, primarily to access small, burrowed reptiles (Bliege Bird et al., 2008, Bliege Bird et al., 2012). Burning is recognised to carry longer-term benefits by increasing food plant abundance for people and animals (Bird et al., 2016, Bliege Bird et al., 2008). Today, fires mostly occur within 50 km of communities (Bird et al., 2013), which has created a transition of anthropogenic to lightning fire across the landscape. Fires close to communities are mainly set by Martu and fires more than two hours from communities are mainly ignited by lightning (Bliege Bird et al., 2018, Greenwood et al., 2021). Fire frequency is highest near Martu communities and declines sharply with travel distance (Greenwood et al., 2021).

Here, we aimed to improve understanding of how fire influences plant communities in semi-arid spinifex grasslands on Martu Native Title. Specifically, we explored how time-since-fire and fire frequency influenced plant richness and diversity, vegetation structure, and plant composition. We investigated several plant groups —e.g., sub-shrubs and edible species— to investigate how fire influences different plant groups. We also explored how travel time from Martu communities (used as a proxy for land-use intensity) influenced plant richness and diversity, including edible plants. We interpreted our results through an Indigenous burning lens by linking our previous work that shows that Martu increase time-since-fire landscape heterogeneity and increase the frequency that landscapes are burnt (Bliege Bird et al., 2018, Greenwood et al., 2021).

Methods

Study system

Our study area was within Martu Native Title and Karlamilyi National Park in Western Australia (Fig. 3.1). This research is part of a larger, long-term collaborative project with

Martu communities on the social and ecological dynamics of Martu cultural landscapes (Bliege Bird et al., 2012, Bliege Bird et al., 2018). The climate is characterised by high evaporation rates, fluctuating temperatures (10 – 40 °C), and low, variable rainfall (113 – 817 mm; annual average 370 mm) (BOM, 2019). There is a diversity of rare and unique flora (~1145 taxa) and a high richness of *Acacia* species (81 taxa) (Department of Biodiversity Conservation and Attractions, 2021). The main ecological communities are sandplains and dunes dominated by spinifex (primarily *T. schinzii* and *T. basedowii* complex), wattles (including *Acacia pachycarpa* and *A. ligulata*), and desert bloodwoods (*Corymbia chippendalei*); rocky ranges dominated by spinifex and wattles; watercourse margins and wash areas sparingly dominated by eucalypts (primarily *Eucalyptus victrix* and *E. camaldulensis*); lateritic uplands dominated by mulga (*Acacia aneura*) woodlands; and *Senna* shrublands.

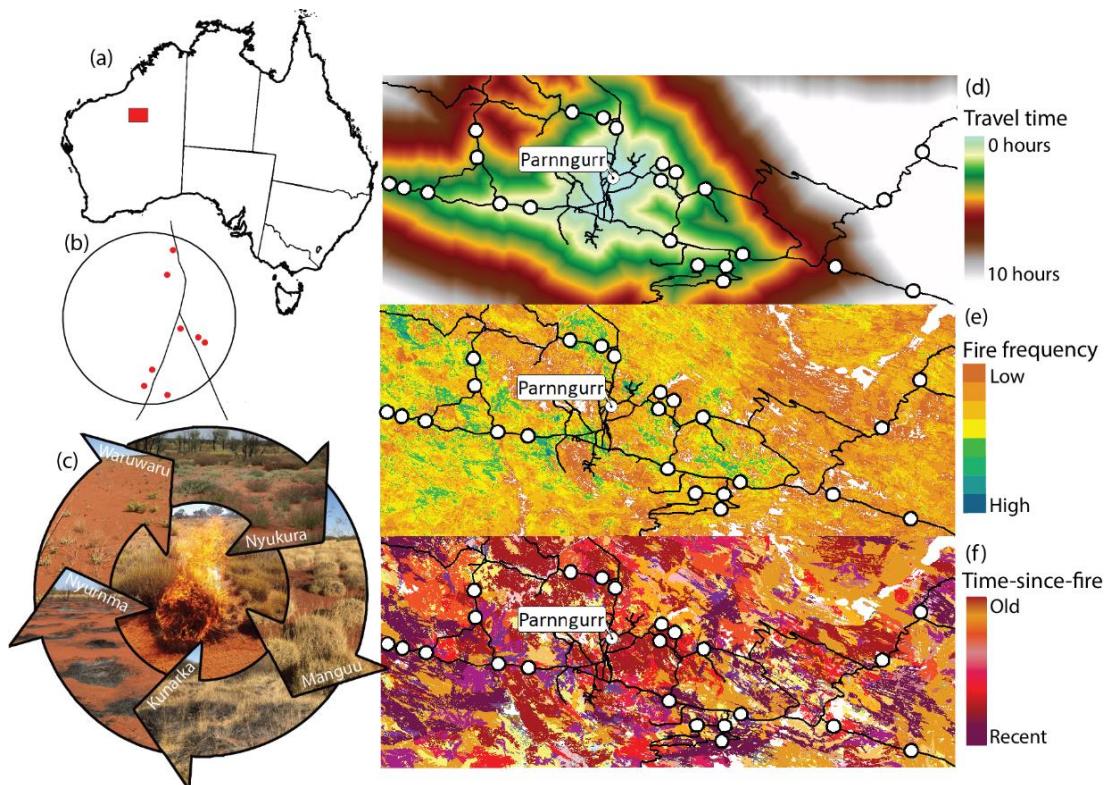


Figure 3.1 (a) Study area (red rectangle) in Australia, (b) example of one of the 23 study landscapes (5 km in diameter) with eight sites embedded (red dots) along road (black lines), and (c) post-fire plant successional model defined by Martu. Representation of (d) travel time from Martu communities' layer, (e) fire frequency layer, and (f) time-since-fire layer. White circles: 23 study landscapes, black lines: roads, white circles with central dot: Martu community of Parnngurr.

Fire mapping

We used detailed fire maps created by RBB to quantify the fire histories across our study area. RBB digitised every fire footprint 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 – 2019 (see Bliege Bird et al., 2012 for more details).

Site selection

Using the fire maps, we selected 184 sites for plant surveys nested within 23 study landscapes (circular areas with a 5 km diameter). We chose 5 km landscape scales because of strong fire diversity patterns (chapter 1), to ensure independence between sites, and to ensure access to sites from roads. We chose sites to capture variation in time-since-fire ages (ranged from 0 to 20 years since fire), fire frequencies (ranged from burnt 0 to 7 times), and unique combinations of time-since-fire ages and fire frequencies. We were not able to calculate other attributes of the fire regime because of the nature of the Landsat fire maps. For example, we were not able to distinguish fire season because Landsat images were taken at six-month intervals, and we had no reliable measure of fire intensity. In addition to capturing a gradient of time-since-fire ages, we ensured that we had replicate sites across successional stages. Martu recognise several successional stages; *nyurnma*: recently burnt patches, *waru waru*: plants re-sprout after 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 classified sites in terms of their post-fire age based loosely on Martu successional stages: ‘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 did not use the Martu terms because our categorisations relied solely on time-since-fire, whereas Martu successional stages are far more nuanced and can vary with other processes such as rainfall (Bliege Bird et al., 2008). As the timing of *waru waru* is particularly variable and dependent on rainfall (which was scarce prior to surveys), we did not have an equivalent fire-age category.

Sites also varied substantially in terms of travel times from Martu communities (ranged from 0.5 to 7 hours from communities) (see section 2.6) (Fig. 3.1). Each site was in spinifex sandplain (sandy substrate, dominated by spinifex, with minimal trees) because it is the most common vegetation type, and it is where Martu conduct most of their burning (Bliege Bird et al., 2008). All sites were within 2 km of a road to ensure ease of access and

avoided *ngarlu* (sacred) areas. Additionally, all sites were at least 500 m from the nearest site to enhance independence.

Plant surveys

We sampled sites between June and August 2019. At each site, we established a north-south 50 m transect. At 1 m intervals along each transect, we used a structure pole to record the habitat structure (plant type). We classified grasses as all grasses not including spinifex, spinifex as all *Triodia* spp., herbs as plants without woody stems, sub-shrubs as plants with multiple woody stems that did not grow higher than 2 m, shrubs as plants with multiple woody stems that grew higher than 2 m, and trees as plants with a single main stem or trunk. We recorded the number of times each plant lifeform touched the pole within five height classes (i.e., < 0.5, 0.5 – 1, 1 – 1.5, 1.5 – 2, and > 2 m). We counted live species and those that had died from causes other than fire (i.e., that were not obviously burnt). We then established three quadrats 10 × 10 m centred at 25 m of each transect. LG recorded each plant species within each quadrat and visually estimated its cover percentage, which we then combined to produce an estimate of site total cover percentage. We collected specimens of all new species to identify using plant identification keys on FloraBase (Department of Biodiversity Conservation and Attractions, 2021). Identification was aided by expert botanist SVL.

Response variables

From the plant surveys, we calculated several plant response variables: (i) species richness (total number of species across all three quadrats for each site), (ii) species diversity (total species percentage cover across all three quadrats and their evenness using Shannon's diversity index H'), (iii) sub-shrub richness, (iv) edible species richness, (v) edible sub-shrub presence, and (vi) edible shrub and tree richness. We identified edible plants from ethnobotanical 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 investigated sub-shrubs and shrubs and trees separately because we assumed that fire would have different effects due to life histories (i.e., short/long lived) and post-fire regeneration methods (i.e., seed/re-sprout) (Nano and Clarke, 2011). We grouped high shrubs and trees as our sites had few trees.

From the 50 m vegetation structure transects, we calculated vegetation structure variables as: (i) counts of grass (i.e., counts of grass on the structure pole along the 50 m

transect), (ii) counts of spinifex < 0.5 m (i.e., ‘low spinifex cover’), (iii) counts of spinifex > 0.5 m (i.e., ‘high spinifex cover’), and (iv) counts of shrubs and trees (included all sub-shrubs, shrubs, and trees). We investigated low spinifex cover and high spinifex cover separately as low spinifex is indicative of early- to mid-succession and high spinifex is indicative of late-succession.

Predictor variables

To quantify time-since-fire and fire frequency, we built fire histories for each site in ArcMap (ESRI. ArcGIS Desktop: Release 10.7.1. Redlands, California: Environmental Systems Research Institute, 2019). From these maps, we measured time-since-fire for each site as the number of years since the last recorded fire prior to vegetation surveys in 2019 (Fig. 3.1). We measured fire frequency as the number of times each site had burnt from 1990 to 2019 (29-year period) (Fig. 3.1). Land-use by Martu likely affects plant communities through a variety of mechanisms, including direct interactions with plants, as well as indirect effects of their fire regimes (Bliege Bird and Nimmo, 2018). Martu land-use intensity is well predicted by central place models, in which people are tethered to residential sites and use landscapes according to a distance-decay function (Bliege Bird et al., 2008). Thus, as a surrogate for land-use intensity, we estimated the time it would take for Martu to reach any point in our study landscape using a cost-distance raster layer based on travel time by vehicle from the Martu communities of Parnngurr or Punmu to any other raster cell (1 x 1 m) within the study area (Fig. 3.1) (see Greenwood et al., 2021).

In this ecosystem, spinifex is the main fuel load component, although other plants can contribute to fuel loads after heavy rainfall (Allan and Southgate, 2002). Following fire, rainfall dictates how quickly spinifex accumulates biomass and can once again carry fire (Allan and Southgate, 2002, Burrows, 2006, Edwards et al., 2008). Thus, rainfall largely dictates fire activity (Allan and Southgate, 2002, Burrows, 2006, Edwards et al., 2008). To explore how rainfall affected response variables we downloaded monthly grids (5 km resolution) from the Bureau of Meteorology (www.bom.gov.au) and extracted monthly rainfall for each site. 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 29-year period. We investigated which rainfall variable was most appropriate to retain by creating a global model that included all predictor variables and only one of the four rainfall variables. To assess the fit of the models, we

used Akaike Information Criterion adjusted for smaller sample sizes (AICc), retaining the rainfall variable with the lowest AICc for further analysis (Burnham and Anderson, 2002). For simplification, we examined parameter estimates and only retained the rainfall variable in models if it was influential (i.e., confidence intervals did not overlap 0).

Data analysis: richness, diversity, and vegetation structure

The relationship between time-since-fire (continuous variable) and several plant richness and diversity response variables were non-linear, identified via data exploration, so we fit generalised additive mixed models (GAMMs). GAMMs use a non-linear smoothing function to summarise the relationship between two variables, rather than a slope parameter (Zuur et al., 2009). We limited the smoothing function (k) to six dimensions to limit complexity and avoid overfitting. To account for the nested study design (i.e., eight sites within each landscape) we included landscape ID as a random effect. Richness variables were discrete and modelled assuming a Poisson distribution, diversity variables were continuous and modelled assuming a Gaussian distribution, and presence/absence was binary and modelled assuming a binomial distribution (Zuur et al., 2009). If discrete data was over dispersed (i.e., when dispersion parameters were > 1.5) we fitted negative binomial models (Zuur et al., 2009).

For plant richness and diversity variables, we explored two models: (i) time-since-fire, fire frequency, travel time from Martu communities, and rainfall as main effects (hereafter ‘main effects models’), and (ii) time-since-fire and fire frequency as an interaction, and travel time and rainfall as main effects (hereafter ‘interaction models’). For vegetation structure, we explored two models: (i) time-since-fire, fire frequency, and rainfall as main effects (‘main effects model’), and (ii) time-since-fire and fire frequency as an interaction, and rainfall as a main effect (‘interaction model’). We did not examine travel time in the vegetation structure models because we assumed that vegetation structure would primarily be affected by fire, whereas we assumed that plant richness and diversity variables would be impacted by fire and people due to ecological roles that Martu fulfil (Bliege Bird and Nimmo, 2018). We compared the main effects models to the interaction models for each plant response variable, assuming the model with the lowest AICc was the most parsimonious (Burnham and Anderson, 2002). While response variables were modelled in relation to time-since-fire as a continuous variable, we overlayed post-fire successional stages to demonstrate how changes in response variables correspond with

successional stages (i.e., recently burnt, mid-succession, late-succession, and long unburnt).

Data analysis: plant species and lifeform composition

For the multivariate analysis we square root transformed plant abundance data, as we were equally interested in compositional changes in dominant plant species as rare species (Clarke and Ainsworth, 1993). To test whether there were differences in plant species composition along the time-since-fire and fire frequency gradients, we used permutational multivariate analysis of variance (permANOVA) with a Bray-Curtis distance measure, 999 permutations, and landscape as a random effect (Anderson, 2001, Bray and Curtis, 1957). PermANOVA compares the difference between groups to the difference within groups (based on the centroid of each group cluster) and obtains p-values using permutations (Anderson, 2001). Next, we investigated how plant species composition differed between post-fire successional stages and fire frequency classes using multilevel pairwise comparison (Martinez Arbizu, 2020). To compare pairs, we grouped time-since-fire and fire frequency into discrete categories. Time-since-fire was grouped into recently burnt, mid-succession, late-succession, and long burnt. For the fire frequency classes, we grouped sites that had been burnt 0 – 2 times over the 29-year period as ‘low fire frequency’ and sites that had been burnt 3 – 7 times as ‘high fire frequency’. Next, we identified which species were characteristic of each successional stage and fire frequency class using indicator species analysis, where high indicator values indicate high frequency and abundance within successional stages or fire frequency classes (Dufrêne and Legendre, 1997, Cáceres and Legendre, 2009). Finally, we used non-metric multidimensional scaling (NMDS) to visualise the differences in plant species composition. NMDS does not produce a unique solution, so we set random starts to 200 (Kenkel, 2006). NMDS also requires the number of axes to be set a priori to analysis, thus we used scree plots to determine the minimum number of axes with ≤ 0.2 stress (i.e., distortion) to ensure interpretability (Clarke, 1993). All analyses were conducted in R version 2.1 (R Core Team, 2018) using gamm4 (Wood and Scheipl, 2017), vegan (Oksanen et al., 2020), and indicspecies (De Cáceres et al., 2016) packages.

Results

We identified 148 plant species from 26 families. Five taxa could only be identified to family, 28 to genus, and ten remained unidentified due to immaturity or lack of sufficient

plant material. Identifications of grasses and spinifex may have some inaccuracy due to lack of seed heads and alive plant material. Low species numbers may be a result of prolonged droughts preceding our plant surveys. *Triodia schinzii*, *Aristida contorta*, *Scaevola parvifolia* subsp. *parvifolia*, and *Dicrastylis exsuccosa* occurred the most frequently across all sites. Preliminary analysis indicated that (i) cumulative 1-year rainfall was the best rainfall variable for edible species richness, edible sub-shrub presence, and sub-shrub cover, (ii) cumulative 2-year rainfall was the best for plant richness and edible shrub and tree richness, and (iii) cumulative 3-year rainfall was the best for plant diversity, low spinifex cover, and high spinifex cover, and (iv) average annual rainfall was the best for sub-shrub richness, grass cover, and shrub and tree cover (Table S3.1).

How does fire and travel time influence plant richness and diversity?

The top model for plant richness was the main effects model ($R^2 = 32\%$) (Table S3.2). Plant richness increased rapidly between 0 – 3.5 years post-fire, peaked at 3.5 years post-fire, declined between 3.5 – 8.5 years post-fire, and plateaued at 8.5 + years post-fire (Table 3.1 and Fig. 3.2). Plant richness declined with increasing travel time, but fire frequency was not influential (Table 3.2, Fig. S3.1). The top model for plant diversity was the main effects model ($R^2 = 32\%$) (Table S3.2). Plant diversity followed similar patterns post-fire as plant richness, peaking at 3.5 years post-fire, but neither fire frequency nor travel time was influential (Table 3.2 and 3.3, Fig. 3.2). The best model for sub-shrub richness was the main effects model ($R^2 = 26\%$) (Table S3.2). Sub-shrub richness followed similar succession patterns post-fire, peaking at 3.5 years post-fire, declined with increasing travel time, but fire frequency was not influential (Table 3.2 and 3.3, Fig. 3.2 and S3.1).

The top model for edible plant richness was the main effects model ($R^2 = 21\%$) (Table S3.2). Edible plant richness followed similar patterns post-fire as plant richness and diversity, peaking at 3.5 years post-fire, and declined with increasing travel time, but fire frequency was not influential (Table 3.2 and 3.3, Fig. 3.2 and S3.1). The top model for edible sub-shrub presence was the main effects model ($R^2 = 13\%$) (Table S3.2). Edible sub-shrub presence increased with fire frequency but neither time-since-fire nor travel time was influential (Table 3.2 and 3.3, Fig. 3.4). The top model for edible shrub and tree richness was the interaction model ($R^2 = 18\%$) (Table S3.2). Edible shrub and tree richness was mostly consistent across all time-since-fire and fire frequency combinations but

peaked in long unburnt sites (18 + years post-fire) that had been burnt frequently (Table 3.2, Fig. 3.5). Additionally, edible shrub and tree richness declined with increasing travel time (Table 3.3, Fig. S3.1).

How does fire influence vegetation structure?

The best models for grass cover and low spinifex cover were the main effects models ($R^2 = 15\%$ and 66% , respectively) (Table S3.2). Grass cover followed similar patterns to richness and diversity variables, peaking at 3.5 years post-fire, and increased with more frequent fires (Table 3.2 and 3.3, Fig. 3.3 and 3.4). Low spinifex cover increased rapidly between 0 – 5 years post-fire, increased at a slower rate 5 + years post-fire, peaked at 20 + years post-fire, and decreased with more frequent fires (Table 3.2 and 3.3, Fig. 3.3 and 3.4). The best model for high spinifex cover was the interaction model ($R^2 = 19\%$) (Table S3.2). At all time-since-fire ages high spinifex cover was lower under high fire frequencies than low fire frequencies, except 18 years + post-fire when high spinifex peaked under moderate fire frequencies (Fig. 3.5).

Table 3.1 GAMM non-linear effects of time-since-fire or the interaction between time-since-fire and fire frequency on response variables. Model: whether time-since-fire and fire frequency were included as main effects or an interaction, edf: estimated degrees of freedom or degree of ‘wiggliness’ (edf = 1 represents a linear relationship), p-value: significance ($p \leq 0.05$ deemed significant).

Response variable	Predictor(s)	Model	edf	p-value
Species richness	Time-since-fire	Main effects	4.72	0.000
Species diversity	Time-since-fire	Main effects	4.57	0.000
Sub-shrub richness	Time-since-fire	Main effects	3.82	0.000
Edible species richness	Time-since-fire	Main effects	4.26	0.002
Edible sub-shrub presence	Time-since-fire	Main effects	1.00	0.515
Edible shrub and tree richness	Time-since-fire + fire frequency	Interaction	5.67	0.003
Grass cover	Time-since-fire	Main effects	4.88	0.009
Low spinifex cover	Time-since-fire	Main effects	4.93	0.000
High spinifex cover	Time-since-fire + fire frequency	Interaction	8.69	0.000
Shrub and tree cover	Time-since-fire	Main effects	4.02	0.000

Table 3.2 GAMM linear effects of fire frequency, travel time from Martu communities, and antecedent rainfall on response variables. SE: standard error, p-value: significance ($p \leq 0.05$ deemed significant).

Response variable	Predictor	Estimate	SE	p-value
Species richness	Fire frequency	0.01	0.03	0.807
	Travel time	-0.09	0.05	0.025
Species diversity	Fire frequency	0.05	0.05	0.239
	Travel time	-0.08	0.05	0.310
Sub-shrub richness	Fire frequency	-0.01	0.03	0.586
	Travel time	-0.17	0.06	0.001
Edible species richness	Fire frequency	0.07	0.04	0.126
	Travel time	-0.12	0.06	0.050
Edible sub-shrub presence	Fire frequency	0.50	0.21	0.021
	Travel time	0.03	0.10	0.928
	1-year rain	-0.71	0.29	0.017
Edible shrub and tree richness	Travel time	-0.23	0.09	0.001
Grass cover	Fire frequency	0.41	0.07	0.002
Low spinifex cover	Fire frequency	-0.09	0.03	0.018
	3-year rain	0.09	0.04	0.031
High spinifex cover	1-year rain	0.13	0.06	0.038
Shrub and tree cover	Fire frequency	-0.05	0.09	0.539

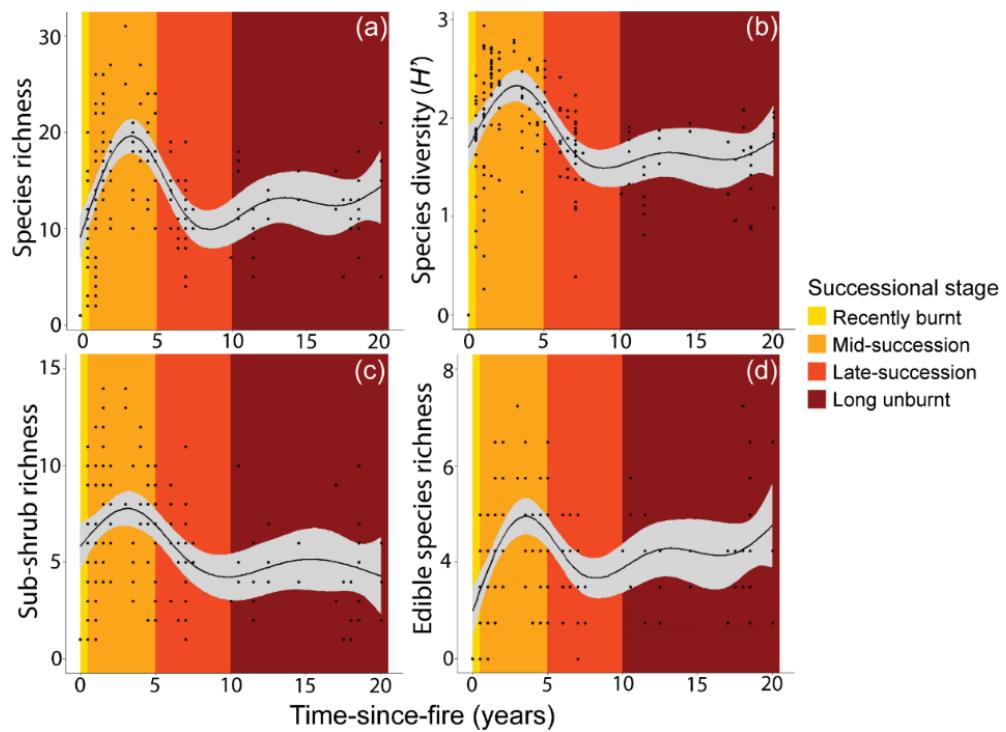


Figure 3.2 Effect of time-since-fire on (a) species richness, (b) species diversity (H'), (c) sub-shrub richness, and (d) edible species richness. Black dots: observed data, black lines: model predictions, grey shading: 95 % confidence intervals.

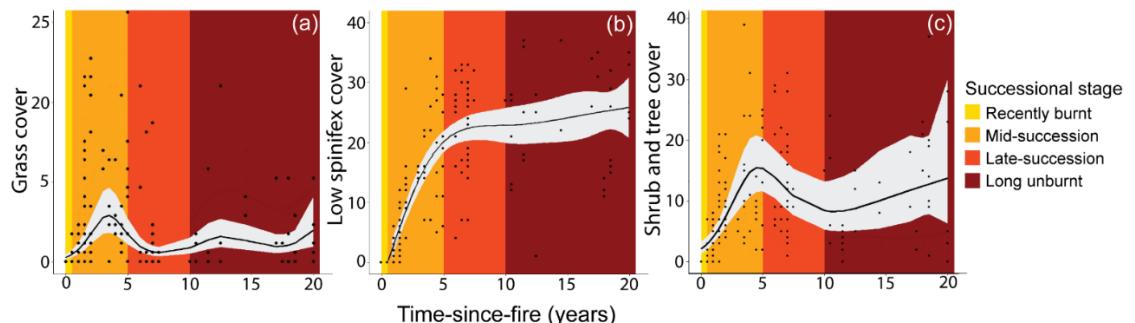


Figure 3.3 Effect of time-since-fire on (a) grass cover, (b) low spinifex (*Triodia* spp.) cover, and (c) shrub and tree cover. Black dots: observed data, black lines: model predictions, grey shading: 95 % confidence intervals.

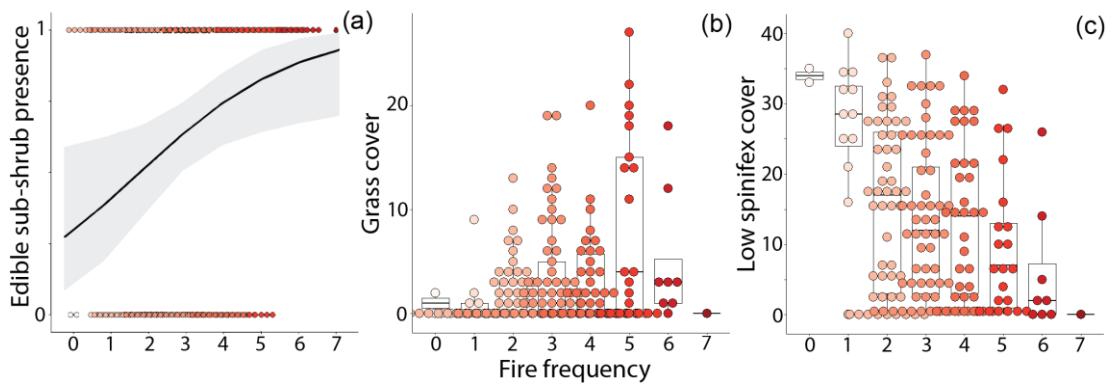


Figure 3.4 Effect of fire frequency over a 29-year period on (a) edible sub-shrub presence (black line: model predictions, grey shading: 95 % confidence intervals), (b) grass cover, and (c) low spinifex (*Triodia* spp.) cover. Dots: observed data coloured by fire frequency.

