Impact of fire and post-fire recovery of tropical and subtropical plant biodiversity

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Covid impact statement

The original plan of this thesis was to conduct fieldwork in Nepal, where I have some previous botanical field survey experience. The fieldwork aimed to collect and analyse data from high-risk wildfire areas nationwide. The goal was to evaluate the impact and risk of fire on biodiversity, ecosystem services, carbon emissions, and socioeconomic factors. The studentship commenced in Oct 2019, and the first six months were primarily focused on becoming familiar with the ecological literature on the impacts of fire and commencing fieldwork planning. When the COVID-19 pandemic emerged, it became clear that fieldwork would not be possible. It also meant I could not travel from my home (Grantham, Lincolnshire) for face-to-face interactions with supervisors and members of my research group; at the same time, I had to manage home schooling of two children – aged 16 and 10 (autistic) with support from my wife. It is difficult to estimate precisely how much time was lost due to this situation, but I estimate it was around six months. Unfortunately, as a self-funded student using graduate loans to support myself during the PhD, I couldn't benefit from funded extensions to recoup this lost time. I hoped fieldwork would be possible in 2021 as travel restrictions ease, but the situation in Nepal did not enable this. Consequently, I was forced to shift to an entirely desk-based study. This situation became challenging as my fieldwork skill was better developed by studying the literature when I started the PhD than my big data handling skills. Learning coding, data handling and analysis skills took much time while working independently from home.

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Thesis abstract

Fires are a key environmental driver that modifies ecosystems and global biodiversity. Within biodiverse tropical and subtropical regions, fire occurrence has increased in recent decades and is predicted to increase due to climate and land use changes. Fire can have both negative and positive impacts on biodiversity and ecosystem functioning. Moreover, the fire pattern is also changing in these regions due to fire suppression and fire ignition measures. The impact of fire on biodiversity and ecosystem is very complex and can vary according to taxa, fire variables, level of disturbance and historical exposure to fire. To add more knowledge and shed light on this intricate relationship between fire and biodiversity, I carried out a pan-tropical analysis on the impact of fire and post-fire recovery on the taxonomic, phylogenetic, and functional diversity of plant communities using data from published field-level studies.

In Chapter 2, this thesis addresses this issue by exploring the impact of fire on taxonomic diversity (species richness and species turnover) of four life form groups: trees/shrubs, forbs, graminoids and climbers. In Chapter 3, I constructed the phylogenetic trees of four life form groups to establish the impact of fire on phylogenetic diversity, including phylogenetic clustering or phylogenetic over-dispersion. In Chapter 4, I collected the traits data for the trees/shrubs and worked on the functional diversity, functional richness, and functional turnover.

This thesis found that the impact of fire and the recovery of plant communities after a fire depends not only on the fire variables (time since fire and prescribed vs. non-prescribed fire)

but also on the life form (trees/shrubs, forbs, graminoids, and climbers), protection status (protected vs non-protected), and a biome with the level of historical exposure to fire. Fire impacts were found to vary across the taxonomic, phylogenetic, and functional diversity as well as across the life forms that are underrepresented in ecological studies, such as forbs, graminoids and climbers. My analysis revealed that the impact could continue to worsen due to increasing fire activities arising from climate and land use change. Although my research adds complementary knowledge to the existing knowledge, it should still be interpreted cautiously due to the limited dataset, and, in some cases, limited predictive power of the models. Hence, this research informs the need to conduct comparative studies of different under-represented life forms and focus more on phylogenetic and functional diversity.

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I want to remember my father-in-law, Bishnu Prasad Sharma, who unexpectedly passed away just before I began my PhD. He had always been my inspiration and support in the difficult time. My brother-in-law, Sagar Sharma, a big heart and a selfless supporter, also passed away before I could submit this thesis. I also want to pay tribute Mohamud Hafiz Abdullah, our batch-mate at Edwards Lab, who unfortunately passed away during his second year. I missed you all.

I am incredibly thankful for the cooperation and friendship of all my friends and relatives, whether near or far, in the UK, Nepal, or anywhere else.

Statement of declaration

I hereby confirm that the thesis submitted is solely my own and that I am the primary author and corresponding author for any publications from this work. I confirm that I have properly acknowledged the contributions of others in my thesis by providing appropriate credit where necessary. I hereby declare that this work has not been previously submitted for an award at this university or any other educational institution.

My supervisors - Dr Karl Evans and Professor David Edwards, and I developed the concepts and methodology for all data chapters. My supervisors also provided comprehensive feedback regarding the structure and content of each chapter.

Chapter 2

This chapter has been submitted to Ecology and Evolution for publication as-.
Sapkota, D.P., Edwards, D.P., Massam M. R. & Evans K.L "**A pantropical analysis of fire impacts and post-fire recovery on tropical plant diversity and species composition**".

This manuscript is reproduced in this thesis with minor alterations in the format. Author contributions are: DPS, KLE, and DPE conceived the ideas and designed the methodology; DPS collected the data; DPS analysed the data with the help of MRM; DPS led the writing of the manuscript. All authors contributed to the manuscript drafts.

Chapter 3

This chapter is currently under preparation for submission.

Sapkota, D.P., Edwards, D.P., Massam M. R. & Evans K.L "**Impact of fire and post-fire recovery of phylogenetic diversity of plant community in tropical and subtropical regions.**"

Author contributions are: DPS, KLE, and DPE conceived the ideas and designed the methodology; DPS collected the data; DPS analysed the data with the help of MRM; DPS led the writing of the manuscript. KLE and DPE gave substantial feedback on the structure and content of each chapter.

Chapter 4

This chapter is currently under preparation for submission.

Sapkota, D.P., Edwards, D.P. & Evans K.L "**Impact of fire and post-fire recovery of functional diversity of trees/shrubs community in tropical and subtropical regions**".

Author contributions are: DPS, KLE, and DPE conceived the ideas and designed the methodology; DPS collected and analysed the data; DPS led the writing of the manuscript; KLE and DPE gave feedback regarding the structure and content of each chapter.

“We cannot even begin to look at how biodiversity is distributed or how fast it is disappearing unless we can put units on it”.

Purvis & Hector (2000)

Purvis, A., & Hector, A. "Getting the measure of biodiversity." *Nature*, vol. 405, no. 6783, 11 May 2000, pp. 212

Chapter One

General introduction

CHAPTER 1

General introduction

1.1 Background

For millions of years, fires have played a significant role in shaping the Earth's ecosystem; it is believed to have existed since the emergence of plant species approximately 420 million years ago (Archibald et al., 2011; He et al., 2019; Scott et al., 2016). Globally, an average of 4.63 Mkm^2 of forest is burned yearly (Lizundia-Loiola et al., 2020). These fires directly impact human health (Lelieveld et al., 2015), ecosystem services, and biodiversity (Barlow et al., 2007; Bowman et al., 2009; Grala et al., 2017). For example, the Australian mega-fire in 2019/2020 killed 33 people and nearly 3 billion animals, including a staggering 2.46 billion reptiles (WWF, 2020; Wintle et al., 2020). Moreover, between 113 and 236 TgC of CO_2 were emitted due to biomass burning, while reduced ecosystem productivity resulted in an additional 19 to 52 TgC emission of CO_2 (Byrne et al., 2022).

Fires can occur naturally by lightning, volcanic eruption, or induced by humans either for deforestation or pyromania (Archibald et al., 2011; Pausas & Keeley, 2019). Various factors, such as historical and geographical exposure to fire and climate elements like temperature, humidity, wind, and precipitation, can impact the likelihood and severity of wildfires (Mhawej et al., 2015). In addition, the forest management system, vegetation structure, biomass, and the amount of fuel available for burning can also determine the size and intensity of the fire (Balde et al., 2023; Rouet-Leduc et al., 2021). While the occurrence of fires has risen in recent times, there has been a 25% decline in global burned areas from 1998 to 2015, mostly due to agricultural expansion in grasslands and savannas (Andela et al., 2017;

Zheng et al., 2021), where fires are an integral part of the ecosystem functioning (Joubert et al., 2012). Moreover, the extent of fires is increasing in tropical forests due to forest degradation and deforestation, warmer, prolonged dry weather, and reduced rainfall (Nobre et al., 2016). If further actions are not taken to combat the impacts of climate change, the decreasing global trend of burned areas could reverse and start increasing again (WWF, BGC, 2020).

Although climatic reasons exacerbate fires, humans ignite over 90 % of forest fires globally (FAO, 2007). Humans have been using fire for millennia to keep warm, cook food, drive game, and clear land (Thompson et al., 2021). Using fires, humans have created vegetational heterogeneity and some ecological benefits, maintaining certain ecosystems (Hoffman et al., 2021). Humans thus play a significant role in altering fire regimes when they start and extinguish fires and alter the composition of vegetation in the area (Lasslop & Kloster, 2017; Harris et al., 2023), causing changes to the fire season and fuel conditions (Archibald et al., 2011).

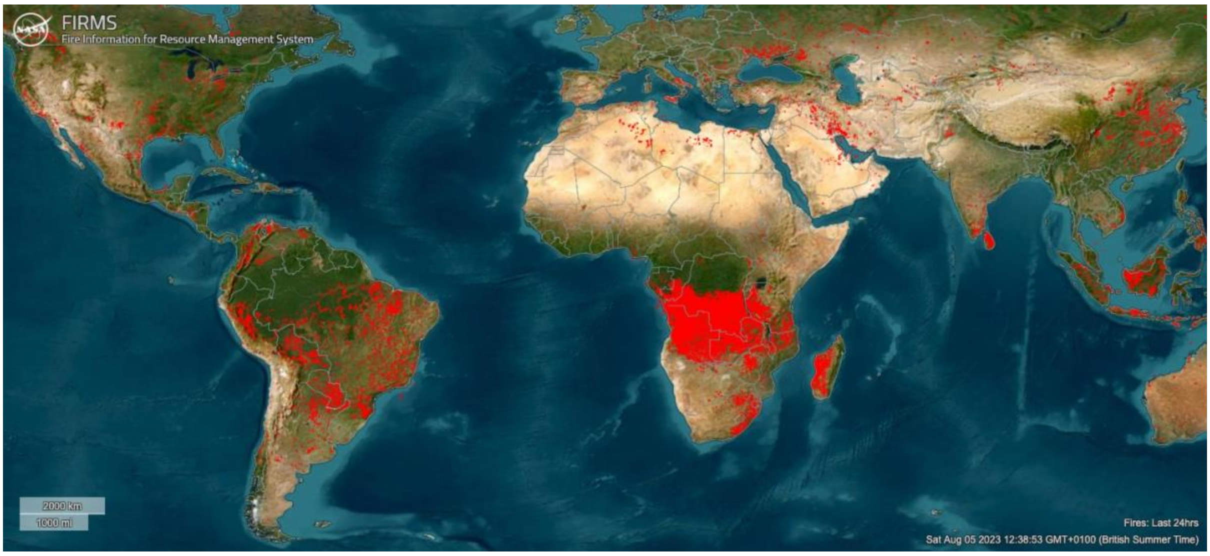

Fig 1.1 Global map showing fire areas during the last 24 hours between 04-05 August 2023, as recorded by satellite observation by NASA/FIRMS.

Fire ecologists recognise that fires are complex ecological phenomena greatly influenced by human activities and climate change (McLauchlan et al., 2020). Climate change can alter fire regimes, but human activities may intensify them by increasing their frequency and severity (Bowman et al., 2009). Hence, it is important to understand the connection between future climate changes and fire patterns, both geographically and historically, to prepare for potential impacts (Krawachuk et al., 2009).

Research has shown that the impact of a fire on an ecosystem can vary according to its characteristics, e.g., intensity, severity, frequency, and time since the last fire (Watson et al., 2004; Knuckey et al., 2016; Arroyo-Vargas et al., 2019; Turner et al., 2013; Morrison et al., 1995; Plumanns-Pouton et al., 2023). For example, a longer period since the last burn positively impacts plant species as they can regrow and fully mature as the time since fire progressed (Plumanns-Pouton et al., 2023; Morrison et al., 1995; Arroyo-Vargas et al., 2019). Similarly, higher fire frequency greatly reduces species richness and changes species composition (Watson et al., 2004; Knuckey et al., 2016). High-severity and low-severity fires have different impacts on species recovery after a fire. Recovery is slower after a high-severity fire (Arroyo-Vargas et al., 2019).

1.2 Consequences of fire

Although fires are largely perceived to be natural disturbances in the Earth's ecosystem, they can alter landscape heterogeneity and plant productivity with resultant impacts on biodiversity and ecosystem services (He et al., 2019; Pickett & White, 1985; Turner et al., 2013; Pausas & Keeley, 2019). Yet the impact of fire on the natural ecosystem and biodiversity remains equivocal because the studies on fire ecology suggest that fire occurrence can have positive and negative impacts (Pausas & Keeley, 2019) on human health and livelihoods, ecosystem services, and biodiversity.

1.2.1 Human health impacts

Fire causes natural habitat fragmentation and houses in burned areas and endangers human health through the smoke it produces. Additionally, it can trigger post-fire erosion, flooding, and water supply contamination (Scott et al., 2016). It is widely recognised that general air pollution caused by wildfires can harm human health (French et al., 2021). Studies have found significant links between respiratory health problems and wildfire smoke, which contains atmospheric pollutants (Liu et al., 2015; van der Werf et al., 2017).

1.2.2 Impact on ecosystem services

Fire can significantly interrupt the ecosystem dynamics, biodiversity, and carbon cycle (Bowman et al., 2009). Fire can impact plants and animals, but the impact can vary based on the nature of fire and the species' traits (Pocknee et al., 2023). After a wildfire, changes to the habitat's structure greatly reduce the ability of animals to recolonise the area. This is because the animals rely on the food, warmth, and shelter provided by the vegetation that regrows after the fire (Puig-Gironès et al., 2018).

Fires can cause enormous changes in carbon stock and lead to forest carbon imbalance (van der Werf et al., 2009). An estimated two gigatons of carbon is emitted annually into the atmosphere due to forest fires alone (van der Werf et al., 2017). The IPCC Synthesis Report 2007 brought attention to the fact that forest fires can contribute to the risks of climate change and ecological imbalances (IPCC, 2007). A rising concern exists about the feedback circle between fire and climate change. This is due to the release of forest carbon emissions caused by fire, which increases the fire risk due to climate change (Benali et al., 2017; Bowman et al., 2009; Clarke et al., 2022; Zheng et al., 2021).

Fire has played an important role in the evolution of many ecosystems throughout history, creating fire-dependent and fire-resilient ecosystems (McLauchlan et al., 2020). Various provisioning ecosystem services, such as food, pollination, and regulating water and carbon cycles, can be negatively affected by wildfires (Fried et al., 2004; Banza et al., 2019). However, the fire also supports most ecosystem services by opening the gap for the light-loving plants and animals that can provide food, pollination, tourism, and recreation (Pausas & Keeley, 2019).

1.2.3 Impact on biodiversity

The term “biodiversity” was first introduced at the United Nations Earth Summit in Rio de Janeiro in 1992. It defined biodiversity as “The variability among living organisms from all sources, including *inter alia*, terrestrial, marine, and other aquatic ecosystem, and the ecological complexes of which they are part: this includes diversity within species, between species and ecosystem” (CBD, 1992). Biodiversity encompasses living and dead organisms, ranging from microorganisms to large plants and animals in different Earth environments (MEA, 2005).

Taxonomic diversity is the most common and widely used diversity metric in ecology. Taxonomic diversity can be quantified through different methods such as alpha, which measures species richness or abundance; beta, which measures species turnover or nestedness; and gamma, which is the total diversity alpha and gamma of a given landscape

(Whittaker, 1972; Moore, 2013; Arellano & Halffter, 2003). While taxonomic diversity is a popular method of exploring biodiversity, it fails to consider the significance of evolutionary history and the various roles that different species play in an ecosystem and community (Faith, 1992; Díaz & Cabido, 2001).

Phylogenetic diversity (PD) is a diversity measure that allows the inclusion of evolutionary relations of species in a community (Cavender-Bares & Wilczek, 2003). Preserving phylogenetic diversity is crucial for safeguarding distinct ecological and phenotypic traits and enhancing ecosystems' stability and functioning (Edwards et al., 2017). On the other hand, functional diversity is a diversity of functions performed by organisms within a community and ecosystem (Díaz and Cabido, 2001; Petchey & Gatson, 2006). It is the key indicator of how an ecosystem functions (Petchey & Gatson, 2006) by providing the magnitude of ecosystem productivity and stability (Díaz & Cabido, 2001; Gagic et al., 2015).

The tropical and subtropical regions have very high biodiversity compared to other regions (Dirzo & Raven, 2003; CBD, 1992). Tropical regions are home to most of the world's land-based biodiversity, with more than two-thirds of biodiversity inhabiting these regions (Barlow et al., 2018). Tropical forests contain the world's largest variety of tree species, and approximately 53,000 species of trees are found in these forests (Slik et al., 2015). The higher temperatures in the tropics lead to faster mutation rates and shorter generation times, contributing to greater species diversity in the region (Rohde, 1992). Despite their high taxonomic diversity, these forests are being lost and degraded at a high rate (Alroy, 2017). As a result of climate and land use change, these forests are at the forefront of current and future extinctions (Barlow et al., 2016; Edwards et al., 2019). The excessive exploitation and degradation of tropical forests have severe adverse effects on plant and animal biodiversity (Gibson et al., 2011).

Wildfire in the tropics was uncommon in the past but has increased rapidly in recent decades (Cochrane, 2003). Additionally, the fires are decreasing in the tropical grasslands and savannas and increasing in the moist forests, resulting in the degradation of ecosystems and modifications to biodiversity (Kelly et al., 2020).

The impact of fire on biodiversity is very complex as the fire impact depends on the taxa, the ecosystem, and the level of human and other disturbances during the post-fire recovery (Kelly & Brotons, 2017). Small and non-mobile animals are more affected than large and mobile ones. For example, birds and other large animals can quickly escape a fire (Pastro et al., 2014) compared to small and slow-moving animals such as amphibians and reptiles (Cano & Lwynaud, 2009). Wildfires also greatly affect moth diversity, causing a reduction in nocturnal pollination (Banza et al., 2019). Similarly, smaller trees are killed more than large ones (Bennett et al., 2013), and trees with thick bark can better sustain fire than those with thin bark (Brando et al., 2012).

The role of fire can differ depending on the specific biomes in which they are present. For example, plant species in tropical dry forests can withstand wildfires and recover through resprouting and survival mechanisms (Mostacedo et al., 2022). In biomes such as grasslands and savannas, where fire is common, species require fire to evolve and regenerate (Herranz et al., 1998). Modification or removal of fire can have a negative impact on species in such ecosystems (Giorgis et al., 2021; Abreu et al., 2017). For example, fire suppression measures in tropical and subtropical grasslands and savannas can support the emergence of shrubs and tree species (Case & Staver, 2016; Stevens et al., 2016). Despite having the potential to develop into forests, vast areas of tropical and subtropical regions are maintained as grasslands and savannas due to fire (Beckage et al., 2011).

Fires are historically rare in tropical and subtropical moist forests and are dominated by fire-sensitive species (Cochrane & Schulze, 1999; Giorgis et al., 2021). Over the past few decades, an increase in droughts and El Niño occurrences, along with selective logging and deforestation, has led to a rise in wildfires in tropical rainforests (Aragão et al., 2018; Asner et al., 2010; Cochrane, 2003). In such forests, species recovery following a fire can be much slower than in biomes that traditionally experience fire (Nelson et al., 2014). Consequently, fires are a primary driver of tropical moist forest degradation and biodiversity loss (Barlow et al., 2019; Lewis et al., 2015). Frequent fires can transform humid tropical forests into savannas over time (Flores & Holmgren, 2021).

The impact of a fire can vary on taxonomic, phylogenetic, and functional diversity metrics; however, it also depends on the ecological landscapes and life forms (de L Dantas et al., 2013). In tropical forests, loss of species richness is expected to be lower than losses in phylogenetic and functional diversity (Rosell et al., 2014). Nóbrega et al. (2019) reported that woody species' functional and phylogenetic diversity reduced greatly after a fire compared to their taxonomic diversity. This is because plant functional traits show a different response to fire (Kelly & Brotons, 2017; Brando et al., 2012). Trees with thick barks (Brando et al., 2012) and herbaceous species with belowground meristem can endure and remain alive in a fire (Loiola et al., 2010). Conducting research on phylogenetic and functional diversity on top of taxonomic diversity in various ecological landscapes could offer a further understanding of how fires impact the plant diversity in a specific ecosystem (Cianciaruso et al., 2012; Nóbrega et al., 2019).

Plants play a vital role in the terrestrial ecosystem by providing food and resources and supporting ecological phenomena. The impact of fire on plants may vary according to the life forms, which can have different recovery responses to fire (Maginel et al., 2019; Foster et al., 2018; Peterson & Reich, 2008). For example, herbaceous species, e.g., forbs and grasses, often recover much quicker from fire than woody trees and shrubs due to traits such as shorter generation times and faster growth rates (Peterson & Reich, 2008; Machida et al., 2021). Moreover, Fires can strongly impact community composition by generating species turnover (i.e., beta diversity) across multiple life forms (Gordijn et al., 2018; Durigan et al., 2020; Peterson & Reich, 2008).

1.3 Strategies to reduce fire risk and impacts on biodiversity

Arguably, one of today's biggest challenges is unprecedented rates of biodiversity loss, which is further exacerbated by climate change. The last five hundred years have seen the extinction or increased likelihood of extinction of one-third of biodiversity (Isbell et al., 2022). The recovery of biodiversity after a fire is a complicated process that relies on several factors, including habitat fragmentation, invasive species, herbivory, and climate changes (He et al., 2019; Blackhall et al., 2017).

As the fire regime is controlled by climate, the change in the climate also changes the fire regime (Lamont, 2022). These changes will likely increase the frequency and severity of wildfires (Flannigan et al., 2013; IPCC Core Writing Team, 2014). Hence, it is very important to forecast potential fire occurrences in different climate change scenarios and land management approaches (Bowman et al., 2014).

Reducing carbon emissions as a climate change mitigation strategy and decreasing the amount of land use help limit the predicted rise in wildfires in the future; even if emissions are not sufficiently reduced, reducing the intensity of land use alone can still effectively mitigate fires during moderate climate change (Le Page et al., 2017). However, it may not be enough to prevent severe wildfire outbreaks in extreme climate scenarios (Le Page et al., 2017). Moreover, incorporating fire management strategies into national plans for preserving biodiversity and adhering to global agreements such as the UN Convention on Biological Diversity can significantly enhance conservation efforts (Kelly et al., 2020).