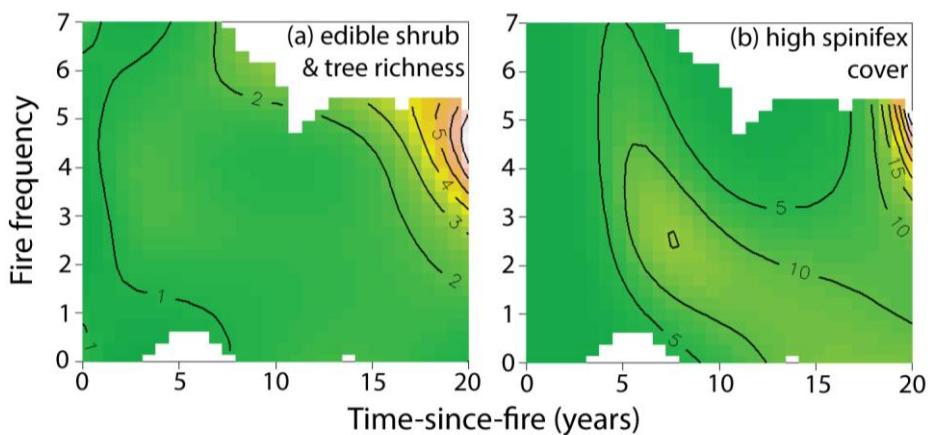


Figure 3.5 Interactive effects between time-since-fire and fire frequency (over a 29-year period) on (a) edible shrub and tree richness and (b) high spinifex (*Triodia* spp.) cover. Green: low, yellow: moderate, and red: high cover/richness. Contour lines are representative of response variable scale and model predictions only extrapolated 20 % beyond the data.

How does fire influence plant species composition?

PermANOVA indicated that there were significant differences in plant species composition between time-since-fire ages (sums of squares [SS] = 3.42, F = 11.68, R² = 6 %, p = 0.001). Pairwise comparisons suggested small to moderate differences in species

composition between pairs of successional stages ($R^2 = 5 - 26\%$) (Table 3.3, Fig. 3.6). Plant species composition differed the most between recently burnt and late-succession ($R^2 = 17\%$), and recently burnt and late-succession ($R^2 = 26\%$) (Table 3.3, Fig. 3.6). Indicator species analysis revealed that recently burnt was characterised by sub-shrubs *Goodenia azurea* subsp. *hesperia* (Table 3.4). Mid-succession was characterised predominantly by grasses and sub-shrubs, such as *Paraneurachne muelleri* and *Sida cardiophylla*, as well as edible species *Eragrostis setifolia* and *Solanum centrale* (Table 3.4). Late-succession was characterised by spinifex, shrubs, and trees, such as *Triodia angusta*, *Calytrix carinata*, and *Acacia* spear trees (Table 3.4). Long unburnt was characterised by spinifex and shrub species *Triodia schinzii* and edible *Acacia dictyophleba* (Table 3.4).

PermANOVA indicated that there were significant differences in plant species composition between fire frequencies ($SS = 2.13$, $R^2 = 4\%$, $F = 7.09$, $p = 0.001$). Pairwise comparisons suggested small differences in plant species composition between low and high fire frequency classes ($R^2 = 2\%$) (Table 3.3, Fig. 3.6). Species indicator analysis revealed that low fire frequency sites were characterised by *Triodia schinzii* and high fire frequency sites were characterised by sub-shrubs such as *Aristida contorta* and *Bonamia erecta*, and edible *S. centrale* (Table 3.4).

Table 3.3 Pair-wise comparisons of plant species composition between post-fire successional stages and fire frequency classes. F: variance between groups, R^2 : dissimilarity between pair, p-value: significance ($p \leq 0.05$ deemed significant), recently burnt: 0 – 6 months post-fire, mid-succession: 1 – 5 years post-fire, late-succession: 5 – 10 years post-fire, long unburnt: 10+ years post-fire, low fire frequency: burnt 0 – 2 times over 29-year period, high fire frequency: burnt 3 – 7 times over 29-year period.

Group	Pair comparison	F	R^2	p-value
Successional stages	Recently burnt vs mid-succession	6.76	6%	0.01
	Recently burnt vs late-succession	11.35	17%	0.01
	Recently burnt vs long unburnt	18.50	26%	0.01
	Mid-succession vs late-succession	8.92	7%	0.01
	Mid-succession vs long unburnt	12.99	9%	0.01
Fire frequency classes	Late-succession vs long unburnt	3.55	5%	0.02
	Low vs high	5.17	2%	0.00

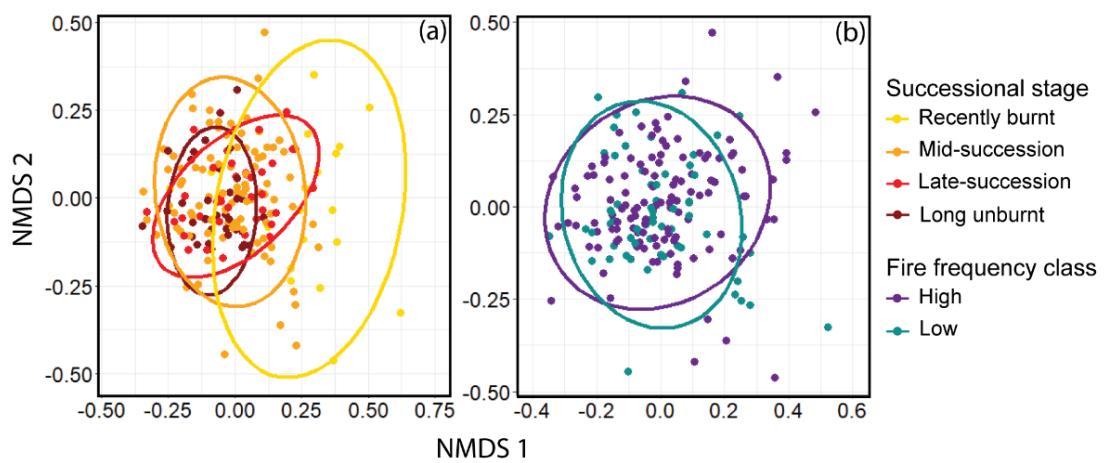


Figure 3.6 NMDS ordination, based on Bray-Curtis distances, of plant species composition and (a) successional stages and (b) fire frequency classes (axes = 3, stress = 0.19, $R^2 = 68\%$). Recently burnt: 0 – 6 months post-fire, mid-succession: 6 months – 5 years post-fire, late succession: 5 – 10 years post-fire, long unburnt: 10 + years post-fire, low fire frequency: burnt 0 – 2 times over 29-year period, high fire frequency: burnt 3 – 7 times over 29-year period.

Table 3.4 Indicator species analysis showing associations of plant species with post-fire successional stages and fire frequency classes. IndVal (indicator value): strength of association to group, p-value: significance ($p \leq 0.05$ deemed significant), recently burnt: 0 – 6 months post-fire, mid-succession: 1 – 5 years post-fire, late-succession: 5 – 10 years post-fire, long unburnt: 10 + years post-fire, low fire frequency: burnt 0 – 2 times over 29-year period, high fire frequency: burnt 3 – 7 times over 29-year period. Species only shown if indicator value ≥ 0.25 and $p \leq 0.05$.

Group	Species	IndVal	p-value
Recently burnt	<i>Goodenia azurea</i> subsp. <i>hesperia</i>	0.26	0.01
	<i>Eragrostis setifolia</i> *	0.47	0.01
	<i>Sida cardiophylla</i>	0.37	0.01
	<i>Goodenia armitiana</i>	0.33	0.01
	<i>Sida</i> sp. <i>excedentifolia</i>	0.29	0.01
Mid-succession	<i>Isotropis atropurpurea</i>	0.28	0.01
	<i>Heliotropium</i> spp.	0.26	0.01
	<i>Paraneurachne muelleri</i>	0.25	0.02
	<i>Solanum centrale</i> *	0.25	0.02
	<i>Scaevola parvifolia</i> subsp. <i>parvifolia</i> *	0.26	0.02
Mid-succession and late-succession	<i>Gompholobium simplicifolium</i>	0.34	0.00
	<i>Triodia angusta</i>	0.33	0.01
	Undescribed <i>Acacia</i> spear tree	0.27	0.01
	<i>Calytrix carinata</i>	0.26	0.01
	<i>Gyrostemon</i> spp.	0.26	0.01
Late-succession and long unburnt	<i>Triodia schinzii</i>	0.70	0.00
Long unburnt	<i>Acacia dictyophleba</i> *	0.32	0.00
Low fire frequency	<i>Triodia schinzii</i>	0.27	0.00
High fire frequency	<i>Bonamia erecta</i>	0.30	0.00
	<i>Aristida contorta</i>	0.25	0.00
	<i>Isotropis atropurpurea</i>	0.25	0.00
	<i>Solanum centrale</i> *	0.25	0.00

* Edible plant

Discussion

Fire plays a prominent role in shaping the richness, diversity, and composition of plant communities across Australia's western desert ecosystems. Consistent with the "initial floristic composition" model, plant richness and diversity increased soon after fire, before undergoing a reduction coincident with an increase in the cover of spinifex. The composition of plant communities differed between post-fire successional stages, consistent with the Martu model of post-fire succession. Edible plant species increased soon after fire and edible sub-shrub presence was higher in areas subject to frequent fire, consistent with the hypothesis that fire increases the productivity of landscapes for Indigenous people in arid Australia (Gould, 1971).

Time-since-fire was a strong driver of the richness and diversity of plants overall and of several plant groups, including edible species and sub-shrubs. In each case, richness and diversity increased soon after fire, before declining in late-succession and plateauing in long unburnt. A peak in species richness and diversity in mid-succession is common throughout spinifex grasslands (Burrows et al., 2020, Marsden-Smedley et al., 2012, Wright and Clarke, 2007) and interpreting these patterns is aided by considering the contemporaneous response of spinifex. Low spinifex cover increased rapidly to 5 years post-fire, and then plateaued, coincident with declines in plant richness and diversity. Spinifex is a superior competitor that out-competes most plants for water and nutrients—both limiting factors in arid environments (Burrows et al., 2006b, Nano and Clarke, 2010). By killing or reducing spinifex to its roots, fire removes the competitive pressure of spinifex and increases soil organic matter, nutrients, and moisture (Muñoz-Rojas et al., 2016, Wright and Clarke, 2007). Concurrently, fire acts on seed dormancy, triggering germination through heat and smoke cues (Commander et al., 2008, Commander et al., 2017). When spinifex regains dominance in late-succession, many of the smaller, short-lived plants (e.g., herbs, grasses, and sub-shrubs) are once again outcompeted (Burrows et al., 2020, Marsden-Smedley et al., 2012). Small increases in species richness and diversity in late-succession may be a result of spinifex senescence (Allan and Southgate, 2002). These patterns—an increase in diversity soon after fire followed by a decline—broadly align with the "initial floristics composition" model (Egler, 1954).

Fire frequency had a weaker effect than time-since-fire on plant communities, but higher fire frequencies, characteristic of Martu fire regimes (Greenwood et al., 2021), promoted edible sub-shrubs and grass cover, and reduced spinifex cover. High fire frequencies could promote small short-lived species by ensuring seeds are at the correct depth for germination (Auld and Denham, 2006) and limiting seed degradation (Commander et al., 2008, Commander et al., 2017). Additionally, high fire frequencies could promote sub-shrubs and grass by reducing spinifex cover; both *T. schinzii* and *T. basedowii* seedling abundance can decline under short fire intervals (Wright and Clarke, 2007). While Wright and Clarke (2007) found that the effects of fire frequency on spinifex are short-lived, our results suggest that the effects of higher fire frequencies can persist for several years. Given our study only spanned 29-years, our measured fire attributes may not accurately reflect the response of long-lived species and seedbanks.

We find evidence that burning increases the productivity of arid areas for Indigenous people (Bliege Bird et al., 2008, Gould, 1971, Jones, 1969). Edible plant richness peaked shortly after fire in mid-succession, which roughly corresponds to *nyukura*, a stage that Martu recognise for edible flowering and fruiting plants (Bliege Bird et al., 2008). This is consistent with the “fire-stick farming” hypothesis; by reducing spinifex cover in recently burnt sites, Indigenous burning increases the availability of edible plants (Gould, 1971). While not explicit, the “fire-stick farming” hypothesis also implies that fire frequency could play a role in increasing site productivity (Gould, 1971, Jones, 1969). We have previously shown that Martu increase the frequency that landscapes are burnt (Greenwood et al., 2021). Martu are more likely to return to frequently burnt landscapes and further increase fire frequency, which Bliege Bird et al. (2020) hypothesise is because they are more productive for people, creating a positive feedback loop. Here, we find support for that notion, as edible plants were more likely to occur in areas that were frequently burnt.

Multivariate analysis showed differences in the composition of plant communities between post-fire successional stages and fire frequency classes, highlighting that distinct communities arise along the post-fire successional axis and under different fire frequencies. Composition changes are likely underpinned by functional traits (Keeley et al., 2011). This is already well known by Martu, who describe a more nuanced suite of successional stages characterised by different subsets of species that arise through the

interplay of fire and rainfall (Bliege Bird et al., 2008). It has previously been shown that Martu fire regimes enhance the number of successional stages and diversity of fire frequency patches present in landscapes (Bliege Bird et al., 2008, Greenwood et al., 2021). It is therefore likely that the provision of fine-scale fire mosaics at the landscape-scale enhances landscape-scale plant diversity by creating a more diverse suite of successional stages and fire frequencies that are characterised by distinctive assemblages. This pattern would be consistent with the “pyrodiversity begets biodiversity” hypothesis (Jones and Tingley, 2021), which predicts that more diverse fire mosaics contain higher biodiversity (Martin and Sapsis, 1992). Verification of this hypothesis would require a landscape-scale study, comparing plant diversity between landscapes that differ in pyrodiversity (Jones and Tingley, 2021).

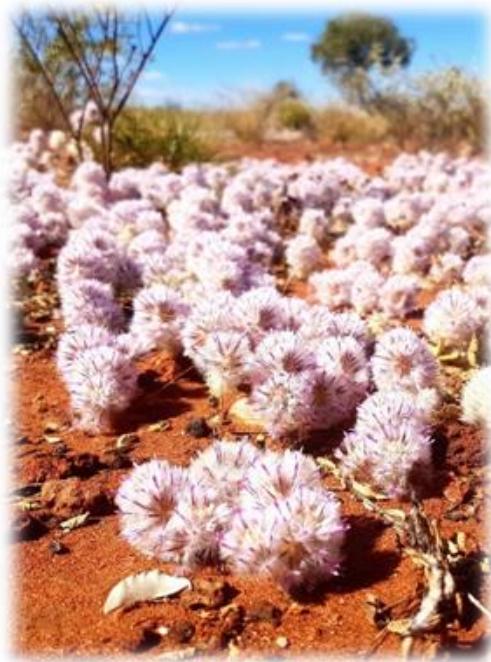
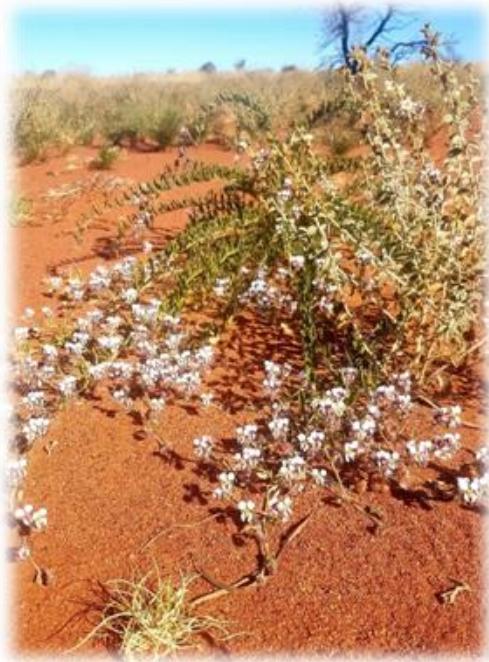
Several measures of plant richness and diversity, including edible species, were higher close to Martu communities where Martu frequent more often. These patterns could be driven by other aspects of the fire regime that we did not measure, such as fire season or intensity (Gill, 1975). While disentangling these effects are challenging, this association could be because of broader ecological roles that Martu fulfil within ecosystems to benefit plant communities, such as hunting pressure, improved soil turn over and aeration through digging for monitor lizards and other underground resources, and dispersal of plant propagules (Bliege Bird and Nimmo, 2018, Silcock, 2018). These results point to important roles that Indigenous people fulfil within ecological communities outside of burning (Bliege Bird, 2015).

This research adds further evidence of the importance of fire in promoting and maintaining diverse plant communities in spinifex grasslands (Burrows et al., 2020, Marsden-Smedley et al., 2012, Wright and Clarke, 2007). Additionally, we demonstrate the importance of Indigenous burning for promoting culturally significant edible plants in Australia’s western deserts (Bliege Bird et al., 2008, Gould, 1971, Jones, 1969). Combined with our previous work that shows the effects of Indigenous burning on fire regimes (Bliege Bird et al., 2008, Greenwood et al., 2021), we show the significant role of Indigenous burning in the maintenance of plant diversity, including edible plants, in these regions. We contribute to the global building narrative of the importance of Indigenous fire regimes in maintaining biodiversity (Ellis et al., 2021a, Garnett et al., 2018, Hoffman et al., 2021) and that the displacement of Indigenous people and the cessation of their

fire regimes has contributed to species decline and loss across the globe (Liebmann et al., 2016, Woinarski et al., 2015). Indigenous-led burning could offer solutions to restoring appropriate fire regimes, limiting fire size, conserving global biodiversity, and concurrently provide important benefits for Indigenous community wellbeing (Ansell and Evans, 2019, Hoffman et al., 2021, Millhauser and Earle, 2022).

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Chapter four: Indigenous pyrodiversity promotes plant richness and diversity in semi-arid Australia

Manuscript in preparation for submission

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Abstract

Pyrodiversity (i.e., temporally and spatially diverse fire histories) is thought to promote biodiversity by replicating Indigenous fire regimes. Pyrodiversity can be measured by the visible (i.e., the most recent and visible fire patterns) and invisible fire mosaic (i.e., long term, underlying spatiotemporal fire patterns). Here, we explored whether Indigenous pyrodiversity promoted plant richness and diversity in arid spinifex (*Triodia* spp.) grasslands of Western Australia. We selected landscapes that ranged from highly pyrodiverse under active Indigenous burning to more coarse-scale and less diverse mosaics under lightning fire regimes. We used generalised linear models to investigate 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 promoted higher total plant richness and diversity; fire frequency diversity promoted higher total plant diversity; and total plant diversity decreased with increasing maximum proportion of landscape burnt. Additionally, we found that edible species richness and diversity declined with higher proportions of recently burnt; total species richness and diversity, sub-shrub richness and

diversity, and edible species richness increased with higher proportions of mid-successional stages; and edible species richness and edible sub-shrub richness declined with higher proportions of long unburnt. By linking our previous work that shows Indigenous burning promotes pyrodiversity and reduces fire size, we find evidence for the notion that Indigenous pyrodiversity promotes plant richness and diversity. This highlights the importance of Indigenous burning for maintaining and promoting plant diversity in fire-prone ecosystems.

Introduction

Ecosystems have long evolved with fire over millions of years (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 (Burrows et al., 2006a, Liebmann et al., 2016, Price and Bowman, 1994, 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 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 other show that plant diversity peaks at moderate levels of

pyrodiversity (McGranahan et al., 2018). Gordijn and O'Connor (2021) highlight that plant groups can respond differently to pyrodiversity.

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, Parr and Andersen, 2006). 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 and purposeful (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). 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). Our finding that each post-fire successional stage promotes distinct plant communities (chapter two) suggests 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 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 because pyrodiversity is thought to beget biodiversity.

2. Sub-shrub and edible sub-shrub richness and diversity would increase with extent of mid-successional stages because 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.
3. Edible shrub and tree richness and diversity would increase with extent of late-successional stage because these species are able to persist into later successional stages despite spinifex regaining dominance.
4. Total and edible richness and diversity would decline with maximum area of landscape burnt because pyrodiversity is thought to limit fire size, and pyrodiversity is thought to beget biodiversity.

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).

Methods

Study system

Our study area was within the Martu Native Title determination and Karlamilyi National Park in Western Australia (Fig. 4.1). 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*); lateritic uplands dominated by mulga (*Acacia aneura*) woodlands; and *Senna* shrublands.

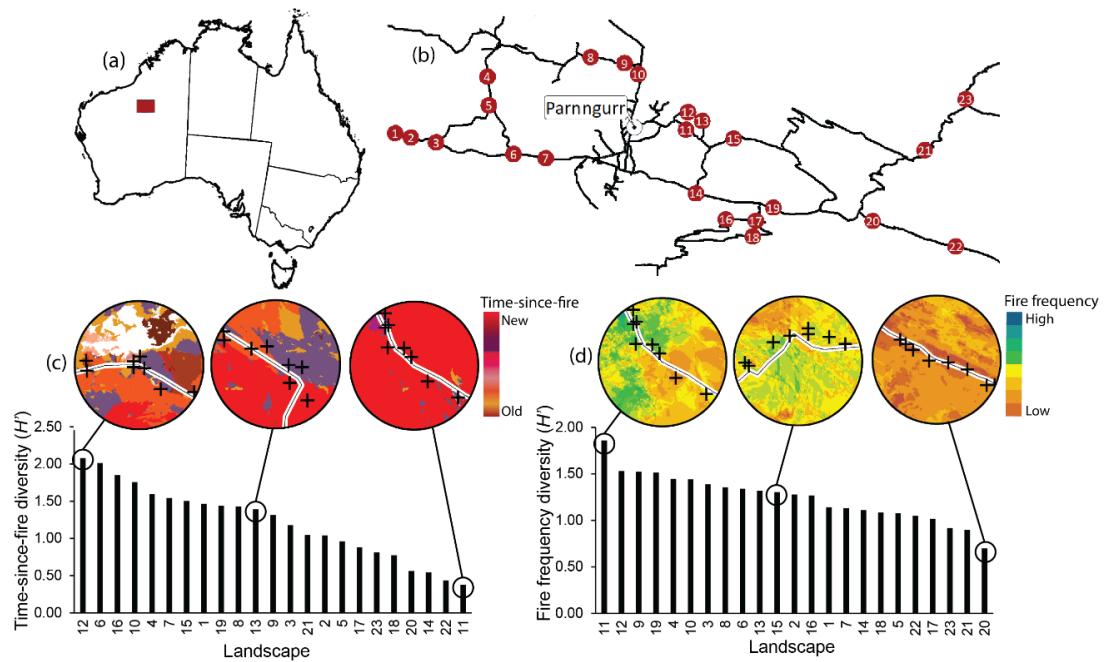


Figure 4.1 (a) Study area in Australia highlighted by red rectangle and (b) 23 study landscape (5 km diameters), black lines: roads. Diversity of (c) time-since-fire ages (H') and (d) fire frequency patches (H') for study landscapes, white lines: roads, crosses: sites.

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 – 2019 (see Bliege Bird et al., 2012 for more details).

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). We chose 5 km landscape scales because of strong fire diversity patterns (chapter 1), to ensure independence between sites, and to ensure access to sites from roads. 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. 4.1). Our final 23 landscapes ranged from 3 – 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 hours from Martu communities (Table S4.1, Fig. 4.1).

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).

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.

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.

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. 4.1). 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. 4.1). 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 several 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 percentage 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). To explore how rainfall affected response variables we downloaded monthly grids (5 km resolution) from the Bureau of Meteorology (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.

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 discrete variables followed Poisson distributions. If discrete 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 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 Δ AICc of the top model) (Burnham and Anderson, 2002). We deemed predictor variables important if 95 % 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.

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-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 S4.2). 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 (Fig. S4.1 and S4.2).

The top models for total plant richness explained a high amount of variation (78 – 82 %) and all included time-since-fire diversity and proportion of mid-succession (Table 4.1 and S4.3, Fig. 4.2). Total plant richness was higher in landscapes with high time-since-fire diversity and high proportions of mid-succession (Table S4.3, Fig. 4.4 and 4.6). The top

model for total plant diversity explained a high amount of variation (56 %) and included maximum proportion of landscape burnt, proportion of mid-succession, and average rainfall (Table 4.1 and S4.3, Fig. 4.2). Total plant diversity was lower where the maximum proportion of a landscape burnt was higher, and higher with high proportions of mid-succession (Table S4.3, Fig. 4.5 and 4.6).

For sub-shrub richness, there was considerable model uncertainty (Table 4.1). Top models explained a moderate amount of variation (37 – 52 %) and all included the proportion of mid-succession (Table 4.1 and S4.3, Fig. 4.2). Sub-shrub richness was higher in landscapes with high time-since-fire diversity and high proportions of mid-succession (Table S4.3, Fig. 4.4 and 4.6). There was also model uncertainty for sub-shrub diversity (Table 4.1). 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 (Table 4.1 and S4.3, Fig. 4.2). 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 (Fig. 4.4 – 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 (Table 4.1 and S4.3, Fig. 4.3). 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. 4.6). The top models for edible species diversity explained a small amount of variation (21 – 28 %) and all included proportion of recently burnt (Table 4.1 and S4.3, Fig. 4.3). Edible species diversity was higher in landscapes with high proportions of recently burnt (Fig. 4.6). For edible sub-shrub richness, the top model explained a modest amount of variation (28 %) and only included the proportion of long unburnt (Table 4.1 and S4.3, Fig. 4.3). Edible sub-shrub richness was higher in landscapes with high proportions of long unburnt (Fig. 4.6). 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 (Table 4.1 and S4.3, Fig. 4.3). For edible shrub and tree diversity the top models explained a moderate amount of variation (21 – 25 %) and all included the proportion of spinifex sandplain, but again showed no significant relationships with our fire predictor variables (Table 4.1 and S4.3, Fig. 4.3).

Table 4.1 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, ΔAICc : 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 ΔAICc are shown.

Response variable	Model	AICc	ΔAICc	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
Sub-shrub richness	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
	Mid-suc + spinifex	145.74	1.97	0.05	0.43
Sub-shrub diversity	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
	Spinifex + rain	157.91	0.00	0.11	0.26
Edible species richness	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
	TSFDiv + mid-suc	159.56	1.50	0.05	0.20
Edible species diversity	Recent	4.33	0.00	0.17	0.21
	Recent + rain	4.92	0.59	0.13	0.28
	MaxBurnt + recent + rain	6.09	1.76	0.07	0.25
Edible sub-shrub richness	Unburnt	122.04	0.00	0.28	0.28
Edible sub-shrub diversity	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
Edible shrub and tree richness	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

Edible shrub and tree diversity	FFDiv + spinifex	28.85	1.64	0.10	0.25
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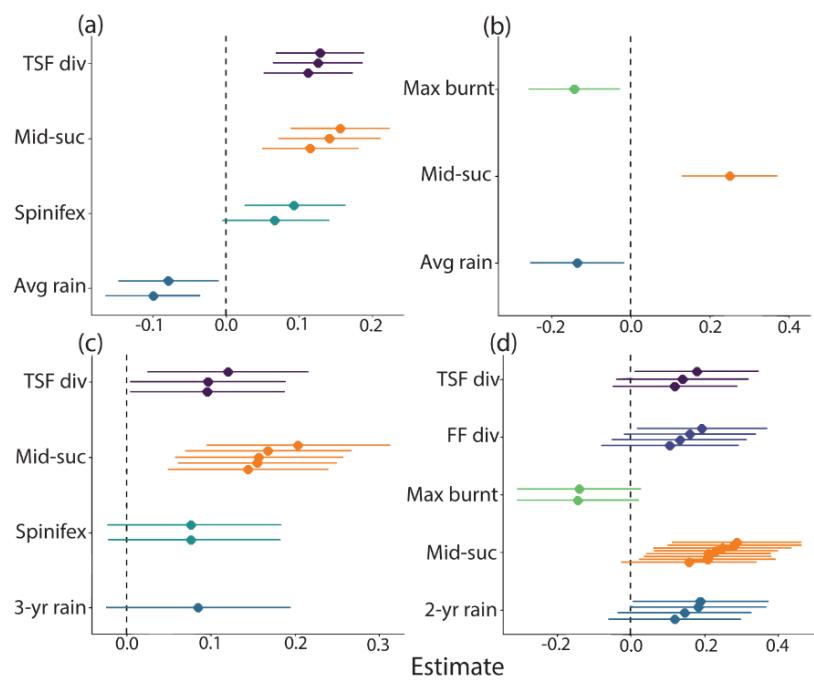


Figure 4.2 Estimated model coefficients (dots) and 95 % confidence intervals (lines) from models with substantial support (i.e., $w_i < 2$) for (a) total species richness, (b) total species diversity (H'), (c) sub-shrub richness, and (d) sub-shrub diversity (H'). TSF div: time-since-fire diversity (H'), FF div: fire frequency diversity (H'), max burnt: maximum landscape proportion burnt, mid-suc: post-fire mid-successional stage, spinifex: percentage of spinifex sandplain, 2-year rain: cumulative annual 2-year rainfall prior to surveys, 3-year rain: cumulative annual rainfall 3-years prior to surveys, avg rain: average annual rainfall.