Since fire cannot be avoided entirely in most ecosystems worldwide, some theories have been proposed to maximise the benefit of fire on biodiversity. Pyrodiversity or patch mosaic burn (PMB) theory describes the process of applying a variation of fires (e.g., time since fire, frequency, intensity) in a landscape that can maximise the biodiversity, often called “pyrodiversity begets biodiversity” (Parr & Andersen, 2006). Similarly, the intermediate disturbance hypothesis (IDH) suggests that a moderate level of disturbance promotes biodiversity more than low or high levels of disturbance (Connell, 1978) because low levels of disturbance can result in competition and exclusion among taxa, while high levels can cause species to become extinct (Osman, 2015). However, based on scientific evidence, the PMB or IDH may not be effective in predicting the diversity of vertebrates (Pastro et al., 2014) and termites (Davies et al., 2012). These theories can be applicable in areas with a long history of burning, and any biodiversity benefits of fire may be restricted to such biomes (Parr & Andersen, 2006). Adverse biodiversity impacts of fire are more likely to arise in biomes that traditionally rarely experience fire, such as tropical and subtropical moist forests (Lewis et al., 2015; Cochrane, 2003).

Prescribed fire or burning is a fire management tool applied under specific weather and fuel conditions (Hiers et al., 2020) to manage forest species and habitats and reduce fuel loads to avoid wildfire (Penman et al., 2020; Bennett et al., 2010; Ryan et al., 2013). In some cases, prescribed fires are used as a substitute for wildfire to get the benefit of wildfire (Pausas & Keeley, 2019). However, the prescribed burn's efficacy over wildfire remains controversial (Bell & Oliveras, 2006). Pastro et al. (2011) and Nesmith et al. (2011) identified that the impact of prescribed fire versus non-prescribed is not different.

In recent decades, numerous policies and frameworks, such as the Convention on Biological Diversity (CBD), The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), Sustainable Development Goals (SDG), and Millennium Ecosystem Assessment (MEA), have been formulated and implemented to preserve and sustain biodiversity. However, party members of these policies are not obligated to follow these policies. Further, they have not significantly improved the situation of biodiversity and, in some instances, have worsened. An example of biodiversity conservation goals is the Aichi target of 2020. In 2010, 20 goals were envisioned to prevent biodiversity loss to value, conserve, restore, and wisely use biodiversity by 2020. This vision is meant to sustain a healthy planet and benefit everyone by maintaining ecosystem services (CBD, 2010). Despite the rise in efforts to preserve biodiversity through policies and actions, the indicators show a further decline in biodiversity from 2011 to 2020. Regrettably, none of the 20 Aichi Biodiversity Targets agreed upon by Parties to the CBD in 2010 have been fully met globally (IUCN, 2022).

The ability of species and ecosystems to recover after a fire depends on the level of disturbance they experience. Protected areas effectively prevent land clearance and reduce activities such as logging, hunting, fire, and grazing (Bruner et al. 2001). Protected areas, where resources are managed strictly, typically experience less disturbance, allowing for faster recovery from disturbances than non-protected areas (Rodrigues et al., 2004). However, the effectiveness of protected areas in reducing the impact of fires on biodiversity is uncertain because protected area management often fails to reduce fire risk compared to nearby unprotected areas (Busch & Ferretti-Gallon, 2017; Laurance et al., 2012). It is important to note that some reports suggest fires in protected areas can even decrease species diversity (White et al., 2011; Roman-Cuesta & Martinez-Vilalta, 2006). One possible explanation is that fire suppression measures are implemented in protected areas, causing the formation of communities that are more susceptible to fires compared to those residing in unprotected areas (Barber et al., 2004; De Groot et al., 2009), but no consensus has yet been reached regarding the extent to which protected area status is associated with species responses to fire.

1.4 Thesis aim and overview

The central aim of this thesis is to assess the impact of fire and post-fire recovery of plant biodiversity in tropical and sub-tropical regions by examining how fire metrics (fire type and time since fire) responses in the plant community vary in protected and non-protected areas and across tropical and subtropical biomes. We evaluate this across four key life form groups: trees/shrubs, forbs, graminoids, and climbers. We focus on plant diversity because it comprises a wide range of life forms and life history strategies and provides the habitat structure and resources other taxonomic groups exploit (Corlett, 2016). It also plays a key role in ecosystem services, including carbon sequestration and climate change (Daba & Dejene, 2018). First, I searched the literature and selected the studies that met my selection criteria. In total, there were 28 studies included in the final set. These studies comprised 101 control (unburnt) and treatment (burnt) sites and 5311 observations. An observation was counted each time a species was found in a burnt or unburnt plot. These datasets are the foundation of the data for all data chapters (2, 3, & 4) to see whether fire impacts are similar or different among taxonomic, phylogenetic, and functional diversity. In the last chapter (5), I evaluated the results from the three data chapters together.

Chapter 2: This chapter focuses on the impact of fire on taxonomic diversity. While much research in the past has focused on the effects of fire on plant diversity in terms of species richness and abundance, the impact on species turnover and composition has received less attention. This chapter's main objective is to examine fire's impact on species richness and species turnover.

Chapter 3: This chapter focuses on the impact of fire on phylogenetic diversity. Although taxonomic diversity is a popular measure of biodiversity, it fails to fully capture the evolutionary history and its association with biodiversity. Phylogenetic diversity provides additional information on whether the species are closely related or distantly related. I constructed phylogenetic trees for each of the four life form groups. I calculated the impact of fire on three important phylogenetic diversity metrics – Phylogenetic Diversity (PD), Mean Pairwise Distance (MPD), and Mean Nearest Taxon Distance (MNTD) and their standardised effect sizes (SESs).

Chapter 4: This chapter evaluates how fire affects the functional diversity of the trees/shrubs community using trait data obtained from TRY and other global datasets (BIEN, Austraits, BROT). I focused on trees/shrubs because there is insufficient trait data for other life forms. Furthermore, trees/shrubs comprise almost two-thirds of our dataset, making them a significant sample. I analysed dendrogram-based functional diversity (FD) as well as multidimensional space-based functional diversity metrics (Functional richness and Functional turnover) to determine the impact of fire on functional diversity.

Chapter 5: In this chapter, I connect the previous three chapters (Chapters 2, 3, and 4). I discuss, compare, and contrast the findings from these chapters and synthesise the overall outcome of the thesis. Furthermore, I suggest the potential implications of our research and areas for further investigation while also recognising the strengths and weaknesses of my study.

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Chapter Two

A pantropical analysis of fire impacts and post-fire recovery on tropical plant diversity and species composition

CHAPTER 2

A pantropical analysis of fire impacts and post-fire recovery on tropical plant diversity and species composition

Abstract

Fire increasingly drives the loss and degradation of tropical habitats, but factors influencing biodiversity responses to fire are inadequately understood. We conduct a pan-tropical analysis of systematically collated data – 5257 observations of 1705 plant species (trees and shrubs, forbs, graminoids and climbers) in burnt and unburnt plots from 28 studies. We use model averaging of mixed effect models assessing how plant species richness and turnover (comparing burnt and unburnt communities) vary with time since fire, fire type, protected area status and biome type. More long-term studies are needed, but our analyses highlight three key findings. First, prescribed and non-prescribed burns have contrasting impacts on plant communities, the direction of which depends on the focal life-form and biome. Forb richness, for example, increases following non-prescribed (but not prescribed) burns in savannahs and flooded grasslands, but in moist broadleaved forests, forb richness increases strongly following prescribed (but not non-prescribed) burns. Second, protected areas mitigate fire impacts on plant communities. Species richness of trees/shrubs increased (~50%) following fires in non-protected sites but tended to remain similar in protected sites. Similarly, ten years after a fire event, graminoid community composition had recovered fully to resemble non-burnt communities in protected areas but remained highly divergent in unprotected sites. Finally, this persistence in the divergence of community composition following fire events occurs across a number of life forms. The composition of tree/shrub communities remained divergent from unburnt communities ten years after a fire, and the composition of forb communities only returned to those of unburnt sites after ten years. Fire

intervals are already less than ten years in some tropical locations, and future climate and land use changes are predicted to further shorten these intervals. Plant communities across much of the tropics are thus likely to change substantially in response to increased exposure to fire.

2.1 Introduction

Globally, the distribution, seasonality, frequency, and intensity of fires have changed in recent decades due to anthropogenic global change drivers, including climate change, land-use change (with fire often used to clear vegetation to facilitate land-use change) and, in some cases, invasion by more flammable species (McLauchlan et al., 2020; Kelly et al., 2020). These changes are predicted to accelerate over the next few decades (Sheehan et al., 2019; Enright et al., 2015; Aragão et al., 2008). There is particular concern regarding the impacts on fire-sensitive tropical ecosystems, many of which are being rapidly lost and degraded (Alroy, 2017; Busch & Ferretti-Gallon, 2017), making the tropics the epicentre of current and future extinction risk (Edwards et al., 2019). Given these changing fire regimes, it is crucial to understand how fire influences biodiversity and the recovery rate following fire events (Kelly et al., 2020). This need is widely recognised, for example, by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019) and the UNFCC REDD+ program (UNFCC, 2019).

The impacts of fire on biodiversity are, however, complex and incompletely understood (Gill et al., 2013; McLauchlan et al., 2020; Tingley et al., 2016), with positive and negative impacts reported (Kelly et al., 2020; Giorgis et al., 2021). Some tropical biomes, such as woody savannas and grasslands, are frequently exposed to fire, and several species that are characteristic of these biomes require fires to persist (Simon & Pennington, 2012). In such biomes, fire positively influences the diversity of photophilic floras and faunas (Pausas & Keeley, 2019), with a landscape mosaic of vegetation patches that vary in the time since they were burnt typically maximising biodiversity (Driscoll et al., 2010). Long-term suppression of fire in these systems typically generates more homogenous vegetation patches that support fewer species (Giorgis et al., 2021; Abreu et al., 2017), promotes woody species and gradual shifts from grasslands to woody savannas, and then shrublands and forests (Probert et al., 2019).

In other biomes, such as tropical moist forests, fire is historically extremely rare, and most plant species are susceptible to fire (Cochrane & Schulze, 1999; Giorgis et al., 2021). Consequently, recent increases in the number of fires are a primary driver of tropical moist forest degradation and biodiversity loss (Barlow et al., 2019; Lewis et al., 2015), including tree (Galvao de Melo & Durigan, 2010; Cochrane & Schulze, 1999) and forb communities (Gordijn et al., 2018). Increased exposure to fire can also eventually convert moist tropical forest ecosystems into open habitats and savannas (Flores & Holmgren, 2021).

Biodiversity will gradually recover following a fire event and should increasingly resemble the pre-fire community as time increases (Machida et al., 2021). Frequent fire events can, however, prevent full recovery by driving fire-sensitive species to regional extinction (Gallagher et al., 2021), and species recovery following a fire can be much slower in fire-sensitive biomes than those that traditionally experience fire (Nelson et al., 2014). Understanding of how biodiversity recovers following fire events is, however, still insufficiently developed. In part, this is because many studies of biodiversity responses to fire focus exclusively on species richness, even though fires have strong impacts on community composition and generate considerable turnover, i.e., beta diversity (Gordijn et al., 2018; Durigan et al., 2020, Peterson & Reich, 2008). The influence of landscape context on biodiversity recovery following fire is also insufficiently understood. Recovery rates are likely to be faster within relatively intact ecosystems (i.e., effectively protected from anthropogenic stressors) in which a greater abundance of natural vegetation increases the availability of propagules that can recolonise burnt sites. Well-managed protected areas may thus facilitate faster recovery from fires, although tropical protected areas vary greatly in their effectiveness, including in reducing fire risk (Laurance et al., 2012).

Most studies assessing fire impacts on plant biodiversity focus on single study locations. Meta-analyses are scarce but have assessed the relative fire sensitivity of native and exotic plant species (Jauni et al., 2015; Alba et al., 2014; Aslan & Dickson, 2020). Here, we build upon a systematic compilation of data from published studies of tropical and sub-tropical plant community responses to fire. We work on plants as they comprise a wide range of life forms and life history strategies and provide the habitat structure and resources that are exploited by other taxonomic groups. We assess post-fire recovery of plant species richness and composition following fire events. Specifically, we test whether species richness and beta diversity (i.e., species turnover) between burnt and unburnt plots respond differently to time since fire and fire type (prescribed burns versus non-prescribed burns). We also assess if protected area status (protected vs. unprotected) moderates the responses of species richness and species turnover to fire events. Our analyses take biome identity into account and distinguishes between prescribed and non-prescribed burns. We do so as prescribed burns are often used in management programmes to reduce the amount of flammable material and, thus, the size and intensity of subsequent fires. The practice has, however, been criticised (Ryan et al., 2013), with some studies suggesting that prescribed burns can alter plant communities in a manner similar to non-prescribed burns (Ffolliott et al., 2012; Pastro et al., 2011).

2.2 Methods

2.2.1 Literature search

A systematic literature search was conducted following the PRISMA guidelines (Liberati et al., 2009; Moher et al., 2009) in January 2020 and updated in March 2023. Three searches were carried out using the 'Web of Science', with the search terms: i) fire* AND "species richness" AND plant*; ii) burn* AND "species richness" AND plant*; and iii) fire*AND "species richness" AND tree*. Our objective was to retain papers that were empirical field-based studies conducted in the tropics or sub-tropics, i.e., 30° north to 30° south (Corlett, 2013), and that provided complete species lists for control (unburnt or sites sampled before a fire) and treatment sites (those with fires). We only selected studies with equal sampling effort in control and treatment sites, as such biases in study design can impact conclusions regarding fire impacts on biodiversity (Kelly et al., 2017).

The data collection process took place in five stages (Table 2.1). After collecting the papers from the initial search, titles were scanned to identify papers that could be used to understand the impacts of fire on plant diversity in tropical and sub-tropical locations. Duplicate papers were removed, and abstracts were then scanned. Papers were only accepted if the study met our criteria of being an empirical field-based study located in the tropics or sub-tropics. We then read each paper in full and removed those for which sampling effort was uneven across control (unburnt) and treatment (burnt) sites or did not provide a complete species list for each type of site. A list of retained papers is given in **Supplementary Materials, Appendix 1**.

Table 2.1: The selection stages, procedure, and total number of papers obtained in the literature search.

Selection Procedure	Number of papers
1. Papers yielded from initial search	8970
2. Papers left after scanning titles	1431
3. Papers left after removing duplicates	1065
4. Papers left after reading the abstract	460
5. Papers left after reading in full and checking selection criteria are met	28

2.2.2 Data extraction & quality control

The final set of 28 studies contained 101 pairwise control (unburnt) and treatment (burnt) plots and 5311 observations, where one observation equates to a species being present in a burnt or unburnt plot (**Supplementary Materials, Table S1**). Some studies reported changes in tree and shrub communities but used plot sizes that are widely considered too small for accurate estimates of the species richness of these groups as the plots could only contain one or two mature individuals of these life forms. We thus did not include observations for calculating tree species richness when plots were less than 100 m^2, or for shrub species richness when plots were less than 16 m^2 (see Mueller-Dombois et al., 2008). Most studies (n = 24; 85 %) provided their study site's latitude and longitude but when these were not provided, they were obtained using the description of the study site location and the online tool https://www.latlong.net/. Not all studies provided data on species' abundances (density or percentage cover), so we converted data into a presence/absence matrix for each burnt and unburnt site.

From each study, we extracted data on two fire metrics – time since fire (number of years between the most recent fire and sampling period), and fire type (prescribed or non-prescribed burns). We defined each site as protected if it was within the boundaries of a protected area (IUCN categories I to VI) as defined by the World Database on Protected Areas (WDPA) database (UNEP-WCMC & IUCN, 2020).

Biomes were classified according to Olson et al. (2001) as i) Tropical and Subtropical Moist Broadleaf Forests (TSMBF; 5 papers & 1846 observations) ii) Tropical and Subtropical Dry Broadleaf Forests (TSDBF, 6 papers & 859 observations) iii) Tropical and Subtropical Coniferous Forests (TSCF, 1 paper & 31 observations), iv) Tropical and Subtropical Grasslands, Shrublands & Savannas (TSGSS, 13 papers and 2433 observations) and v) Flooded Grasslands and Savannas (FGS, 3 papers and 142 observations).

2.2.3 Standardising taxonomy and life form classification

Species, genus, and family names were standardised according to The Plant List, R packages *Taxonstand* version 2.4 (Cayuela et al., 2012) and The World Flora, R package *WorldFlora* version 1.10 (Kindt, 2020). Species that differ in their life-history strategies, especially plants, can exhibit divergent recovery responses to fire (Maginel et al., 2019; Foster et al., 2018; Peterson & Reich, 2008). Forbs and grasses, for example, often recover much quicker from fire than tree species due to traits such as shorter generation times and faster growth rates (Peterson & Reich, 2008; Machida et al., 2021). There is also much inter-specific variation in plant species' responses to fire within life forms (Simpson et al., 2020; Trouvé et al., 2021). Hence, we then classified each species to one of nine life forms: tree/shrub, forb, climber, graminoid, fern, succulent, lichen, and moss using eight datasets from the TRY database (Kattge et al., 2020); Botanical Information and Ecology Network (BIEN) database in R using the package *BIEN*, version 1.2.6 (Maitner et al., 2017) and AusTraits, a curated plant trait database for the Australian flora using the package *aurstraits* in R (Falster et al., 2021). This allowed us to classify 88 % of species; the remaining species were classified using authenticated online sources or the life-form classification used in the original study (**Supplementary Material, Table S2**). Ferns, succulents, lichens, and mosses were excluded from further analysis as they were recorded in too few studies (fewer than five). A list of plant groups and the number of i) studies that recorded them, ii) observations and iii) species recorded is presented in **Supplementary Material, Table S3.**

2.2.4 Biodiversity metrics

We calculated two response variables (relative species richness – alpha diversity; beta-diversity - pairwise dissimilarity) for each of the four analysed life forms, i.e., trees/shrubs, forbs, graminoids, and climbers. Relative species richness was calculated following Burivalova et al., (2014) as the total number of species in the burnt site divided by the total number of species in the unburnt site. Consequently, values of one represent situations where fire has no impact on species richness, values less than one represent situations where fire reduces species richness, and values greater than one represent situations where fire increases species richness.

Species turnover (beta diversity) was calculated as Sørensen pairwise dissimilarity index (Sørensen, 1948), which is widely used to measure the spatial turnover for presence/absence data in ecology and is independent of species richness (Koleff et al., 2003; Socolar et al., 2016). A value of 0 means the composition of two communities is identical, and a value of 1 means the two communities do not share any species in common.

2.2.5 Data analysis

All analyses were conducted in R 4.2.2 (R Core development team, 2023). Continuous variables were centred prior to analysis, and we used the equivalent sum to zero contrasts approach for categorical variables (Schielzeth, 2010). Centering variables reduces problems that otherwise arise with model averaging when interaction terms are included as predictors (Schielzeth, 2010; Cade, 2015; Tyre, 2017). We modelled relative species richness and Sørensen index of i) trees/shrubs, ii) forbs, iii) graminoids, and iv) climbers using linear mixed-effects methods with study ID as a random effect, using the lme4 package (Bates et al., 2015).

In all cases, models had Variance Inflation Factors (VIF) less than 10, indicating that results are not markedly impacted by collinearity between predictors (Hair et al., 1992; Craney & Surles, 2002). We also checked for the linearity of responses by including square terms and comparing the model fit to equivalent models that only included a linear term. The fit of all models was also checked using model diagnostic plots.

We constructed all possible ecologically realistic models (n = 32; **Supplementary Materials, Table S4**) given our suite of predictor variables, i.e., time since fire (years; ln transformed), fire type (fixed factor: prescribed/non-prescribed burns), biomes (fixed factor: TSMBF, TSBDF, TSCF, TSGSS & FGS), and protection status (fixed factor: protected/non-protected). We included interaction terms between each of our two fire metrics (time since fire, and fire type) and i) biomes, and ii) protection status to test whether biome type or protected area status moderated the relationships between each fire metric and our outcome variables.

We used D^2 as a measure of explanatory capacity; $D^2 = (ND - RD)/ND$ where ND is the null deviance, and RD is the residual deviance, which cannot be explained by the models thus, 'ND–RD' is the explained deviance. D^2 varies between zero and one and equals one when the deviance can be explained completely by the model (Guisan & Zimmermann, 2000).

We used an information-theoretic criterion approach to obtain a set of models whose Δ AICc values were within two points of the best-performing model, i.e., that with the lowest AICc value, and then conducted model averaging (Burnham & Anderson, 2004).

2.3 Results

2.3.1 Study locations

Our final set of 28 studies were located across the tropics (n = 22) and sub-tropics (n = 6), although studies from South America (n=10) and Australasia (n = 7) dominated (Fig 1). Five studies were in the Tropical and Subtropical Moist Broadleaf Forests (TSMBF), six in the TSDBF (Tropical and Subtropical Dry Broadleaf Forests), one in TSCF (Tropical and Subtropical Coniferous Forests), 13 in the TSGSS (Tropical and Subtropical Grasslands, Shrublands and Savannas), and three in the FGS (Flooded Grasslands and Savannas) biomes (Fig 2.1).

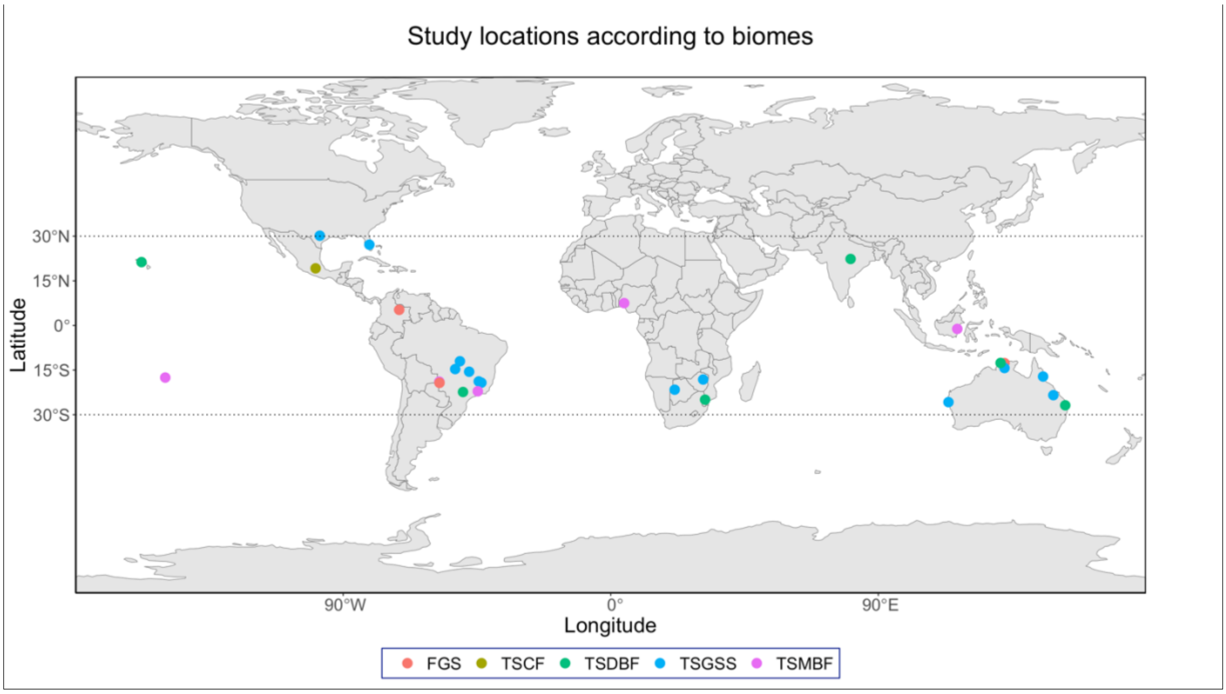

Fig 2.1 Study locations coded by biomes. FGS (Flooded Grasslands and Savannas); TSCF (Tropical and Sub-tropical Coniferous Forests); TSDBF (Tropical and Sub-tropical Dry Broadleaf Forests); TSGSS (Tropical and Sub-tropical Grasslands, Shrublands and Savannas); and TSMBF (Tropical and Sub-tropical Moist Broadleaf Forests). The dotted lines show the boundary of the sub-tropical zone.

2.3.2 Relative species richness

Models of the relative species richness of trees/shrubs in burnt and unburnt plots had limited explanatory power (i.e., 5.78%), and model averaging revealed that the 95% confidence intervals of most parameter estimates overlapped zero (Table 2.2). Protection status did, however, influence the relative species richness of trees/shrubs – with species richness increasing at burnt sites relative to unburnt controls in unprotected sites, whilst within protected sites, species richness was more similar in burnt and unburnt sites (Table 2.2; Fig. 2.2a).

Table 2.2: Results from model averaging across multiple regression models of relative species richness in burnt sites relative to control (unburnt) sites for trees/shrubs, forbs, and climbers. Results for graminoids are not included as no model had a lower AICc than the null model (i.e., one that lacked predictors). Parameter estimates are provided with 95% confidence intervals in brackets. FGS (Flooded Grasslands and Savannas); TSCF (Tropical and Sub-tropical Coniferous Forests); TSDBF (Tropical and Sub-tropical Dry Broadleaf Forests); TSGSS (Tropical and Sub-tropical Grasslands, Shrublands and Savannas); and TSMBF (Tropical and Sub-tropical Moist Broadleaf Forests).

	Life Forms		
	Trees/Shrubs	**Forbs**	**Climbers**
Predictors	**Parameter estimate (95 % CI)**		
Fire Type (Non-prescribed)	-0.051 (-0.264, 0.162)	-0.071 (-0.267, 0.141)	-0.365 (-0.672, -0.057)
Protection Status (Non-protected)	0.245 (0.008, 0.482)		0.077 (-0.188, 0.344)
Biomes (FGS)	-0.046 (-0.446, 0.354)	0.959 (0.528, 1.392)	--
Biomes (TSCF)	1.010 (-0.330, 2.352)	-0.417 (-1.051, 0.232)	--
Biomes (TSDBF)	-0.195 (-0.552, 0.161)	-1.272 (-1.667, -0.871)	--
Biomes (TSGSS)	-0.370 (-0.875, 0.134)	-1.252 (-1.574, -0.921)	--
Fire Type (Non-prescribed): Biomes (FGS)	--	2.821 (2.268, 3.362)	--
Fire Type (Non-prescribed): Biomes (TSDBF)	--	0.380 (-0.020, 0.769)	--
Fire Type (Non-prescribed): Protection Status (Non-protected)	0.023 (-0.123, 0.171)	--	--
Model Explanatory Power (D^2)	**5.78 %**	**41. 74 %**	**5.17%**

Models of forb relative species richness in burnt and unburnt plots had much higher explanatory power (i.e., 41.74%) than models for other life forms (Table 2.2). Model averaging revealed interactions between biome type and type of fire. In flooded grasslands and savannas, forb species richness increased in plots experiencing non-prescribed burns relative to unburnt controls, with species richness being more similar in burnt and unburnt controls following prescribed burns (Table 2.2; Fig. 2.2b). In contrast, in moist broadleaved forest prescribed burns increased forb species richness relative to unburnt controls, whilst non-prescribed burns resulted in similar species richness in burnt and unburnt controls (Table 2.2; Fig. 2.2b).

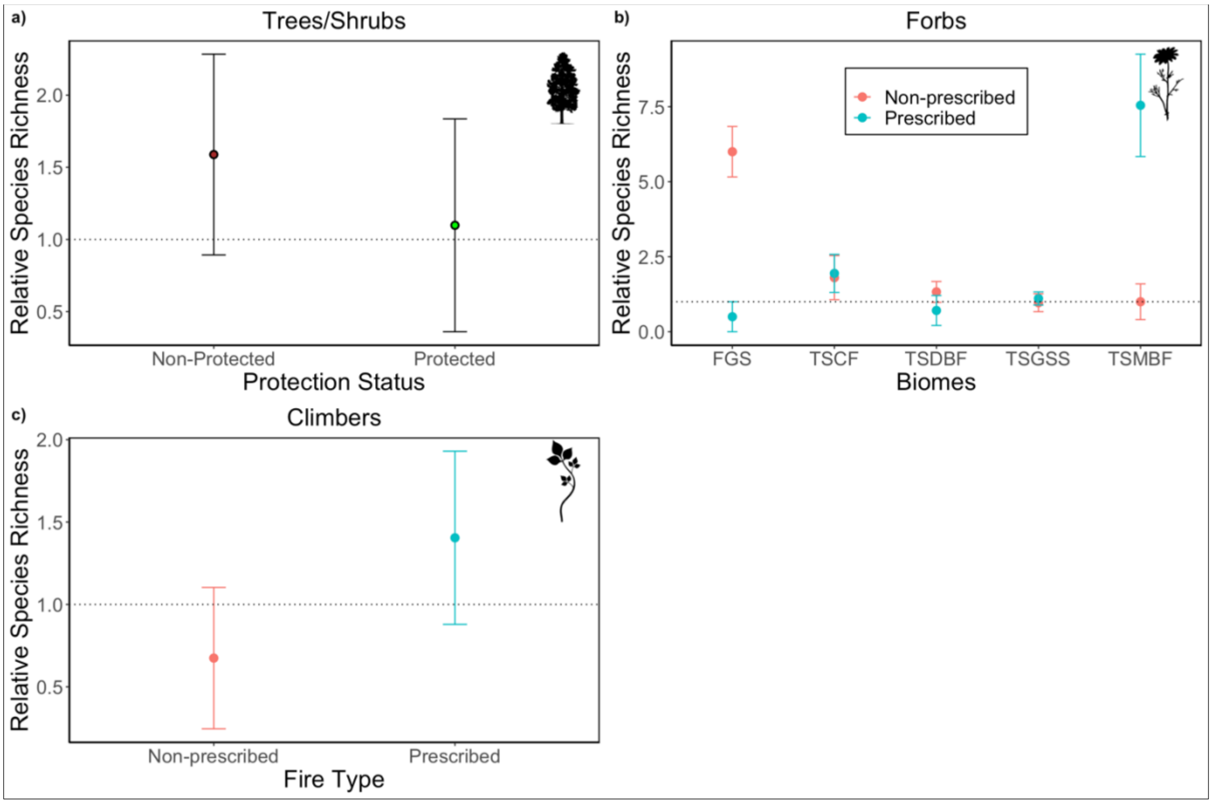

Fig 2.2. Impact of fire on relative species richness (species richness in burnt sites divided by richness in the control sites a) Trees/Shrubs (Non-Protected (n =34), Protected (n = 46), b) Forbs: FGS (n = 5), TSCF (n = 2), TSDBF (n =12), TSGSS (n = 40), TSMBF (n = 2) and c) Climbers (Non-prescribed (n =33), Prescribed (n =27). The error bars represent the 95% confidence interval. The dotted lines represent a relative species richness of 1, i.e., equal species richness in both burnt and unburnt plots.

Models of the relative species richness of climbers in burnt and unburnt sites also had relatively limited explanatory power (i.e., 5.17%), with model averaging revealing that prescribed burns resulted in climber richness increasing in burnt plots relative to unburnt ones, whilst non-prescribed burns resulted in species richness declining in burnt sites relative to unburnt controls (Table 2.2; Fig. 2.2c). The best model of graminoid relative species richness had a higher AICc (88.90) than that of the null model, which lacked predictors (AICc 86.97).

2.3.3 Species turnover

Models of turnover in species composition of tree/shrub, forb and graminoid communities between burnt and unburnt plots consistently had good explanatory power, which (except for forbs) was higher than equivalent models of relative species richness (trees/shrubs: 32.99 %, forbs: 27.60%, and graminoids: 64.95%). Dissimilarity in species composition of tree/shrub and forb communities was initially marked (Table 2.3; Fig.2.3a, 3b).

Table 2.3: Results from model averaging across multiple regression models of species turnover for trees/shrubs, forbs, and graminoids. Results for climbers are not included as no model had a lower AICc than the null model (i.e., one that lacked predictors). Parameter estimates are provided with 95% confidence intervals in brackets.

	Life Forms		
	Trees/Shrubs	**Forbs**	**Graminoids**
Predictors	**Parameter estimate (95 % CI)**		
Time Since Fire (ln transformed)	-0.059 (-0.117, -0.001)	-0.155 (-0.235, -0.076)	-0.102 (-0.160, -0.044)
Protection Status (Non-protected)	--	--	-0.027 (-0.141, 0.084)
Time Since Fire (ln): Protection Status (Non-Protected)	--	--	0.115 (0.051, 0.176)
Model Explanatory Power (D^2)	**32.99 %**	**27.60 %**	**64.95 %**

The composition of forb communities had returned to that of pre-fire communities approximately ten years after a fire (Fig. 2.3b), the composition of tree and shrub communities remained dissimilar to that of pre-fire communities ten years after the fire event (Fig. 2.3a).

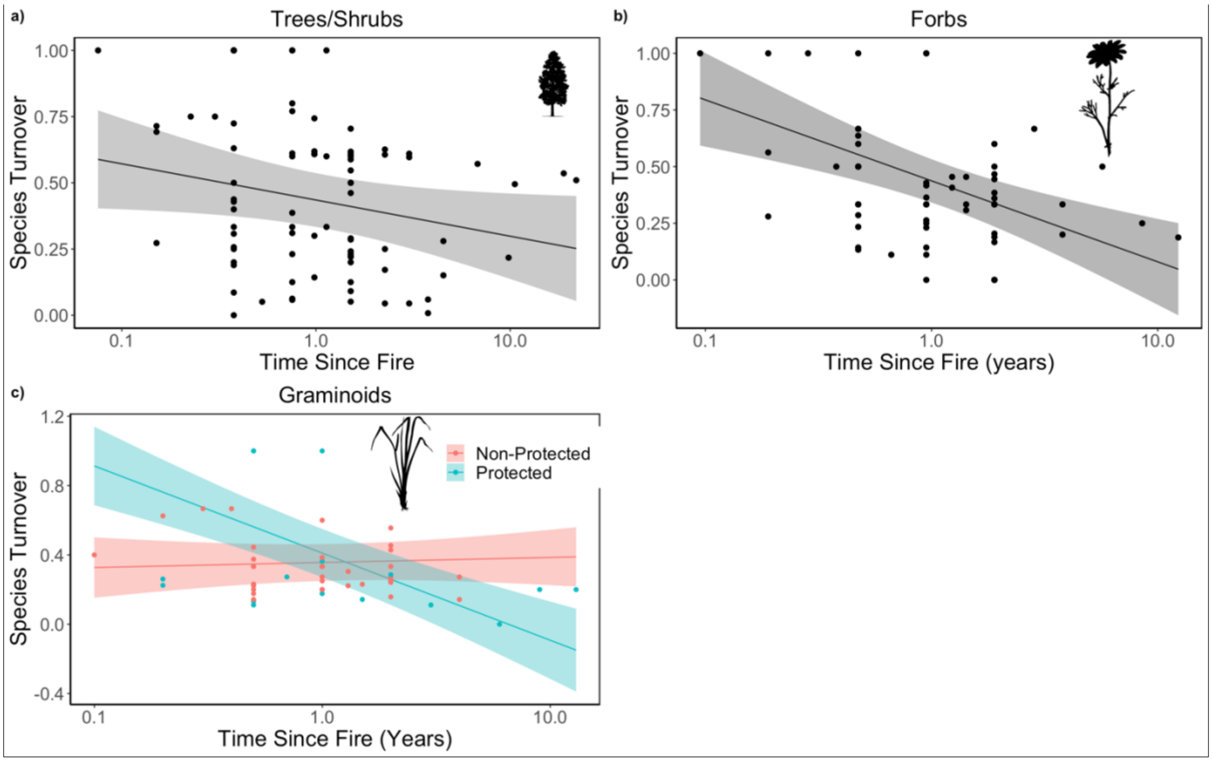

Fig 2.3. Impact of fire on species turnover between burnt and unburnt sites on a) Trees/Shrubs, (n = 84), b) Forbs (n = 61), and c) Graminoids: Non-protected (n = 40), Protected (n =16). Each point represents the number of sites. The X-axis is plotted on a log scale. The shaded area represents the 95% confidence interval.

Within protected areas, graminoid communities exhibited marked turnover immediately following fire events, but these communities resembled pre-fire communities ten tears after the fire event (Table 2.3; Fig. 2.3c). Turnover in graminoid species composition in non-protected areas was much lower immediately after a fire than in non-protected areas, but this dissimilarity increased slightly over the ten years following a fire (Fig. 2.3c). Species turnover in the composition of climber communities did not appear to be associated with any of our predictor variables as the best model had a higher AICc (79.27) than the null model which lacked predictors (AICc 78.14).

2.4 Discussion

Fire has played an important role in shaping tropical biodiversity for millennia (Kelly et al., 2020), with studies reporting contrasting impacts on biodiversity (Kelly et al., 2020; He et al., 2019). To explain this heterogeneity, we analysed a systematic compilation of data quantifying species richness and community composition responses to fire in tropical communities of major plant life forms. Our analyses account for variation across biomes, quantify responses to time since fire and fire type (prescribed or non-prescribed burns), and assess if protected area status modifies plant community responses.

Despite conducting a comprehensive literature search, we only found 28 studies that met our data analysis requirements. There is thus a clear need for additional empirical fieldwork that assesses plant community responses to fire; such studies should follow the open science principles of making underlying datasets freely available to facilitate meta-analyses. Our focal studies included ones that assessed biodiversity recovery up to twenty-nine years following fire events, but most studies were conducted within ten years of a fire event. Given that we find plant community composition can remain impacted by fires ten years after they occur (see below discussion), there is a particular need for long-term (> ten years) longitudinal studies. Our results indicate that changes in species richness and recovery of community composition following fire events vary across plant life forms. This heterogeneity across life forms suggests that apparent contradictions in the published literature regarding the impacts of fire on plant communities may arise from variations in which life forms dominate the focal plant communities. We thus encourage future studies to take this into account in their study design and interpretation. Despite the limitations of data availability and duration of studies, our analyses provide important novel preliminary insights regarding biodiversity responses and recovery from fire events.

2.4.1 Variation across biomes

Some biome types are poorly represented within our dataset, further underlining the need for additional field studies. Our analyses, however, reveal divergent responses of forb species richness to fire events depending on the biome in which they are located, with these relationships being moderated by fire type (prescribed burn or non-prescribed burn) that may be related to the biome's historical exposure to fire (see below discussion of fire type effects). Species richness and community composition of other life forms exhibited similar responses to fire across our focal biome types. Our results thus support evidence that the increasing frequency of fire events across the tropics can influence plant communities and other taxonomic groups across a wide range of habitat types (Feng et al., 2021; Kodandapani et al., 2004), including ones which traditionally experience fire (Andersen et al., 2005, Corey et al., 2019).

2.4.2 Protection status

The role of protected areas in limiting adverse impacts of fire on biodiversity is often considered to focus on reducing fire risk rather than mitigating impacts once a fire occurs (Eklund et al., 2022; Kearney et al., 2020). Indeed, there is concern that fire suppression in protected areas can result in a substantial accumulation of flammable material that increases adverse ecological consequences of fires when they arise and encourage the formation of communities that are more sensitive to fire than areas lacking protection (De Groot et al., 2009; Pereira et al., 2012). We find, however, that protected areas have an stabilising influence that can limit the magnitude of fire-induced changes in plant communities. Species richness of trees/shrubs increased (~50%) following fires in non-protected sites but tended to remain similar in protected sites. Similarly, graminoid community composition resembled that occurring at unburnt control sites approximately ten years after a fire event in protected sites, yet unprotected sites, graminoid communities remained highly divergent from those in control sites ten years after a fire. Whilst tropical protected areas are not always managed as effectively as possible (Laurence et al., 2012), our results suggest that protected areas can reduce the impacts of fire on tropical plant communities and promote more rapid recovery due to having low anthropogenic pressure (Geldmann et al., 2019) and suitable ecological conditions for the diverse community (Gray et al., 2016). Accelerated recovery will be expected if unburnt areas within protected sites enable faster re-colonisation of burnt patches than in unprotected landscapes in which the distance to large intact habitat patches is greater (Gray et al., 2016). Faster recovery in protected areas may also arise due to protection from subsequent human activity following fire events, such as increased grazing, hunting, logging, collecting firewood, etc. (Andam et al., 2008), which enables faster recovery.

2.4.3 Effects of fire type

Previous studies reported that non-prescribed burns, specifically wildfires, and prescribed burns have equivalent effects on plant communities (Ffolliott et al., 2012; Pastro et al., 2011) and survival (Nesmith et al., 2011). Our analyses provide rare evidence that prescribed and non-prescribed fires can have divergent impacts on plant communities.

Prescribed burns increased climber species richness, whilst non-prescribed burns tended to reduce climber species richness. These results extend previous work suggesting reduced species richness of climbers in burnt compared to unburnt plots, irrespective of the fire type (e.g., Addo-Fordjour et al., 2020; Balch et al., 2011). Climbers can play a key role in vegetation dynamics; for example, fire-resilient lianas can protect trees from further fire (Uhl et al., 1988); conversely, lianas are often associated with reduced tree growth rates and higher subsequent mortality (Becknell et al., 2022; Finlayson et al., 2022). Given the roles of climbers in vegetation dynamics and the use of prescribed burns as a conservation tool to reduce the probability of larger, more intense fires, it is important to understand the mechanisms driving the difference in impacts of prescribed and non-prescribed burns. Climbers proliferate in tropical habitats when disturbance events increase light levels or soil nutrients (Magnago et al., 2017), which will happen following a fire. It is plausible that prescribed burns enable this proliferation to occur, increasing climber richness, but the greater intensity of non-prescribed fires (Marshall et al., 2020) limits such proliferation. We also found evidence that in moist broad-leaved forests, prescribed burns increased forb species richness whilst non-prescribed burns had negligible impact on it. Such patterns may also be driven by prescribed burns beneficially altering abiotic conditions for forbs, but greater intensity of non-prescribed burns preventing forb communities from benefitting from these conditions. It is unclear why the opposite pattern, increased forb richness following non-prescribed burns and negligible impact of prescribed burns, occurs in flooded grasslands and savannas - although it may be linked to such biomes having greater historical exposure to fire.

2.4.4 Effects of time since fire

Whilst we find no effects of time since fire on species richness, the species composition of tree/shrub, forb and graminoid communities changes markedly following a fire. Increased species turnover immediately after the fire is likely to be due to the loss of species due to mortality or their inability to tolerate novel environmental conditions (including micro-climates, nutrient and light levels), and the recruitment of new species that favour the altered environmental conditions (Doherty et al., 2017; Kaewsong et al., 2022; Keeley et al., 2005). Biodiversity should gradually recover after a fire event and increasingly resemble the pre-fire community (Machida et al., 2021). In forb communities, recovery tends to be close to completion ten years after a fire event, but recovery of tree/shrub community composition is incomplete after ten years. Moreover, there is no evidence of any recovery in graminoid communities outside protected sites after ten years. The long-term persistence of these compositional changes is probably driven by multiple factors, including the long-term legacy of altered nutrient availability post-fire (Verma et al., 2019), fire-induced reductions in tree growth rates (Bucini & Hanan, 2007), and (especially outside protected areas) altered land-use patterns following fire events (Butsic et al. 2015). Our results underline the need to avoid fire for at least ten years to allow forb communities to recover, and longer for trees/shrubs – and to protect burnt locations from human activities that could disturb regenerating vegetation. It is thus notable that fire return rates in many tropical areas are already shorter than ten years (Archibald et al. 2013), and in some locations, such as the central highlands of Vietnam, have increased in recent decades primarily due to changes in human activity (Nguyen et al. 2023). Indeed, the number of fires in the tropics has increased at ~5% per annum since 2001 (Tyukavina et al., 2022), and is projected to increase further due to both climate change and human activity across a wide range of tropical regions and biomes (Wu et al., 2021; Li et al., 2023). There is, thus, an increasing probability that fire return intervals will decrease to the extent that plant communities will be unable to recover community composition before the next fire occurs, especially in the drier tropical biomes that currently have the shortest fire return intervals (Archibald et al. 2013).

2.5 Conclusions

Our data compilation and analysis of tropical/sub-tropical plant community responses to fire generates important findings that inform knowledge of fire impacts and mitigation strategies and help shape future research agendas. Despite increasing awareness of changing tropical fire regimes, limited studies address plant community responses to key fire features, and long-term longitudinal studies that can quantify recovery times are particularly scarce. More focused research is needed to assess how recovery rates are influenced by landscape composition and configuration. We uncover considerable heterogeneity across plant life forms in their responses to fire metrics and encourage researchers to consider this when reporting fire impact studies. Our research makes four important contributions. First, we uncover evidence that fire impacts on species richness and recovery of community composition can vary with protection status, with protected areas appearing to be able to buffer some plant communities from fire-induced changes. Second, we find that prescribed and non-prescribed burns can vary in their impacts on plant communities, and this should be considered when designing prescribed burning strategies to reduce the risk of larger, more intense non-prescribed fires. Third, there were no differences in fire impacts between fire-adapted and fire-sensitive biomes regarding species richness and community composition of life forms, except in the forb’s community. Finally, and most importantly, we find major shifts in species composition of plant communities, which are often detectable ten years after a fire. Tropical/sub-tropical plant communities thus appear particularly vulnerable to compositional changes from the observed and projected future increases in fire frequency that reduce recovery time between fire events.