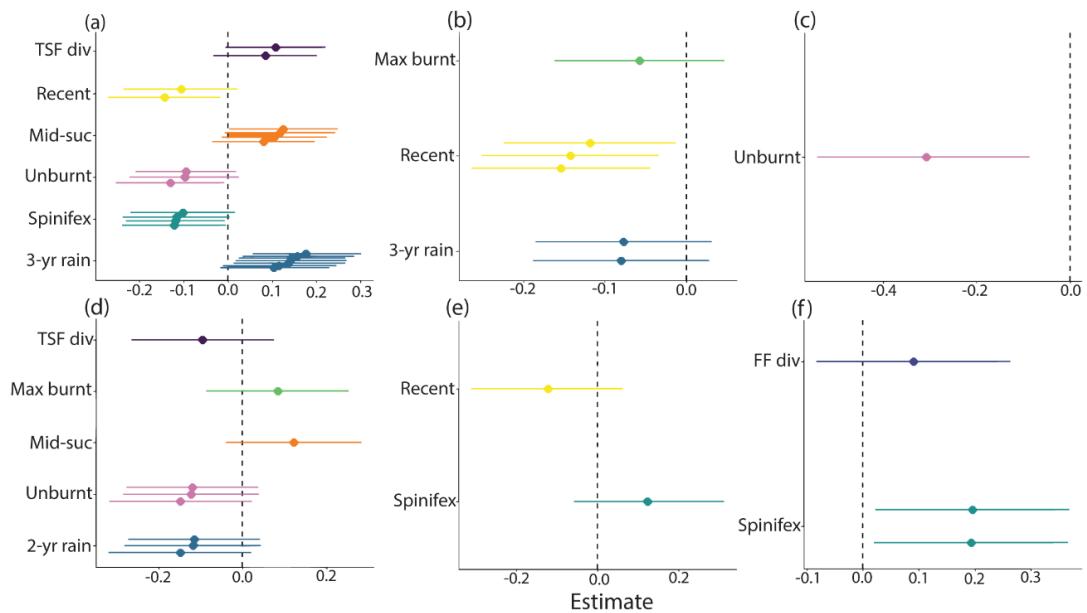


Figure 4.3 Estimated model coefficients (dots) and 95 % confidence intervals (lines) from models with substantial support (i.e., $w_i < 2$) for (a) edible species richness, (b) edible species diversity (H'), (c) edible sub-shrub richness, (d) edible sub-shrub diversity (H'), (e) edible shrub and tree richness, and (f) edible shrub and tree diversity (H'). TSF div: time-since-fire diversity (H'), FF div: fire frequency diversity (H'), max burnt: maximum landscape proportion burnt, recent: recently burnt, mid-suc: post-fire mid-successional stage, unburnt: long unburnt, spinifex: percentage of spinifex sandplain, 2-year rain: cumulative annual 2-year rainfall prior to surveys, 3-year rain: cumulative annual rainfall 3-years prior to surveys, avg rain: average annual rainfall.

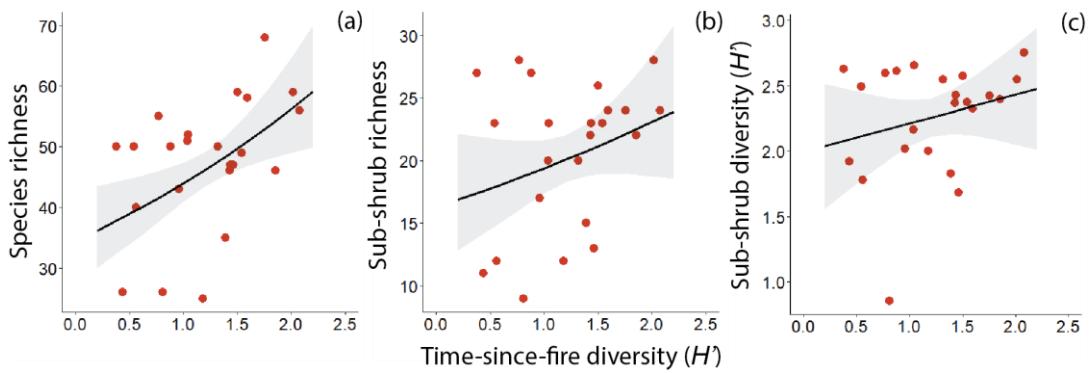


Figure 4.4 Relationship between time-since-fire diversity (H') and (a) total species richness, (b) sub-shrub richness, and (c) sub-shrub diversity (H'). Points: raw data, black lines: model trendline, grey shading: 95 % confidence intervals.

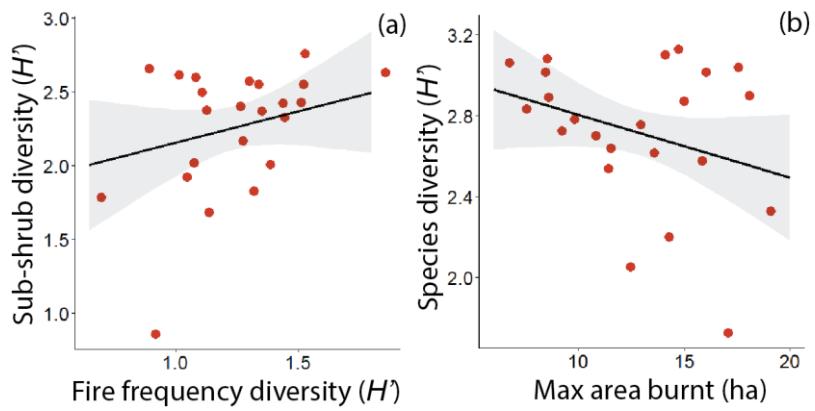


Figure 4.5 Relationship between (a) diversity of fire frequency patches (H') and sub-shrub diversity (H'), and relationship between (b) maximum landscape area burnt (ha) and total species diversity (H'). Points: raw data, black lines: model trendline, grey shading: 95 % confidence intervals.

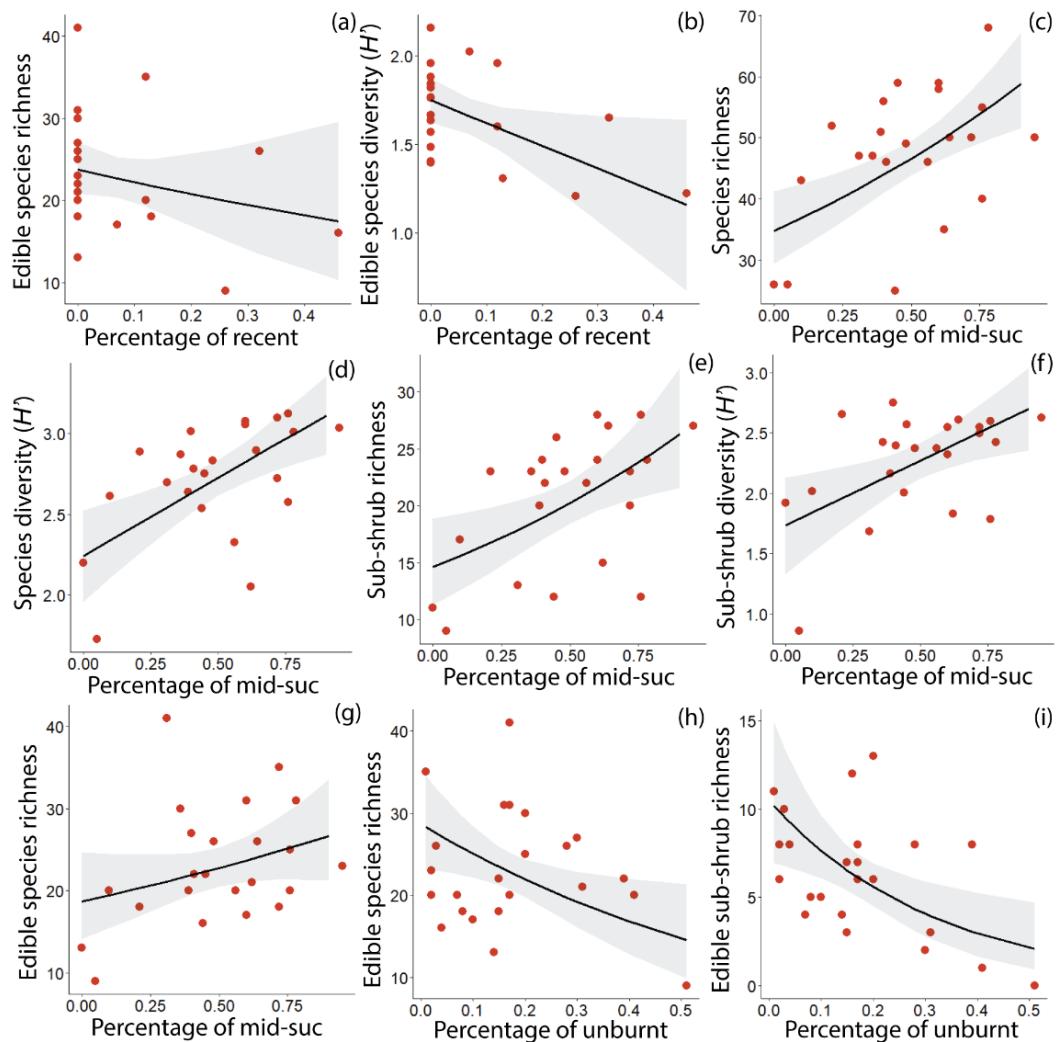


Figure 4.6 Relationship between percentage of recently burnt (recent) and edible species (a) richness, and (b) diversity (H'). Relationship between percentage of mid-succession (mid-suc) and total species (c) richness and (d) diversity (H'), sub-shrub (e) richness and (f) diversity (H'), and (g) edible 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.

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 previously shown that Martu burning increases the diversity and 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 ecosystem (Fig. 4.7).

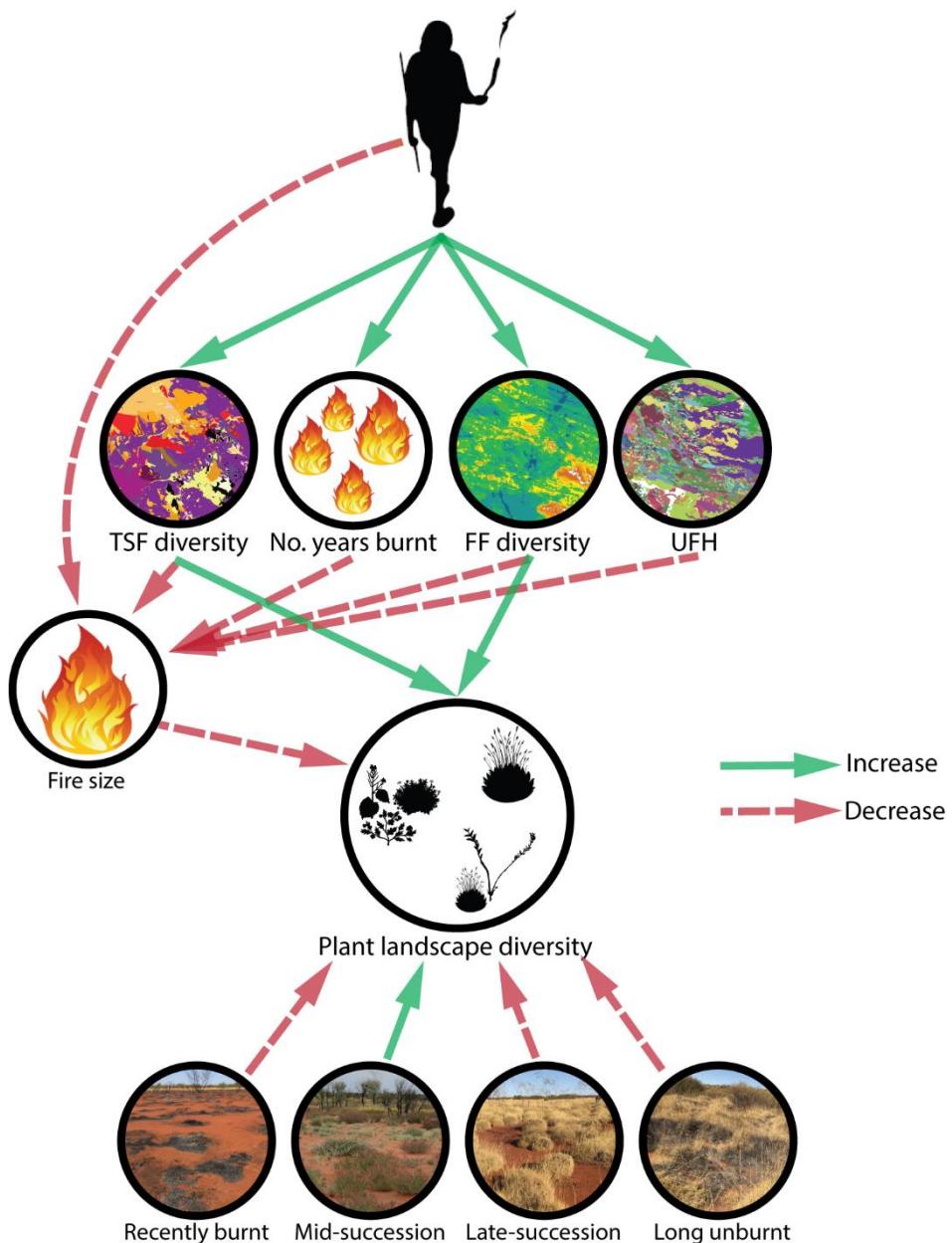


Figure 4.7 Conceptual model linking chapters two, three, and four. Martu increase the frequency that landscapes are burnt, increase visible fire diversity (i.e., time-since-fire diversity H'), increase invisible fire diversity (i.e., number of years burnt, diversity of fire frequency patches H' , and the number of unique fire histories), and reduce fire size. Pyrodiversity increases the richness and diversity of several plant groups and fire size reduces plant diversity, at the landscape scale. Thus, through increasing pyrodiversity and reducing fire size, Martu increase plant diversity at the landscape scale.

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. (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. We have previously shown that time-since-fire can overshadow the effects of underlying fire histories in determining plant community composition (chapter three). Different aged patches support different compositions of species by providing different resources (e.g., light, space) (Davis et al., 2018, Martin and Sapsis, 1992, Pastro et al., 2011). For example, immediately following fire, nutrients and water are more available due to volatisation of nutrients and competitive pressure release from spinifex when fire kills or reduces spinifex to its roots (Burrows et al., 2020, Wright and Clarke, 2007). Additionally, fire is important to break seed dormancy and trigger germination through heat and smoke cues (Commander et al., 2008, Commander et al., 2017). Different successional stages support different plant communities (chapter two), and it is the combination of these different plant communities within pyrodiverse landscapes that contributes to landscape-scale richness and diversity (Fig. 4.7). 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 have higher plant diversity than landscapes without Martu. 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, Codding 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, Trauernicht et al., 2012). 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 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).

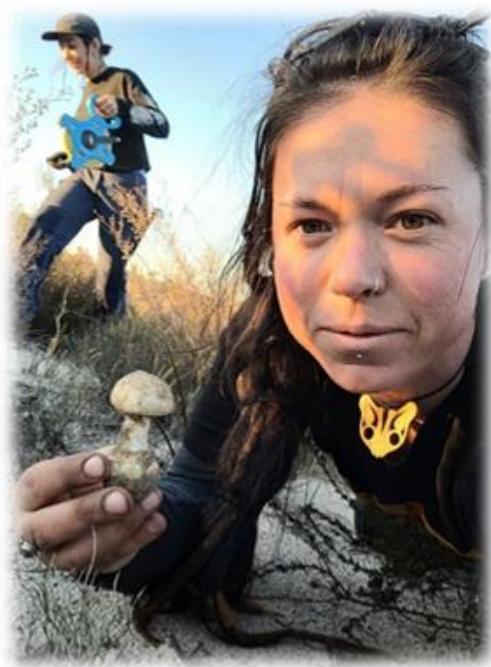
We find support for the notion that large fires can cause declines in species diversity at the landscape scale. Large fires could work to reduce species diversity by homogenising landscapes and burning at higher severities than smaller fires (Williams et al., 2015), reducing soil seed bank viability, 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 shaped by the fire regimes that they evolved under (Pausas and Keeley, 2009) and people have been burning across global ecosystems for thousands of years (Ellis et al., 2021a). It also suggests that the displacement of Indigenous people and their fire regimes can lead to local species decline and extirpation (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 (Ansoll and Evans, 2019, Hoffman et al., 2021, Millhauser and Earle, 2022).

Acknowledgements

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Chapter five: Fire shapes fungal guild diversity and composition through direct and indirect pathways

Manuscript in preparation for submission

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Abstract

Fire has shaped global ecosystems for millennia by directly killing organisms and indirectly altering habitat and resources. Fire is a key driver of fungal diversity, yet the responses of fungal communities to fire attributes other than time-since-fire and in semi-arid ecosystems are not well understood. Here, we collected soil samples and vegetation measurements across sites with differing time-since-fire ages and fire frequencies. Fungal DNA was extracted from soil samples, sequenced using high-throughput sequencing, and assigned taxonomically and to trophic guilds. We used structural equation models to examine direct, indirect, and total effects of time-since-fire and fire frequency on total fungal, ectomycorrhizal, saprotrophic, and pathogenic richness. Additionally, we used multivariate analyses to investigate how total fungal, ectomycorrhizal, saprotrophic, and pathogenic species composition differed between post-fire successional stages and fire frequency classes. Time-since-fire was an important driver of saprotrophic richness; directly, saprotroph richness increased with time-since-fire, and indirectly, declined with time-since-fire, mediated through substrates. Frequently burnt sites had lower numbers of saprotrophic and pathogenic species. Post-fire successional stages and fire frequency classes were characterised by distinct fungal communities, with large differences in ectomycorrhizal species composition. We shed new light on the importance of fire in shaping fungal communities in semi-arid heathlands of south-eastern Australia. We highlight that the complex responses of fungal communities to fire can be improved by exploring how the effects of fire flow through ecosystems and that diverse fire histories may be important for maintaining diverse fungal communities in these regions.

Introduction

Fire has burnt global ecosystems for over 400 million years (Bond and Keeley, 2005, Bowman et al., 2009, Scott, 2018) and is a key driver of biodiversity globally (Fox et al., 2022, He et al., 2019). Fire can influence ecological communities directly by killing organisms via heat and combustion (Klopatek et al., 1988, Neary et al., 1999) and indirectly by altering habitat and energy sources (Hart et al., 2005, Neary et al., 1999). The cumulative effects of fires, such as the frequency that sites are burnt, can also have large effects on ecological communities (Gill, 1975, Bradstock et al., 2005, Haslem et al., 2016). For example, soils burnt frequently can have lower mineral nitrogen and higher pH than soils burnt infrequently (Nichols et al., 2021). Compared to the effects of fire on aboveground communities (Bond and Keeley, 2005, He et al., 2019, Pulsford et al., 2016), the impact of fire on belowground microbiota is not well understood. This is surprising considering that soil biota play important roles in post-fire ecosystems and in overall ecosystem functioning (Dove et al., 2022, Wagg et al., 2014).

Soil-inhabiting fungi occupy critical roles within ecosystems, being essential to plant productivity, plant community composition (Tedersoo et al., 2020), decomposition, and nutrient cycling (Frac et al., 2018, Ferris and Tuomisto, 2015). Fire is a key driver of fungal communities (Fox et al., 2022). Fire can affect soil-inhabiting fungi directly, by killing mycelia and spores through soil heating and combustion of substrates (lethal temperatures are around 60°C for most fungal species) (Klopatek et al., 1988, Neary et al., 1999). However, some fungal species thrive and prolifically fruit shortly after fire, suggesting fire-resistance or fire-stimulation (McMullan-Fisher et al., 2011, Raudabaugh et al., 2020). Indirectly, fire can impact soil-inhabiting fungi by abruptly altering soil nutrients (e.g., carbon and nitrogen), soil properties (e.g., pH) (Neary et al., 1999), substrates (e.g., coarse woody debris) (Whitford and McCaw, 2019), and plant hosts (Hart et al., 2005). These changes can be long-lived, affecting fungal community dynamics for decades (Bowd et al., 2019).

The effects of fire on fungi are primarily explored through how fungal communities change with time-since-fire (i.e., the amount of time that has progressed since the last fire) (Dove and Hart, 2017, Holden and Treseder, 2013, McMullan-Fisher et al., 2011). Fungal communities show a variety of responses to time-since-fire; however, most studies point to a decline in fungal richness shortly after fire, and an increase as time-

since-fire progresses (Dooley and Treseder, 2012, Semenova-Nelsen et al., 2019). Differences in fungal responses are attributed to differences in ecosystems (Dooley and Treseder, 2012, Semenova-Nelsen et al., 2019, Smith et al., 2021), fungal adaptations (Fox et al., 2022), and fungal guild groups (Dooley and Treseder, 2012, Dove and Hart, 2017, McMullan-Fisher et al., 2011). For example, the richness of mycorrhizal fungi, which form symbiotic associations with plants, can decline shortly after fire due to the loss of plant hosts (Dove and Hart, 2017), while saprotrophic (decomposer) fungal richness can increase because of fire created substrates (Semenova-Nelsen et al., 2019).

Although less explored, fungal communities also show mixed responses to fire frequency (O'Bryan et al., 2009, Bowd et al., 2021, Semenova-Nelsen et al., 2019). Fire frequency can alter fungal communities by affecting development of fungal hyphae (Holden et al., 2013), creating long term changes in nutrients (Toberman et al., 2014), and altering plant communities (Hart et al., 2005). As a result, several studies suggest that frequent fires can promote distinct fungal communities by favouring those species that are adapted or tolerant to fire over fire sensitive species (Oliver et al., 2015, Semenova-Nelsen et al., 2019). Fire frequency can affect fungal guilds differently, for example, frequent fires can be detrimental for ectomycorrhizal fungi, because of repeated loss of plant hosts (Hart et al., 2005, Brown et al., 2013), while plant pathogens can increase under high fire frequencies (Beals et al., 2022).

In semi-arid environments, fungal communities are thought to be relatively resilient to fire because semi-arid ecosystems have evolved alongside frequent fires and hot temperatures (Allen et al., 2011, Neary et al., 1999, Peterson et al., n.d.). The nature of fires in semi-arid areas are also thought to minimise the effects of fire on fungal communities (Allen et al., 2011, Fultz et al., 2016, Neary et al., 1999). For example, low soil moisture in semi-arid soils can reduce the amount of heat transferred to soils, low plant biomass can reduce fire severity, and soil property alterations post-fire can be minimal or short-lived because of nutrient poor soils (Allen et al., 2011, Fultz et al., 2016, Neary et al., 1999). Some studies support this idea (Peterson et al., n.d., Haskins and Gehring, 2004). For example, Peterson et al. (n.d.) found no changes in fungal diversity between burnt and unburnt plots in a semi-arid savanna and Haskins and Gehring (2004) found no changes in arbuscular mycorrhizal fungal inoculum between burnt and unburnt sites in a semi-arid woodland. In contrast, others point to changes in fungal communities

along the post-fire successional axis (Fultz et al., 2016, Hinojosa et al., 2016, Muñoz-Rojas et al., 2016, O'Dea, 2007). For example, both Fultz et al. (2016) and Muñoz-Rojas et al. (2016) found that fungal composition differed between unburnt and burnt plots in semi-arid grasslands, and Hinojosa et al. (2016) found that fungal biomass was reduced in burnt plots, compared to unburnt plots in semi-arid shrublands. The effects of fire frequency on semi-arid fungal communities are even less understood. Fultz et al. (2016) found lower abundances of fungi in frequently burnt sites in semi-arid woodlands, but their results were insignificant.

Here, we aimed to explore the effects of fire on fungal richness and composition, and fungal guild richness and composition in the semi-arid heathlands of south-eastern Australia. Soil samples and vegetation measurements were collected in 60 sites with differing time-since-fire ages and fire frequencies. Fungal DNA was extracted from soil samples, sequenced using high-throughput sequencing, assigned taxonomically, and assigned to trophic guilds (i.e., groups of species that exploit the same resources in a similar manner). We used structural equation models (SEMs) to examine the direct, indirect —through interactions between fire, fungi, soil properties, substrates, and plant interactions— and total effects of time-since-fire and fire frequency on fungal richness, ectomycorrhizal richness, saprotrophic richness, and pathogenic richness. Finally, we used multivariate analysis to investigate how total fungal, ectomycorrhizal, saprotrophic, and pathogenic species composition differed between post-fire successional stages and fire frequency classes, because while richness can remain unchanged, composition can differ significantly (Egidi et al., 2016).

Methods

Study area

Our study sites were within the 132 000 ha semi-arid Little Desert National Park, south-eastern Australia (Fig. 5.1). The climate is characterised by cool winters and hot summers, with temperatures ranging between 3 – 31 °C, and low rainfall, varying between 168 – 471 mm (average annual 339 mm) (BOM, 2022). The soils are nutrient poor and sandy, dispersed over low irregular Quaternary sand dunes and sand sheets (Clarke et al., 2021, Department of Natural Resources and Environment, 1996). The National Park is an IUCN Category 2 protected area, supporting a diversity of plants (631 species) and fungi (Department of Natural Resources and Environment, 1996). The main plant communities

are heathlands, Mallee-broombush, Mallee, Yellow gum, Blackbox and desert Stringybark woodlands, and open forest (Department of Natural Resources and Environment, 1996). Fire is a prominent aspect of the landscape (Clarke et al., 2021).

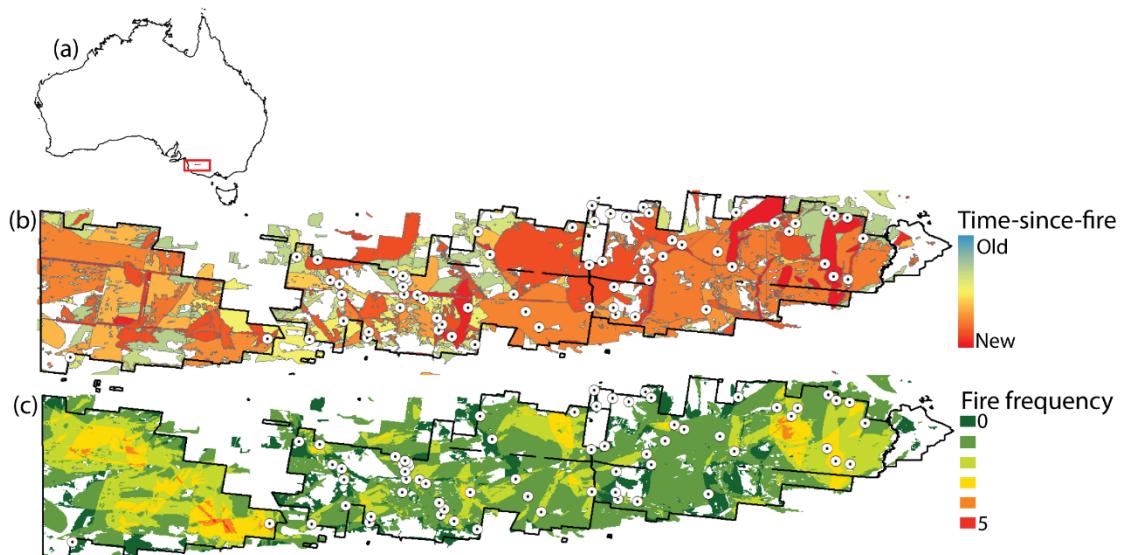


Figure 5.1 (a) Study area (red rectangle) in Australia, (b) time-since-fire layer, and (c) fire frequency layer. White circles with central black dot: 60 sites.

Fire mapping

We used fire maps downloaded from DataVic (Department of Environment, 2022). Fire maps were constructed using record searches, aerial photographs, and regional fire records (Department of Environment, 2022). To quantify time-since-fire and fire frequency, we built fire histories in ArcMap (ESRI. ArcGIS Desktop: Release 10.7.1. Redlands, California: Environmental Systems Research Institute, 2019) (Fig. 5.1). From these maps, we measured time-since-fire as the number of years since the last recorded fire prior to soil surveys in 2021 (since 1946) and fire frequency as the number of times burnt between 1992 and 2021 (29-year period).

Site selection and sample collection

We selected a subset of sites from the Ecosystem Resilience Program (ERP), which aims to examine the effects of fires on biodiversity in the Little Desert. ERP sites were chosen to first capture variation in time-since-fire ages (ranged from 0 to 75 years-since-fire) within each ecological fire group within the Little Desert (Cheal, 2010). ERP researchers also ensured a variation in fire intervals was captured. Sites only encompassed one time-since-fire age and one ecological fire group. Additionally, sites were at least 800 m apart, at least 100 m from roads and tracks, and at least 100 m from time-since-fire and ecological fire group boundaries. Each time-since-fire age was ground truthed prior to

surveys. For this study, we selected a subset of ERP sites. We chose to focus sampling in heath vegetation (included damp heathland, dune field heathland, heathy woodland, and tea-tree heath), which resulted in a total of 60 sites. Our sites ranged in time-since-fire ages from 0 – 75 years-since-fire (mean = 22 years) and fire frequencies, burnt 0 – 5 times (mean = burnt twice) (Table S5.1, Fig. 5.1).

ERP researchers conducted plant surveys at all 60 sites in spring and summer of 2019 and 2020. At each site, they established a north-south 100 m transect. At 1 m intervals along each transect, they used a structure pole to record the substrate (ground type) and habitat structure (plant type). They recorded the number of times plant types touched the pole within five height classes (i.e., < 0 – 0.2, 0.2 – 0.5, 0.5 – 1, 1 – 2, 2 – 4 m). For our analysis, we only retained coarse woody debris cover, elevated dead cover, and shrub cover. ERP researchers classified ‘coarse woody debris’ as plant debris with a diameter of 1 – 5 cm, ‘elevated dead’ as dead material suspended off the ground (including attached to living plants), and ‘shrub’ as plants with multiple woody stems.

We collected soil samples at all 60 sites in winter of 2021. At each site, we established a 10 x 10 m plot in the centre of the 100 m transect. We collected a subsample of soil at the corners of the plot, the centre point between each corner, and in the centre of the plot (totalling 9 subsamples per plot) (Bowd et al., 2021, Bissett et al., 2016). We removed debris or litter from the soil surface, then used a 4 cm diameter soil core to collect soil to a depth of 10 cm. We combined and mixed the subsamples together thoroughly and then divided the mixture into two; one for fungal DNA analysis and one for soil property analysis. All soil samples were immediately stored in a transportable freezer at -10°C. We cleaned shoes and tools between sites to minimise contamination. Soil samples were stored at -10°C until analysed.

Soil, substrate, and plant variables

Environmental Analysis Laboratory (EAL) at Charles Sturt University calculated ammonia (NH_3), nitrate (NO_3^-), total organic carbon (TOC), and pH for each of our sites (Rayment and Lyons, 2011). Ammonia and nitrate were extracted with 2 M KCl at a 1:10 soil/solution ratio for 1 hour, distilled, reduced, and calculated following titration with dilute mineral acid to pH 5 (Rayment and Lyons, 2011). Total organic carbon was measured using Dumas high temperature combustion and infrared/thermal conductivity

and pH was measured using 1:5 soil/water suspension method (Rayment and Lyons, 2011).

From the 100 m vegetation structure transects, we calculated (i) proportion of coarse woody debris (i.e., proportion of coarse woody debris substrate along the 100 m transect), (ii) elevated dead (i.e., counts of elevated dead on the structure pole along the 100 m transect), and (iii) shrub cover (i.e., counts of shrubs on the structure pole along the 100 m transect). We chose elevated dead and coarse woody debris to reflect the decomposing aspects of the environment, which we assumed would be particularly important drivers of ectomycorrhizal and saprotrophic fungi (Fernandez and Kennedy, 2016, Mäkipää et al., 2017) (Table S5.2). We chose shrub cover to reflect the living component of the environment, as shrub cover largely reflects plant cover in our heathland sites. We assumed that shrub cover would be a particularly important driver for ectomycorrhizal and pathogenic fungi because they either form partnerships with plants or require plants as hosts (Dean et al., 2012, Smith and Read, 2008) (Table S5.2).

Data processing

We extracted fungal DNA from soil samples using DNeasy Powersoil Pro kits (Qiagen, GmbH, Hilden, Germany) according to manufacturer's instructions. Samples were sent to Western Sydney University's Next-Generation Sequencing Facility (NSW, Australia). The DNA was purified using the Agencourt AMPure XP Beads (Beckman Coulter) and quality assessed using Qunat-iT™ PicoGreen fluorescence-based analysis (ThermoFisher Scientific, North Ryde, NSW, Australia). The purified DNA was amplified using polymerase chain reaction (PCR), targeting the internal transcribed spacer (ITS) region 2 (Blaalid et al., 2013) using the primer set FITS7/ITS4 (Ihrmark et al., 2012). Briefly, PCR reactions consisted of 5 µl Q5® High-Fidelity DNA Polymerase 2 x master mix (New England Biolabs, Notting Hill, Victoria, Australia), 0.2 µl of 10 µM forward and reverse primer with 2 µl of DNA, total volume of the reaction was 10 µl. PCR reactions were as described in Caporaso et al. (2018). A short second PCR was conducted to the amplified PCR product to attach the Illumina Nextera XT v2 index set (Illumina, Melbourne, Australia) as per manufacturer's instructions. Each reaction consisted of 3.8 µl of Q5® High-Fidelity DNA Polymerase 2 x master mix (NEB), 1.5 µl of each index (Illumina) and 2.3 µl of PCR product, total reaction volume was 7.6 µl. The amplicons were diluted and assessed using the Qunat-iT™ PicoGreen (ThermoFisher Scientific) assay and normalised library pools were

constructed using the Eppendorf epMotion. The libraries were cleaned-up and prepared for sequencing following the Illumina MiSeq protocol. Sequencing was performed on the Illumina MiSeq platform using the Illumina MiSeq reagent kit v3 2 x 300 bps paired-end chemistry as per manufacturer's instructions.

We processed the fungal raw sequences using qiime2 (qiime2-2021.11 Bolyen et al., 2019). We performed sequence quality control, denoising, chimera detection, and clustering into amplicon sequence variants (ASVs) (i.e., functional equivalent of species-level taxa) using "DADA2" (Callahan et al., 2016) with parameters: --p-trunc-len-f 200 --p-trunc-len-r 200. We removed ASVs with < 10 reads across all samples. We assigned each ASV taxonomically using classify-sklearn and the UNITE database (v.8) (Abarenkov et al., 2020) and grouped ASVs into trophic guilds using the FungalTraits database (Pöhlme et al., 2020). We rarefied ASV samples to a sequencing depth of 17 583 reads (Fig. S5.1) to adjust for different sample sizes across sites (Weiss et al., 2017). Rarefaction involves identifying the site with the lowest number of sequences and then randomly discarding reads from larger samples so that all samples have the same sequencing depth (i.e., 17 583 in our case) (Weiss et al., 2017).

We found a total of 2 088 436 sequences, which ranged from 17 583 – 40 008 (mean = 32,130) per site and included 5520 unique ASVs. Nearly half (43 %) of the ASVs (i.e., 2388 ASVs) were only found in one site and did not re-occur. We assigned 4272 ASVs (77 %) to phylum level, 1975 (36 %) to genus level, and 358 (6 %) to species level. Ascomycota was the most abundant phyla (75 %), followed by Basidiomycota (21 %), Mucoromycota (2 %), Chytridiomycota (0.7 %), Rozellomycota (0.5 %), Mortierellomycota (0.5 %), and Olpidiomycota (0.02 %). *Oidiodendron* was the most common genus, followed by *Coniochaeta*, *Cortinarius*, *Sebaci*, *Talaromyces*, *Cladophialophora*, *Exophiala*, and *Penicillium*. The most common species were *Oidiodendron griseum*, *Leohumicola lenta*, *Coniochaeta discospora*, *Umbelopsis dimorpha*, *Exophiala bergeri*, and *Penicillium spinulosum*.

We assigned 1712 (31 %) ASVs to trophic guilds: 1204 (22 %) were saprotrophic fungi (dung, nectar, pollen, litter, soil, and wood saprotrophs), 224 (4 %) were plant pathogens, 142 (3 %) were parasitic (algal, animal, and myco-parasites), 96 (2 %) were ectomycorrhizal, 16 (0.3 %) were endophytic, 11 (0.2 %) were epiphytic, 10 (0.1 %) were lichenised, and 10 (0.1 %) were soot-moulds. For the fungal trophic guild analysis, we

chose to focus on ectomycorrhizal, saprotrophic, and pathogenic fungal richness because they were the most common guilds in our study system. We omitted algal, animal, and myco-parasitic fungi because we assumed they would not respond strongly to soil properties or substrate variables.

Data analysis

We used piecewise structural equation models (SEMs) to explore the relationships between fire, fungi, soil properties, substrates, and plants (Lefcheck, 2016). Belowground and aboveground communities are inherently linked (Fierer et al., 2009, Wardle et al., 2004) and thus, fungal communities are affected both by direct and indirect effects of fire (Fox et al., 2022). SEMs provide a powerful tool to explore the direct effects of fire on fungal communities as well as the flow on effects of fire through ecosystem elements, such as soil properties and substrates (Grace et al., 2012). In piecewise SEMs, each response variable is modelled and evaluated separately, allowing a variety of distributions to be fitted to the data (Lefcheck, 2016).

We built two global SEMs based on conceptual models from existing knowledge (see Table S5.2) (Grace et al., 2012): one that only included total fungal richness as a fungal response variable, and one that included ectomycorrhizal richness, saprotrophic richness, and pathogenic richness as fungal response variables. Initially, all pathways from our theoretical models were included in the SEMs. Richness and soil property variables were continuous and fitted using linear models (LMs) (Zuur et al., 2009). Coarse woody debris cover, elevated dead cover, and plant cover were proportions that we logit transformed (Warton and Hui, 2011) and fitted using LMs (Zuur et al., 2009). We removed pathways if they were not significant (Stenegren et al., 2017). We identified missing pathways using *d-sep* and included the paths in models if 95 % confidence intervals did not overlap with 0 (Shipley, 2013). Additionally, we removed paths if they did not connect directly or indirectly to our fungal response variables. The fit of nodes was assessed by calculating R^2 (amount of variation explained by the models) (Lefcheck, 2016). We evaluated the final models using a chi-square test (deeming models as a good fit if the test was non-significant). We calculated the direct effects using the piecewise package (Lefcheck, 2016) and indirect and total effects using the semEFF package (Murphy, 2021). The semEFF package estimates the indirect and total effects by evaluating each effect through bootstrapping (Murphy, 2021). Indirect effects combine all direct effects along causal

pathways and total effects are the sum of direct and indirect effects (Murphy, 2021). Finally, we scaled all effects by their relevant range, which measures how a variable changes in proportion to its range (i.e., minimum and maximum), to allow comparison between effects (Grace and Bollen, 2005). We calculated 95 % confidence intervals for all effects, deeming variables influential if the confidence intervals did not overlap 0.

To explore how the composition of all fungal species, ectomycorrhizal species, saprotrophic species, and pathogenic species differed with time-since-fire and fire frequency, we used multivariate analyses. We square root transformed fungal abundance matrixes because we were equally as interested in compositional changes in dominant plant species as rare species (Clarke and Ainsworth, 1993). To test whether there were differences in all fungal species and fungal guild species composition along the time-since-fire and fire frequency gradients, we used permutational multivariate analysis of variance (permANOVA) with a Bray-Curtis distance measure and 999 permutations (Anderson, 2001, Bray and Curtis, 1957). PermANOVA compares the difference between groups to the difference within groups (based on the centroid of each group cluster) and obtains p-values using permutations (Anderson, 2001). Next, we investigated how fungal species and fungal guild species composition differed between post-fire successional stages and fire frequency classes using multilevel pairwise comparison (Martinez Arbizu, 2020). To compare pairs, we grouped time-since-fire and fire frequency into discrete categories. Time-since-fire was grouped into ‘recently burnt’: 0 – 2.5 years post-fire, ‘mid-succession’: 2.5 – 8.5 years post-fire, ‘late-succession’: 8.5 – 33.5 years post-fire, and ‘long unburnt’: 33.5 + years post-fire (Cheal, 2010). For the fire frequency classes, we grouped sites that had been burnt 0 – 2 times over the 29-year period as ‘low fire frequency’ and sites that had burnt 3 – 5 times as ‘high fire frequency’ (Cheal, 2010). Next, we identified which species were characteristic of each post-fire successional stage and fire frequency class using indicator species analysis, where high indicator values indicate high frequency and abundance within successional stages or fire frequency classes (Dufrêne and Legendre, 1997, Cáceres and Legendre, 2009). Finally, we used non-metric multidimensional scaling (NMDS) to visualise the differences in fungal species and fungal guild species composition. NMDS does not produce a unique solution, so we set random starts to 200 (Kenkel, 2006). NMDS also requires the number of axes to be set a priori to analysis, thus we used scree plots to determine the minimum number of axes with ≤ 0.2 stress (i.e., similarity of observed distance to ordination distance) to ensure

interpretability (Clarke, 1993). All analyses were conducted in R version 2.1 (R Core Team, 2018) using piecewiseSEM (Lefcheck, 2016), semEFF (Murphy, 2021), and vegan (Oksanen et al., 2020) packages.

Results

Total fungal richness

Total fungal richness was not directly affected by time-since-fire (Table 5.1, Fig. 5.2a). Indirectly, total fungal richness declined with time-since-fire because elevated dead cover increased with time-since-fire and total fungal richness declined with increasing elevated dead cover (Table 5.2, Fig. 5.2a). Overall, the SEM adequately fit the data ($\chi^2 = 23.63$, $p = 0.17$, $df = 18$, AIC = 145.97).

Table 5.1 Direct effects from structural equation models exploring the interactions between fire, total fungal richness, and substrate cover. Est: non-standardised estimate, SE: standard error, LCI: lower 95 % confidence interval, UCI: upper 95 % confidence interval, Std Est: standardised (range) estimate, R^2 : variation explained. Variables deemed influential if confidence intervals do not overlap 0.

Response	Predictor	Est	SE	LCI	UCI	Std Est	R^2
Total fungal richness	Elevated dead	-20.65	9.74	-39.45	-0.78	-0.19	8%
Elevated dead	Time-since-fire	0.02	0.01	0.01	0.03	0.60	18%

Table 5.2 Indirect and total effects from structural equation models exploring the interactions between fire, total fungal richness, and substrate cover. Std Est: standardised (range) estimate, SE: standard error, LCI: lower 95 % confidence interval, UCI: upper 95 % confidence interval. Variables deemed influential if confidence intervals do not overlap 0.

Response	Effect	Predictor	Std Est	SE	LCI	UCI
Total fungal richness	Indirect	Time-since-fire	-0.33	0.20	-0.83	-0.04
	Total	Time-since-fire	-0.33	0.20	-0.83	-0.04
	Total	Elevated dead	-20.65	9.74	-39.45	-0.78
Elevated dead	Total	Time-since-fire	0.02	0.01	0.01	0.03

Fungal guild richness

There were strong interactive effects between the richness of fungal guilds (Table 5.3 and 5.4, Fig. 5.2b). For example, saprotrophic richness increased with increasing ectomycorrhizal richness, and pathogenic richness increased with increasing saprotrophic richness (Table 5.3 and 5.4, Fig. 5.2b). This resulted in indirect interactions between fire, fungal guilds, soil properties, and substrates (Table 5.4, Fig. 5.2b).

Ectomycorrhizal richness was not influenced directly or indirectly by time-since-fire (Table 5.3 and 5.4, Fig. 5.2b). Directly, saprotrophic richness increased with time-since-fire

(Table 5.3, Fig. 5.2b). Indirectly, time-since-fire had contrasting negative effects on saprotrophic richness, mediated through interactions between elevated dead and coarse woody debris (Table 5.4, Fig. 5.2b). For example, saprotrophic richness declined with increasing cover of coarse woody debris, and coarse woody debris increased with time-since-fire (Table 5.3 and 5.4, Fig. 5.2b). As a result, the total effects of time-since-fire on saprotrophic richness were positive (Table 5.4, Fig. 5.2b). While pathogenic richness was not influenced directly by time-since-fire, time-since-fire had positive indirect effects (and thus total effects without direct effects) on pathogenic richness because of mediated interactions between fungal guilds, soil properties, and substrates (Table 5.3 and 5.4, Fig. 5.2b). For example, pathogenic richness increased with increasing richness of saprotrophic richness, and saprotrophic richness increased with time-since-fire (Table 5.3 and 5.4, Fig. 5.2b).

No fungal guilds were influenced by fire frequency directly (Table 5.3, Fig. 5.2b). However, indirectly both saprotrophic richness and pathogenic richness declined under frequent fires, mediated through effects of fire frequency on coarse woody debris and saprotrophic richness (Table 5.4, Fig. 5.2b). For example, fire frequency increased coarse woody debris cover, which reduced saprotrophic richness (Table 5.3 and 5.4, Fig. 5.2b). Overall, the SEM adequately fit the data ($\chi^2 = 32.06$, $p = 0.81$, $df = 40$, AIC = 72.06).

Table 5.3 Direct effects of structural equation models exploring the interaction between fire, fungal trophic guilds richness, soil properties, and substrate cover. Est: non-standardised estimate, SE: standard error, LCI: lower 95 % confidence interval, UCI: upper 95 % confidence interval, Std Est: standardised (range) estimate, R²: variation explained. Variables deemed influential if confidence intervals do not overlap 0.

Response	Predictor	Est	SE	LCI	UCI	Std Est	R ²
Ectomycorrhizal richness	Total organic carbon	-0.000	0.000	-0.010	-0.001	-0.436	13%
	Time-since-fire	0.269	0.085	0.132	0.423	0.373	
Saprotrophic richness	Elevated dead	-6.481	1.895	-10.152	-2.933	-0.283	30%
	Coarse woody debris	-10.015	3.246	-16.733	-3.971	-0.277	
	Ectomycorrhizal richness	1.978	0.779	0.433	3.472	0.283	
Pathogenic richness	Saprotroph richness	0.155	0.032	0.092	0.211	0.543	38%
	pH	-1.516	0.620	-2.724	-0.381	-0.328	
Elevated dead	Time-since-fire	0.016	0.005	0.013	0.031	0.471	18%
Coarse woody debris	Time-since-fire	0.004	0.070	0.013	0.021	0.798	25%
	Fire frequency	0.178	0.070	0.034	0.220	0.564	

Table 5.4 Indirect and total effects from structural equation models exploring the interactions between fire, fungal trophic guilds richness, soil properties, and substrate cover. Est: non-standardised estimate, SE: standard error, LCI: lower 95 % confidence interval, UCI: upper 95 % confidence interval, Std Est: standardised (range) estimate. Variables deemed influential if confidence intervals do not overlap 0.

Response	Effect	Predictor	Est	SE	LCI	UCI	Std Est
Ectomycorrhizal richness	Total	TOC	-0.000	0.000	-0.001	-0.000	-0.44
	Indirect	Time-since-fire	-0.212	0.071	-0.386	-0.098	-0.24
		Fire frequency	-1.143	0.694	-3.215	-0.228	-0.09
Saprotrrophic richness	Total	TOC	-0.001	0.000	-0.002	-0.000	-0.15
		Time-since-fire	0.043	0.077	-0.121	0.185	0.05
		Fire frequency	-1.143	0.694	-0.315	-0.228	-0.09
Pathogenic richness	Indirect	TOC	-0.001	0.001	-0.002	-0.000	-0.15
		Elevated dead	-6.486	1.868	-10.202	-2.929	-0.28
		Coarse woody debris	-10.005	3.192	-16.689	-4.291	-0.28
		Ectomycorrhizal richness	1.951	0.780	0.388	3.454	0.28
		Time-since-fire	0.007	0.001	-0.017	0.031	0.04
	Total	Fire frequency	-0.177	0.104	-0.482	-0.037	-0.05
		TOC	0.000	0.000	0.000	0.000	0.00
		Elevated dead	-1.002	0.327	-1.773	-0.453	-0.14
		Coarse woody debris	-1.546	0.522	-2.805	-0.679	-0.13
		Ectomycorrhizal richness	0.301	0.136	0.063	0.602	0.15
Elevated dead	Total	Time-since-fire	0.007	0.001	-0.017	0.031	0.04
		Fire frequency	-0.177	0.104	-0.482	-0.037	-0.05
	Total	TOC	0.000	0.000	0.000	0.000	0.00
		pH	-1.510	0.024	-2.678	-0.382	-0.33
		Elevated dead	-1.002	0.327	-1.773	-0.453	-0.14
Coarse woody debris	Total	Coarse woody debris	-1.546	0.522	-2.805	-0.679	-0.13
		Ectomycorrhizal richness	0.301	0.136	0.063	0.602	0.15
		Saprotrrophic richness	0.155	0.030	0.093	0.212	0.54
	Total	Time-since-fire	0.016	0.006	0.002	0.026	0.47
		Fire frequency	0.011	0.003	0.005	0.017	0.80

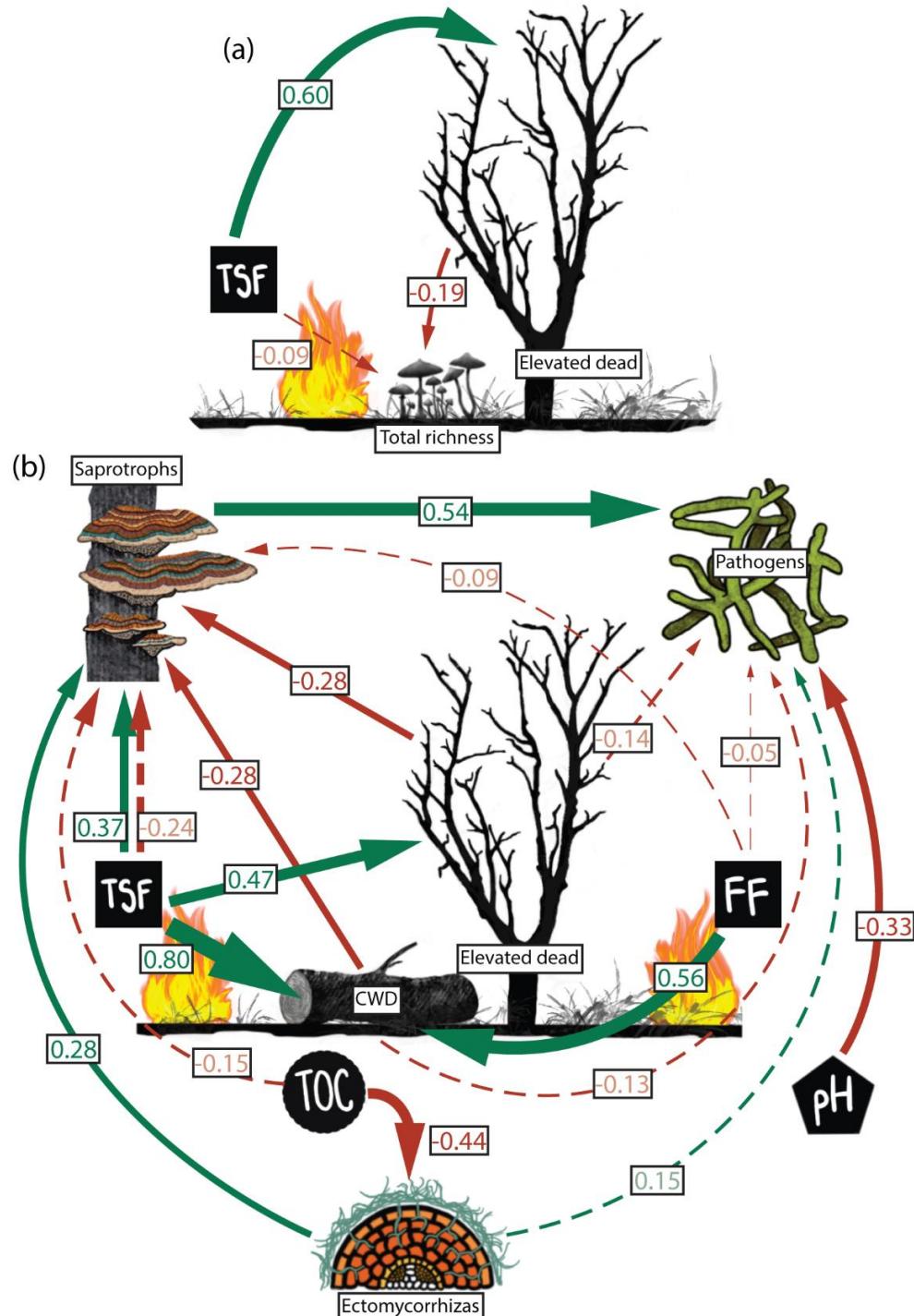


Figure 5.2 Structural equation models (SEMs) exploring the interactions between fire, soil properties, substrate cover, and (a) total fungal richness ($X^2 = 23.63$, $p = 0.17$, $df = 18$, AIC = 145.97), and (b) fungal trophic guild richness ($X^2 = 32.06$, $p = 0.81$, $df = 40$, AIC = 72.06). TSF: time-since-fire, FF: fire frequency, TOC: total organic carbon, CWD: coarse woody debris, solid arrow: direct effect, dashed arrow: indirect effect, green arrow: positive effect, red arrow: negative effect, arrows scaled to demonstrate effect size. Only effects that were influential are included (i.e., 95 % confidence intervals do not overlap with 0).

Total fungal composition

There were significant differences in total fungal species composition between time-since-fire ages (permANOVA: SS = 0.78, $F = 2.93$, $R^2 = 4\%$, $p = 0.001$), but the differences were small (pairwise comparison: $R^2 = 5 - 9$) (Table 5.5, Fig. 5.3a). There were also

significant differences in fungal species composition between low and high fire frequencies (permANOVA: SS = 0.80, F = 3.00, R² = 5 %, p = 0.001), but again, the differences were small (pairwise comparison: R² = 4 %) (Table 5.5, Fig. 5.3a).

Fungal guild composition

There were significant differences in fungal guild composition between time-since-fire ages (Fig. 5.3). Ectomycorrhizal composition significantly differed between time-since-fire ages (permANOVA: SS = 1.22, F = 5.67, R² = 8 %, p = 0.001) (Fig. 5.3b). Differences were small to moderate, with the largest difference in ectomycorrhizal composition between mid-succession and long unburnt (pairwise comparison: R² = 4 – 17 %) (Table 5.5). Ectomycorrhizal ASVs, *Inocybe* spp. and *Scleroderma* spp. showed a preference for recently burnt sites (Table S5.5). Saprotrrophic composition significantly differed between time-since-fire ages (permANOVA: SS = 0.74, F = 2.62, R² = 4 %, p = 0.001), but the differences were small (pairwise comparison: R² = 4 – 8 %) (Table 5.5, Fig. 5.3c). Several saprotrophic ASVs showed a preference for a particular time-since-fire age (Table S5.5). For example, recently burnt sites were characterised by *Acremonium* spp. and *Coniochaeta* spp., mid-succession was characterised by *Clathrus* spp. and *Penicillium* spp., late-succession was characterised by *Arthrocladium* spp. and *Sclerogaster* spp., and long unburnt was characterised by *Acremonium* spp. and *Umbelopsis* spp. (Table S5.5). Pathogenic composition significantly differed between time-since-fire ages (permANOVA: SS = 0.62, F = 2.37, R² = 4 %, p = 0.001), but the differences were small (pairwise comparison: R² = 4 – 7 %) (Table 5.5, Fig. 5.3d). Several pathogenic ASVs showed a preference for a particular time-since-fire age (Table S5.5). For example, recently burnt sites were characterised by *Fusarium* spp. and *Pleurophoma* spp., mid-succession by *Devriesia* spp. and *Dothiorella* spp., late-succession by *Drechslera* spp. and *Sclerotinia* spp., and long unburnt by *Neocatenulostroma* spp. and *Acrodontium* spp. (Table S5.5).

Fungal guild composition also differed between fire frequencies (Fig. 5.3). Ectomycorrhizal composition significantly differed between fire frequencies (permANOVA: SS = 1.02, F = 4.68, R² = 7 %, p = 0.001), but the differences were small (pairwise comparison: R² = 6 %) (Table 5.5, Fig. 5.3b). Ectomycorrhizal ASVs, *Amanita* spp. and *Auritella* spp., showed a preference for frequently burnt sites (Table S5). Saprotrrophic composition significantly differed between fire frequencies (permANOVA: SS = 0.74, F = 2.62, R² = 4 %, p = 0.001), but the differences were small (pairwise

comparison: $R^2 = 3\%$) (Table 5.5, Fig. 5.3c). Several saprotrophic ASVs showed a preference for a particular fire frequency (Table S5.5). For example, *Baudoinia* spp. and *Mortierella* spp. preferred sites that were burnt infrequently and *Arthrocladum* spp. and *Penicillium* spp. showed preference for sites that were burnt frequently (Table S5.5). Pathogenic composition significantly differed between fire frequencies (permANOVA: SS = 0.55, F = 2.12, $R^2 = 4\%$, p = 0.001), but the differences were again small (pairwise comparison: $R^2 = 3\%$) (Table 5.5, Fig. 5.3d). Several pathogenic ASVs showed a preference for a particular fire frequency (Table S5.5). For example, *Acrodontium* spp. was associated with sites that were burnt infrequently and *Coniozyma* spp. and *Devriesia* spp. with sites that were burnt frequently (Table S5.5).