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Chapter Three

Impact of fire and post-fire recovery of phylogenetic diversity of tropical and sub-tropical plant communities

CHAPTER 3

Impact of fire and post-fire recovery of phylogenetic diversity of tropical and sub-tropical plant communities

Abstract

Fire plays a significant role in the degradation of tropical forests and the modification of biodiversity. Climate and land use changes have changed fire patterns across the tropics. Although there has been increasing research on how the taxonomic diversity of plant communities is affected by fire responses of plant phylogenetic diversity to fire and its subsequent recovery is less well explored. We address this by conducting a pan-tropical analysis of a systematically collated dataset from 28 studies that contrast plant communities (trees and shrubs, forbs, graminoids and climbers) in burnt and unburnt controls, assessing how phylogenetic diversity of plant communities vary with time since fire and fire type (prescribed vs non-prescribed), and how protected area status and biomes moderate fire impacts. We used six metrics of phylogenetic diversity (PD, sesPD, MPD, sesMPD, MNTD, and sesMNTD) to evaluate the effects of fire on the phylogenetic diversity of plant communities in tropical and subtropical regions around the world. We discovered that the sesPD and sesMNTD of the trees/shrubs community experienced an initial increase after the fire. However, over time, they gradually decreased and returned to their pre-fire levels after approximately two years. On the other hand, the graminoid MNTD decreased immediately after the fire and then gradually increased, returning to pre-fire levels after approximately five years.

Furthermore, the occurrence of fire results in greater phylogenetic diversity in trees/shrubs and forbs communities in areas that are not protected compared to those in protected areas. The PD of trees/shrubs increased in burnt plots relative to unburnt plots in non-protected areas, whereas it decreased in burnt plots relative to unburnt in protected areas. Similarly, the PD of forbs increased in burnt plots relative to unburnt in the non-prescribed site of non-protected areas but remained similar to the unburnt plots in the prescribed site of non-protected and both prescribed and non-prescribed sites in protected areas. In addition, trees/shrubs' sesMPD increased in burnt plots relative to unburnt in FGS but decreased in TSMBF, whereas in other biomes, e.g., TSDBF, TSGSS and TSCF, the sesMPD remained similar in both burnt and unburnt control plots. Our research indicates that the shifting fire patterns in tropical areas could significantly impact the phylogenetic diversity of plant communities in the future.

3.1 Introduction

Fire is an important driver of tropical forest degradation and modification of biodiversity (He et al., 2019). Fire occurrence is higher in disturbed and degraded ecosystems than in non-degraded ones of a similar type (Brando et al., 2019). Fire occurrence and severity, and thus impacts, are expected to increase due to climate change and land use in tropical regions (Tyukavina et al., 2022). Additionally, fire size and season are being manipulated in both fire-prone and non-fire-prone ecosystems for economic and social gain (Archibald et al., 2013). Although burned areas in the tropics are decreasing, most of the decrease is from grasslands and savannas, where fire is a natural part of the ecosystem (Jiang et al., 2020). The primary factors causing a decrease in burning within these ecosystems are changes in rainfall patterns and the availability of plant fuel (Jiang et al., 2020).

While fire occurrences are decreasing in grasslands and savannas, they are still increasing in tropical forests due to climate and land use change (Kelly et al., 2020). Climate change, decreased rainfall, and higher temperatures increase fire occurrence in rainforests and adjoining savannas and grasslands (Jiang et al., 2020). These changes in the fire regime are likely to affect community assembly, species recovery, and species composition, posing a threat to biodiversity conservation (Armenteras et al., 2021; Kelly et al., 2020).

Ecologists view fire as an evolutionary force for creating new fire-adapted species (McLauchlan et al., 2020; Archibald et al., 2018). To cope with fire impact, some species develop new traits that allow them to adapt to fire and gradually diverge from their ancestors (He et al., 2019). When fires act as an abiotic filter in an ecological process, they can filter fire-sensitive and select fire-tolerant species (Archibald et al., 2018). As fire frequency increases, fire selects the species with similar traits that are tolerant to fire (Cianciaruso et al.,

2012) because ecologically similar species respond similarly to external disturbances due to having similar traits (Pausas & Verdú, 2010; Pausas et al., 2016). In this context, the study of the impact of fire on phylogenetic diversity may provide more in-depth knowledge of the evolutionary consequences of how plant communities respond to fire (Cianciaruso et al., 2012).

Even though taxonomic diversity is widely studied and considered an important metric in biodiversity and ecological research, it fails to depict the evolutionary linkage of the species coexisting in the community (Donoghue, 2008). Instead, phylogenetic diversity allows the inclusion of evolutionary relations of species in a community (Cavender-Bares & Wilczek, 2003). By measuring the phylogenetic difference between species within a community, phylogenetic diversity provides complementary information and offers comparable evolutionary measures of biodiversity (Miller et al., 2018). Faith (1992) proposed the first measure of phylogenetic diversity (PD) as the combined length of all the branches in a phylogenetic tree, capturing the species present in a community. For example, the phylogenetic diversity of two plots with equal species richness may differ significantly if one has more closely related species (less phylogenetic diversity) and the other has more distantly related species (more phylogenetic diversity) (Qian et al., 2023). More diverse phylogenetic communities usually have greater productivity, contribute to a healthy ecosystem, and are more resilient to environmental change (Cadotte et al., 2009; Webb et al., 2002; Li et al., 2015).

The process of phylogenetic community assembly is determined mainly by the traits that respond to the external environment (Cianciaruso et al., 2012; Mayfield & Levine, 2010). When considering phylogenetic diversity, two important and contrasting processes are considered - phylogenetic clustering and overdispersion (Webb et al., 2002; Pausas & Verdú, 2010). Phylogenetic clustering occurs when phylogenetically similar species are assembled because of environmental filtering or niche conservatism. Phylogenetic niche conservatism (PNC) is the pattern where closely related species inherit ecological traits and, thus, niches from their parental species (Wiens & Graham, 2005).

Alternatively, inter-specific competition, i.e., biotic interaction among species for sharing the niche, could result in competitive exclusion, where the species in a community are more phylogenetically dissimilar than expected by chance (Webb et al., 2002). If competitive biotic exclusion dominates the ecological process, phylogenetic evenness or overdispersion occurs (Donoghue, 2008). However, competitive exclusion is a complicated process, where biotic exclusion may sometimes remove distantly related species rather than closely related ones, even when species niches are phylogenetically conserved (Mayfield & Levine, 2010).

Previous research has shown that the impact of fire on plant phylogenetic diversity varies depending on the fire's characteristics and protection status, as well as the ecosystem's sensitivity to fire. For example, the phylogenetic diversity of plant communities with a longer time since the last fire was found to be higher than those with a shorter time since the last fire in Mediterranean shrublands in Valencia, Spain (Pérez-Valera., 2018) and semi-arid shrublands in Iran (Bashirzadeh et al., 2023). Moreover, Nóbrega et al. (2019) discovered that applying prescribed burning every three years resulted in more phylogenetic diversity of trees than an area burnt annually in a neotropical forest in the Amazonia boundary. In contrast, in protected areas in the Brazilian savanna, a higher frequency of fires increases the phylogenetic diversity of woody plants (Cianciaruso et al. 2012).

To date, there is very limited research on the effects of fire on plant phylogenetic diversity, especially in tropical and subtropical plant communities. As such, using data collected from published literature, we conducted a pan-tropical data analysis on the impact of fire on the phylogenetic diversity of four life form groups (trees/shrubs, forbs, graminoids, and climbers) of plants across the tropics and sub-tropical ecosystem. We examine how phylogenetic metrics, i.e., Phylogenetic diversity (PD), Mean pairwise distance (MPD) and Mean Nearest Taxon Distance (MNTD), respond to fire type (prescribed or non-prescribed burn), and time since fire. In addition, we assess if protected area status and tropical and subtropical biome types moderate the impact of fires on phylogenetic diversity.

3.2 Methods

3.2.1 Literature search

A systematic literature search was conducted following the PRISMA guidelines (Liberati et al., 2009; Moher et al., 2009) in January 2020 and updated in March 2023. Three searches were carried out using the 'Web of Science', with the search terms: i) fire* AND "species richness" AND plant*; ii) burn* AND "species richness" AND plant*; and iii) fire*AND "species richness" AND tree*. Our objective was to retain papers that were empirical field-based studies conducted in the tropics or sub-tropics, i.e., 30^o north to 30^o south (Corlett, 2013), and that provided complete species lists for control (unburnt or sites sampled before a fire) and treatment sites (those with fires). We only selected studies with equal sampling effort in control and treatment sites since biases in study design can impact conclusions regarding fire impacts on biodiversity (Kelly et al., 2017).

The data collection process took place in five stages (Table 3.1). After collecting the papers from the initial search, titles were scanned to identify papers that could be used to understand the impacts of fire on plant diversity in tropical and sub-tropical locations. We removed duplicate papers and read the remaining abstracts. Papers were only accepted for inclusion if the study met our criteria of being an empirical field-based study located in the tropics or sub-tropics. We then read each paper in full and removed those for which sampling effort was uneven across control (unburnt) and treatment (burnt) sites or did not provide a complete species list for each type of site. Some studies reported changes in tree and shrub communities but used plot sizes that are widely considered too small for accurate estimates of the community composition of these larger-sized plants, as the plots could only contain one or two mature individuals of these life forms. We thus did not include observations for trees when plots were less than 100 m^2 or for shrub species richness when plots were less than 16 m^2 (see Mueller-Dombois et al., 2008). A list of retained papers is given in **Supplementary Materials, Appendix 1**.

Table 3.1: The selection stages, procedure, and total number of papers obtained in the literature search.

Selection Procedure	Number of papers
1. Papers yielded from initial search	8970
2. Papers left after scanning titles	1431
3. Papers left after removing duplicates	1065
4. Papers left after reading the abstract	460
5. Papers left after reading in full and checking selection criteria are met	28

3.2.2 Data extraction & quality control

The final set of 28 studies contained 101 pairwise control (unburnt) and treatment (burnt) plots and 5311 observations, where one observation equates to a species being present in a burnt or unburnt plot (**Supplementary Material, Table S1)**. Most studies (n = 24; 85 %)

provided their location's latitude and longitude, but when these were not provided, they were obtained using the description of the study site location and the online tool https://www.latlong.net/. Not all studies provided data on species' abundances (density or percentage cover), so we converted data into a presence/absence matrix for each burnt and unburnt site.

From each study, we extracted data on two fire metrics – time since fire (number of years between the most recent fire and sampling period) and fire type (prescribed or non-prescribed burns). We defined each site as protected if it was within the boundaries of a protected area (IUCN categories I to VI) as defined by the World Database on Protected Areas (WDPA) database (UNEP-WCMC & IUCN, 2020); this was achieved using the *wdpar* R package version 1.3.2 (Hanson, 2020).

Biomes were classified according to Olson et al. (2001) as i) Tropical and Subtropical Moist Broadleaf Forests (TSMBF; five papers & 1846 observations), ii) Tropical and Subtropical Dry Broadleaf Forests (TSDBF, six papers & 859 observations), iii) Tropical and Subtropical Coniferous Forests (TSCF, one paper & 31 observations), iv) Tropical and Subtropical Grasslands, Shrublands & Savannas (TSGSS, 13 papers and 2433 observations) and v) Flooded Grasslands and Savannas (FGS, three papers and 142 observations).

3.2.3 Standardising taxonomy and life form classification

Species, genus, and family names were standardised according to The Plant List, R packages *Taxonstand* version 2.4 (Cayuela et al., 2012) and The World Flora, R package *WorldFlora* version 1.10 (Kindt, 2020). We then classified each species to one of nine life-forms: tree/shrub, forb, climber, graminoid, fern, succulent, lichen, and moss using eight datasets from the TRY database (Kattge et al., 2020); Botanical Information and Ecology Network (BIEN) database in R using the package *BIEN*, version 1.2.6 (Maitner, et al, 2017) and AusTraits, a curated plant trait database for the Australian flora using the package *aurstraits* in R (Falster et al., 2021). This allowed us to classify 88% of species; the remaining species were classified using authenticated online sources or the life-form classification used in the original study (**Supplementary Materials, Table S2)**. Ferns, succulents, lichens, and mosses were excluded from further analysis as they were recorded in too few studies (fewer than five). A list of plant groups and the number of i) studies that recorded them, ii) observations and iii) species recorded are presented in **Supplementary Materials, Table S3.**

3.2.4 Phylogenetic tree

We built a phylogenetic tree of all four life forms (Trees/Shrubs, Forbs, Graminoids and Climbers) at the global and regional species level in R using the V.phylomaker package. The V.Phylomaker is a comprehensive software package developed by Jin & Qian (2019) that contains the sequencing of 74,533 species and all families of vascular plants. This software is an updated version of the mega-tree developed by Smith & Brown (2018), the phylogeny for seed plants (i.e., GBOTB), which includes nearly 80 % of genera of vascular plants in the world (Qian & Jin, 2023). When constructing the tree, we applied "scenario 3" in the V.Phylomaker package. "Scenario 3" is the most widely used approach and can include missing genera or species in the phylogeny by adding them with known branch lengths (Qian & Jin, 2020, 2023).

3.2.5 Phylogenetic diversity metrics

We calculated phylogenetic diversity for Trees/Shrubs, Forbs, Graminoids and Climbers**.** We calculated six phylogenetic diversity metrics in R using the *Picante* package, version 1.8.2

(Kembel et al., 2010). These were: Phylogenetic Diversity (PD), Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD); and their standardised effect sizes, sesPD, sesMPD, sesMNTD, respectively.

Phylogenetic Diversity (PD) is the sum of the entire branch length of a phylogenetic tree in a specific location or group of organisms (Faith, 1992); it thus represents the sum of the evolutionary history present at a site. Mean Pairwise Distance (MPD) is the average value of the phylogenetic distance between all combinations of paired species in a community (Webb et al., 2002). Higher MPD values indicate that species within the community are less closely related (phylogenetically overdispersed). In contrast, lower MPD values mean the species present are closely related (phylogenetically clustered). Mean Nearest Taxon Distance (MNTD) is the average phylogenetic distance between the species of terminal branches that are the closest relative (Webb et al., 2002). Lower MNTD indicates that species in the community are closely related, whereas higher MNTD means species are distantly related.

Observed PD, MPD, and MNTD values tend to correlate with species richness (Swenson, 2014). Hence, we calculated their standardized effect sizes, such as sesPD, sesMPD, and sesMNTD, by comparing the observed value with the null community of equal species richness. We carried out a 999-time randomisation from the regional species pool using the "independent swap" algorithm (Edwards et al., 2017; Gotelli, 2000). Species pools at the regional level were created using our continent-level datasets since local variation in community patterns arises from historical diversification and distribution at continental and geographical levels (Zobel, 2015). All standardised effect sizes (*ses)* metrics were calculated as follows (Swenson, 2014):

Standardised Effect Size (ses) = (Observed-Null)/ SD(Null)

(*Where Observed is the PD of our observed community, Null is the mean PD of the 999 times randomised null community, SD(Null) is the standard deviation of the PD of that null community*)

A negative value of these standardized effect sizes (ses) implies that PD, MPD, and MNTD are lower than expected by chance. This indicates that fire causes more phylogenetic clustering than expected, given the community's species richness (Swenson, 2014). In contrast, a positive value suggests the observed values are greater than expected by chance, given the community's species richness (Swenson, 2014), suggesting fire leads to overdispersion.

We calculated the response variables of six phylogenetic diversity metrics as diversity in burnt relative to unburnt sites. We used a natural log response ratio for relative PD, MPD, and MNTD (Hedges et al., 1999), e.g., Relative PD = log (PD in burnt/PD in unburnt). For *ses*PD, *ses*MPD, and *ses*MNTD, we calculated raw differences between burnt and unburnt sites, e.g., Relative sesPD = sesPD in burnt – sesPD in unburnt (Hughes et al., 2020), because the value of *ses* metrics can be negative. For example, if the burnt plot's *ses* is more negative than the unburnt plot's *ses*, the difference is negative, which shows that burnt plots have lower values than unburnt plots. In both cases, values of zero (0) represent situations where fire has no impact on phylogenetic diversity, negative values represent situations where fire reduces phylogenetic diversity (i.e., phylogenetic clustering), and positive values represent situations where fire increases phylogenetic diversity (i.e., phylogenetic over-dispersion).

3.2.6 Data analysis

All analyses were conducted in R programme language version 4.2.2 (R Core development team, 2023). Time since fire was natural log-transformed (ln) and centred before analysis, and we used the equivalent sum to zero contrasts approach (Schielzeth, 2010) for categorical variables (fire type, protection status and biomes). Centering variables reduces problems that otherwise arise with model averaging when interaction terms are included as predictors (Schielzeth, 2010; Cade, 2015; Tyre, 2017). We modelled all PD metrics of i) trees/shrubs, ii) forbs, iii) graminoids, and iv) climbers using linear mixed-effects methods with study ID as a random effect, using the lme4 package (Bates et al., 2015).

In all cases, models had Variance Inflation Factors (VIF) less than ten indicating that results are not markedly impacted by collinearity between predictors (Hair et al., 1992; Craney & Surles, 2002). We also checked for the linearity of responses by including square terms and comparing the model fit to equivalent models that only included a linear term. The fit of all models was also checked using model diagnostic plots.

We constructed all possible ecologically realistic models (n = 32; **Supplementary Table S4**) given our suite of predictor variables, i.e., time since fire (years; ln transformed), fire type (fixed factor: prescribed/non-prescribed burns), biomes (fixed factor: TSMBF, TSBDF, TSCF, TSGSS, & FGS), and protection status (fixed factor: protected/non-protected). We included interaction terms between our fire metrics (time since fire, and fire type) and i) biomes and ii) protection status to test whether biome type or protected area status moderated the relationships between each fire metric and our outcome variables.

We used D^2 to measure explanatory capacity; $D^2 = (ND - RD)/ND$ where ND is the null deviance, and RD is the residual deviance, which the model cannot explain; thus, (ND–RD)/ ND is the explained deviance. D^2 varies between zero and one and equals one when the model can explain the deviance completely (Guisan & Zimmermann, 2000).

We used an information-theoretic criterion (AICc) approach to obtain a set of models whose Δ AICc values were within two points of the best-performing model, i.e., that with the lowest AICc value, and then conducted model averaging (Burnham & Anderson, 2004).

3.3 Results

3.3.1 Phylogenetic trees

We built a phylogenetic tree of four focal life forms: trees/shrubs (n = 991; Supplementary Material Fig. S1), forbs (n =341; Supplementary Material Fig. S2), graminoids (n =222; Supplementary Material Fig. S3) and climbers (n = 132; Supplementary Material Fig. S4). For all four of our focal life forms, there was no clear clustering within the phylogenetic tree of species with shared responses to fire (Fig 3.1; **Supplementary Materials Table S5**).

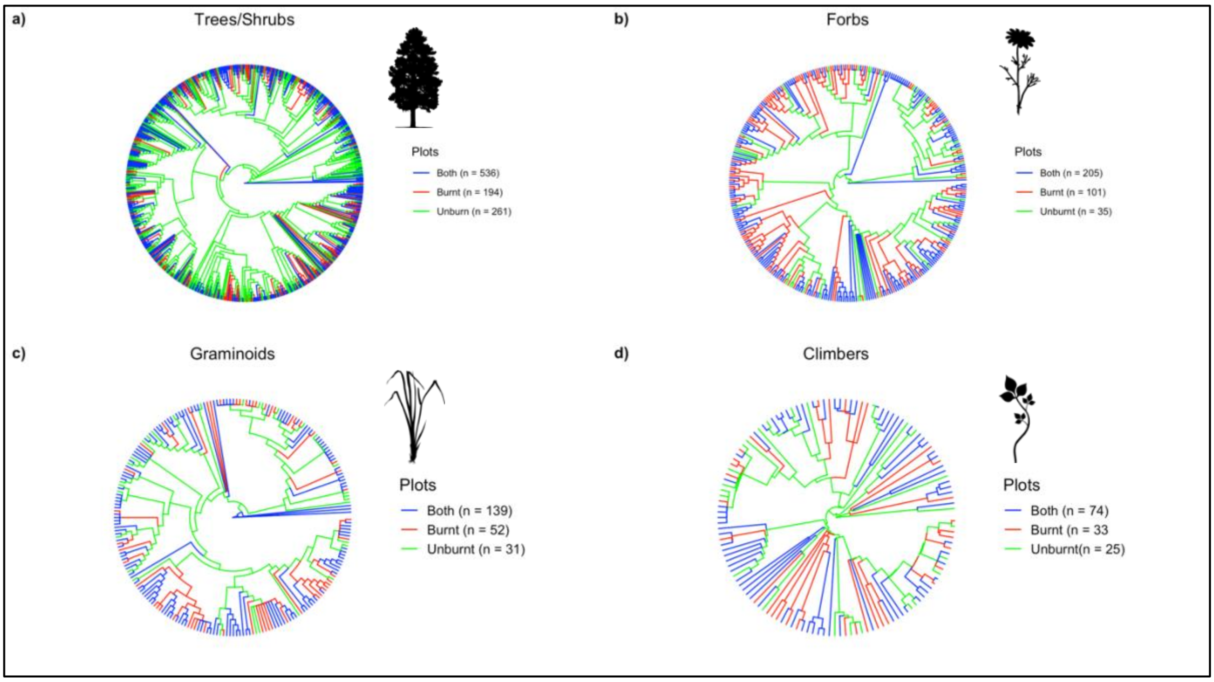

Fig. 3.1. The phylogenetic tree of a) trees/shrubs, b) forbs, c) graminoids, and d) climbers. The tip colour shows species found in burnt (red), unburnt (green) and both (blue) plots. The number of species found in each plot is given in brackets.

3.3.2 Phylogenetic diversity (PD) & sesPD

The model of the relative phylogenetic diversity (PD) of tree/shrub in burnt plots relative to unburnt controls was associated with protection status (D^2 = 12.67 %), with higher values in non-protected sites than in protected sites (Table 3.2). The relative PD was higher in burnt sites relative to unburnt controls in non-protected sites, whereas relative PD was lower in burnt sites relative to unburnt within protected sites (Table 3.2; Fig. 3.2a).

Models of the relative PD of forbs in burnt plots relative to unburnt had higher explanatory power (D^2 = 21.32%) than trees/shrubs; however, the model averaging revealed that 95% confidence intervals of parameter estimates overlapped zero except the interaction between fire type and protection status (Table 3.2). In non-protected sites, relative PD increased in plots experiencing non-prescribed burns relative to unburnt controls, with relative PD being more similar in burnt and unburnt controls following prescribed burns (Table 3.2; Fig. 3.2b). In contrast, in protected sites, prescribed burns increased forb PD in burnt relative to unburnt controls, whereas non-prescribed burns resulted in decreased relative PD in burnt and unburnt controls (Table 3.2; Fig. 3.2b).