There were several ASVs that showed a preference for a specific combination of post-fire successional stage and fire frequency class (Table S5.5). For example, *Alterria* spp. and *Cairneyella* spp. were associated with recently burnt sites that were burnt frequently, and *Acrodontium* spp. and *Umbelopsis* spp. were associated with long unburnt sites that were burnt infrequently (Table S5.5).

Table 5.5 Pair-wise comparisons of fungal species and trophic guild species composition between post-fire successional stages and fire frequency classes. F: variance between groups, R²: amount of dissimilarity between pair, p-value: significance (p ≤ 0.05 deemed significant), recently burnt: 0 – 2.5 years post-fire, mid-succession: 2.5 – 8.5 years post-fire, late-succession: 8.5 – 33.5 years post-fire, long unburnt: 33.5 + years post-fire, low fire frequency: burnt ≤ 2 times over 29-year period, high fire frequency: burnt 3 – 5 times over 29-year period.

Fungi group	Fire measure	Pair	F	R ²	p-value
Total fungal species	Successional stage	Recently burnt vs mid-succession	1.91	7%	0.02
		Recently burnt vs late-succession	2.32	8%	0.01
		Recently burnt vs long unburnt	2.59	8%	0.01
		Mid-succession vs late-succession	2.01	6%	0.01
		Mid-succession vs long unburnt	3.11	9%	0.01
		Late-succession vs long unburnt	1.64	5%	0.01
	Fire frequency class	Low vs high	2.32	4%	0.00
		Recently burnt vs mid-succession	3.05	10%	0.01
		Recently burnt vs late-succession	3.80	12%	0.01
		Recently burnt vs long unburnt	4.69	14%	0.01
		Mid-succession vs late-succession	4.57	12%	0.01
		Mid-succession vs long unburnt	6.80	17%	0.01
	Ectomycorrhizas	Late-succession vs long unburnt	1.42	4%	0.06
		Low vs high	4.00	6%	0.00
		Recently burnt vs mid-succession	1.75	6%	0.03
		Recently burnt vs late-succession	2.07	7%	0.01
		Recently burnt vs long unburnt	2.34	8%	0.01
		Mid-succession vs late-succession	1.94	6%	0.01
	Saprotophorts	Mid-succession vs long unburnt	2.80	8%	0.01
		Late-succession vs long unburnt	1.53	4%	0.04
		Low vs high	1.99	3%	0.00
		Recently burnt vs mid-succession	0.98	4%	1.00
		Recently burnt vs late-succession	1.82	6%	0.03
		Recently burnt vs long unburnt	1.50	5%	0.29
	Pathogens	Mid-succession vs late-succession	1.93	6%	0.04
		Mid-succession vs long unburnt	2.45	7%	0.01
		Late-succession vs long unburnt	1.64	5%	0.13
		Low vs high	1.58	3%	0.06

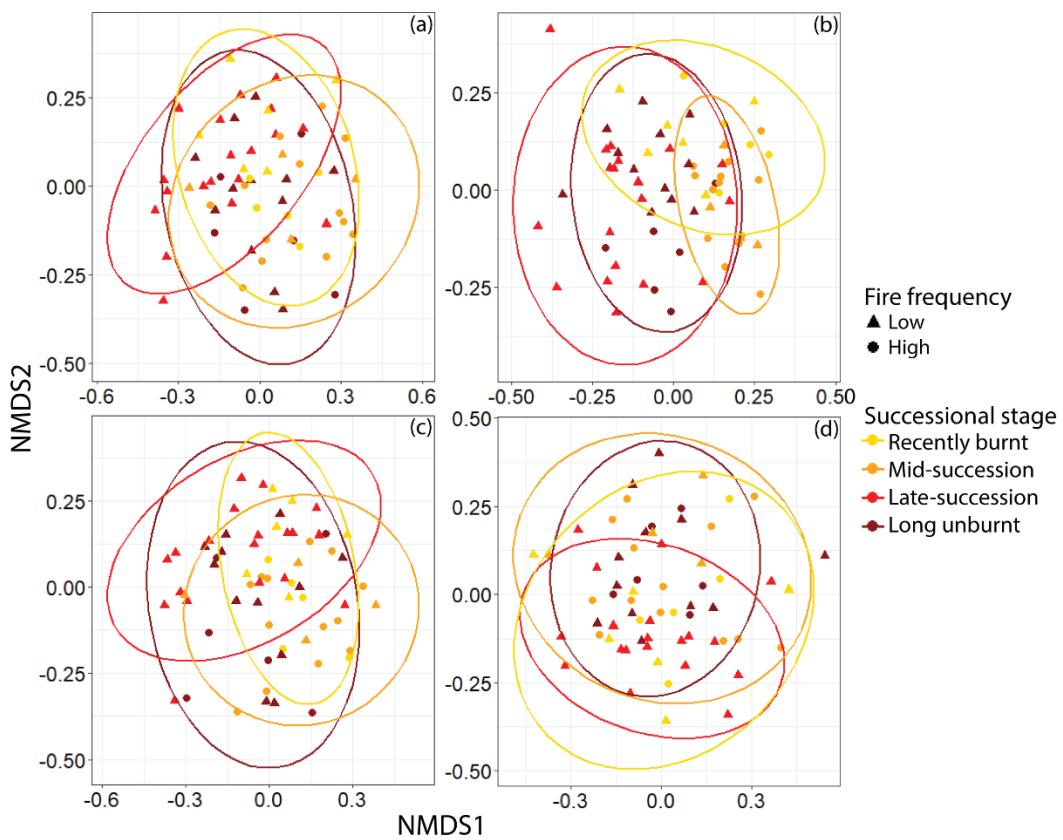


Figure 5.3 NMDS ordination, based on Bray-Curtis distances, of (a) total fungal species composition (stress = 0.16, axes = 3, R^2 = 75 %), (b) ectomycorrhizal species composition (stress = 0.18, axes = 3, R^2 = 79 %), (c) saprotrophic species composition (stress = 0.19, axes = 3, R^2 = 70 %), and (d) pathogenic species composition (stress = 0.19, axes = 3, R^2 = 71 %) with post-fire successional stages and fire frequency classes. Recently burnt: 0 – 2.5 years post-fire, mid-succession: 2.5 – 8.5 years post-fire, late-succession: 8.5 – 33.5 years post-fire, long unburnt: 33.5 + years post-fire, low fire frequency: burnt \leq 2 times over 29-year period, high fire frequency: burnt 3 – 5 times over 29-year period.

Discussion

Fire plays a prominent role in shaping the diversity and composition of fungal communities in the semi-arid heathlands of south-eastern Australia—both directly and indirectly—mediated through interactions between fire, fungal guilds, and substrates. Time-since-fire was an important driver of saprotrophic richness. Directly, saprotrophic richness increased with time-since-fire, and indirectly, saprotrophic richness declined with time-since-fire, mediated through substrates, resulting in an overall positive effect. Fire frequency only influenced fungal communities indirectly through interactions between fire, fungal guild interactions, and substrates. Nonetheless, frequently burnt sites had lower numbers of saprotrophic and pathogenic species. Post-fire successional stages and fire frequency classes were characterised by distinct fungal communities, with large differences in ectomycorrhizal species composition. Hundreds of ASVs showed

preference for a particular post-fire successional stage and fire frequency class, with several ASVs showing preference for a specific combination of both.

Total fungal richness

Our semi-arid heathland sites were highly diverse mycobiomes; nearly half of the ASVs (43 %) were only found at one site, which may explain why we found minimal effects of fire on total fungal richness. In contrast to our assumptions, total fungal richness declined with time-since-fire because elevated dead cover increased with increasing time-since-fire and total fungal richness declined with increasing elevated cover. The response of increasing elevated dead with time-since-fire aligns with other studies, as vegetation complexity increases along the post-fire succession axis (Burrows et al., 2021, Gosper et al., 2012b). However, lower fungal richness under higher covers of elevated dead is more difficult to explain. It could reflect competition between species as substrates build up (Bödeker et al., 2016, Künzler, 2018), but diverse and dense covers of substrates can support diverse fungal communities (Yang et al., 2021a). Alternatively, aboveground substrates could inaccurately reflect soil-inhabiting fungal communities, as some species specialise in above-ground or below-ground resources (Mäkipää et al., 2017). Additionally, patterns in fungal richness may have been driven by unmeasured factors, such as climate variability and soil moisture (Kivlin et al., 2011, Tedersoo et al., 2014). Minimal responses of total fungal richness to fire suggests that total fungal richness is too crude a measurement for the highly diverse fungal kingdom (Naranjo-Ortiz and Gabaldón, 2019). Deeper insight can be attained by exploring functional groups (Lindenmayer et al., 2015, Pölme et al., 2020) and compositional changes (Egidi et al., 2016).

Fungal guilds

Limited direct or indirect effects of time-since-fire and fire frequency on ectomycorrhizal richness could point to fire-adapted ectomycorrhizal species that have co-evolved with fire-adapted hosts (Baynes et al., 2012). Ectomycorrhizal fungi form partnerships with plants, and thus their survival during and after fire events is largely tied to their plant host's survival (and vice versa) (Hart et al., 2005, Smith and Read, 2008). Given most plants in semi-arid heath resprout post-fire, ectomycorrhizal fungi could survive fires inside their plant host's roots (Pausas and Bradstock, 2007). It could also indicate quick recovery post-fire, as ectomycorrhizal species can germinate quickly from heat-resistant or heat-stimulated spores to take advantage of reduced competition (Glassman et al.,

2016). Alternatively, it could point to limited effects of fire on soil in this environment, because of low soil moisture in semi-arid soils reducing the amount of heat transferred to soils and low plant biomass reducing fire severity, and soil property alterations post-fire can be minimal or short-lived because of nutrient poor soils (Allen et al., 2011, Fultz et al., 2016, Neary et al., 1999).

While fire did not influence ectomycorrhizal richness, distinct ectomycorrhizal communities arose under different post-fire successional stages and fire frequency classes, and several ectomycorrhizal ASVs showed strong associations to particular time-since-fire ages and fire frequencies. This may also reflect the relationship between ectomycorrhizal fungi species and their plant hosts (Hart et al., 2005, Rodríguez-Echeverría et al., 2016). As plant composition changes along the post-fire temporal axis and under differing fire frequencies (Pausas and Bradstock, 2007, Clarke et al., 2010, Gosper et al., 2012b), ectomycorrhizal species that are host-specific (Lofgren et al., 2018) may undergo changes (Hart et al., 2005). Simultaneously, changes in ectomycorrhizal composition between time-since-fire ages and fire frequencies could have implications for plant productivity (Anthony et al., 2022), plant composition (Albornoz et al., 2016), and biogeochemical cycles (Averill and Hawkes, 2016, Zak et al., 2019) because ectomycorrhizal species vary in their nutrient acquisition abilities (Leake, 2001, Zak et al., 2019).

Of the trophic fungal guilds, saprotrophs were the most impacted by fire, directly and indirectly, through mediated interactions between fire and substrates. Directly, saprotrophic richness declined shortly after fire, likely due to fire heating the soil to lethal temperatures, killing non-pyrophilous species (Klopatek et al., 1988, Neary et al., 1999). Saprotrophs may be particularly vulnerable to fire because of their position in the environment (i.e., shallower soil depths) (Fernandez and Kennedy, 2016) and position in substrates (Bowd et al., 2022, McMullan-Fisher et al., 2002). For example, litter dwelling saprotrophs could be killed by fire as fire often consumes litter (Bowd et al., 2022, McMullan-Fisher et al., 2011, Haslem et al., 2010). As time-since-fire progresses, saprotrophic richness may increase as species recolonise sites from surviving spores and hyphal fragments or dispersal from adjacent sites (Claridge et al., 2009, Glassman et al., 2016, Pattinson et al., 1999). Temporal variation in saprotrophic species returning may be driven by return rates of substrates and their decay along the post-fire succession axis

(Burton et al., 2021, Haslem et al., 2010), and the competitive interactions that ensue (Fernandez and Kennedy, 2016, Mäkipää et al., 2017, Yang et al., 2021a). For example, saprotrophs can prefer specific types of wood and decay states that may not return to a site until late-succession (Gates et al., 2011, Wardlaw et al., 2009, Yang et al., 2021a). Fire frequency did not directly affect saprotrophic richness, suggesting that saprotrophs are more vulnerable to changes in substrates under differing fire frequencies than the direct effects of re-occurring fires (Mäkipää et al., 2017, Yang et al., 2021a).

Saprotrophs can be particularly sensitive to the indirect effects of time-since-fire and fire frequency because of their reliance on substrates, which are often removed or altered by fire (Alem et al., 2020, O'Dea, 2007, Haslem et al., 2010). For example, our study species decompose dung, nectar, pollen, litter, soil, and wood, which can be entirely consumed or altered by fires (Haslem et al., 2010). The build-up of both elevated dead (Burrows et al., 2021, Gosper et al., 2012b) and coarse woody debris (Haslem et al., 2010) as vegetation complexity increases along the post-fire successional axis aligns with other studies. Decreases in coarse woody debris under frequent fires contrasts our assumption, however it has been reported elsewhere, attributed to low intensity fires, reduced potential of debris burning because of regular charring, and increased debris from repeatedly burnt re-sprouting plants (Whitford and McCaw, 2019). The mechanisms underlying the negative effects of high elevated dead and coarse woody debris cover on saprotrophic richness are not clear, but may have similar explanations to the response of total fungal richness; competition between species as substrates build up (Bödeker et al., 2016, Künzler, 2018) or that aboveground debris is not an accurate substrate measurement for soil-inhabiting saprotrophs (Mäkipää et al., 2017). Opposing direct and indirect effects of time-since-fire on saprotrophs suggests that complex interactions could be overlooked if the flow on effects of fire through ecosystems are not explored.

Saprotrophic fungi are key regulators of decomposition, nutrient cycling, and nutrient distribution in ecosystems (Guhr et al., 2015, Frac et al., 2018), but photodegradation can also play an important role in semi-arid environments (Austin and Vivanco, 2006). As saprotrophs demonstrate functional diversity and different preferences for substrates and decay rates (Gates et al., 2011, Yang et al., 2021a), reduced saprotrophic richness in early successional stages and under high fire frequencies could alter decomposition rates and the distribution of water and nutrients throughout soils (Guhr et al., 2015). This could

have large implications for soil and plant communities and the behaviour of future fires through altered fuel loads.

Frequent fires indirectly reduced pathogenic richness, in contrast to other studies (Bär et al., 2019, Beals et al., 2022). Pathogenic richness declined under high fire frequencies because coarse woody debris cover increased under frequent fires, which reduced saprotrophic richness (discussed above), which increased pathogenic richness. This could reflect true ecological responses (Chen et al., 2020, Lekberg et al., 2021) as saprotrophs excrete anti-fungal properties (Kepler et al., 2017, Lekberg et al., 2021). Alternatively, the relationship could be causal (i.e., similar underlying drivers) because both saprotroph richness and pathogen richness declined under increasing total organic carbon and elevated dead cover. It is also important to note that under a third of our ASVs were assigned to guilds, and saprotrophs and pathogens can shift between lifestyles (e.g., 77 % of the plant pathogens in our study had the potential to switch to saprotrophs) (Veneault-Fourrey and Martin, 2011, Kuo et al., 2014). Reduced numbers of plant pathogen species under high fire frequencies could reduce plant disease and mortality, with profound implications on plant community structure and composition (Gilbert, 2002).

Ectomycorrhizal richness directly enhanced saprotrophic richness and indirectly enhanced pathogenic richness, through the interaction between ectomycorrhizas and saprotrophs. This directly contrasts the “Gadgil effect”, which suggests that ectomycorrhizal fungi reduce saprotrophic richness through direct competition, releasing antibiotics, altering soil properties, and parasitising on saprotrophs (Gadgil and Gadgil, 1971, Fernandez and Kennedy, 2016). The “Gadgil effect” is thought to be more pronounced in arid environments because soils are nutrient poor and have low soil moisture (Fernandez and Kennedy, 2016). Here, we find that diverse ectomycorrhizal fungal communities can enhance the diversity of saprotrophic species (Yang et al., 2021b) even in semi-arid ecosystems. Ectomycorrhizal fungi can create beneficial environments for saprotrophs by mineralising nutrients, translocating nutrients between different substrates, and increasing the amount of decaying matter in soils (Lindahl et al., 2002, Yang et al., 2021b).

While it is important to recognise the limitations of eDNA in profiling fungal communities (Carini et al., 2016), we found that distinct fungal community assemblages and distinct

assemblages of ectomycorrhizal, saprotrophic, and pathogenic species can arise under different post-fire successional stages and fire frequency classes (Anderson et al., 2007, Berglund et al., 2011). Importantly, this suggests that pyrodiverse landscapes, which have a diversity of temporal and spatial fire histories, could be important in maintaining diverse fungal communities, by creating a higher diversity of niches to suit a higher diversity of species needs (Fox et al., 2022, Martin and Sapsis, 1992).

We shed new light on the importance of fire in shaping fungal communities in south-eastern Australia's semi-arid heathlands. We highlight that exploring fungal guilds can be more insightful than simply exploring the response of all fungal species to fire and that fungal guilds can respond differently to time-since-fire and fire frequency. Importantly, the direct and indirect effects of fire can have opposing effects on fungal communities, suggesting that understanding the complex responses of fungal communities to fire can be improved by exploring how the effects of fire flow through ecosystems. Finally, we highlight that distinct fungal communities can arise under differing combinations of post-fire successional stages and fire frequency classes, which suggests that pyrodiverse landscapes may be important in maintaining diverse fungal communities in these ecosystems.

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Chapter six: Summary

Chapters two, three, and four

Fire ecologists and managers are still grappling with how best to apply fire in fire-prone areas to maintain and promote diversity (Driscoll et al., 2010, Fox et al., 2022, He et al., 2019, Kelly et al., 2020). This is further complicated by fire regimes rapidly departing from their historical patterns because of the compounding effects of climate change, landscape degradation, and the displacement of Indigenous people and their fire regimes (Driscoll et al., 2010, Fletcher et al., 2021b, Kelly et al., 2020). The role that people have played in shaping historical fire regimes (Ellis et al., 2021a) and the implications of this for species and ecological communities continues to build (Hoffman et al., 2021). Understanding how Indigenous people shape fire regimes and how species and ecological communities respond to their fire regimes offer solutions to improve fire management and biodiversity conservation. In this thesis, I have contributed towards understanding the important role of Indigenous fire regimes in maintaining and enhancing plant diversity. I hope that this work will serve as an important case-study of the vital importance of people to landscapes in Australia and around the world.

In **chapter two**, I examined how Indigenous fire regimes influenced visible and invisible fire mosaics in Australia's western deserts. I calculated how long it would take Martu to travel from their communities to each of the study landscapes (used as a proxy for land-use intensity) and explored how differing travel times influenced several measurements of the visible and invisible fire mosaic. I found that Martu fire regimes profoundly transformed landscapes into fine-scale pyrodiverse landscapes with high diversities of time-since-fire ages, fire frequency patches, and unique combinations of fire histories (seasons, interval lengths, and time-since-fire ages), compared to landscapes under lightning fire regimes. I also found that these pyrodiverse landscapes reduced the size of fires. While several studies around the world show that Indigenous burning increases diversity in the visible fire mosaic (Roos et al., 2021, Sheuyange et al., 2005, Trauernicht et al., 2015) and indicate that Indigenous burning can reduce fire size (Bliege Bird et al., 2012), a key result is that Indigenous burning substantially increases diversity in the invisible fire mosaic.

In **chapter three**, I built on my second chapter by examining how plant communities responded to time-since-fire and fire frequency in the semi-arid spinifex grasslands of Australia's western deserts. I explored how several plant richness and diversity variables (including edible plants) and vegetation structure responded to time-since-fire and fire frequency, and how plant composition differed between post-fire successional stages and fire frequency classes. By investigating edible plant groups, I was able to explore the long-standing "fire-stick farming" hypothesis, that burning increases the availability of food plants for Indigenous people (Jones, 1969, Gould, 1971). Aligned with other studies in spinifex grasslands, I found that fire was a strong driver of plant communities, and that spinifex played a key role, with patterns largely following the "initial floristic composition" model (Burrows et al., 2020, Egler, 1954, Wright and Clarke, 2007). A key result, consistent with the "fire-stick farming" hypothesis, was that burning enhanced the productivity of areas for Indigenous people; edible plant richness peaked shortly after fire and frequent fires enhanced the availability of edible plants (Jones, 1969, Gould, 1971). Importantly, by linking my results from **chapter one**, which suggested that Martu increase the frequency that landscapes are burnt, I highlight that Martu fire regimes enhance the availability of edible plants. Additionally, consistent with the Martu model of post-fire succession, I found that distinct plant communities arose under differing post-fire successional stages and fire frequency classes, providing hypotheses for chapter four.

In **chapter four**, I investigated the ecological implications of chapter two by exploring whether pyrodiversity maintained by Indigenous people promoted plant richness and diversity in semi-arid spinifex grasslands. I explored how plant richness and diversity differed across landscapes that ranged from highly pyrodiverse under active Indigenous burning, in both visible and invisible fire diversity, to more coarse-scale and less diverse mosaics under lightning fire regimes. A key result from this chapter is that Indigenous created pyrodiversity increases plant diversity. While adding support for the "pyrodiversity begets biodiversity" hypothesis (Jones and Tingley, 2021, Martin and Sapsis, 1992), my results highlight the importance of considering the historical levels of pyrodiversity, which in many cases are those created by Indigenous burning, and the configuration and extent of post-fire successional stages (Bliege Bird et al., 2018, Parr and Andersen, 2006, Taylor et al., 2012). Additionally, I found that plant diversity declined with increasing extent of landscape burnt. By linking my results from **chapter**

two, that suggest that Martu reduce the size of fires, I further highlight the importance of Indigenous burning in maintaining diverse plant communities.

Collectively, my results from **chapters two, three, and four** suggest that by increasing the frequency that landscapes are burnt, increasing visible and invisible fire diversity, and reducing fire size, Indigenous people enhance plant diversity and the productivity of landscapes for people (Fig. 4.7). My results contribute to the global building narrative of the importance of Indigenous fire regimes in maintaining biodiversity by aligning with the historical fire regimes that species evolved under and reducing fire size (Ellis et al., 2021a, Garnett et al., 2018, Hoffman et al., 2021). This has large and wide-reaching implications and further supports the idea that the displacement of Indigenous people and the cessation of their fire regimes has contributed to species decline and loss across the globe (Liebmann et al., 2016, Woinarski et al., 2015). Global biodiversity continues to decline (Tilman et al., 2017), with 15 % of species declines attributed to inappropriate fire regimes (Kelly et al., 2020). Fire regimes continue to rapidly depart from historical patterns (Ellis et al., 2021b), with the displacement of Indigenous people and their fire regimes likely playing a major role (Burrows et al., 2006a, Fletcher et al., 2021a, Stambaugh et al., 2018). Indigenous-led burning could offer solutions to restoring appropriate fire regimes, limiting fire size, conserving global biodiversity, and concurrently provide important benefits for Indigenous community wellbeing (Ansell and Evans, 2019, Hoffman et al., 2021, Millhauser and Earle, 2022).

Chapter five

We have a limited understanding of how to apply fire to maintain diverse semi-arid fungal communities (Fox et al., 2022). Understanding the responses of fungal communities to fire patterns across different ecosystems and in the long-term is key, given the functional roles that fungi play within ecosystems, including in post-fire environments (Claridge et al., 2009, Dove et al., 2022, Wagg et al., 2014). In this thesis, I have increased our understanding of how fire regimes shape semi-arid fungal diversity and composition.

In **chapter five**, I investigated how the direct and indirect effects of time-since-fire and fire frequency influenced total fungal richness and the richness of ectomycorrhizas, saprotrophs, and plant pathogens in the semi-arid heathlands of south-eastern Australia. Additionally, I explored how fungal composition differed across post-fire successional stages and fire frequency classes. A key result was that saprotrophic richness was

particularly impacted by fire, but that direct and indirect effects had opposing impacts, highlighting the importance of exploring the flow on effects of fire through ecosystems. Additionally, I found that distinct fungal communities arose under different post-fire successional stages and fire frequency classes, with substantial differences in ectomycorrhizal species composition. This suggests that pyrodiversity could be important for maintaining diverse fungal communities in semi-arid heathlands, an important question for future research.

Research from my final chapter describes the highly diverse soil microbiome of the semi-arid heathlands of the Little Desert National Park and provides new insight into the role of fire in shaping these fungal communities (Allen et al., 2011, Neary et al., 1999, Peterson et al., n.d.). While fire is routinely applied across semi-arid areas to maintain diversity in aboveground ecosystems, the responses of fungal communities are largely unknown and rarely considered. Integrating fungi into future fire management planning and post-fire studies is crucial to ensure appropriate fire regimes to maintain and promote diverse fungal communities (May and McMullan-Fisher, 2012), as well as diverse and productive aboveground communities (Claridge et al., 2009, Dove et al., 2022, Wagg et al., 2014).

Appendix A: Supplementary material for chapter two

Table S2.1 Model selection for the most appropriate rainfall variables to include for each landscape response variable. Models included all predictor variables, i.e., travel time from Martu communities, proportion of spinifex sandplain, proportion of claypans and lakes, and the interaction between travel time and rainfall, as well as a varying rainfall variable. Model: the rainfall variable included in the model, AICc: model rank, ΔAICc : difference between top model and described model, w_i : Akaike weight (i.e., the likelihood of the model being the best in the candidate set).

Landscape response variable	Model	AICc	ΔAICc	w_i
Number of years burnt	3-year rain	20985.60	0.00	1
	2-year rain	21155.20	169.60	0
	15-year rain	21240.69	255.09	0
	1-year rain	21242.55	256.95	0
	Coefficient in 15-year rainfall	21270.03	284.43	0
Diversity of time since fire patches	3-year rain	-586.59	0.00	1
	2-year rain	-471.90	114.68	0
	1 year rain	-408.05	178.54	0
	15-year rain	-403.52	183.07	0
	Coefficient in 15-year rainfall	-373.41	213.18	0
Diversity of fire frequency patches	3-year rain	-1671.61	0.00	1
	15-year rain	-1603.84	67.73	0
	2-year rain	-1478.70	192.89	0
	1 year rain	-1364.58	307.01	0
	Coefficient in 15-year rainfall	-1331.47	340.11	0
Number of unique fire histories	3-year rain	41433.42	0.00	1
	Coefficient in 15-year rainfall	41786.70	953.41	0
	2-year rain	41796.29	1069.85	0
	15-year rain	41813.01	1611.20	0
	1-year rain	41917.80	1682.35	0

Table S2.2 Estimated model coefficients from models with substantial support (i.e., $w_i < 2$) for each landscape response variable. Est: estimate, SE: standard error of parameter estimates, CI: 95 % confidence intervals (significance indicated by no overlap with 0).

Landscape response variable	Model	Predictor variable	Est	SE	CI
Number of years burnt	time + rain	Log (travel time)	-0.60	0.03	-0.66 – -0.55
	+ claylake	Cumulative 3-year rain	0.13	0.01	0.11 – 0.14
	+ claylake	Claypan and lake	-0.11	0.03	-0.16 – -0.06
	time*rain	Travel time*rain	-0.03	0.01	-0.05 – -0.02
	time + rain	Log (travel time)	-0.60	0.03	-0.66 – -0.55
Diversity of time-since-fire patches	+ spinifex + claylake + time*rain	Cumulative 3-year rain	0.13	0.01	0.11 – 0.14
	+ spinifex + claylake + time*rain	Spinifex sandplain	0.12	0.03	-0.07 – 0.04
	+ spinifex + claylake + time*rain	Claypan and lake	-0.12	0.03	-0.17 – -0.06
	+ spinifex + claylake + time*rain	Travel time*rain	-0.03	0.01	-0.05 – -0.02
	time + rain	Log (travel time)	-0.18	0.01	-0.21 – -0.15
	+ spinifex + claylake	Cumulative 3-year rain	0.04	0.00	0.04 – 0.05
	+ spinifex + claylake	Spinifex sandplain	-0.02	0.01	-0.05 – 0.01
	+ spinifex + claylake	Claypan and lake	-0.04	0.01	-0.07 – -0.01

	time + rain + claylake	Log (travel time)	-0.19	0.01	-0.22 – -0.16
		Cumulative 3-year rain	0.04	0.00	0.04 – 0.05
		Claypan and lake	-0.03	0.01	-0.06 – -0.01
	time + rain + spinifex + claylake + time*rain	Log (travel time)	-0.18	0.02	-0.21 – -0.16
		Cumulative 3-year rain	0.04	0.00	0.04 – 0.05
		Spinifex sandplain	-0.02	0.01	-0.05 – 0.01
		Claypan and lake	-0.04	0.02	-0.07 – -0.01
		Travel time*rain	0.00	0.00	-0.00 – 0.01
	time + rain + claylake + time*rain	Log (travel time)	-0.19	0.01	-0.21 – -0.16
		Cumulative 3-year rain	0.04	0.00	0.04 – 0.05
		Claypan and lake	-0.03	0.01	-0.06 – -0.01
		Travel time*rain	0.00	0.00	-0.00 – 0.01
	time + rain + claylake	Log (travel time)	-0.16	0.01	-0.18 – -0.14
		Cumulative 3-year rain	0.05	0.00	0.04 – 0.05
		Claypan and lake	-0.06	0.01	-0.08 – -0.04
Diversity of fire frequency patches	time + rain + claylake + time*rain	Log (travel time)	-0.16	0.01	-0.18 – -0.13
		Cumulative 3-year rain	0.05	0.00	0.04 – 0.05
		Claypan and lake	-0.06	0.01	-0.08 – -0.04
	time + rain + spinifex + claylake	Log (travel time)	-0.16	0.01	-0.18 – -0.14
		Cumulative 3-year rain	0.05	0.00	0.04 – 0.05
		Spinifex sandplain	0.01	0.01	-0.02 – 0.03
		Claypan and lake	-0.06	0.01	-0.08 – -0.04
	time + rain + spinifex + claylake	Log (travel time)	-0.55	0.03	-0.60 – -0.50
		Cumulative 3-year rain	0.11	0.02	0.10 – 0.11
		Spinifex sandplain	0.04	0.03	-0.01 – 0.09
		Claypan and lake	-0.14	0.03	-0.19 – -0.09
Number of unique fire histories	time + rain + claylake	Log (travel time)	-0.55	0.03	-0.60 – -0.50
		Cumulative 3-year rain	0.11	0.02	0.10 – 0.11
		Claypan and lake	-0.15	0.03	-0.20 – -0.10
	time + rain + spinifex + claylake + time*rain	Log (travel time)	-0.56	0.03	-0.60 – -0.50
		Cumulative 3-year rain	0.11	0.01	0.10 – 0.11
		Spinifex sandplain	0.04	0.03	-0.01 – 0.09
		Claypan and lake	-0.14	0.03	-0.20 – -0.10
		Travel time * rain	0.01	0.01	-0.01 – 0.01

Additional analysis to investigate how travel time from Martu communities influences the proportion of each successional stage.

We calculated the proportional cover of each Martu successional stage—*nyurnma* (0 – 6 months post-fire), *nyukura* (6 months – 5 years post-fire), *manguu* (5 – 10 years post-fire), and *kunarka* (10 + years post-fire)—to investigate how travel time (hours) from Martu communities influenced the proportion of young and old patches within pyrodiverse landscapes. We chose to omit *waru waru* as its dependence on the timing of rainfall resulted in significant temporal overlap with *nyukura*. To calculate the proportion of each successional stage for each landscape, we defined fire polygons by their time-

since-fire age, assigned each patch to each successional stage, and then summed their cover for each landscape.

The cover of successional stages was proportional and followed a binomial distribution, so we fitted generalised linear mixed models (GLMMs). First, we investigated which rainfall variable was most appropriate to retain in the models by creating a global model that included all predictor variables (i.e., travel time from Martu communities, proportion of spinifex sandplain, and proportion of claypans and lakes), 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. Next, for each successional stage response variable, we created a model candidate set with all combinations of the predictor variables. Models were deemed parsimonious and retained if they were within 2 AICc of the top model. To assess the significance of the predictor variables, we calculated the 95 % confidence intervals around the estimate, deeming variables important if the confidence intervals did not overlap zero. For all models we included landscape ID as a random effect to account for spatial (i.e., landscapes closer together may share more similarities than those further apart) and temporal effects (i.e., repeating landscapes over 13 temporal windows). The models for the proportion of *nyurnma* and *nyukura* were over dispersed, thus we included an additional random effect—the observation number (i.e., row number).

Table S2.3 Model selection for the most appropriate rainfall variables to include for each Martu successional stage response variable. Models included all predictor variables, i.e., travel time from Martu communities, proportion of spinifex sandplain, and proportion of claypans and lakes, as well as a varying rainfall variable. Model: the rainfall variable included in the model, AICc: model rank, ΔAICc : difference between top model and described model, w_i : Akaike weight (i.e., the likelihood of the model being the best in the candidate set).

Successional stage	Model	AICc	ΔAICc	w_i
<i>Nyurnma</i> (0 – 6 months post-fire)	1-year rain	146.06	0.00	0.42
	3-year rain	147.10	1.04	0.25
	2-year rain	147.54	1.48	0.20
	15-year rain	149.13	3.07	0.09
	Coefficient in 15-year rainfall	151.37	5.32	0.03
<i>Nyukura</i> (6 months – 5 years post-fire)	3-year rain	889.82	0.00	1
	2-year rain	915.86	26.04	0
	15-year rain	916.79	26.97	0
	Coefficient in 15-year rainfall	925.20	35.38	0
	1-year rain	925.41	35.59	0
	1-year rain	6043.39	0.00	1

	2-year rain	6122.78	79.39	0
<i>Manguu</i> (5 – 10 years post-fire)	Coefficient in 15-year rainfall	6159.98	116.59	0
	3-year rain	6161.90	118.51	0
	15-year rain	6161.97	118.57	0
	1-year rain	4692.52	0.00	1
<i>Kunarka</i> (10 + years post-fire)	2-year rain	4735.38	42.86	0
	3-year rain	4775.46	82.95	0
	Coefficient in 15-year rainfall	4804.50	111.98	0
	15-year rain	4807.91	115.39	0

Table S2.4 Model selection for how travel time (hours) from Martu communities (time), rain (antecedent rainfall variable), percentage of spinifex sandplain (spinifex), and percentage of claypan and lake (claylake) effect the cover of Martu successional stages. AICc: model rank, ΔAICc : difference between top model and described model, w_i : Akaike weight (i.e., the likelihood of the model being the best in the candidate set), R^2 : model fit. Only models with $\Delta\text{AICc} \leq 2$ are shown.

Successional stage	Model	AICc	ΔAICc	w_i	R^2
<i>Nyurnma</i> (0 – 6 months post-fire) cover	time + rain	144.88	0.00	0.37	2%
	time + rain + claylake	146.33	1.45	0.18	2%
	time + rain + spinifex	146.68	1.80	0.15	2%
<i>Nyukura</i> (6 months – 5 years post-fire) cover	time + rain + spinifex + claylake	891.83	0.00	0.77	6%
<i>Manguu</i> (5 – 10 years post-fire) cover	time + rain + spinifex + claylake	6043.39	0.00	1.00	11%
<i>Kunarka</i> (10 + years post-fire) cover	time + rain + claylake	4691.31	0.00	0.65	12%
	time + rain + spinifex + claylake	4692.52	1.20	0.35	12%

Table S2.5 Estimated model coefficients from the models for each Martu successional stage. SE: standard error of parameter estimates, CI: 95 % confidence intervals (significance indicated by no overlap with 0), travel time: travel time (hours) from Martu communities, spinifex: percentage of spinifex sandplain, claypan and lake: percentage of claypan and lake.

Successional stage	Model	Predictor variable	Coefficient	SE	CI
<i>Nyurnma</i> (0 – 6 months post-fire) cover	time + rain	Travel time	0.69	0.26	0.17 – 1.18
		Cumulative 1 year rain	-0.80	0.36	-1.56 – -0.13
		Claypan and lake	-0.57	1.03	-4.76 – 0.42
	time + rain + claylake	Travel time	0.66	0.25	0.15 – 1.17
		Cumulative 1-year rain	-0.80	0.36	-1.56 – -0.13
		Claypan and lake	-0.57	1.03	-4.76 – 0.42
	time + rain + spinifex	Travel time	0.72	0.27	0.19 – 1.25
		Cumulative 1-year rain	-0.80	0.36	-1.50 – -0.09
		Spinifex sandplain	-0.16	0.34	-0.82 – 0.51
<i>Nyukura</i> (6 months – 5 years post-fire) cover	time + rain + spinifex + claylake	Travel time	0.49	0.10	0.29 – 0.69
		Cumulative 3-year rain	0.64	0.11	0.43 – 0.85
		Spinifex sandplain	-0.21	0.09	-0.39 – -0.02
		Claypan and lake	-0.91	0.49	-2.19 – -0.21
<i>Manguu</i> (5 – 10 years post-fire) cover	time + rain + spinifex + claylake	Travel time	-0.25	0.03	-0.32 – -0.19
		Cumulative 1-year rain	0.35	0.03	0.29 – 0.41
		Spinifex sandplain	0.16	0.03	0.10 – 0.22
		Claypan and lake	-0.53	0.04	-0.61 – -0.46
<i>Kunarka</i> (10 + years post-fire) cover	time + rain + claylake	Travel time	0.31	0.04	0.24 – 0.38
		Cumulative 1-year rain	-0.41	0.04	-0.49 – -0.34

	Claypan and lake	0.55	0.03	0.49 – 0.62
time + rain	Travel time	0.31	0.04	0.24 – 0.38
+ spinifex +	Cumulative 1-year rain	-0.41	0.04	-0.49 – -0.34
claylake	Spinifex sandplain	0.04	0.04	-0.04 – 0.12
	Claypan and lake	0.56	0.03	0.49 – 0.62

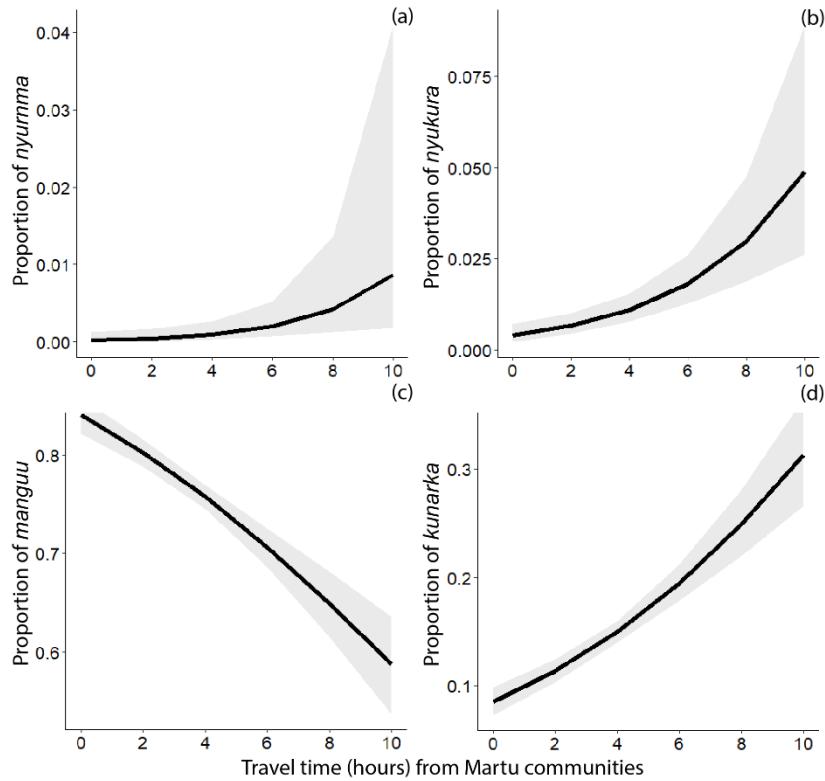


Figure S2.1 Relationship between travel time (hours) from Martu communities and proportion of (a) *nyurnma* (0 – 6 months post-fire), (b) *nyukura* (6 months – 5 years post-fire), (c) *manguu* (5 – 10 years post-fire), and (d) *kunarka* (10 + years post-fire). Black lines: fitted relationships derived from regression models, grey shading: 95 % confidence intervals.

Appendix B: Supplementary material for chapter three

Table S3.1 Model selection for the most appropriate rainfall variables to include for each plant response variable. TSF: time-since-fire, FF: fire frequency, TT: travel time (hours from Martu communities), AICc: model rank, ΔAICc : difference between top model and described model, w_i : Akaike weight (i.e., the likelihood of the model being the best in the candidate set).

Response variable	Predictor variables	AICc	ΔAICc	w_i
Species richness	TSF + FF + TT + 2YearRain	1116.80	0.00	0.29
	TSF + FF + TT + 1YearRain	1116.82	0.02	0.29
	TSF + FF + TT + 3YearRain	1117.43	0.63	0.21
	TSF + FF + TT + AverageRain	1117.52	0.72	0.20
Species diversity	TSF + FF + TT + 3YearRain	263.23	0.00	0.29
	TSF + FF + TT + 1YearRain	263.51	0.28	0.25
	TSF + FF + TT + 2YearRain	263.63	0.40	0.23
	TSF + FF + TT + AverageRain	263.68	0.45	0.23
Sub-shrub richness	TSF + FF + TT + AverageRain	880.35	0.00	0.49
	TSF + FF + TT + 3YearRain	882.05	1.70	0.21
	TSF + FF + TT + 2YearRain	882.36	2.01	0.18
	TSF + FF + TT + 1YearRain	883.02	2.67	0.13
Edible species richness	TSF + FF + TT + 1YearRain	679.16	0.00	0.46
	TSF + FF + TT + 3YearRain	680.94	1.78	0.19
	TSF + FF + TT + AverageRain	681.00	1.84	0.18
	TSF + FF + TT + 2YearRain	681.11	1.95	0.17
Edible sub-shrub presence	TSF + FF + TT + 1YearRain	223.09	0.00	0.51
	TSF + FF + TT + 2YearRain	224.54	1.45	0.25
	TSF + FF + TT + 3YearRain	224.95	1.86	0.20
	TSF + FF + TT + AverageRain	227.84	4.75	0.05
Edible shrub and tree richness	TSF + FF + TT + 2YearRain	528.96	0.00	0.31
	TSF + FF + TT + 1YearRain	529.03	0.07	0.30
	TSF + FF + TT + 3YearRain	529.11	0.15	0.29
	TSF + FF + TT + AverageRain	530.96	2.00	0.01
Grass cover	TSF + FF + AverageRain	1042.15	0.00	0.60
	TSF + FF + 1YearRain	1045.02	2.87	0.14
	TSF + FF + 3YearRain	1045.08	2.94	0.14
	TSF + FF + 2YearRain	1045.32	3.17	0.12
Low spinifex cover	TSF + FF + 3YearRain	1322.91	0.00	0.34
	TSF + FF + 2YearRain	1323.01	0.10	0.32
	TSF + FF + 1YearRain	1323.19	0.19	0.30
	TSF + FF + AverageRain	1327.26	4.35	0.04
High spinifex cover	TSF + FF + 1YearRain	777.14	0.00	0.38
	TSF + FF + 3YearRain	777.90	0.77	0.26
	TSF + FF + TT + 2YearRain	778.13	0.99	0.23
	TSF + FF + TT + AverageRain	779.26	2.12	0.13
Shrub and tree cover	TSF + FF + 1YearRain	1176.51	0.00	0.35
	TSF + FF + 3YearRain	1177.30	0.79	0.23
	TSF + FF + AverageRain	1177.34	0.83	0.23
	TSF + FF + 2YearRain	1177.70	1.19	0.19

Table S3.2 Model selection for effect of time-since-fire (TSF), fire frequency (FF), travel time from Martu communities (TT), and one of four antecedent rainfall variables on plant response variables. Model: whether TSF and FF were included as main effects or an interaction, AICc: model rank, ΔAICc : difference between top model and described model, w_i : Akaike weight (i.e., the likelihood of the model being the best in the candidate set), R^2 : model fit.

Response variable	Predictor variables	Model	AICc	ΔAICc	w_i	R^2
Species richness	TSF + FF + TT	Main effects	1115.36	0.00	1.00	32%
		Interaction	1149.53	34.17	0.00	20%
Species diversity	TSF + FF + TT	Main effects	257.54	0.00	1.00	32%
		Interaction	277.39	19.85	0.00	24%
Sub-shrub richness	TSF + FF + TT	Main effects	881.17	0.00	0.63	26%
		Interaction	882.27	1.10	0.37	26%
Edible species richness	TSF + FF + TT	Main effects	677.12	0.00	0.91	21%
		Interaction	681.63	4.51	0.09	18%
Edible sub-shrub presence	TSF + FF + TT + 1YearRain	Main effects	223.09	0.00	0.96	13%
		Interaction	229.64	6.55	0.04	12%
Edible shrub and tree richness	TSF + FF + TT	Interaction	528.93	0.00	0.51	18%
		Main effects	529.04	0.11	0.49	9%
Grass cover	TSF + FF	Main effects	1043.31	0.00	1.00	15%
		Interaction	1079.61	36.30	0.00	13%
Low spinifex cover	TSF + FF + 3YearRain	Main effects	1322.91	0.00	0.85	66%
		Interaction	1326.36	3.45	0.15	67%
High spinifex cover	TSF + FF + 1YearRain	Interaction	774.65	0.00	0.78	58%
		Main effects	777.14	2.49	0.22	54%
Shrub and tree cover	TSF + FF	Main effects	1158.07	0.00	0.96	19%
		Interaction	1163.70	5.63	0.06	18%

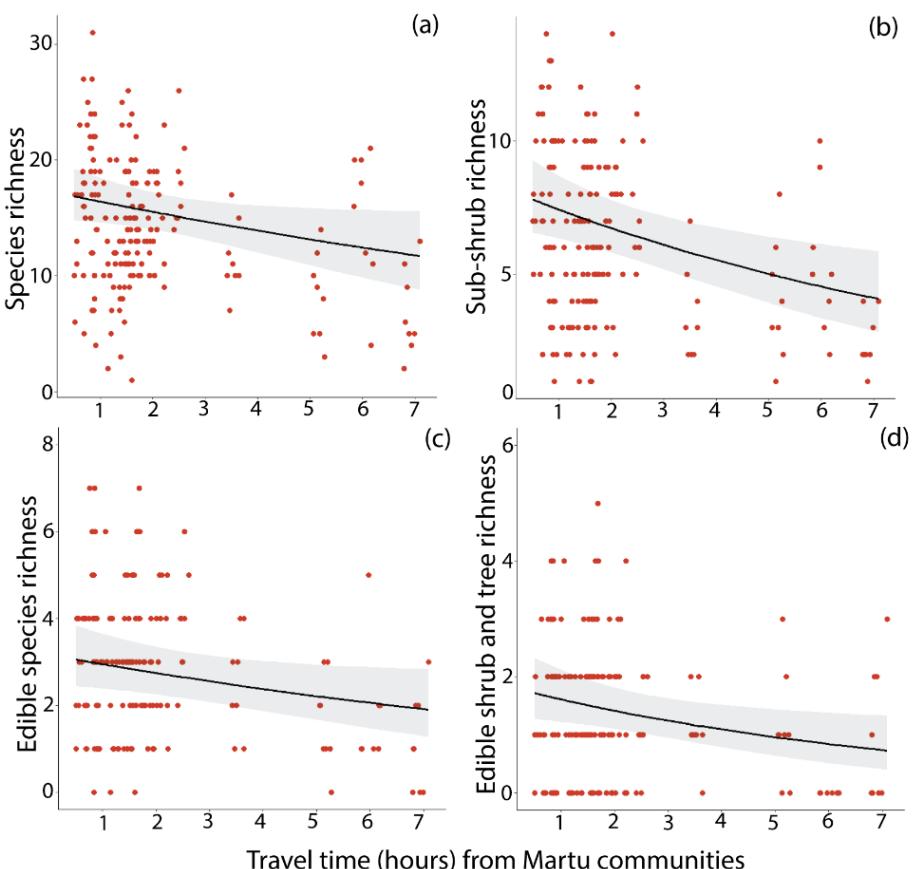


Figure S3.1 The effect of travel time (hours) from Martu communities on (a) species richness, (b) sub-shrub richness, (c) edible species richness, and (d) edible shrub and tree richness. Red dots: observed data, black lines: model predictions, grey shading: 95 % confidence intervals.

Table S3.3 Goodness of fit of time-since-fire, successional stages, fire frequency, and fire frequency classes on plant species composition based on the *envfit* function using NMDS plots.

Predictor	R ²	p-value
Time-since-fire	12%	0.001
Successional stages	19%	0.001
Fire frequency	1%	0.585
Fire frequency classes	1%	0.262

Appendix C: Supplementary material for chapter four

Table S4.1 The spread of travel time (hours) from Martu communities, diversity of time-since-fire patches (H'), and diversity of fire frequency patches (H'), for each of our study landscapes. Green: high values, white: moderate values, red: low values within each separate category.

Landscape	Travel time	Time-since-fire diversity	Fire frequency diversity
158	3.59	0.56	0.70
201	1.27	1.32	1.52
235	0.89	1.76	1.44
237	1.91	1.43	1.35
254	2.59	1.60	1.44
287	0.87	2.08	1.53
304	2.09	0.96	1.08
311	1.15	1.39	1.32
312	0.66	0.38	1.86
323	6.96	0.81	0.92
326	1.74	1.46	1.14
327	1.64	1.04	1.28
337	1.58	1.50	1.30
355	0.77	1.54	1.13
370	6.05	1.05	0.90
379	0.96	2.01	1.34
411	0.90	0.54	1.11
414	1.55	1.44	1.51
435	1.63	0.88	1.01
437	2.16	0.77	1.08
438	1.63	1.85	1.27
447	5.25	0.43	1.05
452	1.48	1.18	1.39

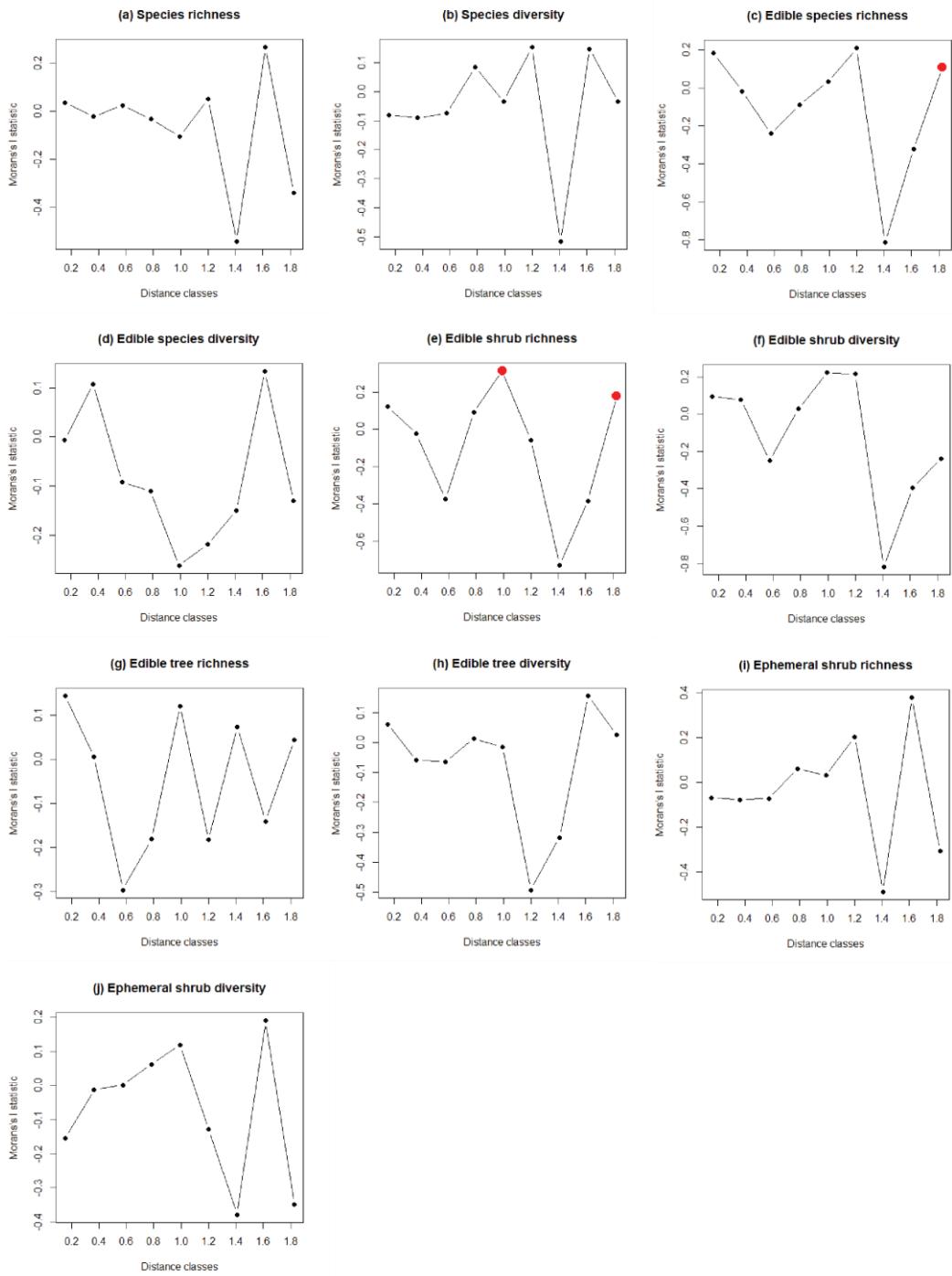


Figure S4.1 Correlograms of model residuals based on Moran's I statistic indicating level of spatial autocorrelation between landscapes for: (a) species richness, (b) species diversity (in terms of Shannon's diversity index H'), (c) edible species richness, (d) edible species diversity (H'), (e) edible shrub richness, edible shrub diversity (H'), (f) edible tree richness, (g) edible tree diversity (H'), (h) ephemeral shrub richness, and (i) ephemeral shrub diversity (H'). Significance (i.e., $p < 0.05$) indicated by red points.

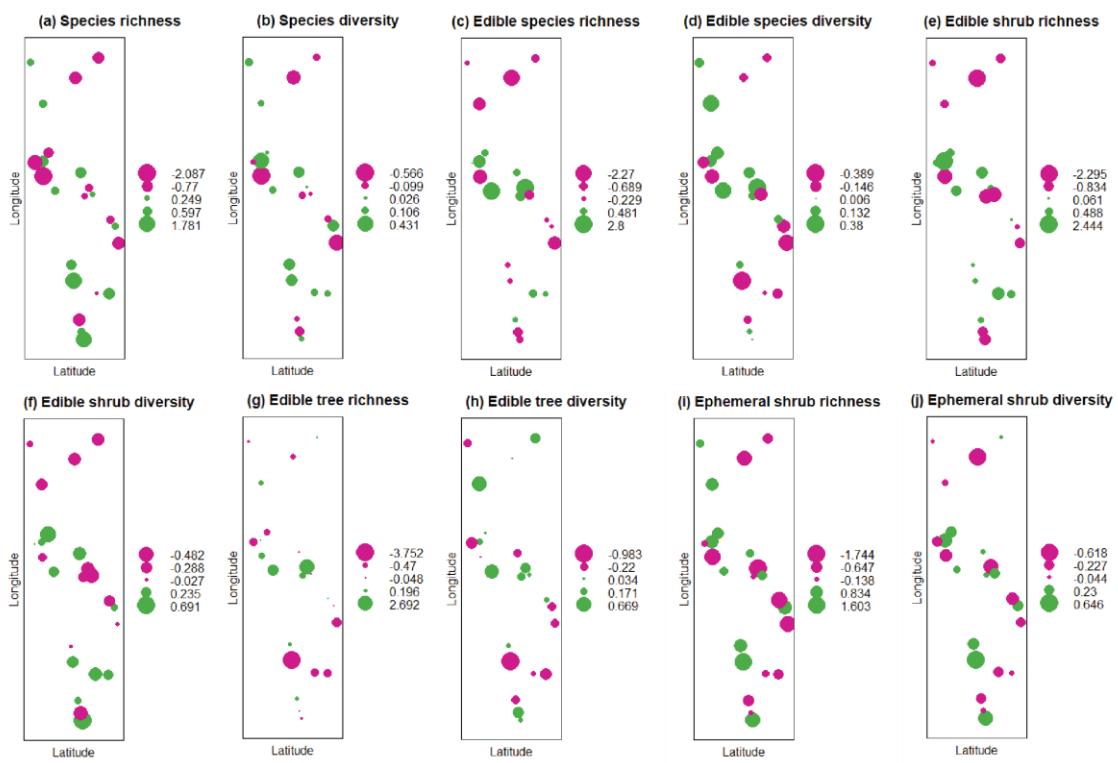


Figure S4.2 Bubble plots of model residuals indicating level of spatial autocorrelation between landscapes for: (a) plant richness, (b) plant diversity (in terms of Shannon's diversity index H'), (c) edible species richness, (d) edible species diversity (H'), (e) edible sub-shrub richness, edible sub-shrub diversity (H'), (f) edible shrub and tree richness, (g) edible shrub and tree diversity (H'), (h) sub-shrub richness, and (i) sub-shrub diversity (H').