The relative PD of graminoids and climbers in burnt plots relative to unburn control was not associated with any of our focal fire metrics or other predictor variables, as the null models (no predictors) had the lowest AICc values.

The relative sesPD of trees/shrubs in burnt plots relative to unburnt was only associated with time since fire, which had limited explanatory power (D^2 = 3.96%; Table 3.2). Immediately after a fire event, burnt plots contained higher sesPD of trees/shrubs than control (unburnt plots), with the sesPD declining over the period and returning to the level of unburnt control plots approximately after two years (Table 3.2, Fig 3.2c). There was no evidence that any other predictor variables, including interaction terms, influenced the relative sesPD of trees/shrubs.

The relative sesPD of forbs, graminoids, and climbers was not associated with our focal fire metrics or other predictor variables, with the null model (no predictors) having the lowest AICc value.

3.3.3 Mean pairwise distance (MPD) & sesMPD

The best model of relative Mean Pairwise Distance (MPD) of trees/shrubs in burnt plots relative to unburnt ones was associated with biomes. However, despite being the best model in AICc ranking, the explained deviance of the fitted model was negative (D^2 = -87.31 %) due to the negative deviance of both the null and fitted models (Table 3.2). As the null model possessed negative deviance, it resulted in negative D^2 (explained deviance), no matter how well the model fitted the data and whether it had the lowest AICc value. We could not proceed with the analysis using the current fitted model since the explained deviance was much lower than the reference boundary.

Similarly, the relative MPD of other life forms- forbs, graminoids, and climbers was not associated with the focal fire metrics or other predictor variables, with the null model (no predictors) having the lowest AICc value.

Table 3.2. Results from model averaging across multiple regression models of relative phylogenetic diversity metrics (PD, sesPD, MPD, sesMPD, MNTD and sesMNTD) in burnt sites relative to control (unburnt) for trees/shrubs, forbs and graminoids. Results for climbers are not included as no model had a lower AICc than the null model (i.e., one that lacked predictors). Parameter estimates are provided with 95% confidence intervals in brackets.

Relative PD metrics	**Life Forms**	**Predictors**								***Model Explanatory Power (D^2) (%)***
		Time Since Fire (ln transformed)	***Fire Type (Non-prescribed)***	***Protection Status (Non-protected)***	***Biomes (FGS)***	***Biomes (TSCF)***	***Biomes (TSDBF)***	***Biomes (TSGSS)***	***Fire Type: Protection Status***	
		Parameter estimates with 95% CI								
PD	Trees/ Shrubs	--	---	0.149 (0.008, 0.285)	---	---	---	---	---	12.67
	Forbs	0.015 (-0.091, 0.123)	0.026 (-0.102, 0.155)	0.118 (-0.029, 0.265)					0.240 (0.043, 0.437)	21.32
sesPD	Trees/ Shrubs	-0.413 (-0.687, -0.135)	---	---					---	3.96
MPD	Trees/ Shrubs	---		---	2.038 (2.006, 2.069)	-0.508 (-0.555, -0.462)	-0.509 (-0.528, -0.490)	-0.500 (-0.517, -0.483)	---	-87.31
sesMPD	Trees/ Shrubs	---	---	---	2.374 (1.261, 3.471)	-0.466 (-1.946, 1.009)	-0.432 (-1.100, 0.220)	-0.359 (-0.941, 0.211)	---	7.92
MNTD	Trees /Shrubs	-0.122 (-0.181 -0.063)			1.621 (1.320, 1.922)	-0.484 (-0.836, -0.131)	-0.342 (-0.514, -0.167)	-0.448 (-0.595, -0.301)	---	217.73
	Graminoids	0.170 (0.011, 0.341)	---						--	7.2
sesMNTD	Trees Shrubs	-0.427 (-0.684, -0.170)			---				---	4.78

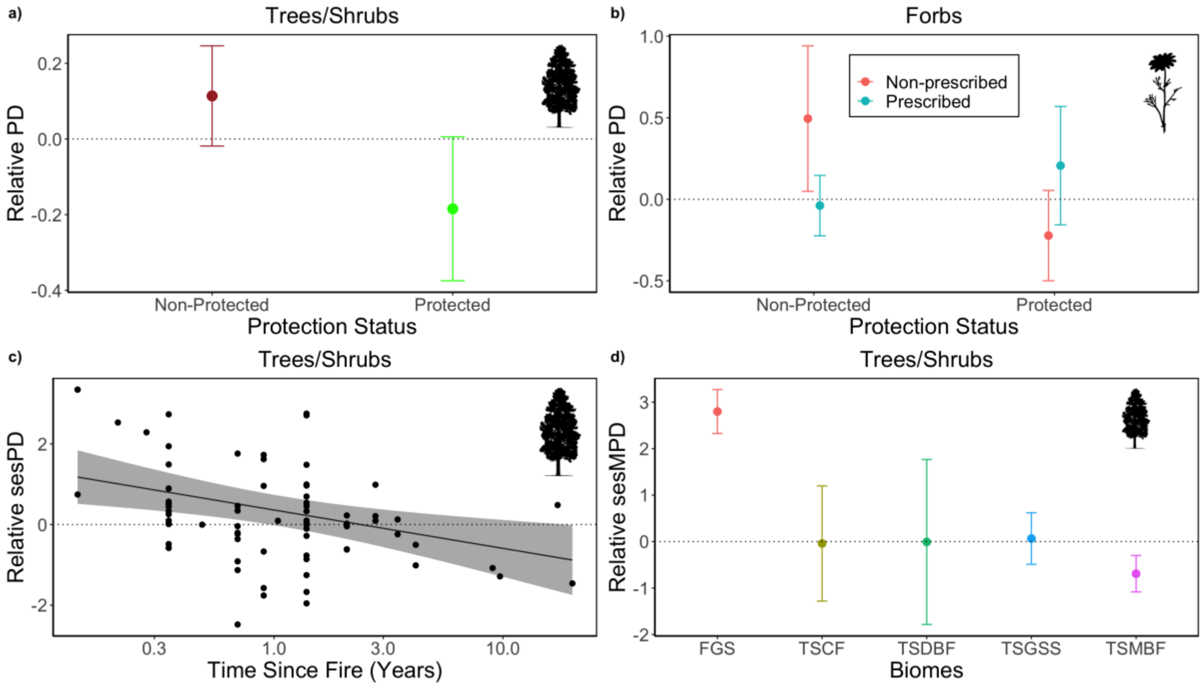

Fig. 3.2. Impact of fire on relative PD and sesPD and sesMPD in burnt plots relative to unburnt plots on two different groups of plants – a, c & d) Tree/Shrubs, & b) Forbs. The X-axis for c is plotted on a log scale. The error bars or shaded area shows the 95% confidence intervals. The dotted line at 0 on the Y-axis represents an equal amount of PD, sesPD or sesMPD in both burnt and unburnt sites.

The relative sesMPD of trees/shrubs in burnt relative to unburnt plots differed across biomes, although the model explanatory power also remained limited (D^2 = 7.92 %). Relative sesMPD of trees/shrubs in burnt plots relative to unburn control was significantly higher in biome FGS and lower in TSMBF (Table 3.2, Fig 3.2d). Whilst relative sesMPD was similar in TSCF, TSDBF & TSGSS biomes in burnt plots relative to unburnt control, the 95% confidence intervals of the parameter estimates overlapped zero. There was no evidence that any other predictor variable, including interaction terms, influenced the relative sesMPD of trees/shrubs.

The relative sesMPD of forbs, graminoids and climbers in burnt plots relative to unburn was not associated with the focal fire metrics or other predictor variables, with the null model (no predictors) having the lowest AICc value.

3.3.4 Mean nearest taxon distance (MNTD) & sesMNTD

The best model of the mean nearest taxon distance (MNTD) of trees/shrubs was associated with time since fire and biome type. However, despite having the best model in the AICc ranking, the explained deviance of the fitted model appeared to have been much higher than expected (D^2 = 217 %) due to the negative residual deviance of the fitted model (Table 1). The null model always has a higher null deviance than the residual deviance of a fitted model. If a fitted model has negative deviance, it can cause the explained deviance of the model to exceed 100%. The analysis cannot proceed with the fitted model as the explained deviance falls outside the reference boundary.

The relative MNTD of the graminoid community in burnt plots relative to unburnt ones was associated with time since fire. The relative MNTD in burnt plots relative to unburnt ones decreased immediately after the fire but increased over the period and reached the level of unburnt controls after ~5 years (Table 3.2, Fig 3.3a). There was no evidence that any other predictor variable, including interaction terms, influenced the relative MNTD in the graminoid community.

Relative MNTD of forbs and climbers was not associated with our focal fire metrics or other predictor variables, with the null model (i.e., the one which lacked predictors) having the lowest AICc value.

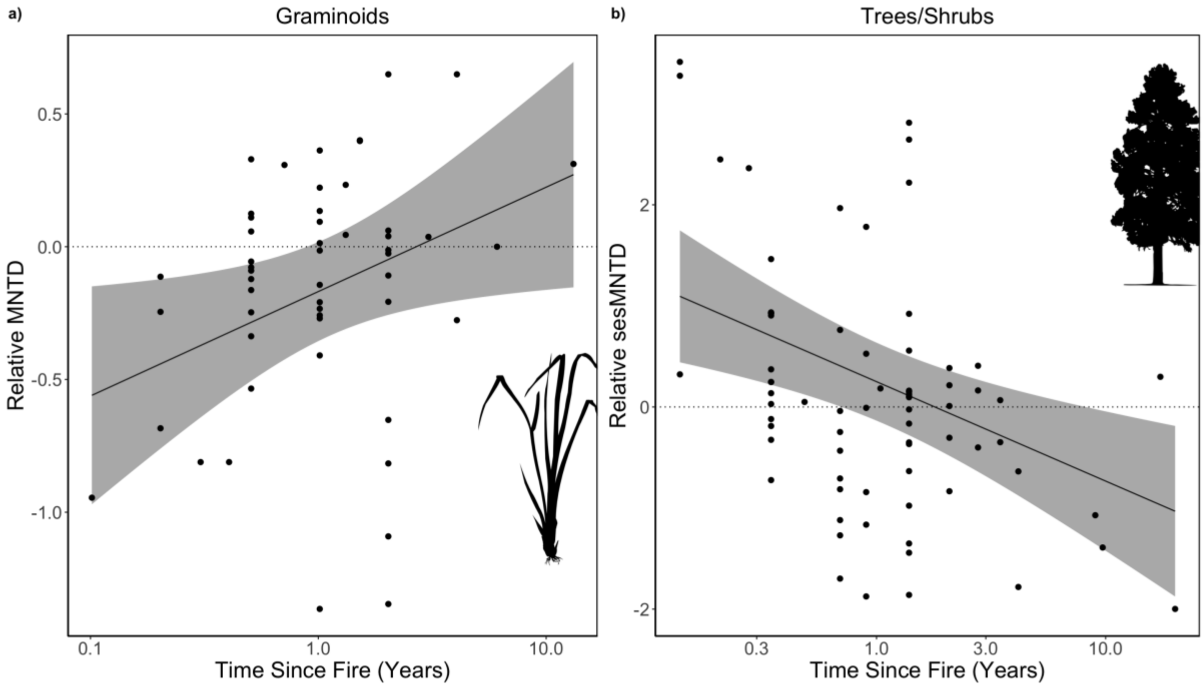

Fig. 3.3 Impact of fire on relative MNTD and sesMNTD in burnt plots relative to unburnt on two different groups of plants – a) Graminoids, b)Trees/Shrubs. The Y-axis represents relative MNTD or relative sesMNTD. The X-axis for both a & b. is plotted on a log scale. The shaded area shows the 95% confidence intervals. The dotted line at 0 on the Y axis represents an equal amount of both MNTD and sesMNTD at both burnt and unburnt sites.

The model of relative sesMNTD of trees/shrubs in burnt plots relative to unburnt was associated with time since fire (Table 3.2, Fig 3.3b); however, the model explanatory power was very low (D^2 = 4.78%). Results showed high relative sesMNTD in burnt plots relative to unburnt control immediately after the fire. Relative sesMNTD decreased with time since fire, returning to values similar to those of unburnt controls after ~2 years. There was no evidence that any other predictor variable, including interaction terms, influenced the relative sesMNTD in the trees/shrubs community.

The relative sesMNTD in burnt plots relative to unburnt of forbs, graminoids and climbers was not associated with our focal fire metrics or other predictor variables, with the null model (i.e., the one which lacked predictors) having the lowest AICc value.

3.4 Discussion

Using pantropical data, we examined the impact of fire and post-fire recovery of phylogenetic diversity in four plant lifeform groups (trees/shrubs, forbs, graminoids and climbers). Using diverse biomes as a focus, we examine whether plant phylogenetic diversity is modified by the time since fire, fire type (prescribed or non-prescribed burns), and protected area status (protected vs. non-protected). To our knowledge, this is the first study to use systematically collated data from previous studies to examine the effects of fire on plant phylogenetic diversity across tropical and subtropical regions. While some of our models had limited explanatory power, we uncovered important insights regarding fire's impact on plant species' phylogenetic diversity.

We discovered that standardised effect size of PD and MNTD of trees/shrubs in burnt relative to unburnt increases immediately after the fire but decreases gradually and reaches the unburnt control level nearly two years after the fire. The PD of trees/shrubs increased in burnt plots relative to unburnt plots in non-protected areas, whereas it decreased in burnt plots relative to unburnt in protected areas. Similarly, biomes Flooded Grasslands and Savannas (FGS) have a higher relative sesMPD in burnt plots relative to unburnt compared to the other focal biomes. Similarly, the PD of forbs increased in burnt plots relative to unburnt in the non-prescribed site of non-protected areas but remained similar to the unburnt plots in the prescribed site of non-protected and both prescribed and non-prescribed sites in protected areas. Moreover, the graminoid community exhibited a rise in MNTD when the duration of time since the fire grew longer and returned to the unburnt/control level nearly after 5 years.

3.4.1 Impact of time since fire

Studies in the past have shown that in the aftermath of a fire, the initial recovery phase of the plant community had reduced phylogenetic diversity, but over time, a gradual increase in phylogenetic diversity was observed (Pérez-Valera et al., 2018; Bashirzadeh et al., 2023). However, we found the opposite trend and observed that the sesPD and sesMNTD of trees/shrubs in burnt plot relative to unburnt was high immediately after the fire but decreased with the increasing time since the fire and reached the unburnt control level nearly two years. This indicates that after controlling for richness, a reduction in phylogenetic overdispersion was observed with increasing time since fire. This finding matches the outcome of Letten et al. (2014), which demonstrated a rise in plant phylogenetic diversity right after a fire, followed by a decline over time, in heathlands in New South Wales, Australia, outside the tropics. Our result also resembles the findings of Verdú and Pausas (2007) that fire occurrence in Mediterranean woodlands leads to decreased phylogenetic diversity and phylogenetic clustering of woody species over time.

Our analyses of the graminoid community discovered that the relative MNTD in the burnt plot relative to the unburnt decreased right after the fire. However, over time, it increased and returned to the unburnt control level at about five years. This suggests that the fire produced a phylogenetic overdispersion of graminoid species that persisted with increased time since fire. This could be because the time since the fire has positively impacted the richness of graminoid species (Durigan et al., 2020), including the recruitment of distantly related taxon. However, none of the previous research found evidence suggesting that the time since fire increased the phylogenetic diversity of graminoids.

3.4.2 Impact of prescribed vs. non-prescribed burns

Generally, prescribed fires are applied to improve the quality of habitats and maintain ecosystem stability (Ryan et al., 2013). Although past studies suggest that non-prescribed and prescribed fire had an equal effect on species richness and composition of plant communities (Pastro et al., 2011; Ffolliott et al., 2012); we found that the impact of fire on the phylogenetic diversity of the forb community varies, but this variation depends on the protection status. According to our findings, in non-protected areas, the recovery of forbs after non-prescribed burn results in more distantly related species than the prescribed burn sites, but there was no difference in the prescribed and non-prescribed fire in protected areas. Our findings align with Bashirzadeh et al. (2023), who studied the impact of non-prescribed burn (wildfire) in non-protected areas and suggested that non-prescribed fire can increase the phylogenetic diversity of plants, particularly forbs, in semi-arid shrublands, outside the tropics. Based on our findings, the effects of prescribed versus non-prescribed fires may vary depending on location and circumstances (Foster et al., 2018).

3.4.3 Protection status

Burnt plots relative to unburnt plots in non-protected areas had increased PD of trees/shrubs but decreased in protected areas. A similar but weaker trend was also observed in the forb community, where the PD in burnt plots relative to unburnt plots was reduced in protected areas after the fire. This result indicates that after a fire, trees/shrubs and forbs are more phylogenetically diverse in non-protected areas than in protected areas. Although the recovery of species in protected forests could perform better and maintain biodiversity by reducing disturbances such as land clearing, grazing and logging (Bruner, 2001; Geldmann et al., 2013), our results indicate an opposite trend that species in burnt plots relative to unburnt in non-protected areas tend to be more phylogenetically diverse. This could be due to the accumulation of flammable materials inside the protected areas due to fire suppression measures, exacerbating the impact of fires and promoting the growth of communities that are more susceptible to fire damage than those in unprotected areas (De Groot et al., 2009; Pereira et al., 2012). Our results suggest that the chance of losing of phylogenetic diversity in protected areas are higher than the non-protected, especially for the trees/shrubs community in the event of fire. Despite this, the importance of phylogenetic diversity in conservation efforts is often overlooked (Winter et al., 2013). Thus, it is crucial to include the importance of preserving phylogenetic diversity in protected area policies and management to achieve the overall biodiversity goal (Larkin et al., 2015).

3.4.4 Impact across biomes

The impact of fire can differ according to the biomes and climate that has experienced fires in the past (Bousquet et al., 2022). Our findings suggest that PD are different between fires in different biomes, although this was only observed in trees/shrubs. We found strong evidence that relative sesMPD in burnt plots relative to unburnt was high in flooded grasslands and savannas (FGS) and low in tropical and subtropical moist broadleaf forests (TSMBF). This suggests that fire facilitates the phylogenetically dissimilarity of trees/shrubs in FGS. One possible reason for this could be that the fire in FGS causes the soil to become dry, which creates a favourable environment for the growth of new and distantly related plant species due to changes in the microclimate (Joyce et al., 2016). According to our research, it is recommended to maintain fires in flooded grasslands and savannas to promote the phylogenetic diversity of trees/shrubs. However, there is a possibility of introducing non-native invasive plant species due to the impact of the fire (Joyce et al., 2016). More research into phylogenetic diversity is necessary for FGS to address the impact of fire. Previous studies have overlooked FGS in comparison to other biomes.

Moreover, our findings also showed a lower sesMPD in the burnt areas relative to the unburnt areas in tropical and subtropical moist broadleaf forests (TSMBF). The reason for this could be the high mortality rate of fire-sensitive species of trees and shrubs and the selection of fire-resistant trees in such biomes (Nóbrega et al., 2019). Our findings suggest avoiding fires in tropical and subtropical moist broadleaf forests to preserve the phylogenetic diversity of the tree/shrub community.

3.5 Conclusions

Our study shows how the time since fire and the prescribed and non-prescribed burns impact the phylogenetic diversity across four plant life forms (trees/shrubs' forbs and graminoids and climbers). The responses to these fire metrics also vary between protected and non-protected areas and across tropical and subtropical biomes. Although we did not see the impact of fire on the phylogenetic diversity of the climber community, we observed some notable results in the rest of the plant communities. i) The phylogenetic diversity is reduced with increasing recovery time; ii) the impact of prescribed and non-prescribed fire can vary phylogenetic diversity; iii) losses of phylogenetic diversity can be high in protected areas and moist broadleaf forests. As the pattern of fire in the tropics is changing by reducing in grasslands and savannas and increasing in moist forests due to fire climate and land use changes, the possibility of this trend persisting could impact the plant communities' phylogenetic diversity. When developing fire management policies and activities, it is important to consider phylogenetic diversity to effectively preserve the overall biological diversity. Our study emphasises the importance of conducting further research on forbs, graminoids, and climbers, as they are currently underrepresented in ecological and phylogenetic diversity studies.

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Chapter Four

Impact of fire and post-fire recovery on the functional diversity and composition of trees and shrubs community: A pantropical data analysis

CHAPTER 4

Impact of fire and post-fire recovery on the functional diversity and composition of trees and shrubs community: A pantropical data analysis

Abstract

Fire has been a major element in shaping ecosystems for millions of years. The human-driven climate and land use changes have altered fire patterns, resulting in changes in biodiversity and ecological systems. Functional diversity is an important indicator of the functioning of an ecosystem, yet it receives considerably less attention than taxonomic diversity in ecological research. Research on the effects of fire on functional diversity has been limited and mainly concentrated on fire-prone ecosystems. We conducted a pan-tropical analysis of systematically collated data from 63 paired burnt and unburnt sites from 19 studies. We calculate five functional diversity metrics using four key traits (pollination syndrome, dispersal syndrome, maximum plant height and wood density) of 951 tree/shrub species. We use model averaging of mixed effect and general linear models to assess how functional diversity, functional richness, and functional turnover between burnt and unburnt plots vary with time since fire, fire type, protected area status and biome type. Our result highlights three main outcomes: First, prescribed fires can have a positive impact on functional richness; second, protected areas can limit fire's impact on functional diversity compared to non-protected areas; and third, functional turnover following a fire event remains very low in grasslands, shrublands and savannas but high in dry broadleaf forests. This result suggests that incorporating functional diversity aspects into fire management policies and strategies can aid in conserving biodiversity and improving the functioning of ecosystems. Whilst our

results are based on a limited dataset, they suggest that changing fire patterns in the tropics due to climate and land-use change will alter the functional diversity and composition of tree/shrub communities.

4.1 Introduction

Fire has been a vital ecological force for millions of years, serving as a major evolutionary driver (Bond & Keeley, 2005; Bowman et al., 2009). Throughout history, humans have altered the ecological system and the relationship between fire and vegetation by controlling the availability of fuels and the frequency and intensity of fires (Liang & Hearteau, 2023). Fire has also become an integral part of some ecosystems that determines which species occur in a particular ecosystem (He et al., 2019; McLauchlan et al., 2020). Climate and land use changes caused by humans affect the frequency and nature of fires on Earth, leading to changes in vegetation patterns, ecological systems, and biodiversity (Cochrane & Barber, 2009; He et al., 2019).

The functioning of an ecosystem depends on how living beings interact with each other and the surrounding environment (Díaz & Cabido, 2001). A highly diverse ecosystem tends to be healthy, productive, and resilient to external disturbance (Cleland, 2011; Ricotta et al., 2020). Hence, biodiversity loss drastically impacts ecosystem function (Hooper et al., 2012). The traditional measure of diversity is counting the number of species (richness) or individuals (abundance), but these measures do not reflect the diversity of the community's ecosystem functions (Abedi et al., 2022; Mouchet et al., 2010). Functional diversity, therefore, bridges such gaps and provides complementary data on species’ functions within such communities (Tilman, 2001; Petchey & Gaston, 2006; Ricotta & Burrascano, 2008). An ecosystem where most species perform similar functions is less functionally diverse than one where most perform contrasting functions (Ricotta & Burrascano, 2008). A functionally diverse community tends to have higher productivity and stability in its ecosystem compared to a less diverse community (Díaz & Cabido, 2001; Gagic et al., 2015).

As research into functional diversity in ecology has grown over the past few decades, various functional diversity metrics have been proposed in the literature (Hatfield et al., 2018; Mouchet et al., 2010). Functional diversity (FD) refers to the diversity of functions of organisms in a community within an ecosystem (Petchey & Gatson, 2006). Functional richness refers to the volume of functional spaces species occupy within a group of organisms (Mason et al., 2005; Villéger et al., 2008). In addition, functional turnover, i.e., functional beta diversity, reflects the functional dissimilarity of species between two communities (Siefert et al., 2012). All functional diversity metrics are based on species' functional traits, i.e., morphological, physiological, reproductive, and behavioural traits (Tilman, 2001; Schleuter et al., 2010; Pérez-Harguindeguy et al., 2013). An individual's traits are measurable characteristics that may affect performance or fitness (Cadotte et al., 2011). Hence, functional diversity is also called trait diversity (Fontana et al., 2015). Traits are the key to understanding how species influence community assembly and ecosystem function (Echeverría-Londoño et al., 2018; Díaz et al., 2007).

A functionally diverse community has lower levels of inter-specific competition as the species present have dissimilar traits and, thus, functional roles tend to be more stable than a less functionally diverse community (Allan et al., 2011). Communities facing strong environmental pressures tend to have low functional diversity as species must possess a limited range of traits to pass through the selection filter imposed by strong selection pressure; they thus tend to have reduced functional diversity (Rosenfield & Müller, 2020). In contrast, competition among species for resources tends to select functionally diverse species that can avoid inter-specific competition through niche segregation, thus increasing functional diversity (Kluge & Kessler, 2010).

Fire is one of the most prominent disturbance/selection pressures impacting functional diversity (Abedi et al., 2022). Although fire's impact on taxonomic diversity is well studied, phylogenetic and functional diversity has received less attention (Bashirzadeh et al., 2023). The impact of fire on functional diversity can be different across different biomes, such as moist broadleaf forests that do not experience fire (Giorgis et al., 2021), compared to fire-prone biomes such as grasslands, shrublands and savannas. For example, in tropical savanna, the recurrent fire favours enhanced functional diversity compared to long unburned plots due to an established plant regeneration strategy (Teixeira et al., 2022). In the neotropical forest, where fires are generally infrequent, regular fire decreases the functional diversity (Nóbrega et al., 2019).

The effect of fire on plant functional diversity has been studied mostly in fire-prone habitats (e.g., Nóbrega et al., 2019; Meza et al., 2023; Smith et al., 2022; Teixeira et al., 2022; Rainsford et al., 2021), suggesting that fire loses both taxonomic and functional diversity. However, some research (e.g., Abedi et al., 2022, Bashirzadeh et al., 2023) identified the variation in the impact on plants' taxonomic and functional diversity. Fire impact on functional diversity may vary depending on the types of fire (prescribed and non-prescribed) and the recovery time since the last fire event (Enright et al., 2015). Moreover, the impacts on functional diversity may be different in areas with protected and unprotected areas. Although protected areas do not sufficiently reduce the risk and impact of fire (De Groot et al., 2009; Laurance et al., 2012), they can shield the disturbances and allow for the fastest recovery compared to unprotected areas (Rodrigues et al., 2004).

Plants' response to fire mostly depends on traits related to post-fire recovery, recruitment, and growth strategy (Pausas et al., 2004; Schaffhauser et al., 2008). Fire forces individuals to develop traits that enable them to adapt to fire-prone environments (Keeley et al., 2011). Many studies have focused mainly on the traits relevant to fire survival, i.e., bark thickness, resprouting capacity, and tolerance to fire (e.g., Nóbrega et al.; Clarke et al., 2012; Mostacedo et al., 2022). For example, some fire-tolerant species have specific traits such as thick bark and higher wood density (Brando et al., 2012), underground rootstock (Brathen et al., 2021), higher specific leaf area (SLA) and lower dry leaf matter content (Keeley et al., 2011) that either reduce fire impacts or allow them to recover more quickly afterwards. Other traits that influence the function of plant communities but are not linked to plant responses to fire, such as dispersal and pollination syndrome, are also fundamental to understanding how fire impacts functional diversity (Brown et al., 2016; Meza et al., 2023). For example, fire reduces the diversity of plant species whose seeds are dispersed by animals (Meza et al., 2023). Similarly, the moth-pollinated plants are also impacted if the fire frequency increases as the diversity of moths is reduced by fire (Banza et al., 2019). Wood density and plant height are also important traits that can help save plants in fire (Cornelissen et al., 2003). Here, we will explore the impact of fire on functional diversity by filtering the trees/shrubs community from datasets used in the previous chapters and identify how fire responds to the functional diversity of the trees/shrubs community. We have chosen trees/shrubs for two reasons – first, most of the fire impacts we observed in Chapters 2 and 3 were in the trees/shrubs community, and second, trait data are available for a larger proportion of the tree/shrub species in our dataset than in the case for other life forms. Our core objectives are to answer the following questions.

1. How does time since fire and fire type impact the functional richness and diversity across tropical and subtropical biomes, and does this vary between protected and non-protected areas?

2. How does time since fire and fire type impact the functional turnover and composition across tropical and subtropical biomes, and does this vary between protected and non-protected areas?

4.2 Methods

4.2.1 Literature search

A systematic literature search was conducted following the PRISMA guidelines (Liberati et al., 2009; Moher et al., 2009) in January 2020 and updated in March 2023. Three searches were carried out using ‘Web of Science’, with the search terms: i) fire* AND “species richness” AND plant*; ii) burn* AND “species richness” AND plant*; and iii) fire*AND “species richness” AND tree*. Our objective was to retain papers that were empirical field-based studies, conducted in the tropics or sub-tropics, i.e., 30^o north to 30^o south (Corlett, 2013), and that provided complete species lists for control (unburnt or sites sampled before a fire) and treatment sites (those with fires). We only selected studies with equal sampling effort in control and treatment sites, as such biases in study design can impact conclusions regarding fire impacts on biodiversity (Kelly et al., 2017).

The data collection process took place in five stages (Table 4.1). After collecting the papers from the initial search, titles were scanned to identify papers that could be used to understand the impacts of fire on plant diversity in tropical and sub-tropical locations. Duplicate papers were removed, and abstracts were then scanned. Papers were only accepted if the study met our criteria of being an empirical field-based study located in the tropics or sub-tropics. We then read each paper in full and removed those for which sampling effort was uneven across control (unburnt) and treatment (burnt) sites or did not provide a complete species list for each type of site. Some studies reported changes in tree and shrub communities but used plot sizes that are widely considered too small for accurate estimates of the species richness of these groups, as the plots could only contain one or two mature individuals of these life forms. We thus did not include observations when plots were less than 100 m^2, or for shrub species richness when plots were less than 16 m^2 (see Mueller-Dombois et al., 2008). A list of retained papers is given in **Supplementary Materials, Appendix 1**.

Table 4.1: The selection stages, procedure, and total no. of papers obtained in the literature search.

Selection Procedure	Number of papers
6. Papers yielded from initial search	8970
7. Papers left after scanning titles	1431
8. Papers left after removing duplicates	1065
9. Papers left after reading the abstract	460
10. Papers left after reading in full and checking selection criteria are met	28

4.2.2 Data extraction & quality control

The final set of 28 studies contained 101 pairwise control (unburnt) and treatment (burnt) plots and 5311 observations, where one observation equates to a species being present in a burnt or unburnt plot (**Supplementary Material**, **Table S1**). Most studies (n = 24; 85 %) provided their study site's latitude and longitude, but when these were not provided, they were obtained using the description of the study site location and the online tool https://www.latlong.net/. Not all studies provided data on species' abundances (density or percentage cover), so we converted data into a presence/absence matrix for each burnt and unburnt site.

From each study, we extracted data on two fire metrics – time since fire (number of years between the most recent fire and sampling period), and fire type (prescribed or non-prescribed burns). We defined each site as protected if it was within the boundaries of a protected area (IUCN categories I to VI) as defined by the World Database on Protected Areas (WDPA) database (UNEP-WCMC & IUCN, 2020.

Biomes were classified according to Olson et al. (2001) as i) Tropical and Subtropical Moist Broadleaf Forests (TSMBF; 5 papers & 1846 observations) ii) Tropical and Subtropical Dry Broadleaf Forests (TSDBF, 6 papers & 859 observations) iii) Tropical and Subtropical Coniferous Forests (TSCF, 1 paper & 31 observations), iv) Tropical and Subtropical Grasslands, Shrublands & Savannas (TSGSS, 13 papers and 2433 observations) and v) Flooded Grasslands and Savannas (FGS, three papers and 142 observations).

4.2.3 Standardising taxonomy and life form classification

Species, genus, and family names were standardised according to The Plant List, R packages *Taxonstand* version 2.4 (Cayuela et al., 2012) and The World Flora, R package *WorldFlora* version 1.10 (Kindt, 2020). From these datasets, we extracted all observations relating to trees/shrubs using life form classifications from the TRY database (Kattge et al., 2020); Botanical Information and Ecology Network (BIEN) database in R using the package *BIEN*, version 1.2.6 (Maitner et al., 2017), AusTraits, a curated plant trait database for the Australian flora using the package *aurstraits* in R (Falster et al., 2021) and authenticated online sources or the life-form classification used in the original study (**Supplementary Material, Table S2**).

4.2.4 Functional traits and dataset

Accurate assessments of functional diversity primarily rely on selecting ecologically significant traits (Laureto et al., 2015) because the selection of traits significantly impacts the ecological findings obtained through functional diversity (Zhu et al., 2017). Selecting the right traits is essential, yet it is important to differentiate between ‘effect’ and ‘response’ traits when considering functional redundancy (Pillar et al., 2013). Response traits pertain to the way communities react to environmental change, whereas effect traits concern the fitness and impact on ecosystem processes (Lavorel & Garnier 2002; Violle et al., 2007). Here, focus on all response traits since they relate to the responding environmental change from a wildfire, although some of the traits (e.g., wood density, maximum plant height) are related to both effects and response traits.

We aimed to collect at least seven functional traits (Dispersal syndrome, Pollination syndrome, Wood density, Maximum plant height, Seed mass, Specific leaf area and Leaf nitrogen content). However, we were only able to obtain sufficient trait data for four traits (maximum plant height, wood density, dispersal syndrome and pollination syndrome) (Table 4.2).

Due to having only four traits, we could only calculate the functional diversity of the sites with more than four species. Hence, we had to exclude the 310 observations from 21 sites that had less than four species. As a result, we have only been able to calculate the functional diversity metrics of 3215 observations of 63 sites from 19 studies containing 951 species from three biomes i) Tropical and Subtropical Moist Broadleaf Forests (TSMBF; 4 papers & 1773 observations) ii) Tropical and Subtropical Dry Broadleaf Forests (TSDBF; 4 papers & 531observations) iii) Tropical and Subtropical Grasslands, Shrublands & Savannas (TSGSS, 11 papers and 911 observations) (**Supplementary Material Table S6**)

Table 4.2: List of plant traits used in the study with their, units, trait types, functions, and ecological importance.

SN	Traits	Units	Types	Function	Ecological Importance
1	Dispersal Syndrome	Categorical Biotic: *Animal* Abiotic: *Wind, Gravity, Water*	Reproductive	Germination, Reproduction and regeneration	Migration and diversity and food for seed-dispersing animals (Howe, 2016)
2	Wood Density	mg/cm3	Morphological	Growth, strength, stiffness of a stem	Forest structure, carbon storage, timber stock (Pérez-Harguindeguy et al., 2013, Phillips et al, 2009)
3	Maximum Plant Height	meter	Morphological	Competitive strength, response to soil resources. Access to sunlight and photosynthesis	Forest structure, climate response, response to disturbance, Effects on plant geochemical cycle. Provide shade and shelter to other creatures (Cornelissen et al., 2003)
4	Pollination Syndrome	Categorical Biotic: *Animal* Abiotic: *Wind, Gravity, Water*	Reproductive	Reproduction and regeneration	Diversity of pollinator community, the evolution of a flower (Dellinger, 2020; Rosas-Guerrero et al., 2014)

Traits were collected from various sources such as TRY database (Kattge et al., 2020), Botanical Information and Ecology Network (BIEN) database in R using the package *BIEN*, version 1.2.6 (Maitner, et al, 2017), AusTraits, a curated plant trait database for the Australian flora using the package *aurstraits* in R (Falster et al, 2021), BROT.2 (Tavşanoğlu & Pausas, 2018), Dispersal Distance Data (Tamme et al., 2014), original studies and online sources. The wood density trait was collected using the *biomass* package in R (Réjou-Méchain et al., 2017). A detailed list of the species' traits and source is available in **Supplementary Material, Table S7.**

Categorical traits - pollination syndrome and dispersal syndrome were classified to binary (biotic or abiotic) levels. Missing traits for species were extracted by doing phylogenetic imputation in the *Rphylopar* package in R (Goolsby et al., 2016). The *Rphylopar* package does not work for the imputation of categorical traits; hence we first converted the binary data to numerical traits as 0 for abiotic and 1 for the biotic. Then the imputed data for the pollination and dispersal syndrome were generated between 0 and 1, where values > 0.5 were converted to 1, and those < 0.5 were converted to 0 (Ma et al., 2011). Before imputing, we checked each trait's phylogenetic signal (Pagel's lambda) for the species. Lambda value ranges between 0 and 1, where lambda greater than 0.6 is considered a strong phylogenetic signal for the phylogenetic imputation (González-del-Pliego et al., 2019). The detail of missing traits and the phylogenetic signal of collected data is given in **Table 4.3.**

Table 4.3: List of traits, units of the traits, species identified with trait data, species with missing trait data and the phylogenetic signals (Pagels's Lambda) for the traits used in the study.

Traits	Units	Species with trait data (%)	Species with missing trait data (%)	Pagels's Lambda
Dispersal syndrome	Categorical binary (Biotic/abiotic)	75.24	24.76	0.96
Pollination syndrome	Categorical binary (Biotic/abiotic)	65.80	34.20	0.95
Maximum plant height	Meters	81.21	18.79	0.74
Wood density	(mg/cm^3)	100	0	0.99

4.2.5 Functional diversity metrics

We calculated five functional diversity metrics – Functional Diversity (FD), standardised effect sizes of FD (sesFD), Functional Richness (FRic), standardised effect sizes of FRic (sesFRic) and functional beta diversity (functional turnover) of trees/shrubs community by using presence-absence data. FD is a functional diversity metric measured based on the total branch length of the functional dendrogram of species in an assemblage (Petchey & Gatson, 2002) and was calculated using the *picante* package in R version 1.8.2 (Kembel et al., 2010). Functional richness refers to the total functional spaces occupied by species in the community (Villéger et al., 2008) and was calculated as the multidimensional space trait-based approach using mFD package in R (Magneville et al., 2021). As the FD and FRic are correlated with the species richness (Swenson, 2014), the standardised effect sizes of FD (sesFD) and standardised effect size of FRic (sesFRic) were calculated by creating the null community of equal species richness from a regional species pool (continental level) and did a randomization 999 times using the "richness" algorithm (Gotelli, 2000). All standardised effect sizes (*ses)* metrics were calculated as follows (Swenson, 2014):

$$\text{Standardized Effect Size (ses)} = (\text{Observed-Null})/\ \text{SD}(\text{Null})$$

(*Where Observed is the FD of our observed community, Null is the mean FD of the 999 times randomised null community, SD is the standard deviation of the FD of that null community*)

A value below zero (0) of these standardised effect sizes (ses) implies that FD and FRic are lower than expected by chance, which indicates that fire reduces functional diversity. In contrast, a value above zero (0) suggests the observed values are greater than expected by chance (Swenson, 2014), suggesting fire increases functional diversity.

4.2.6 Relative FD, sesFD, FRic and sesFRic and functional turnover

We used a natural log response ratio to calculate relative FD and FRic (Hedges et al., 1999), e.g., Relative FD = log (FD in burnt/FD in unburnt). For *ses*FD, and *ses*FRic, we calculated raw differences between burnt and unburnt sites because the value of *ses* metrics can be negative. For example, if the burnt plot's *ses* is more negative than the unburnt plot's *ses*, the difference is negative, which shows that burnt plots have lower values than unburnt plots. In both cases, values of zero (0) represent situations where fire has no impact on functional diversity, negative values represent situations where fire reduces functional diversity, and positive values represent situations where fire increases functional diversity.

The functional beta diversity i.e., functional turnover, was calculated as Sorenson functional beta diversity was calculated in R using the package *mFD*. A greater value indicates higher functional turnover.

4.2.7 Data analysis

All analyses were conducted in R programme language version 4.2.2 (R Core development team, 2023). Time since fire was centred before analysis, and we used the equivalent “sum to zero contrasts” approach (Schielzeth, 2010) for categorical variables – fire type, protection status and biomes. Centring variables reduces problems that otherwise arise with model averaging when interaction terms are included as predictors (Schielzeth, 2010; Cade, 2015; Tyre, 2017). We modelled relative FD and sesFD using linear mixed effect methods, with study ID as a random effect, using the lme4 package (Bates et al., 2015). We modelled FRic, sesFRic, and Functional turnover as a general linear model (without study ID) as the mixed models were overfitted when adding study ID as a random effect.

In all cases, models had Variance Inflation Factors (VIF) less than ten indicating that results are not markedly impacted by collinearity between predictors (Hair et al., 1992, Craney & Surles, 2002). We also checked for the linearity of responses by including square terms and comparing the model fit to equivalent models that only included a linear term. The fit of all models was also checked using model diagnostic plots.

We constructed all possible but ecologically realistic models (n = 32; **Supplementary Material, Table S4**) given our suite of predictor variables, i.e., time since fire (years; ln transformed), fire type (fixed factor: prescribed/non-prescribed), biomes (fixed factor: TSMBF, TSBDF, TSGSS), and protection status (fixed factor: protected/non-protected). We included interaction terms between our fire metrics (time since fire and fire type) and i) biomes and ii) protection status to test whether biome type or protected area status moderated the relationships between each fire metric and our outcome variables.

For the mixed effect models, we used D^2 as a measure of explanatory capacity; $D^2 = (ND - RD)/ND$ where ND is the null deviance, and RD is the residual deviance, which the model cannot explain, thus '(ND–RD)/ND' is the explained deviance. D^2 varies between zero and one and equals one when the model can explain the deviance completely (Guisan & Zimmermann, 2000). We used R^2 to measure explanatory capacity in all general linear models.

We used an information-theoretic criterion (AICc) approach to obtain a set of models whose Δ AICc values were within two points of the best-performing model, i.e., that with the lowest AICc value, and then conducted model averaging (Burnham & Anderson, 2004).

4.3 Results

4.3.1 Functional diversity (FD) & sesFD

The models of relative FD in burnt plots relative to unburnt ones were associated with time since fire, protection status and fire type. However, despite being the best model in the AICc ranking, the explanatory power of this model appeared to have been negative (D^2 = -16.21%) due to the negative deviance of both the null and fitted models (Table 4.4). As the null model possessed negative deviance, it resulted in negative D^2 (explained deviance), no matter how well the model fitted the data and whether it had the lowest AICc value. As such, we were unable to continue the analysis using the current fitted model as the variance explained by the model was much lower than the reference boundary.

Models of the relative standardised effect size of FD (sesFD) in burnt and unburnt plots had limited explanatory power (i.e., D^2 = 5.28 %). Model averaging revealed that fire type and protection status were associated with the relative sesFD. However, the 95% confidence interval of parameter estimates of fire type overlapped zero (Table 4.4). Protection status did influence the sesFD, with sesFD decreasing at burnt sites relative to unburnt controls in non-protected sites, whilst within protected sites, sesFD was more similar in burnt and unburnt sites (Table 4.4; Fig. 4.1a). There was no evidence that any other predictor variable, including interaction terms, influenced the sesPD.

Table 4.4. Results of model averaging of relative functional diversity metrics (FD, sesFD, FRic) in burnt sites relative to unburnt sites and Functional turnover between burnt and unburnt sites. Results for relative sesFRic are not included as no model had a lower AICc than the null model (i.e., one that lacked predictors). Relative FD and sesFD were modelled using mixed effect models, and relative FRic and Functional turnover were modelled using general linear models. Parameter estimates are provided with 95% confidence intervals in brackets.

FD metrics	**Predictors**					***Model Explanatory Power* (%)**
	Time Since Fire (ln transformed)	***Fire Type (Non-prescribed)***	***Protection Status (Non-protected)***	***Biomes (TSDBF)***	***Biomes (TSGSS)***	
	Parameter estimates with 95% CI					
FD	0.064 (0.018, 0.111)	-0.010 (-0.063, 0.043)	0.009 (-0.038, 0.057)	---	---	-16.21 (D^2)
sesFD	---	0.101 (-0.196, 0.399)	-0.404 (-0.674, -0.134)	---	---	5.28 (D^2)
FRic	---	-0.206 (-0.410, -0.002)	---	---	---	6.27 (R^2)
Functional Turnover	-0.029 (-0.099, 0.041)	---	---	0.108 (0.012, 0.204)	-0.105 (-0.182, -0.029)	16.51 (R^2)

4.3.2 Functional richness (FRic) & sesFRic

The model of the relative functional richness in burnt plots relative to unburnt sites also had relatively limited explanatory power (i.e., $R^2 = 6.27\%$), with the model revealing that prescribed burns resulted in functional richness (FRic) increasing in burnt plots relative to unburnt ones, whilst non-prescribed burns resulted in functional richness declining in burnt sites relative to unburnt controls (Table 4.4; Fig. 4.1b). Relative functional richness (FRic) was not influenced by any other predictor variable, including interaction terms.

The standardised effect size of functional richness (sesFRic) did not appear to be associated with any of our predictor variables, as the best model had a higher AICc (540.21) than the null model that lacked predictors (AICc 537.82).