Table S4.2 Model selection for the most appropriate rainfall variables to retain for each plant response variable. Rainfall variable: the rainfall variable included in the global model. AICc: model rank, ΔAICc : difference between top model and described model, w_i : Akaike weight (i.e., the likelihood of the model being the best in the candidate set). Only models within $2 \Delta\text{AICc}$ are shown.

Plant response variable	Rainfall variable	AICc	ΔAICc	w_i
Plant richness	Average annual rainfall	173.44	0.00	0.38
	Cumulative 1-year rainfall	173.79	0.35	0.32
	Cumulative 2-year rainfall	175.13	1.69	0.16
	Cumulative 3-year rainfall	175.32	1.88	0.15
Plant diversity	Average annual rainfall	26.51	0.00	0.58
	Cumulative 2-year rainfall	28.34	1.82	0.23
	Cumulative 3-year rainfall	29.35	2.84	0.14
	Cumulative 1-year rainfall	31.67	5.15	0.04
Sub-shrub richness	Cumulative 2-year rainfall	161.93	0.00	0.28
	Average annual rainfall	161.99	0.07	0.27
	Cumulative 3-year rainfall	162.17	0.25	0.25
	Cumulative 1-year rainfall	162.73	0.80	0.19
Sub-shrub diversity	Cumulative 2-year rainfall	42.23	0.00	0.47
	Average annual rainfall	43.27	1.04	0.28

	Cumulative 3-year rainfall	44.63	2.39	0.14
	Cumulative 1-year rainfall	45.15	2.91	0.11
Edible species richness	Cumulative 3-year rainfall	172.07	0.00	0.35
	Average annual rainfall	172.47	0.26	0.29
	Cumulative 1-year rainfall	173.05	0.72	0.21
	Cumulative 2-year rainfall	173.77	1.29	0.15
Edible species diversity	Cumulative 3-year rainfall	24.91	0.00	0.38
	Cumulative 2-year rainfall	25.67	0.76	0.26
	Cumulative 1-year rainfall	26.25	1.34	0.19
	Average annual rainfall	26.58	1.67	0.16
Edible sub-shrub richness	Cumulative 1-year rainfall	144.71	0.00	0.29
	Cumulative 3-year rainfall	145.09	0.30	0.24
	Cumulative 2-year rainfall	145.09	0.34	0.24
	Average annual rainfall	145.24	0.51	0.22
Edible sub-shrub diversity	Cumulative 2-year rainfall	47.54	0.00	0.42
	Cumulative 3-year rainfall	48.04	0.50	0.33
	Average annual rainfall	50.00	2.46	0.12
	Cumulative 1-year rainfall	50.02	2.48	0.12
Edible shrub and tree richness	Average annual rainfall	163.79	0.00	0.49
	Cumulative 2-year rainfall	165.81	1.39	0.18
	Cumulative 3-year rainfall	165.83	1.51	0.18
	Cumulative 1-year rainfall	166.03	1.57	0.16
Edible shrub and tree diversity	Cumulative 1-year rainfall	55.61	0.00	0.26
	Cumulative 3-year rainfall	55.63	0.02	0.26
	Average annual rainfall	55.83	0.22	0.24
	Cumulative 2-year rainfall	55.84	0.23	0.24

Table S4.3 Estimated model coefficients from models with substantial support (i.e., within $2 \Delta AICc$) for each plant response variable. Est: estimate, SE: standard error, CI: confidence intervals (significance signified by no overlap with 0).

Plant response variable	Model	Predictor variable	Est	SE	CI
Plant richness	TSFDiv + <i>nyukura</i> + spinifex + rain	Time-since-fire diversity	0.25	0.06	0.13 – 0.38
		<i>Nyukura</i>	0.14	0.04	0.07 – 0.21
		Spinifex sandplain	0.07	0.04	-0.01 – 0.14
		Average rainfall	-0.07	0.04	-0.15 – -0.01
Plant richness	TSFDiv + <i>nyukura</i> + rain	Time-since-fire diversity	0.26	0.06	0.13 – 0.38
		<i>Nyukura</i>	0.16	0.03	0.09 – 0.22
		Average rainfall	-0.10	0.03	-0.16 – -0.03
		Time-since-fire diversity	0.23	0.06	0.11 – 0.35
Plant diversity	TSFDiv + <i>nyukura</i> + spinifex	<i>Nyukura</i>	0.12	0.03	0.05 – 0.18
		Spinifex sandplain	0.09	0.04	0.03 – 0.16
		Max fire size	-0.14	0.06	-0.26 – -0.03
		<i>Nyukura</i>	0.25	0.06	0.13 – 0.37
	Fire size + <i>nyukura</i> + rain	Average rainfall	-0.14	0.06	-0.26 – -0.02
		Time-since-fire diversity	0.19	0.09	0.01 – 0.38

	<i>Nyukura</i>	0.17	0.09	0.07 – 0.27	
	Time-since-fire diversity	0.24	0.10	0.05 – 0.44	
	<i>Nyukura</i>	0.20	0.06	0.09 – 0.31	
	2-year rainfall	0.09	0.06	-0.02 – 0.20	
Sub-shrub richness	Time-since-fire diversity	0.19	0.09	0.01 – 0.38	
	<i>Nyukura</i>	0.16	0.05	0.06 – 0.26	
	Spinifex sandplain	0.08	0.05	-0.02 – 0.18	
	<i>Nyukura</i>	0.16	0.05	0.06 – 0.25	
	<i>Nyukura</i>	0.14	0.05	0.05 – 0.24	
	Spinifex sandplain	0.08	0.05	-0.22 – 0.18	
	Time-since-fire diversity	0.36	0.16	0.02 – 0.70	
	<i>Nyukura</i>	0.29	0.08	0.11 – 0.46	
	2-year rainfall	0.18	0.09	-0.01 – 0.37	
	Fire size + <i>nyukura</i>	Max fire size	-0.14	0.08	-0.31 – 0.03
Sub-shrub diversity	<i>Nyukura</i>	0.23	0.08	0.06 – 0.40	
	<i>Nyukura</i>	0.21	0.08	0.04 – 0.38	
	FFDiv + <i>nyukura</i>	Fire frequency diversity	0.51	0.34	-0.20 – 1.22
	<i>Nyukura</i>	0.16	0.08	-0.02 – 0.34	
	TSFDiv + <i>nyukura</i>	Time-since-fire diversity	0.24	0.16	-0.09 – 0.58
	<i>Nyukura</i>	0.21	0.08	0.04 – 0.38	
	FFDiv + <i>nyukura</i> + rain	Fire frequency diversity	0.62	0.33	-0.07 – 1.32
	<i>Nyukura</i>	0.21	0.08	0.02 – 0.40	
	2-year rainfall	0.15	0.09	-0.04 – 0.39	
	Fire size + <i>nyukura</i> + rain	Max fire size	-0.14	0.08	-0.31 – 0.02
Edible species richness	<i>Nyukura</i>	0.28	0.08	0.10 – 0.46	
	2-year rainfall	0.12	0.09	-0.06 – 0.30	
	FFDiv	Fire frequency diversity	0.75	0.33	0.06 – 1.44
	TSFDiv + FFDiv + <i>nyukura</i> + rain	Time-since-fire diversity	0.28	0.17	-0.08 – 0.64
		Fire frequency diversity	0.42	0.34	-0.31 – 1.13
		<i>Nyukura</i>	0.25	0.08	0.06 – 0.44
		2-year rainfall	0.19	0.09	0.01 – 0.37
	Spinifex + rain	Spinifex sandplain	0.16	0.06	0.03 – 0.29
		3-year rainfall	-0.12	0.06	-0.24 – -0.01
	<i>Nyukura</i>	<i>Nyukura</i>	0.12	0.07	-0.01 – 0.24
	<i>Kunarka</i> + spinifex + rain	<i>Kunarka</i>	-0.10	0.06	-0.21 – 0.02
		Spinifex sandplain	0.18	0.06	0.06 – 0.30
		3-year rainfall	-0.12	0.06	-0.23 – -0.01
	Spinifex	Spinifex sandplain	0.12	0.07	-0.01 – 0.25
	<i>Nyukura</i> + spinifex	<i>Nyukura</i>	0.11	0.06	-0.01 – 0.23
		Spinifex sandplain	0.14	0.07	0.01 – 0.27
	<i>Nyurnma</i> + rain	<i>Nyurnma</i>	-0.14	0.06	-0.27 – -0.02
		3-year rainfall	-0.12	0.06	-0.24 – 0.01
	<i>Nyurnma</i>	<i>Nyurnma</i>	-0.11	0.07	-0.24 – 0.02
	<i>Kunarka</i> + spinifex	<i>Kunarka</i>	-0.10	0.06	-0.22 – 0.02
		Spinifex sandplain	0.10	0.06	-0.02 – 0.23
	TSFDiv + <i>kunarka</i> + spinifex	Time-since-fire diversity	0.22	0.12	-0.01 – 0.45
		<i>Kunarka</i>	-0.13	0.06	-0.25 – -0.01
		Spinifex sandplain	0.14	0.06	0.03 – 0.26

	<i>Nyukura</i> + spinifex + rain	<i>Nyukura</i>	-0.04	0.06	-0.04 – 0.20
		Spinifex sandplain	0.14	0.06	0.02 – 0.27
		3-year rainfall	-0.11	0.06	-0.22 – 0.02
	TSFDiv + <i>nyukura</i>	Time-since-fire diversity	0.22	0.12	-0.01 – 0.45
		<i>Nyukura</i>	0.12	0.06	0.01 – 0.25
	<i>Nyurnma</i>	<i>Nyurnma</i>	-0.12	0.05	-0.22 – -0.01
Edible species diversity	<i>Nyurnma</i> + rain	<i>Nyurnma</i>	-0.14	0.05	-0.25 – -0.03
		3-year rainfall	-0.07	0.05	-0.19 – 0.03
	Fire size + <i>nyurnma</i> + rain	Max fire size	-0.05	0.05	-0.16 – 0.05
		<i>Nyurnma</i>	-0.13	0.05	-0.23 – -0.02
		3-year rainfall	-0.07	0.05	-0.19 – 0.03
Edible sub-shrub richness	<i>Kunarka</i>	<i>Kunarka</i>	-0.31	0.11	-0.54 – -0.09
	<i>Kunarka</i>	<i>Kunarka</i>	-0.12	0.08	-0.28 – 0.04
	<i>Nyukura</i>	<i>Nyukura</i>	0.12	0.08	-0.04 – 0.28
	Rain	2-year rainfall	-0.12	0.08	-0.28 – 0.04
Edible sub-shrub diversity	<i>Kunarka</i> + rain	<i>Kunarka</i>	-0.12	0.08	-0.28 – 0.03
		2-year rainfall	-0.12	0.08	-0.27 – 0.04
	TSFDiv + rain	Time-since-fire diversity	-0.19	0.16	-0.53 – 0.15
		2-year rainfall	-0.15	0.08	-0.32 – 0.02
	Max fire size + <i>kunarka</i>	Max fire size	0.08	0.08	-0.08 – 0.25
Edible shrub and tree richness	<i>Spinifex</i>	<i>Nyurnma</i>	-0.12	0.09	-0.31 – 0.06
	<i>Nyurnma</i>	Spinifex sandplain	0.12	0.10	-0.06 – 0.31
Edible shrub and tree diversity	<i>Spinifex</i>	Spinifex sandplain	0.20	0.08	0.02 – 0.40
	FFDiv + <i>spinifex</i>	Fire frequency diversity	0.35	0.32	-0.32 – 1.02
		Spinifex sandplain	0.19	0.08	0.02 – 0.37

Appendix D: Supplementary material for chapter five

Table S5.1 The number of years-since-fire and the number of times each site was burnt (i.e., fire frequency) for each site.

Site	Years-since-fire	Fire frequency			
1	44	1	47	4	3
2	13	1	48	6	2
3	4	3	49	4	3
4	44	1	50	6	3
5	4	5	51	6	4
6	43	1	52	4	4
7	44	1	53	4	5
8	37	1	54	37	1
9	38	1	55	2	2
10	39	1	56	26	1
11	5	2	57	44	1
12	42	1	58	0	2
13	42	1	59	1	3
14	39	1	60	1	2
15	1	3			
16	1	3			
17	44	1			
18	39	2			
19	27	3			
20	24	4			
21	26	1			
22	25	2			
23	23	2			
24	32	2			
25	32	3			
26	27	2			
27	26	2			
28	12	2			
29	17	1			
30	5	3			
31	14	2			
32	13	2			
33	18	3			
34	14	4			
35	13	3			
36	6	2			
37	7	2			
38	75	0			
39	75	0			
40	75	0			
41	75	0			
42	75	0			
43	8	4			
44	6	3			
45	6	4			
46	3	3			

Table S5.2 Rationale for causal direction of paths used in SEMs. NH₃: nitrate, NO₃-: ammonia, TOC: total organic carbon.

Response	Predictor	Rationale
Total fungal richness	Time-since-fire	Altered by time-since-fire (Bowd et al., 2021, Dooley and Treseder, 2012, McMullan-Fisher et al., 2011, Smith et al., 2021).
	Fire frequency	Altered by fire frequency (Bowd et al., 2021, Dooley and Treseder, 2012, McMullan-Fisher et al., 2011, Smith et al., 2021).
	NH ₃ , and TOC	Soil properties are key drivers of fungal communities (Chai et al., 2019, Fierer et al., 2009, Tedersoo et al., 2014), especially carbon and nitrogen (Schimel and Weintraub, 2003).
	pH	pH is a key driver of fungal composition (Lauber et al., 2009, Rousk et al., 2010).
	Coarse woody debris	Altered by coarse woody debris cover (Mäkipää et al., 2017, Mikryukov et al., 2021).
	Elevated dead	Altered by elevated dead cover and decay rate (Mäkipää et al., 2017).
Ectomycorrhizal richness	Plant cover	Altered by plant cover because of available soil resources, nutrients, and plant hosts (Hart et al., 2005, Shen et al., 2021, Wardle et al., 2004).
	Time-since-fire	Altered by time-since-fire (Bowd et al., 2021, Dove and Hart, 2017).
	Fire frequency	Altered by fire frequency (Brown et al., 2013, Buscardo et al., 2010).
	NH ₃ and TOC	Influenced by nitrogen (Bauman et al., 2016, Tedersoo et al., 2014, Treseder, 2004) and to a lesser degree carbon (because they receive it from plants) (Smith and Read, 2008).
	pH	Influenced by pH (Bauman et al., 2016, Tedersoo et al., 2014, Treseder, 2004).
	Coarse woody debris	Some ectomycorrhizal lineages still decompose wood and thus, may be influenced by changes in coarse woody debris (Fernandez and Kennedy, 2016).
Saprotrophic richness	Elevated dead	Some ectomycorrhizal lineages still decompose wood and thus, may be influenced by changes in elevated dead (Fernandez and Kennedy, 2016).
	Shrub cover	Rely on carbon allocated from their hosts in the form of simple sugars (Averill et al., 2022, Smith and Read, 2008) and thus, are vulnerable to changes in plant communities (Lindahl et al., 2010).
	Time-since-fire	Altered by time-since-fire (Day et al., 2019, Semenova-Nelsen et al., 2019).
	Fire frequency	Altered by fire frequency (Bowd et al., 2021).
	NH ₃ and TOC	Influenced by carbon (Fernandez and Kennedy, 2016) and nitrogen (Tedersoo et al., 2014).
	Coarse woody debris	Influenced by coarse woody debris (Kutszegi et al., 2021, Mäkipää et al., 2017, Saitonen, 2001).

	Elevated dead	Influenced by elevated dead (Mäkipää et al., 2017, Siitonens, 2001).
	Shrub cover	Influenced by plant groups, due to differences in C:N ratios and lignin content of plant tissue (Francioli et al., 2021).
Pathogenic richness	Time-since-fire	Altered by time-since-fire (Beals et al., 2022, Bowd et al., 2021).
	Fire frequency	Altered by fire frequency (Beals et al., 2022, Bowd et al., 2021).
	NH ₃ and TOC	Influenced by carbon and nitrogen (Tedersoo et al., 2014).
	pH	Influenced by pH (Bowd et al., 2022, Lekberg et al., 2021).
	Shrub cover	Influenced by plant cover (Borowicz, 2001, Dean et al., 2012).
NH ₃ and TOC	Time-since-fire	Fire can volatise nutrients, alter mineralisation rates, change soil nutrient ratios, and cause nutrient erosion and leaching (Certini, 2005, González-Pérez et al., 2004, Neary et al., 1999).
	Fire frequency	Altered by fire frequency (Certini, 2005, González-Pérez et al., 2004, Neary et al., 1999).
pH	Time-since-fire	Altered by time-since-fire (Certini, 2005, González-Pérez et al., 2004, Neary et al., 1999).
	Fire frequency	Altered by fire frequency (Nichols et al., 2021).
Coarse woody debris	Time-since-fire	Altered by time-since-fire (Haslem et al., 2010, Whitford and McCaw, 2019)
	Fire frequency	Altered by fire frequency (Whitford and McCaw, 2019).
Elevated dead	Time-since-fire	Altered by time-since-fire (Burrows et al., 2021, Gosper et al., 2012b).
	Fire frequency	Altered by fire frequency (Collins et al., 2019).
Shrub cover	Time-since-fire	Altered by time-since-fire (Pulsford et al., 2016, He et al., 2019, Keeley et al., 2011)
	Fire frequency	Altered by fire frequency (Pausas and Keeley, 2014, Vigilante et al., 2004).

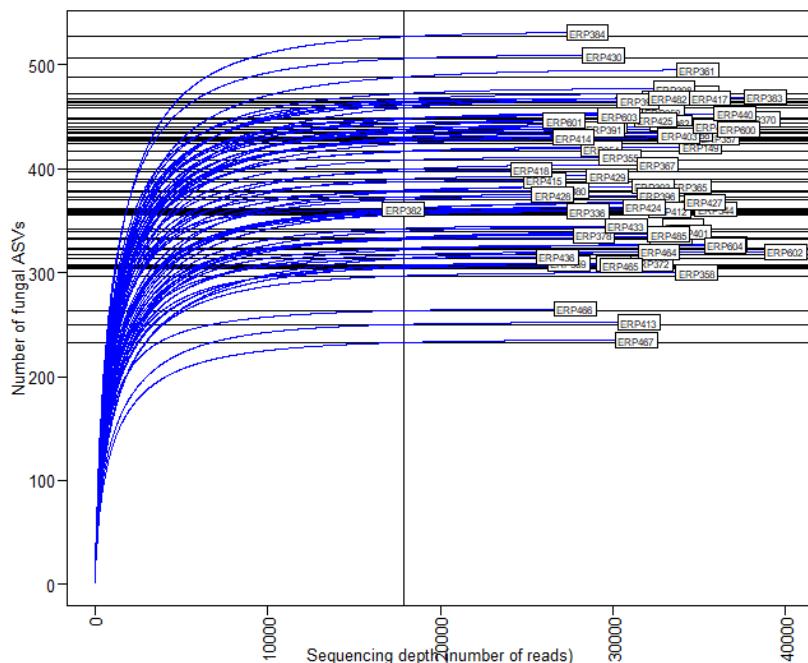


Figure S5.1 Rarefaction curves of fungal ASVs (Amplicon Sequence Variant) in samples. Vertical line indicates the site with the lowest number of reads (17,853 reads).

Table S5.3 Goodness of fit of time-since-fire, successional stages, fire frequency, and fire frequency classes on fungi and trophic guild composition based on the *envfit* function using NMDS plots.

Predictor	Total fungi		Ectomycorrhizas		Saprotophs		Pathogens	
	R ²	p-value	R ²	p-value	R ²	p-value	R ²	p-value
Time-since-fire	13%	0.016	47%	0.001	13%	0.019	12%	0.024
Successional stages	16%	0.002	40%	0.001	15%	0.004	11%	0.032
Fire frequency	34%	0.001	37%	0.001	34%	0.001	12%	0.036
Fire frequency classes	13%	0.001	16%	0.001	12%	0.002	3%	0.024

Table S5.4 Indicator species analysis showing associations of fungal species with post-fire successional stages and fire frequency classes. Indicator value (Ind Val): strength of association to group, p-value: significance ($p \leq 0.05$ deemed significant), recently burnt: 0 – 2.5 years post-fire, mid-succession: 2.5 – 8.5 years post-fire, late-succession: 8.5 – 33.5 years post-fire, long unburnt: 33.5 + years post-fire, low fire frequency: burnt ≤ 2 times over 29-year period, high fire frequency: burnt 3 – 5 times over 29-year period. Species only shown if indicator value ≥ 0.25 , significant, and if unique to one group. ASVs bolded if they show a preference for both a post-fire successional stage and a fire frequency class.

Group	ASV ID	Phylum	Family	Genus	Species	Guild	Ind Val	p-value
Recently burnt	ASV59	Basidiomycota	Geminibasidiaceae	Geminibasidium		saprotroph	0.73	0.000
	ASV301	Ascomycota					0.69	0.000
	ASV25	Ascomycota	Herpotrichiellaceae	Cladophialophora		saprotroph	0.66	0.000
	ASV424						0.65	0.000
	ASV391	Basidiomycota	Cortiriaceae				0.64	0.000
	ASV281	Ascomycota	Herpotrichiellaceae				0.64	0.000
	ASV248	Ascomycota					0.64	0.000
	ASV104	Chytridiomycota	Powellomyctaceae	Powellomyces		saprotroph	0.61	0.000
	ASV201	Ascomycota	Herpotrichiellaceae				0.59	0.000
	ASV67	Ascomycota	Hypocreales	Leucosphaeri			0.59	0.000
	ASV360	Ascomycota					0.59	0.000
	ASV120	Basidiomycota	Sclerodermataceae	Scleroderma	albidum	ectomycorrhizal	0.59	0.000
	ASV266	Ascomycota	Lasiosphaeriaceae				0.58	0.000
	ASV156	Basidiomycota	Boletaceae				0.53	0.000
	ASV295	Ascomycota	Herpotrichiellaceae				0.53	0.000
	ASV438						0.53	0.000
	ASV368	Ascomycota	Herpotrichiellaceae				0.52	0.001
	ASV53	Basidiomycota	Filobasidiaceae	Filobasidium	globisporum	saprotroph	0.51	0.000
	ASV269						0.50	0.001
	ASV97	Ascomycota	Aspergillaceae	Penicillium		saprotroph	0.49	0.001
	ASV113	Ascomycota	Herpotrichiellaceae	Rhinocladiella		saprotroph	0.49	0.001
	ASV214						0.49	0.001
	ASV423	Ascomycota					0.49	0.000
	ASV6	Ascomycota	Pleosporaceae	Alterria	alterta		0.49	0.000
	ASV119	Basidiomycota	Sclerodermataceae	Scleroderma		ectomycorrhizal	0.49	0.001
	ASV110	Ascomycota	Trichocomaceae	Rasamsonia		saprotroph	0.49	0.001
	ASV258	Ascomycota	Herpotrichiellaceae				0.48	0.001

Recently burnt	ASV213	Ascomycota	Teratosphaeriaceae			0.48	0.001	
	ASV173	Ascomycota				0.47	0.001	
	ASV341	Ascomycota	Herpotrichiellaceae			0.45	0.001	
	ASV325					0.45	0.002	
	ASV346	Ascomycota				0.45	0.001	
	ASV65	Ascomycota	Helotiales	Leohumicola	lenta	saprotroph	0.44	0.005
	ASV398	Ascomycota	Herpotrichiellaceae				0.44	0.003
	ASV198	Basidiomycota	Lycoperdaceae				0.44	0.005
	ASV207						0.44	0.005
	ASV226						0.44	0.003
	ASV243						0.44	0.001
	ASV246	Ascomycota					0.44	0.003
	ASV28	Ascomycota	Coniochaetaceae	Coniochaeta	discospora	saprotroph	0.43	0.004
	ASV19	Ascomycota	Helotiaceae	Cairneyella	variabilis	endophyte	0.43	0.003
	ASV195	Ascomycota	Herpotrichiellaceae				0.43	0.005
	ASV426	Ascomycota	Herpotrichiellaceae				0.43	0.003
	ASV188	Ascomycota					0.43	0.004
	ASV141	Mucoromycota	Umbelopsidaceae	Umbelopsis	dimorpha	saprotroph	0.43	0.005
	ASV30	Ascomycota	Coniochaetaceae	Coniochaeta	cipro	saprotroph	0.42	0.005
	ASV118	Ascomycota	Debaryomycetaceae	Schwanniomyces	vanrijiae	saprotroph	0.42	0.004
	ASV93	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.42	0.005
	ASV276						0.42	0.004
	ASV324	Ascomycota					0.42	0.005
	ASV5	Ascomycota	Pleosporaceae	Alterria	infectoria		0.42	0.005
	ASV103	Ascomycota	Lentitheciaceae	Pleurophoma		pathogen	0.41	0.009
	ASV310						0.41	0.004
	ASV407						0.41	0.004
	ASV96	Ascomycota	Aspergillaceae	Penicillium		saprotroph	0.40	0.004
	ASV38	Basidiomycota	Corticiaceae	Cortirius			0.40	0.005
	ASV63	Basidiomycota	Inocybaceae	Inocybe		ectomycorrhizal	0.40	0.004
	ASV72	Mortierellomycota	Mortierellaceae	Mortierella	fimbricystis	saprotroph	0.40	0.002
	ASV313	Ascomycota	Myxotrichaceae				0.40	0.005
	ASV319	Ascomycota					0.40	0.009
	ASV101	Ascomycota	Aspergillaceae	Penicillium		saprotroph	0.39	0.001

Recently burnt	ASV107	Ascomycota	Sarcosomataceae	Pseudoplectania		saprotroph	0.39	0.010
	ASV363	Ascomycota	Herpotrichiellaceae				0.38	0.022
	ASV18	Basidiomycota	Lycoperdaceae	Bovista	aestivalis	saprotroph	0.38	0.011
	ASV177	Ascomycota					0.38	0.017
	ASV167	Ascomycota					0.37	0.020
	ASV302						0.37	0.015
	ASV21	Ascomycota	Cladoniaceae	Cladonia	calyciformis	lichenized	0.36	0.030
	ASV40	Basidiomycota	Cortiriaceae	Cortirius			0.36	0.033
	ASV41	Basidiomycota	Cortiriaceae	Cortirius			0.36	0.033
	ASV43	Basidiomycota	Cortiriaceae	Cortirius			0.36	0.027
	ASV175	Ascomycota	Herpotrichiellaceae				0.36	0.030
	ASV193	Ascomycota	Herpotrichiellaceae				0.36	0.032
	ASV430	Ascomycota	Herpotrichiellaceae				0.36	0.033
	ASV307	Ascomycota	Hyaloscypheaceae				0.36	0.030
	ASV88	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.36	0.023
	ASV270						0.36	0.032
	ASV316	Basidiomycota					0.36	0.035
	ASV318	Ascomycota					0.36	0.030
	ASV339	Ascomycota					0.36	0.031
	ASV342	Ascomycota					0.36	0.031
	ASV373						0.36	0.017
	ASV397	Ascomycota					0.36	0.031
	ASV401	Ascomycota					0.36	0.029
	ASV405	Ascomycota					0.36	0.030
	ASV410						0.36	0.030
	ASV429	Ascomycota					0.36	0.022
	ASV442	Mucoromycota					0.36	0.031
	ASV54	Ascomycota	Nectriaceae	Fusarium		pathogen	0.36	0.031
	ASV306	Ascomycota	Pezizaceae				0.36	0.032
	ASV114	Basidiomycota	Phanerochaetaceae	Rhizochaete	america	saprotroph	0.36	0.022
	ASV249	Ascomycota	Sporormiaceae				0.36	0.030
	ASV145	Ascomycota	Venturiaceae	Venturia		pathogen	0.36	0.032
	ASV300	Basidiomycota	Agaricaceae				0.35	0.024
	ASV29	Ascomycota	Coniochaetaceae	Coniochaeta	africa	saprotroph	0.35	0.030