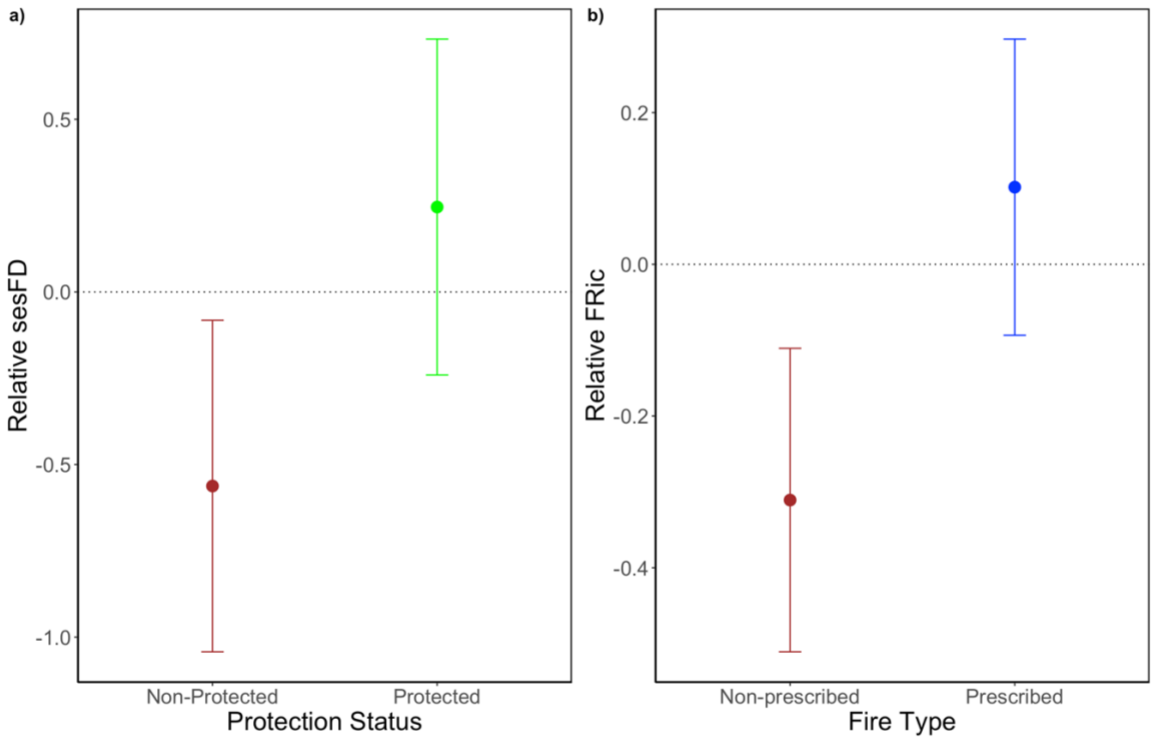

Fig 4.1: Impact of fire on a) Relative sesFD, b) Relative FRic in burnt site relative to unburnt sites. The error bar indicates the 95% confidence interval. The dotted line at 0.0 indicates the equal sesFD and FRic in burnt and unburnt plots.

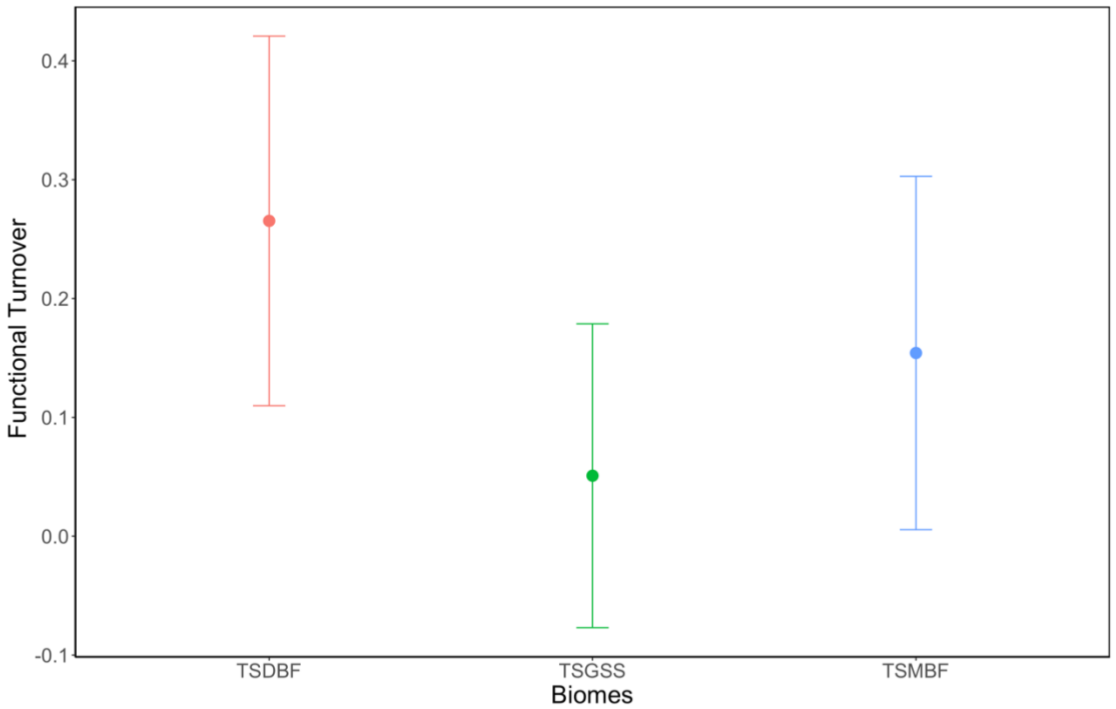

Fig 4.2: Impact of fire on functional turnover between burnt and unburnt plots. The error bar indicates the 95% confidence interval. Biomes (TSDBF: Tropical and Subtropical Dry Broadleaf Forests, TSGSS: Tropical and Subtropical Grasslands Shrublands and Savannas, TSMBF: Tropical and Subtropical Moist Broadleaf Forests)

4.3.3 Functional turnover

Models of functional turnover in functional composition between burnt and unburnt plots had comparatively higher explanatory power ($R^2 = 16.51$ %) than the other response variables. The model revealed that functional turnover is associated with time since fire and biomes. The functional turnover had a negative relationship with the time since fire, but the 95% confidence interval of parameter estimates overlapped zero (Table 4.4). Regarding the biomes, there was a high functional turnover between burnt and unburnt plots in biome TSDBF and a low functional turnover in biome TSGSS in comparison to the biome TSMBF (Table 4.4, Fig 4.2)

4.4 Discussion

Fire is a natural disturbance that can impact species directly or change the availability of resources necessary for survival (Lyet et al., 2009), eventually affecting a community's functional diversity (Abedi et al., 2022). Research on the impact of fire on the functional diversity of plant communities is minimal, and most of the studies that have been conducted on fire-prone habitats. This limits the knowledge of how fire impacts functional diversity and how post-fire recovery of functional diversity of plant communities occurs in fire-sensitive ecosystems experiencing increased fire risk due to anthropogenic activities.

As we have only been able to collect sufficient data for four response traits (dispersal syndrome, pollination syndrome, wood density and maximum plant height), we eventually ended up at the dataset of 63 sites from 19 studies because we could not include plots with species less than four. It is important to note that obtaining the appropriate amount of trait data is an inherent problem in functional diversity measurement (Santos et al., 2023). We recommend conducting further studies on various plant traits and functions at local and regional levels to draw more generalised conclusions about the impact of fire on plant functional diversity.

Due to having small datasets, we have also been unable to run the mixed effect for some of the response variables, as the models were overfitted while including the random effect. In addition, some of the remaining models we encountered had limited explanatory power. Despite these limitations, our study has identified some key findings- i) decreased relative sesFD in burnt plots relative to unburnt ones in non-protected areas compared to protected areas, ii) decreased relative functional richness (FRic) in burnt plots relative to unburnt in non-prescribed fire sites compared to prescribed, and iii) increased functional turnover between burnt and unburnt sites on tropical and subtropical dry broadleaf forests (TSDBF) and decreased functional turnover in tropical and subtropical grasslands, shrublands and savannas (TSGSS) compared to the tropical and subtropical moist broadleaf forests (TSMBF).

4.4.1 Impact of time since fire

Time since fire is an important predictor as it allows to predict how long it takes for functional diversity to recover following a fire event (McLauchlan et al., 2020). It is found that both taxonomic and functional diversity increased longer the time interval since fire than the shorter ones in shrublands in Iran, outside tropics (Bashirzadeh et al., 2023). However, the functional richness decreased with time since fire in Jarrah Forest, Australia, outside the tropics (Standish et al., 2021). We found no evidence of increasing or decreasing functional diversity or functional richness following fire events. Still, we observed weak evidence that increasing time since fire reduces the functional turnover of the trees/shrub community.

4.4.2 Prescribed vs. non-prescribed burn

Prescribed fires are used for various purposes, such as reducing the fuel loads and reducing the risk of wildfire (Penman et al., 2020, Hunter & Robles, 2020), creating a fire break to save fire-sensitive species (Pastro et al., 2011), recovering the historical vegetation assembly, and enhancing habitat quality (Ryan et al., 2013). However, despite these benefits, it is still debated if prescribed fires support biodiversity conservation because prescribed and non-prescribed fires have similar effects on plant biodiversity (Pastro et al., 2011, Glassman et al., 2023). This is because prescribed fire can equally affect plants by killing individuals and changing the landscape structure (Holland et al., 2017). Despite this controversy, prescribed fires are still applied to manage biodiversity in many landscapes (Hunter & Robles, 2020). Although prescribed burning is mostly applied in fire-prone ecosystems, the biodiversity within such ecosystems can be negatively impacted by fire depending on their frequency and magnitude (Harper et al., 2018). Here, we find evidence that prescribed burns can positively impact functional richness. Our result is similar to that of Abedi et al. (2022), who observed a decline in functional richness by the non-prescribed burns in Iran, outside the tropics, Moreover, the taxonomic and functional diversity was greatly reduced in the neotropical forest under non-prescribed because non-prescribed fires filter similar functional traits and create functional similarity (Meza et al., 2023). Here, our study also informs that prescribed fires can positively impact functional richness and functional diversity more than non-prescribed fires.

4.4.3 Protected vs. non-protected status

Protected areas prevent forest and biodiversity loss from the land use change (Geldmann et al., 2019). Although species loss can occur equally in protected and non-protected areas, protected areas still support more species than non-protected ones (Cooke et al., 2023, Bailey et al., 2022). As fire has become one of the threats to ecological systems and biodiversity, protected areas can also mitigate the fire's impact on biodiversity loss (Imron et al., 2022). However, there is still debate on the effectiveness of protected areas in conserving and promoting biodiversity in the event of fire (Biswas et al., 2015; Pereira et al., 2012), as nearly half of the world's established protected areas suffer from fire disturbances (Schulze et al., 2018). Our analysis revealed that protected areas can significantly limit the extent of fire-generated changes in plant communities. Our results showed that burnt sites in non-protected areas lose more functional diversity than those in protected areas. This could be because non-protected areas suffer from high disturbance from anthropogenic activities (logging, fuelwood collection, fires) and fewer resource management practices than protected areas (Geldmann et al., 2019).

4.4.4 Impact across biomes

Some biomes, e.g., tropical and subtropical grasslands and savannas, are historically exposed to fire. Species are adapted to fire in such an ecosystem, and fire is important for maintaining the ecosystem and its biodiversity (Kelly et al., 2020). Reducing the frequency of fires can thus affect species diversity and change the ecosystem's functioning in such ecosystems (Giorgis et al., 2021, Pausas & Keeley, 2019). Our result also indicates that these biomes have significantly less functional turnover following a fire event compared to the other focal biomes that do not traditionally experience fire (e.g., TSMBF and TSDBF). The limited functional turnover in grasslands and savanna forests following fires is probably because the species in these ecosystems are already adapted to fire (Giorgis et al., 2021; Pausas & Keeley, 2014). This could be because fire has created a fire-adaptive species that can be regenerated with fire, and the recovery is thus much faster than elsewhere, enabling species and functional composition to be maintained (Teixeira et al., 2022).

Meanwhile, we found a high functional turnover in Tropical and subtropical dry broadleaf forests (TSDBF). Although the dry broadleaf forests are comparatively low exposure to fire, the impact is very high once the fire occurs (Verma et al., 2017), and an occasional fire can have a greater impact on species diversity and substantial change in species composition (Kodandapani et al., 2009). The number of fires in this biome is growing and expected to grow due to climate change, growing population and land use change, which may substantially impact both species and functional composition (Das & Joshi, 2022).

4.5 Conclusions

Our results suggest that fire can impact functional diversity but these impacts vary across fire and functional diversity metrics, biomes, and protection status. Despite having a limited dataset and explanatory power, our research has brought up some notable outcomes-
First, non-prescribed fire causes a greater loss of functional richness than prescribed fire; hence the employment of prescribed fires not only combat the risk of non-prescribed fires but also prevent the loss of functional diversity. Second, protected areas can contribute to limiting the impact of fire during post-fire recovery of functional diversity that cannot be achieved in non-protected areas. Hence, effectively managed protected areas can alleviate the impact of fire on functional diversity. Third, functional turnover remains very low in the fire-adaptive ecosystem and high in the fire-sensitive ecosystem. Species in fire-prone ecosystems are adapted to fire; hence fire suppression measures in such ecosystems may change the functional richness and composition. Although our results are clear, they should be taken cautiously as the results we obtained are from small datasets but a wider geographical

landscape. Since the pattern of fire is changed in both fire-prone and non-fire-prone ecosystems and is expected to be worse due to climate change, understanding on how fire impacts the functional diversity of plant communities could be an additional asset for preserving biodiversity in the tropics in the future.

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Chapter Five

General Discussion

CHAPTER 5

General Discussion

5.1 Summary

Fire has played a crucial role in shaping the biodiversity of Earth for millions of years (Kelly et al., 2020; Bowman et al., 2009). It is a natural disturbance that can either directly impact species or change the availability of necessary resources for survival, which can eventually affect the diversity of a community (Wu et al., 2021; Lyet et al., 2009; Abedi et al., 2022). Although the impact of fire on the taxonomic diversity (species richness and abundances) of plant communities is well understood by ecologists (He et al., 2019), addressing the fire impact on species composition by species turnover are often overlooked. In addition, fire's effects on phylogenetic and functional diversity have not been given much attention (Abedi et al., 2022; Pausas & Keeley, 2023). Where such research has occurred, they are primarily confined to fire-prone habitats (Meza et al., 2023; Smith et al., 2022; Teixeira et al., 2022; Rainsford et al., 2021). This limits the comparative knowledge of how fire impacts taxonomic, phylogenetic and functional diversity and how post-fire recovery of these metrics occurs in all other ecosystems, particularly those of fire-sensitive biomes. Moreover, fire studies often assess the impact on trees/shrubs communities. Forbs, graminoids, and climbers are often neglected despite their crucial role in maintaining ecological stability and resilience to fire (Stephan et al., 2010; Gallagher & Leishman, 2012).

Here, I analysed a systematic compilation of data quantifying taxonomic, phylogenetic, and functional diversity on responses to fire in tropical and subtropical communities of four major plant life forms (trees/shrubs, forbs, graminoids & climbers. Despite conducting an extensive literature search, I only found 28 studies that met our selection criteria for the objective of my study. Most studies were conducted within ten years of a fire event, suggesting a need for more research to evaluate how the plant community responds to fires over longer time scales. In addition, these studies should adhere to open science principles by providing open access to the underlying data to support meta-analyses.

My results suggest that changes in taxonomic, phylogenetic, and functional diversity following fire events vary across plant life forms. Studies published in the past on the effects of fire on plant communities may have conflicting results due to differences in life forms dominant in each community. Therefore, I highly recommend that future researchers consider this aspect when designing and interpreting their studies. Moreover, some biomes, such as tropical and subtropical coniferous forests (TSCF), flooded grasslands, and savannas (FGS), are poorly represented within our dataset, further underlining the need for additional field studies in these biomes. Although there were challenges with the availability of data and the duration of studies, my analyses offer valuable initial findings on how biodiversity responds and recovers from fire incidents.

This chapter summarises the results of the previous data chapters. It describes how fire has affected plant taxonomic, phylogenetic, and functional diversity according to their response to the life forms (Table 5.1). Here, I compare and contradict my findings to the wider literature relevant to the impact of fire on plant biodiversity. Moreover, I also suggest future work directions and discuss the conservation implications for policymakers, fire managers and practitioners. Although my results have limited generality due to the limited database and predictive power of some models, they can still be used as a reference for future research.

Chapter 2 is about taxonomic diversity (species richness and species turnover). I found that fire impacts on species richness and recovery of community composition can vary with protection status, with protected areas appearing to buffer some plant communities from fire-induced changes. In addition, prescribed and non-prescribed burns can vary in their impacts. Moreover, I found no differences in fire impacts between fire-adapted and fire-sensitive biomes regarding species richness and community composition of life forms, except in the forb's community. I found that non-prescribed burns increased forbs species richness in flooded grasslands and savannas, whereas prescribed burns increased forbs species richness in moist broadleaf forests. In **Chapter 3**, I worked on phylogenetic diversity. I found that standardised effect sizes of PD and MNTD are reduced with increasing time since fire in trees/shrubs and forbs communities; PD of forbs increased in burnt plots relative to unburnt in the non-prescribed site of non-protected areas. Following fire events, PD of trees/shrubs and forbs increased in non-protected areas but decreased in protected sites. The standardised effect size of MPD of trees/shrubs is high in burnt plots relative to unburnt in flooded grasslands and savannas (FGS) and low in moist broadleaf forests (TSMBF). In **Chapter 4,** I filtered the data for the trees/shrubs community and collected the traits of species relevant to the fire response to the plant community. I found that non-prescribed fire causes a greater loss of functional richness than prescribed fire; protected areas can contribute to limiting the impact of fire during post-fire recovery of functional diversity that cannot be achieved in non-protected areas; and functional turnover remains very low in the fire-adaptive ecosystem and high in the fire-sensitive ecosystem.

Table 5.1 Summary of the direction of the effects of fire on taxonomic (relative species richness, species turnover); phylogenetic (PD, sesPD, sesMPD, MNTD, sesMNTD); and functional (sesFD, FRic, functional turnover) diversity on four life forms (trees/shrubs, forbs, graminoids and climbers). The green arrow (⬆) indicates that fire increases, while the red arrow (⬇) shows fire decreases the diversity.

Response variables /Predictors	Relative species richness	Species turnover	PD	ses PD	ses MPD	MNTD	ses MNTD	ses FD	FRic	Functional turnover
Trees/Shrubs										
Time since fire		⬇		⬇			⬇			
Protection status (non-protected)	⬆		⬆					⬇		
Fire type (non-prescribed)									⬇	
Biomes (FGS)					⬆					
Biomes (TSDBF)										⬆
Forbs										
Time since fire		⬇								
Fire type (non-prescribed): Protection status (non-protected)			⬆							
Fire type (non-prescribed): Biomes (FGS)	⬆									
Graminoids										
Time since fire						⬆				
Time since fire: Protection status (non-protected)		⬆								
Climbers										
Fire type (non-prescribed)	⬇									

5.2 Impact of time since fire

Time since fire is an important predictor that reflects the time it takes to recover the taxa from a fire event; understanding time since fire can help to manage fire and biodiversity conservation effectively (Moghli et al., 2021). While some studies suggest that a longer period since a fire can promote the restoration of plant biodiversity (Standish et al., 2021; Pérez-Valera et al., 2018; Bashirzadeh et al., 2023), this is not always the case. I found the variation in the impact of time since fire depends on plant life forms and biodiversity metrics. For example, in **Chapter 2**, I did not find the impact of time since fire on the species richness of any life forms. Still, I found the trees/shrubs and forb species composition gradually recovered over the period and became similar to the unburnt control sites in different time levels.

In contrast, in **Chapter 3**, I found that the phylogenetic diversity of trees/shrubs declined as time progressed. In **Chapter 4**, I did not observe the impact of time since fire on the functional richness or diversity of trees/shrubs. However, the compositional dissimilarity in species diversity and functional diversity remained for 10 years (**Chapters 2 and 4**). This indicates that species and functional composition recovery takes over a decade to reach its pre-fire or unburnt level. The number of fires in the tropics has increased rapidly in the last two decades (Tyukavina et al., 2022) and is projected to increase due to climate change (Wu et al., 2021; Li et al., 2023), indicating that fires in the tropics have direct impacts on the recovery of species composition and functional composition.

Moreover, I also found that the impact of time since fire on graminoid species turnover is linked to the protection status (**Chapter 2**) (described below in protection status).

5.3 Effects of prescribed vs. non-prescribed burn

Even though there is controversy surrounding the use of prescribed fires, they are still utilised to manage biodiversity in various landscapes (Hunter & Robles, 2020). Prescribed burning is typically conducted in fire-prone ecosystems, which can impact negatively on fire-sensitive ecosystems if not applied properly and can decrease biodiversity (Harper et al., 2018). My research shows that prescribed and non-prescribed fires can have contrasting effects on plant life forms and biodiversity metrics.

I did not find an impact of fire type on taxonomic diversity and phylogenetic diversity of the tree/shrub community. However, there was evidence that the prescribed burn positively impacted functional richness over the non-prescribed burns **(Chapter 4)**. This could be due to the non-prescribed burn selecting similar functional traits that can tolerate fires (Meza et al., 2023). Hence, prescribed fires can promote functional richness and functional diversity compared to non-prescribed fires in tree/shrub communities.

In forbs, I found that the impact of fire type on taxonomic diversity varies across biomes (described below in the biomes section), and phylogenetic diversity varies depending on protected area status (described below in the protected vs non-protected section).

In climber communities, non-prescribed burns tended to reduce the species richness, whereas they enhanced the richness at the prescribed burn **(Chapter 2)**. Previous research has shown that the climber species is reduced in areas affected by fire, regardless of the prescribed or non-prescribed fire (Addo-Fordjour et al., 2020; Balch et al., 2011). In tropical habitats, climbers tend to thrive when disturbances increase the amount of light or nutrients in the soil (Magnago et al., 2017). Prescribed burns potentially increase the richness of climbers, whereas non-prescribed fires tend to be more intense (Marshall et al., 2020), which can limit the growth of these plants.

5.4 Variation of fire impact across biomes

One of the most discussed aspects of the fire regime is the fire-adaptive and fire-sensitive ecosystem because the impact of a fire can vary according to the climate and biomes that have experienced fires in the past (Bousquet et al., 2022). Some biomes, e.g., tropical and subtropical grasslands and savannas, are historically exposed to fire. In such biomes, fire is integral to maintaining biodiversity and the ecosystem (Kelly et al., 2020). Removing or reducing fire in such biomes can reduce species diversity and negatively impact the ecosystem's functioning (Giorgis et al., 2021; Pausas and Keeley, 2019). In contrast, biomes, such as tropical rainforests, are poorly exposed to fire and species that live in these forests are sensitive to fire (Cochrane, 2003; Kelly et al., 2020). Increasing fire in such an ecosystem reduces species diversity (Cochrane & Schulze, 1999; Staal et al., 2018). My result indicates some similarities and dissimilarities with those previous findings and identified that impacts also depend on the life forms, biodiversity metrics and types of fire.