Recently burnt	ASV223	Ascomycota	Hyaloscyphaceae			0.35	0.024	
	ASV2	Ascomycota	Hypocreales	Acremonium	polychromum	saprotroph	0.35	0.022
	ASV208	Ascomycota					0.35	0.029
	ASV245	Ascomycota					0.35	0.030
	ASV279						0.35	0.031
	ASV285	Ascomycota					0.35	0.033
	ASV327						0.35	0.026
	ASV336	Ascomycota					0.35	0.031
	ASV386	Basidiomycota					0.35	0.031
	ASV102	Ascomycota	Phaeococomycetaceae	Phaeococomyces		saprotroph	0.35	0.031
	ASV344	Ascomycota	Venturiaceae				0.35	0.029
	ASV62	Basidiomycota	Inocybaceae	Inocybe		ectomycorrhizal	0.34	0.030
	ASV68	Ascomycota	Lophiostomataceae	Lophiostoma	chamaecyparidis	saprotroph	0.34	0.045
	ASV211	Ascomycota					0.34	0.039
	ASV305						0.34	0.032
	ASV399	Ascomycota					0.34	0.032
	ASV406	Ascomycota					0.34	0.036
	ASV64	Ascomycota	Lecanoraceae	Lecidella		lichenized	0.33	0.016
	ASV242	Ascomycota					0.33	0.030
	ASV359	Ascomycota					0.33	0.036
	ASV362	Ascomycota					0.33	0.006
	ASV393						0.33	0.030
	ASV404						0.33	0.029
	ASV263						0.32	0.030
	ASV352	Ascomycota					0.32	0.046
	ASV432						0.32	0.030
	ASV197	Ascomycota	Teratosphaeriaceae				0.32	0.032
	ASV427						0.31	0.032
	ASV91	Ascomycota	Myxotrichaceae	Oidiodendron	chlamydosporicum	saprotroph	0.30	0.022
	ASV254						0.30	0.031
	ASV320	Ascomycota					0.30	0.030
	ASV331	Ascomycota	Herpotrichiellaceae				0.28	0.030
	ASV139	Ascomycota	Hypocreaceae	Trichoderma		parasitic	0.27	0.019
	ASV170	Basidiomycota	Psathyrellaceae				0.62	0.000

Mid-succession	ASV385					0.58	0.000	
	ASV180					0.54	0.000	
	ASV443	Basidiomycota				0.54	0.000	
	ASV132	Basidiomycota	Sphaerobolaceae	Sphaerobolus	saprotoph	0.54	0.000	
	ASV354	Ascomycota				0.53	0.001	
	ASV365	Basidiomycota				0.53	0.000	
	ASV47	Ascomycota	Teratosphaeriaceae	Devriesia	america	pathogen	0.50	0.001
	ASV48	Ascomycota	Botryosphaeriaceae	Dothiorella		pathogen	0.49	0.001
	ASV210	Ascomycota					0.49	0.001
	ASV159	Basidiomycota	Thelephoraceae				0.48	0.001
	ASV408						0.46	0.001
	ASV183	Chytridiomycota					0.45	0.003
	ASV228						0.45	0.003
	ASV20	Ascomycota	Teratosphaeriaceae	Camarosporula	persooniae	epiphyte	0.45	0.002
	ASV403	Ascomycota					0.44	0.002
	ASV227	Mucoromycota					0.43	0.003
	ASV133	Ascomycota	Onygeles	Spiromastix		saprotoph	0.43	0.002
	ASV99	Ascomycota	Aspergillaceae	Penicillium	nodositatum	saprotoph	0.42	0.004
	ASV337	Mucoromycota					0.42	0.004
	ASV340	Ascomycota					0.42	0.004
	ASV112	Ascomycota	Herpotrichiellaceae	Rhinocladiella		saprotoph	0.41	0.000
	ASV152	Ascomycota	Microascaceae	Wardomyopsis	litoralis	saprotoph	0.41	0.004
	ASV261	Ascomycota					0.4	0.010
	ASV308	Ascomycota					0.4	0.008
	ASV422	Basidiomycota	Boletaceae				0.39	0.010
	ASV233	Ascomycota					0.39	0.014
	ASV347	Basidiomycota					0.39	0.011
	ASV439						0.39	0.011
	ASV256	Basidiomycota					0.38	0.014
	ASV350	Ascomycota					0.38	0.014
	ASV123	Ascomycota	Helotiaceae	Scytalidium		saprotoph	0.37	0.019
	ASV334	Ascomycota	Herpotrichiellaceae				0.37	0.015
	ASV80	Ascomycota	Myxotrichaceae	Oidiodendron		saprotoph	0.37	0.015
	ASV252	Ascomycota					0.37	0.020

Mid-succession	ASV309	Ascomycota				0.37	0.023	
	ASV330					0.37	0.020	
	ASV137	Ascomycota	Teichosporaceae	Teichospora	grandicipis	saprotroph	0.37	0.020
	ASV262	Ascomycota	Teichosporaceae				0.37	0.019
	ASV74	Basidiomycota	Tricholomataceae	Myce			0.37	0.024
	ASV27	Basidiomycota	Clathraceae	Clathrus	archeri	saprotroph	0.36	0.019
	ASV45	Ascomycota	Helotiaceae	Crocicreas		saprotroph	0.36	0.022
	ASV166	Ascomycota	Herpotrichiellaceae				0.36	0.023
	ASV387	Ascomycota					0.36	0.020
	ASV434						0.36	0.021
	ASV206	Basidiomycota	Sirobasidiaceae				0.36	0.016
	ASV149	Ascomycota	Sympoventuriaceae	Veroeopsis	simplex		0.36	0.022
	ASV50	Ascomycota	Herpotrichiellaceae	Exophiala		parasitic	0.35	0.022
	ASV204						0.35	0.027
	ASV216						0.35	0.028
	ASV335						0.35	0.021
	ASV420	Ascomycota					0.35	0.028
	ASV431	Ascomycota					0.35	0.022
	ASV73	Basidiomycota	Tricholomataceae	Myce	flosnivium		0.35	0.027
	ASV140	Mucoromycota	Umbelopsidaceae	Umbelopsis	isabelli	saprotroph	0.35	0.022
	ASV37	Basidiomycota	Cortiriaceae	Cortirius			0.34	0.020
	ASV131	Ascomycota	Didymosphaeriaceae	Spegazzinia		saprotroph	0.34	0.036
	ASV36	Basidiomycota	Cortiriaceae	Cortirius			0.33	0.044
	ASV154	Ascomycota	Helotiales	Xylogone		parasitic	0.33	0.036
	ASV86	Ascomycota	Myxotrichaceae	Oidiodendron	griseum	saprotroph	0.33	0.042
	ASV259						0.33	0.043
	ASV264	Mucoromycota					0.33	0.044
	ASV394						0.33	0.023
	ASV56	Basidiomycota	Filobasidiaceae	Ganishia			0.32	0.040
	ASV388	Ascomycota					0.32	0.036
	ASV311						0.31	0.040
Late-succession	ASV49	Ascomycota	Pleosporaceae	Drechslera		pathogen	0.58	0.000
	ASV338	Ascomycota	Venturiaceae				0.52	0.001
	ASV46	Ascomycota	Pleosporaceae	Curvularia		pathogen	0.49	0.001

Late-succession	ASV244	Basidiomycota	Agaricaceae			0.48	0.001
	ASV380					0.47	0.002
	ASV237					0.46	0.002
	ASV127	Basidiomycota	Sebaceae	Sebaci		0.45	0.003
	ASV122	Ascomycota	Sclerotiniaceae	Sclerotinia	pathogen	0.44	0.002
	ASV87	Ascomycota	Myxotrichaceae	Oidiodendron	saprotroph	0.43	0.004
	ASV255	Ascomycota	Herpotrichiellaceae			0.42	0.007
	ASV185	Ascomycota				0.42	0.005
	ASV384					0.42	0.006
	ASV390	Ascomycota				0.42	0.011
	ASV369					0.41	0.007
	ASV116	Basidiomycota	Erythrobasidiales	Sakaguchia	saprotroph	0.40	0.003
	ASV121	Basidiomycota	Sclerogastraceae	Sclerogaster	compactus	0.40	0.009
	ASV89	Ascomycota	Myxotrichaceae	Oidiodendron	cereale	0.38	0.018
	ASV265	Ascomycota				0.38	0.012
	ASV24	Ascomycota	Herpotrichiellaceae	Cladophialophora	saprotroph	0.37	0.021
	ASV161	Ascomycota				0.37	0.021
	ASV433					0.37	0.017
	ASV217	Ascomycota				0.36	0.019
	ASV289	Ascomycota				0.36	0.006
	ASV191					0.35	0.026
	ASV215					0.35	0.034
	ASV293	Ascomycota	Massariceae			0.34	0.028
	ASV353					0.34	0.028
	ASV9	Ascomycota	Chaetomiaceae	Arcopilus	saprotroph	0.33	0.042
	ASV168	Ascomycota				0.33	0.049
	ASV253	Ascomycota				0.33	0.037
	ASV12	Ascomycota	Trichomeriaceae	Arthrocladium	tardum	0.33	0.042
	ASV409					0.32	0.046
	ASV437	Ascomycota	Herpotrichiellaceae			0.31	0.043
Long unburnt	ASV212	Ascomycota				0.65	0.000
	ASV144	Mucoromycota	Umbelopsidaceae	Umbelopsis	isabelli	0.58	0.000
	ASV250	Ascomycota	Herpotrichiellaceae			0.55	0.000
	ASV231	Ascomycota	Herpotrichiellaceae			0.54	0.000

Long unburnt	ASV150	Ascomycota	Tympanidaceae	Vexillomyces	verruculosus	0.54	0.000	
	ASV370					0.53	0.000	
	ASV142	Mucoromycota	Umbelopsidaceae	Umbelopsis	dimorpha	saprotroph	0.51	0.000
	ASV371	Basidiomycota					0.50	0.000
	ASV105	Ascomycota	Sporormiaceae	Preussia		saprotroph	0.50	0.001
	ASV238						0.47	0.001
	ASV412						0.46	0.001
	ASV109	Ascomycota	Trichocomaceae	Rasamsonia		saprotroph	0.46	0.002
	ASV288	Ascomycota					0.45	0.004
	ASV290	Basidiomycota	Lycoperdaceae				0.43	0.004
	ASV90	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.43	0.004
	ASV153	Ascomycota	Xylariaceae	Xylaria		saprotroph	0.43	0.003
	ASV169						0.42	0.004
	ASV345	Ascomycota	Didymellaceae				0.41	0.007
	ASV234						0.41	0.006
	ASV283	Ascomycota	Phaeomoniellaceae				0.41	0.013
	ASV76	Ascomycota	Teratosphaeriaceae	Neocatenulostroma		pathogen	0.41	0.005
	ASV81	Ascomycota	Myxotrichaceae	Oidiodendron	chlamydosporicum	saprotroph	0.40	0.009
	ASV117	Ascomycota	Amphisphaeriaceae	Sarcostroma	restionis	saprotroph	0.39	0.014
	ASV272	Basidiomycota					0.39	0.019
	ASV1	Ascomycota	Hypocreales	Acremonium	polychromum	saprotroph	0.38	0.019
	ASV366	Ascomycota					0.38	0.014
	ASV164	Ascomycota	Didymellaceae				0.37	0.015
	ASV69	Ascomycota	Lophiostomataceae	Lophiostoma		saprotroph	0.37	0.016
	ASV247						0.37	0.016
	ASV287						0.37	0.017
	ASV428						0.37	0.016
	ASV126	Basidiomycota	Sebacieae	Sebaci			0.37	0.014
	ASV436	Basidiomycota	Boletaceae				0.36	0.020
	ASV323	Ascomycota	Herpotrichiellaceae				0.36	0.031
	ASV364	Ascomycota	Hyaloscyphaceae				0.36	0.019
	ASV3	Ascomycota	Mycosphaerellaceae	Acrodontium	hydnicola	pathogen	0.36	0.019
	ASV411	Basidiomycota					0.36	0.024
	ASV413						0.36	0.017

Long unburnt	ASV421	Ascomycota				0.36	0.020	
	ASV31	Ascomycota	Coniochaetaceae	Coniochaeta	saprotroph	0.35	0.020	
	ASV57	Basidiomycota	Gastraceae	Gastrum	hungaricum	saprotroph	0.35	0.023
	ASV194	Ascomycota				0.35	0.022	
	ASV222					0.35	0.033	
	ASV251					0.35	0.028	
	ASV314					0.35	0.031	
	ASV60	Ascomycota	Dothioraceae	Hormonema	viticola	saprotroph	0.34	0.023
	ASV83	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.34	0.040
	ASV176	Ascomycota					0.34	0.033
	ASV203						0.34	0.037
	ASV286						0.34	0.040
	ASV4	Ascomycota	Pleosporaceae	Alterria	alterta		0.34	0.035
	ASV95	Ascomycota	Aspergillaceae	Penicillium		saprotroph	0.33	0.034
	ASV33	Ascomycota	Coniochaetaceae	Coniochaeta	discospora	saprotroph	0.33	0.045
	ASV178	Ascomycota	Lophiotremataceae				0.33	0.039
	ASV275	Ascomycota					0.33	0.040
	ASV292	Ascomycota					0.33	0.044
	ASV415						0.33	0.048
	ASV440	Basidiomycota					0.33	0.044
	ASV17	Ascomycota	Teratosphaeriaceae	Baudoinia	antilliensis	saprotroph	0.33	0.047
	ASV115	Basidiomycota	Trimorphomycetaceae	Saitozyma	podzolica	saprotroph	0.33	0.046
	ASV299	Basidiomycota					0.32	0.049
	ASV378						0.32	0.043
	ASV78	Ascomycota	Sympoventuriaceae	Ochroconis		parasitic	0.32	0.047
	ASV98	Ascomycota	Aspergillaceae	Penicillium		saprotroph	0.31	0.049
	ASV179	Ascomycota					0.31	0.049
	ASV125	Basidiomycota	Sebaciceae	Sebaci			0.31	0.019
	ASV389	Ascomycota					0.29	0.030
Low fire frequency	ASV109	Ascomycota	Trichocomaceae	Rasamsonia		saprotroph	0.50	0.000
	ASV290	Basidiomycota	Lycoperdaceae				0.49	0.000
	ASV366	Ascomycota					0.47	0.000
	ASV163						0.44	0.001
	ASV418						0.44	0.001

Low fire frequency	ASV212	Ascomycota					0.42	0.000
	ASV412						0.42	0.001
	ASV124	Basidiomycota	Sebaciceae	Sebaci			0.42	0.001
	ASV151	Basidiomycota	Bulleribasidiaceae	Vishniacozyma	saprotroph		0.41	0.001
	ASV90	Ascomycota	Myxotrichaceae	Oidiodendron	saprotroph		0.40	0.001
	ASV379						0.40	0.002
	ASV332	Ascomycota	Herpotrichiellaceae				0.38	0.004
	ASV192	Basidiomycota					0.38	0.002
	ASV371	Basidiomycota					0.38	0.003
	ASV229						0.37	0.003
	ASV284						0.36	0.004
	ASV372	Ascomycota					0.34	0.008
	ASV416	Ascomycota					0.34	0.006
	ASV288	Ascomycota					0.33	0.010
	ASV296						0.33	0.007
	ASV143	Mucromycota	Umbelopsidaceae	Umbelopsis	dimorpha	saprotroph	0.33	0.005
	ASV182	Ascomycota	Sporormiaceae				0.32	0.012
	ASV209	Ascomycota	Sporormiaceae				0.32	0.011
	ASV15	Basidiomycota	Exidiaceae	Basidiodendron	saprotroph		0.31	0.023
	ASV52	Ascomycota	Herpotrichiellaceae	Exophiala	xenobiotica	parasitic	0.31	0.014
	ASV169						0.31	0.012
	ASV317	Ascomycota	Phaeosphaeriaceae				0.31	0.021
	ASV202	Ascomycota					0.30	0.025
	ASV238						0.30	0.016
	ASV315	Ascomycota					0.30	0.021
	ASV370						0.30	0.010
	ASV134	Basidiomycota	Sporidiobolaceae	Sporobolomyces	roseus	parasitic	0.30	0.021
	ASV16	Ascomycota	Teratosphaeriaceae	Baudoinia	antilliensis	saprotroph	0.30	0.019
	ASV150	Ascomycota	Tympanidaceae	Vexillomyces	verruculosus		0.30	0.016
	ASV153	Ascomycota	Xylariaceae	Xylaria	saprotroph		0.30	0.014
	ASV22	Ascomycota	Cladoniaceae	Cladonia	calyciformis	lichenized	0.29	0.023
	ASV231	Ascomycota	Herpotrichiellaceae				0.29	0.024
	ASV250	Ascomycota	Herpotrichiellaceae				0.29	0.023
	ASV364	Ascomycota	Hyaloscypheaceae				0.29	0.014

	ASV92	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.29	0.023
Low fire frequency	ASV257						0.29	0.011
	ASV282						0.29	0.037
	ASV326	Ascomycota					0.29	0.038
	ASV351	Ascomycota					0.29	0.037
	ASV71	Mortierellomycota	Mortierellaceae	Mortierella	alpi	saprotroph	0.28	0.038
	ASV234						0.28	0.031
	ASV280	Ascomycota					0.28	0.044
	ASV129	Basidiomycota	Sebaciceae	Sebaci			0.28	0.025
	ASV303	Basidiomycota	Serendipitaceae				0.28	0.026
	ASV10	Ascomycota	Trichomeriaceae	Arthrocladium	tardum	saprotroph	0.28	0.032
	ASV162	Ascomycota	Coniothyriaceae				0.27	0.040
	ASV268						0.27	0.030
	ASV314						0.27	0.044
	ASV329	Basidiomycota					0.27	0.048
	ASV374						0.27	0.028
	ASV128	Basidiomycota	Sebaciceae	Sebaci			0.27	0.037
	ASV105	Ascomycota	Sporormiaceae	Preussia		saprotroph	0.27	0.043
	ASV3	Ascomycota	Mycosphaerellaceae	Acrodontium	hydnicola	pathogen	0.26	0.046
High fire frequency	ASV361						0.26	0.043
	ASV382						0.26	0.042
	ASV402	Ascomycota					0.26	0.032
	ASV26	Ascomycota	Cladosporiaceae	Cladosporium	cladosporioides	saprotroph	0.25	0.031
	ASV241						0.25	0.032
	ASV297	Ascomycota					0.25	0.050
	ASV108	Ascomycota	Sarcosomataceae	Pseudoplectania		saprotroph	0.25	0.046
	ASV125	Basidiomycota	Sebaciceae	Sebaci			0.25	0.004
	ASV357	Ascomycota	Chaetomiaceae				0.61	0.000
	ASV358	Ascomycota					0.52	0.000
	ASV228						0.49	0.000
	ASV181	Ascomycota	Microascaceae				0.48	0.000
	ASV132	Basidiomycota	Sphaerobolaceae	Sphaerobolus		saprotroph	0.48	0.000
	ASV381	Ascomycota	Xylariaceae				0.47	0.000
	ASV334	Ascomycota	Herpotrichiellaceae				0.45	0.000

High fire frequency	ASV383	Ascomycota				0.43	0.001	
	ASV443	Basidiomycota				0.43	0.000	
	ASV55	Basidiomycota	Filibasidiaceae	ganishia		0.41	0.001	
	ASV35	Ascomycota	Dothideomycetidae	Coniozyma	leucospermi	pathogen	0.40	0.001
	ASV240	Ascomycota	Herpotrichiellaceae				0.40	0.002
	ASV367						0.40	0.001
	ASV349						0.39	0.000
	ASV8	Basidiomycota	Amanitaceae	Amanita		ectomycorrhizal	0.38	0.001
	ASV365	Basidiomycota					0.38	0.003
	ASV377	Ascomycota					0.38	0.003
	ASV414	Ascomycota					0.38	0.002
	ASV170	Basidiomycota	Psathyrellaceae				0.38	0.002
	ASV211	Ascomycota					0.37	0.003
	ASV220	Mucromycota					0.36	0.004
	ASV259						0.36	0.001
	ASV271	Ascomycota	Valsaceae				0.36	0.003
	ASV273	Ascomycota					0.35	0.003
	ASV343						0.35	0.007
	ASV99	Ascomycota	Aspergillaceae	Penicillium	nodositatum	saprotroph	0.34	0.006
	ASV199						0.34	0.008
	ASV94	Ascomycota	Phaeosphaeriaceae	Paraphoma		pathogen	0.34	0.006
	ASV190	Ascomycota	Venturiaceae				0.34	0.007
	ASV180						0.33	0.005
	ASV210	Ascomycota					0.33	0.011
	ASV256	Basidiomycota					0.33	0.011
	ASV146	Ascomycota	Venturiaceae	Venturia		pathogen	0.33	0.003
	ASV34	Ascomycota	Coniochaetaceae	Coniochaeta		saprotroph	0.32	0.008
	ASV85	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.32	0.011
	ASV165	Basidiomycota					0.32	0.005
	ASV233	Ascomycota					0.32	0.004
	ASV235	Ascomycota					0.32	0.002
	ASV294	Ascomycota					0.32	0.005
	ASV354	Ascomycota					0.32	0.013
	ASV419	Ascomycota					0.32	0.013

High fire frequency	ASV420	Ascomycota				0.32	0.011	
	ASV425	Ascomycota				0.32	0.013	
	ASV131	Ascomycota	Didymosphaeriaceae	Spegazzinia	saprotroph	0.31	0.018	
	ASV312	Ascomycota	Hyaloscypheaceae			0.31	0.017	
	ASV84	Ascomycota	Myxotrichaceae	Oidiodendron	saprotroph	0.31	0.007	
	ASV39	Basidiomycota	Cortiriaceae	Cortirius		0.30	0.006	
	ASV66	Ascomycota	Helotiales	Leohumicola	lenta	saprotroph	0.30	0.017
	ASV260	Ascomycota	Herpotrichiellaceae			0.30	0.017	
	ASV225	Basidiomycota				0.30	0.015	
	ASV227	Mucoromycota				0.30	0.018	
	ASV333	Ascomycota				0.30	0.015	
	ASV340	Ascomycota				0.30	0.015	
	ASV348	Basidiomycota				0.30	0.005	
	ASV396	Ascomycota				0.30	0.024	
	ASV438					0.30	0.016	
	ASV47	Ascomycota	Teratosphaeriaceae	Devriesia	america	pathogen	0.30	0.022
	ASV155	Ascomycota	Chaetomiaceae	Zopfiella		saprotroph	0.29	0.001
	ASV32	Ascomycota	Coniochaetaceae	Coniochaeta	discospora	saprotroph	0.29	0.016
	ASV42	Basidiomycota	Cortiriaceae	Cortirius			0.29	0.021
	ASV19	Ascomycota	Helotiaceae	Cairneyella	variabilis	endophyte	0.29	0.004
	ASV363	Ascomycota	Herpotrichiellaceae				0.29	0.016
	ASV14	Basidiomycota	Inocybaceae	Auritella	arenicolens	ectomycorrhizal	0.29	0.016
	ASV200	Ascomycota	Lophiostomataceae				0.29	0.015
	ASV157	Basidiomycota					0.29	0.024
	ASV232	Basidiomycota					0.29	0.016
	ASV236	Ascomycota					0.29	0.025
	ASV278						0.29	0.018
	ASV376						0.29	0.025
	ASV403	Ascomycota					0.29	0.022
	ASV135	Ascomycota	Trichocomaceae	Talaromyces		saprotroph	0.29	0.011
	ASV11	Ascomycota	Trichomeriaceae	Arthrocladium	tardum	saprotroph	0.29	0.005
	ASV100	Ascomycota	Aspergillaceae	Penicillium	spinulosum	saprotroph	0.28	0.013
	ASV48	Ascomycota	Botryosphaeriaceae	Dothiorella		pathogen	0.28	0.033
	ASV171	Ascomycota	Herpotrichiellaceae				0.28	0.017

High fire frequency	ASV195	Ascomycota	Herpotrichiellaceae			0.28	0.015	
	ASV160	Rozellomycota				0.28	0.028	
	ASV218	Ascomycota				0.28	0.031	
	ASV224	Basidiomycota				0.28	0.030	
	ASV355	Ascomycota				0.28	0.027	
	ASV375	Ascomycota				0.28	0.017	
	ASV417	Ascomycota				0.28	0.027	
	ASV7	Ascomycota	Pleosporaceae	Alterria	hungarica	0.28	0.022	
	ASV25	Ascomycota	Herpotrichiellaceae	Cladophialophora		saprotroph	0.27	0.036
	ASV112	Ascomycota	Herpotrichiellaceae	Rhinocladiella		saprotroph	0.27	0.001
	ASV70	Ascomycota	Lophiostomataceae	Lophiostoma	chamaecyparidis	saprotroph	0.27	0.033
	ASV79	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.27	0.024
	ASV186	Ascomycota					0.27	0.016
	ASV196						0.27	0.043
	ASV277	Ascomycota					0.27	0.041
	ASV435	Ascomycota					0.27	0.016
	ASV441	Ascomycota					0.27	0.036
	ASV77	Ascomycota	Phaeosphaeriaceae	Neosetophoma	samararum	saprotroph	0.27	0.035
	ASV106	Ascomycota	Didymosphaeriaceae	Pseudopithomyces	karoo	pathogen	0.26	0.047
	ASV58	Basidiomycota	Geastraceae	Geastrum		saprotroph	0.26	0.041
	ASV44	Ascomycota	Helotiaceae	Crocicreas		saprotroph	0.26	0.047
	ASV123	Ascomycota	Helotiaceae	Scytalidium		saprotroph	0.26	0.045
	ASV23	Ascomycota	Herpotrichiellaceae	Cladophialophora		saprotroph	0.26	0.048
	ASV51	Ascomycota	Herpotrichiellaceae	Exophiala		parasitic	0.26	0.043
	ASV138	Ascomycota	Hypocreaceae	Trichoderma	harzianum	parasitic	0.26	0.049
	ASV80	Ascomycota	Myxotrichaceae	Oidiodendron		saprotroph	0.26	0.027
	ASV172	Ascomycota					0.26	0.046
	ASV184						0.26	0.043
	ASV239	Ascomycota					0.26	0.042
	ASV267	Ascomycota					0.26	0.045
	ASV274						0.26	0.048
	ASV298						0.26	0.046
	ASV304	Ascomycota					0.26	0.046
	ASV330						0.26	0.046

High fire frequency	ASV356	Ascomycota				0.26	0.048	
	ASV392	Basidiomycota				0.26	0.016	
	ASV6	Ascomycota	Pleosporaceae	Alterria	alterta	0.26	0.037	
	ASV130	Basidiomycota	Sebacieae	Sebaci		0.26	0.045	
	ASV136	Ascomycota	Trichocomaceae	Talaromyces	pseudostromaticus	saprotroph	0.26	0.047
	ASV74	Basidiomycota	Tricholomataceae	Myce			0.26	0.046
	ASV147	Ascomycota	Venturiaceae	Venturia		pathogen	0.26	0.048
	ASV148	Ascomycota	Venturiaceae	Venturia		pathogen	0.26	0.050
	ASV13	Ascomycota	Aspergillaceae	Aspergillus	lentulus	saprotroph	0.25	0.025
	ASV27	Basidiomycota	Clathraceae	Clathrus	archeri	saprotroph	0.25	0.046
	ASV174	Ascomycota	Herpotrichiellaceae				0.25	0.018
	ASV187	Ascomycota	Herpotrichiellaceae				0.25	0.047
	ASV205	Ascomycota	Herpotrichiellaceae				0.25	0.048
	ASV400	Ascomycota	Hyaloscypheaceae				0.25	0.045
	ASV61	Basidiomycota	Hygrophoraceae	Hygrocybe		saprotroph	0.25	0.045
	ASV158	Ascomycota					0.25	0.044
	ASV219	Ascomycota					0.25	0.047
	ASV221	Ascomycota					0.25	0.046
	ASV230	Ascomycota					0.25	0.030
	ASV291	Ascomycota					0.25	0.049
	ASV321	Basidiomycota					0.25	0.042
	ASV322	Ascomycota					0.25	0.046
	ASV328	Ascomycota					0.25	0.048
	ASV395	Ascomycota					0.25	0.049
	ASV431	Ascomycota					0.25	0.047
	ASV189	Ascomycota	Sporormiaceae				0.25	0.046
	ASV75	Ascomycota	Teratosphaeriaceae	Neocatenulostroma		pathogen	0.25	0.047
	ASV111	Ascomycota	Trichocomaceae	Rasamsonia		saprotroph	0.25	0.046

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