In trees/shrubs, I noticed no impact on the species richness and species turnover in any biomes (**Chapter 2**). I found strong evidence that the sesMPD of phylogenetic diversity in burnt plots relative to unburn was high in flooded grasslands and savannas (FGS) and low in tropical and subtropical moist broadleaf forests (TSMBF) (**Chapter 3**). Although the fire does not impact species diversity, it could reduce the phylogenetic diversity of trees/shrubs in such biomes where species are not adapted to fire (Nóbrega et al., 2019). Similarly, the functional diversity metrics show great variation across biomes. The functional turnover remained high in tropical and subtropical dry broadleaf forests (TSDBF) and low in tropical and subtropical grasslands, shrublands and savannas (TSGSS) (**Chapter 4)**. The low functional turnover in the grasslands could be because fire has already created fire-adaptive species, and the recovery of functional composition takes much faster than elsewhere (Teixeira et al., 2022; Giorgis et al., 2021).

In forbs, I discovered that species richness responds differently to fire events depending on the biome where they dwell. This relationship is further influenced by the fire type (prescribed vs. non-prescribed). In Flooded grasslands and savannas (FGS), the forb richness increases with fire experiencing non-prescribed burn but decreases with a prescribed burn. In contrast, in Tropical and subtropical moist broadleaf forests, the richness remains similar with non-prescribed fire and increases with prescribed fire. The taxonomic diversity of forbs depends on the types of biomes they inhabit and the fire they experience in such biomes (**Chapter 2**). Although I found the variation in taxonomic diversity across biomes, there was no variation observed in forb's phylogenetic diversity across biomes with any fire events because the fire impacts can be different on a plant's taxonomic and phylogenetic diversity (Nóbrega et al., 2019). Even though we observed a notable fire effect on FGS, our dataset has a limited representation of these biomes. This could be because researchers often overlook FGS despite their unique ecological characteristics and historical exposure to fire (Joyce et al., 2016). Hence, more research on FGS and their comparison to other biomes is needed to corroborate our findings.

5.5 Fire impact on protected vs. non-protected areas

Protected areas are vital in preventing the loss of forests and biodiversity caused by land use change and other disturbances (Geldmann et al., 2019). While protected areas are often viewed as a way to reduce the risk of fires rather than simply mitigating their effects once they occur (Eklund et al., 2022; Kearney et al., 2020), there are concerns that efforts to prevent fires in these areas can lead to the accumulation of flammable material, which can have negative ecological consequences when fires do occur (De Groot et al., 2009; Pereira et al., 2012).

Past studies have indicated that while species loss is possible in protected and non-protected areas, protected areas tend to maintain a higher level of biodiversity than unprotected areas (Bailey et al., 2022). As fires have become a major threat to ecological systems and biodiversity, protected areas can help mitigate the impact of fires on biodiversity loss (Imron et al., 2022). There is an ongoing discussion about whether protected areas are successful in preserving and promoting biodiversity during a fire (Biswas et al., 2015; Pereira et al., 2012), as nearly half of global protected areas are affected by fire disturbances (Schulze et al., 2017). My findings suggest that protected areas have the potential to minimise the impact of fires on plant communities.

In trees/shrubs, species richness increased following fires in non-protected sites but tended to remain similar in protected sites (**Chapter 2).** However, the phylogenetic diversity is reduced in protected areas but increased in non-protected areas **(Chapter 3).** Functional richness was similar in burnt sites in protected areas but low in non-protected areas **(Chapter 4)**. Our result suggests that protected areas can limit the loss of taxonomic and functional diversity of trees/shrubs yet fail to maintain phylogenetic diversity. Although the protected areas can maintain taxonomic and functional diversity in the event of a fire**,** our results indicate that the chance of losing the phylogenetic diversity of trees/shrubs is higher than the taxonomic diversity in protected areas. Thus, it is crucial to include the importance and planning of preserving phylogenetic and functional diversity in protected area policies and management to achieve the overall biodiversity goal (Larkin et al., 2015).

In forbs communities, I did not find the variation of fire impact in the taxonomic diversity in burnt and unburnt sites across protected and non-protected areas (**Chapter 2**). However, phylogenetic diversity tended to increase in the burnt sites relative to unburnt in non-protected areas and remains unchanged in protected areas. This relation is, however, influenced by fire type (prescribed vs. non-prescribed), where the increased phylogenetic diversity was observed only with non-prescribed burns in non-protected sites (**Chapter 3**). Bashirzadeh et al. (2023) also found that non-prescribed fire increased the phylogenetic diversity of forbs outside the protected area in semi-arid shrublands. Although establishing the protected areas can protect these areas from disturbances and prevent biodiversity loss (Bailey et al., 2022), my result on the relation between fire and phylogenetic diversity in protected areas is a bit unexpected. Further research is needed to validate the effectiveness of protected areas in conserving phylogenetic diversity in the event of fire.

In the graminoid community, I found that the recovery time after the fire was quicker in protected areas than in unprotected areas **(Chapter 2).** This is likely because these areas experience less human interference and less disturbance compared to unprotected areas following fire events, allowing for faster recovery after a fire (Geldmann et al., 2019; Andam et al., 2008) and suitable ecological conditions for the species diversity (Gray et al., 2016). My findings show that protected areas can effectively mitigate the effects of fires on tropical plant communities.

5.6 Conclusions and implications

My data compilation and analysis of tropical/sub-tropical plant community responses to fire generate important findings that inform knowledge of fire impacts and mitigation strategies and can help shape future research agendas. I uncover considerable heterogeneity across plant life forms in their responses to fire and biodiversity metrics and encourage researchers to consider this when reporting fire impact studies. My research makes some important contributions. A) Fire impacts on plant diversity and recovery of the species and functional composition can vary with protection status, with protected areas appearing to support some plant communities from fire-induced changes. B) Prescribed and non-prescribed burns can vary in their impacts, and this should be considered when designing prescribed burning strategies to reduce the risk of larger, more intense non-prescribed fires. C)There are differences in fire impacts in fire-adapted and fire-sensitive biomes regarding taxonomic, phylogenetic, and functional diversity, and the plant community are vulnerable in both fire-sensitive and fire-adaptive ecosystem. D) The loss of phylogenetic diversity could be higher than the taxonomic diversity in the event of a fire. As the pattern of fire is being changed in both fire-prone and non-fire-prone ecosystems and is expected to be worse due to climate change, the knowledge of how fire impacts the diversity of plants and how they recovers following the fire could be an additional asset for framing biodiversity research in the future.

Although my results are straightforward, they should be taken cautiously as these results are obtained from the limited dataset representative of the wider geographical landscape. Despite increasing awareness of changing tropical fire regimes, only a few studies address plant community responses to key fire features, and long-term longitudinal studies that can quantify recovery times are particularly scarce. More focused research on fire is needed to assess how recovery rates are influenced by landscape composition and configuration.

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Supplementary materials

Appendix 1

List of studies used in the data.

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Supplementary Table S1

This supplementary table includes the raw data collected for the Chapter 2, 3 & 4. It can be found at **https://figshare.shef.ac.uk/articles/dataset/Impact_of_fire_and_post-fire_recovery_of_tropical_and_subtropical_plant_biodiversity_Supplementary_tables/24138651/1**

Supplementary Table S2

This supplementary table includes the classification of species and life forms standardised by various sources. It can be found at **https://figshare.shef.ac.uk/articles/dataset/Impact_of_fire_and_post-fire_recovery_of_tropical_and_subtropical_plant_biodiversity_Supplementary_tables/24138651/1**

Supplementary Table S3

Plant groups and their presence in the number of studies, number of sites, number of observations and total number of species of four life-form groups.

Plant Group	No of Studies	No of sites	Observations	No of species
Trees/Shrubs	26	84	3535	1006
Forbs	20	61	798	343
Graminoids	18	56	651	224
Climbers	24	60	273	132

Supplementary Table S4

Candidate Models

Response variables are either the Relative Species Richness or the Species Turnover (Sorenson Index) for chapter 2; Relative Phylogenetic Diversity (PD), Relative Mean Pairwise Distance (MPD), Relative Mean Nearest Taxon Distance (MNTD), Relative sesPD, Relative sesMPD, and Relative sesMNTD for chapter 3; and Relative Functional Diversity (FD), Relative Functional Richness (FRic), Functional turnover, Relative sesFD, and Relative sesFRic for chapter 4.

Model	Equation
M00	1 + (1|study_ID)
M01	Time Since Fire + (1|study_ID)
M02	Fire Type + (1|study_ID)
M03	Biomes + (1|study_ID)
M04	Protection Status+ (1|study_ID)
M05	Time Since Fire + Fire Type + (1|study_ID)
M06	Time Since Fire +Biomes + (1|study_ID)
M07	Time Since Fire +Protection Status+ (1|study_ID)
M08	Fire Type + Biomes + (1|study_ID)
M09	Fire Type + Protection Status+ (1|study_ID)
M10	Biomes +Protection Status+ (1|study_ID)
M11	Time Since Fire +Fire Type+ Biomes + (1|study_ID)
M12	Time Since Fire +Fire Type+ Protection Status+ (1|study_ID)
M13	Time Since Fire +Biomes + Protection Status+ (1|study_ID)
M14	Fire Type + Biomes + Protection Status+ (1|study_ID)
M15	Time Since Fire +Fire Type + Biomes + Protection Status+(1|study_ID)
M16	Time Since Fire +Biomes + Time Since Fire*Biomes + (1|study_ID)
M17	Time Since Fire + Protection status+ Time Since Fire*Protection Status+ (1|study_ID)
M18	Fire Type + Biomes + Fire Type*Biomes + (1|study_ID)
M19	Fire Type+ Protection Status+ Fire Type*Protection Status+ (1|study_ID)
M20	Fire Type+ Time Since Fire*Biomes + (1|study_ID)
M21	Time Since Fire +Fire Type*Biomes + (1|study_ID)
M22	Fire Type+ Time Since Fire*Protection Status+ (1|study_ID)
M23	Time Since Fire + Fire Type*Protection Status+(1|study_ID)
M24	Protection status+ Time Since Fire*Biomes +(1|study_ID)
M25	Biomes + Time Since Fire*Protection Status+ (1|study_ID)
M26	Protection status+ Fire Type*Biomes + (1|study_ID)
M27	Biomes + Fire Type*Protection Status+ (1|study_ID)
M28	Fire Type + Protection status+ Time Since Fire*Biomes + (1|study_ID)
M29	Time Since Fire +Fire Type + Time Since Fire*Protection Status+ (1|study_ID)
M30	Time Since Fire + Protection status+ Fire Type*Biomes + (1|study_ID)
M31	Time Since Fire +Biomes +Fire Type*Protection Status+ (1|study_ID)

Supplementary Table S5

This supplementary table includes the number of species found in the burn and unburn plots of Trees/Shrubs, Forbs, Graminoids and climbers. The table is found at **https://figshare.shef.ac.uk/articles/dataset/Impact_of_fire_and_post-fire_recovery_of_tropical_and_subtropical_plant_biodiversity_Supplementary_tables/24138651/1**

Supplementary Table S6

This supplementary table includes the dataset for Chapter 4. The data table can be found at **https://figshare.shef.ac.uk/articles/dataset/Impact_of_fire_and_post-fire_recovery_of_tropical_and_subtropical_plant_biodiversity_Supplementary_tables/24138651/1**

Supplementary Table S7

This includes the information on species and their trait data collected from various sources and their references. The table is found at **https://figshare.shef.ac.uk/articles/dataset/Impact_of_fire_and_post-fire_recovery_of_tropical_and_subtropical_plant_biodiversity_Supplementary_tables/24138651/1**

Supplementary Figures

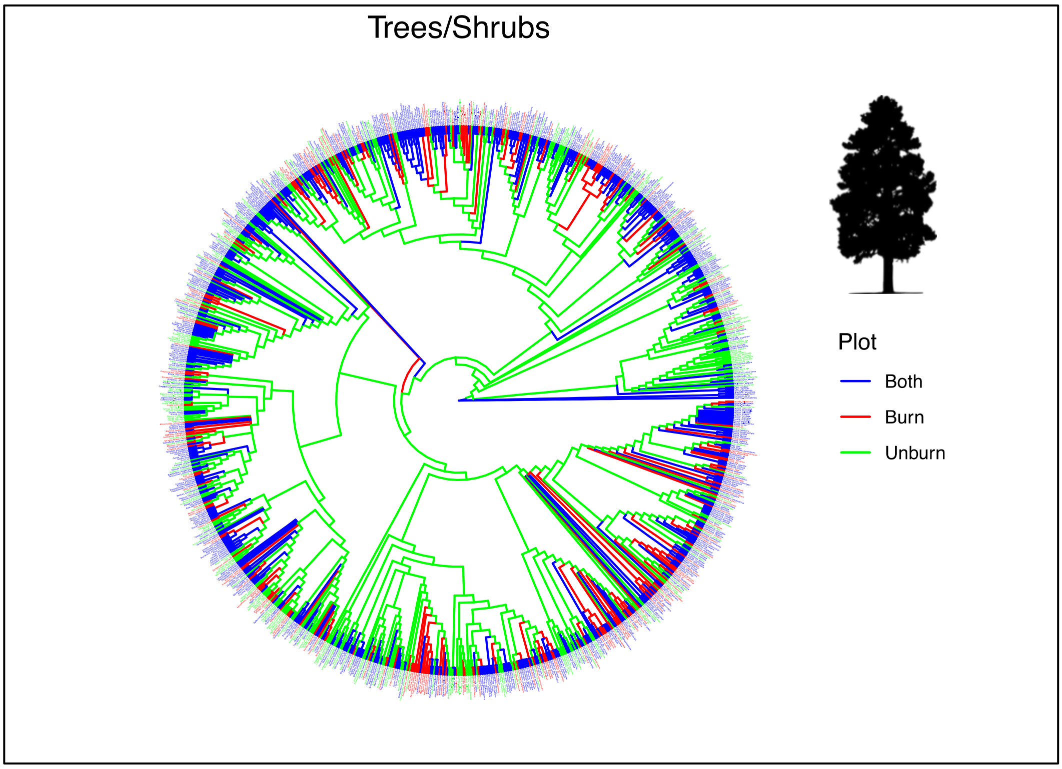

Fig S1. The phylogenetic tree of trees/shrubs community. The tip colour shows species found in burnt only (red, n = 194), unburnt only (green, n = 261) and both burnt and unburnt (blue, n = 536) plots.

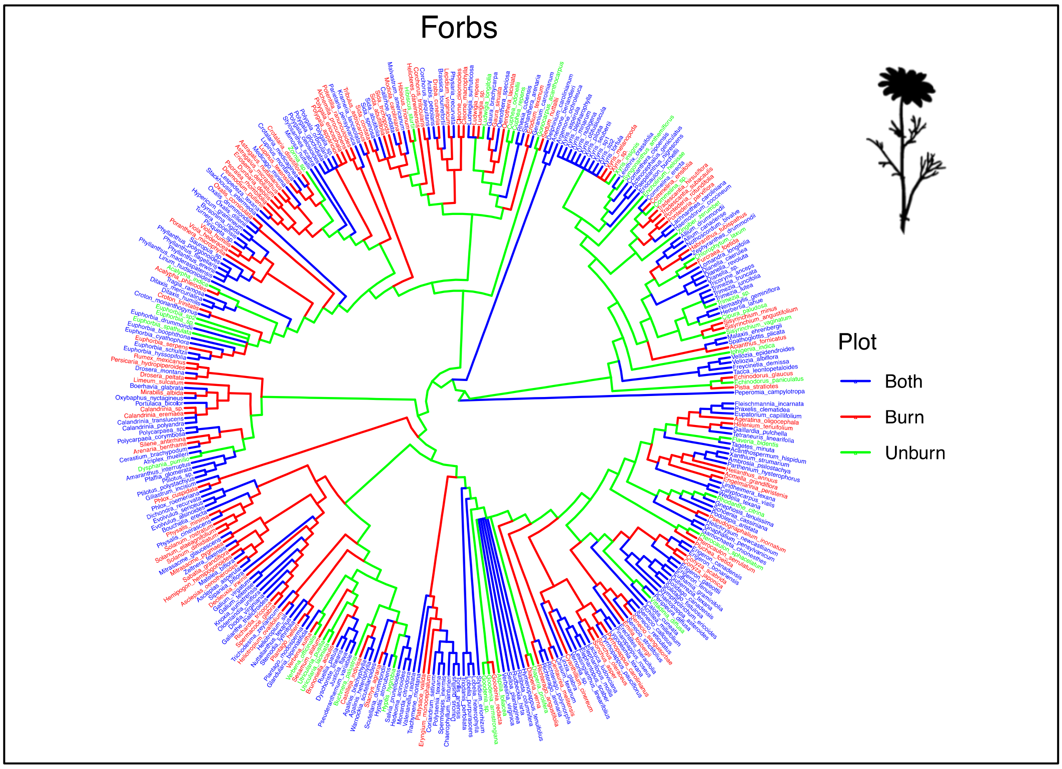

Fig S2. The phylogenetic tree of forb community. The tip colour shows species found in burnt only (red n = 101), unburnt only (green, n = 35) and both burnt and unburnt (blue n = 205) plots.

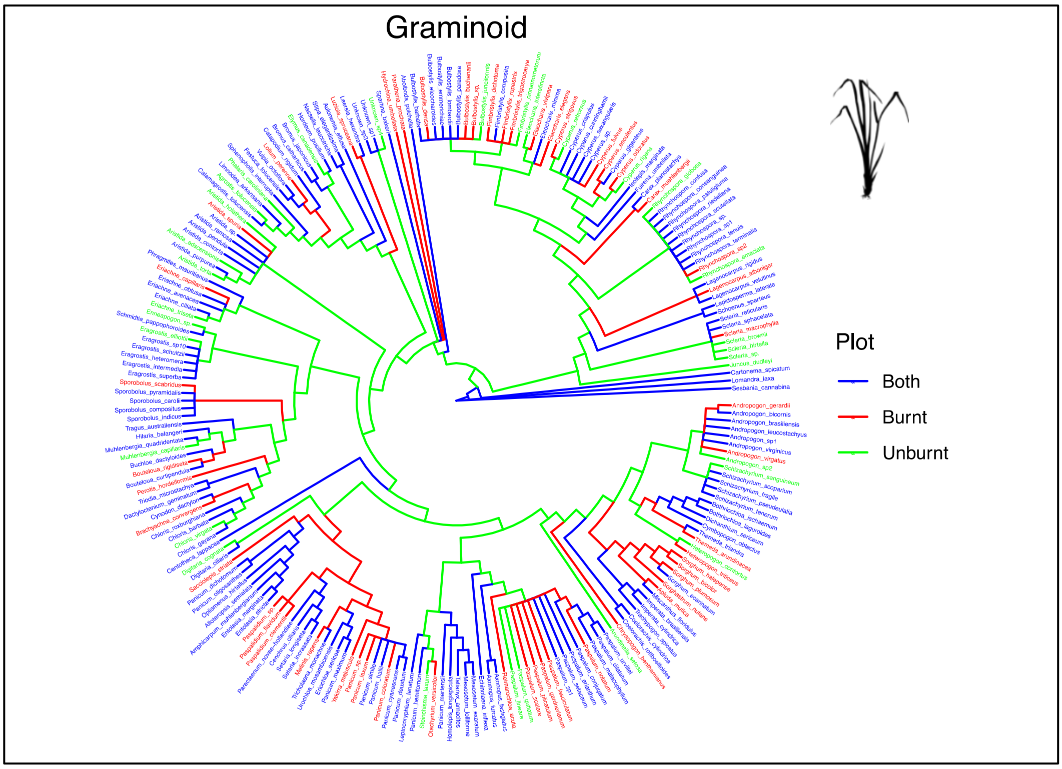

Fig S3. The phylogenetic tree of graminoid community. The tip colour shows species found in burnt only (red n = 52), unburnt only (green, n = 31) and both burnt and unburnt (blue n = 139) plots.

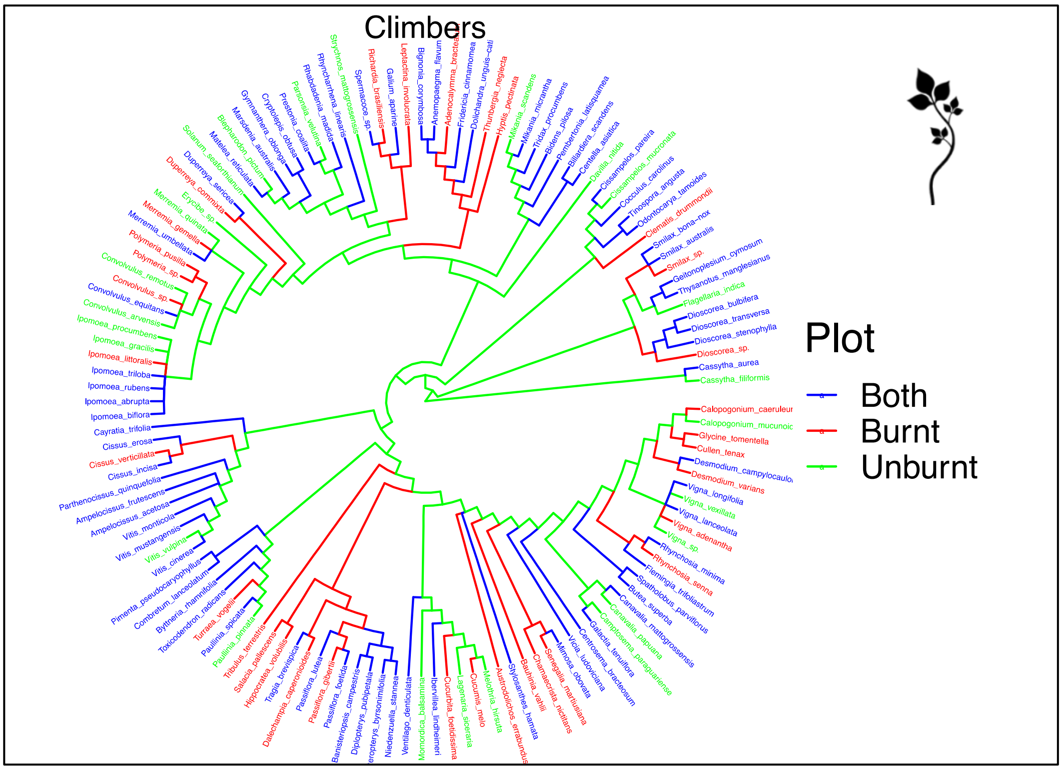

Fig S4. The phylogenetic tree of the climber community. The tip colour shows species found in burnt only (red n = 74), unburnt only (green, n = 33) and both burnt and unburnt (blue n = 25) plots.