

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

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## Abstract

Fire is increasingly driving 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 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 forest 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 (by ~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 divergence of community composition following fire events occurs across a number of life forms. Composition of tree/shrub communities remained divergent from unburnt communities ten years after a fire, and 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 change are predicted to further shorten these intervals. Plant communities across much of the tropics are thus likely to change substantially in response increased exposure to fire.

## Introduction

Globally, the distribution, seasonality, frequency and intensity of fires has 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 rate of recovery 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 UNFCCC REDD+ program (UNFCCC, 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 highly sensitive 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 habitat 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 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 at 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 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).

## Methods

### Literature search

A systematic literature search was conducted following the PRISMA guidelines (Liberati et al., 2009; Moher et al., 2009) and completed 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° 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).

Data collection process took place in five stages (Table 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 at **Appendix 1**.

**Table 1:** The selection stages, procedure, and total no. of papers obtained in the literature search.

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

## 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 (**Appendix 2, 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<sup>2</sup>, or for shrub species richness when plots were less than 16 m<sup>2</sup> (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); 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; 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).

## 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 *aurstrait*s 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 (**Appendix 3, 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 at **Appendix 4, Table S3**.

## 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.

## Data analysis

All analyses were conducted in R 4.2.2 (R Core development team, 2022). 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 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 ( $n = 32$ ; **Appendix 5, 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 model, 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).

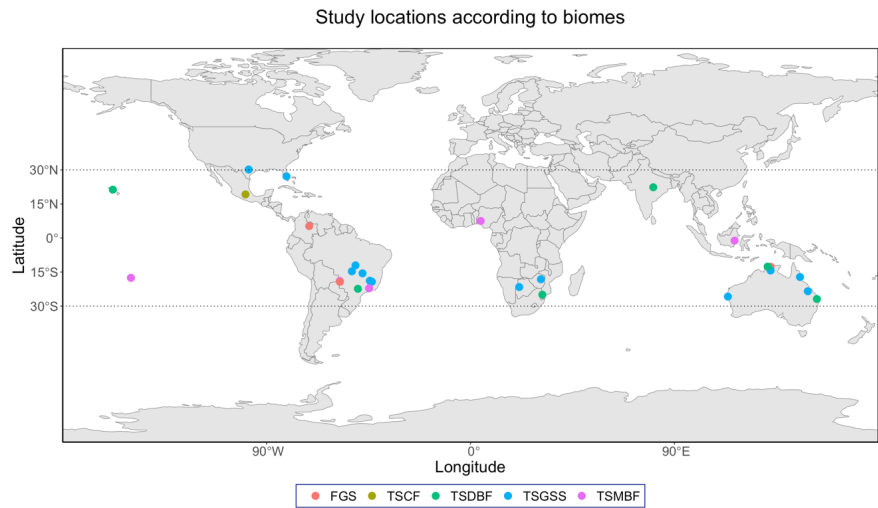
We used an information-theoretic criterion approach to obtain a set of models whose  $\Delta AICc$  values were

within two points of the best performing model, i.e., that with the lowest AICc value, and then conducted model averaging (Burnham & Anderson, 2004).

## Results

### 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 1).



**Fig 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.

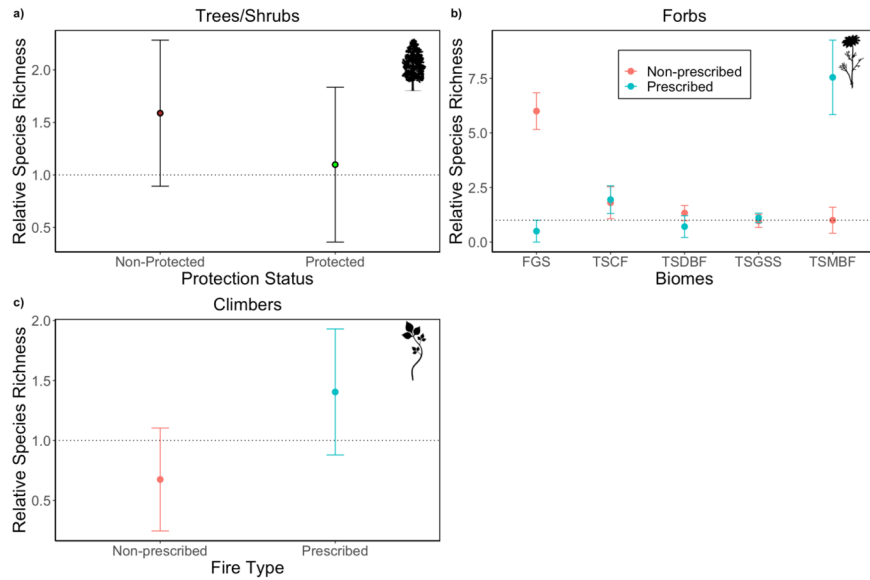
### Relative Species Richness

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). Protection status did, however, influence 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; Fig. 2a). 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). 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; Fig. 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; Fig. 2). 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; Fig. 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).

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



**Fig 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.

### Species Turnover

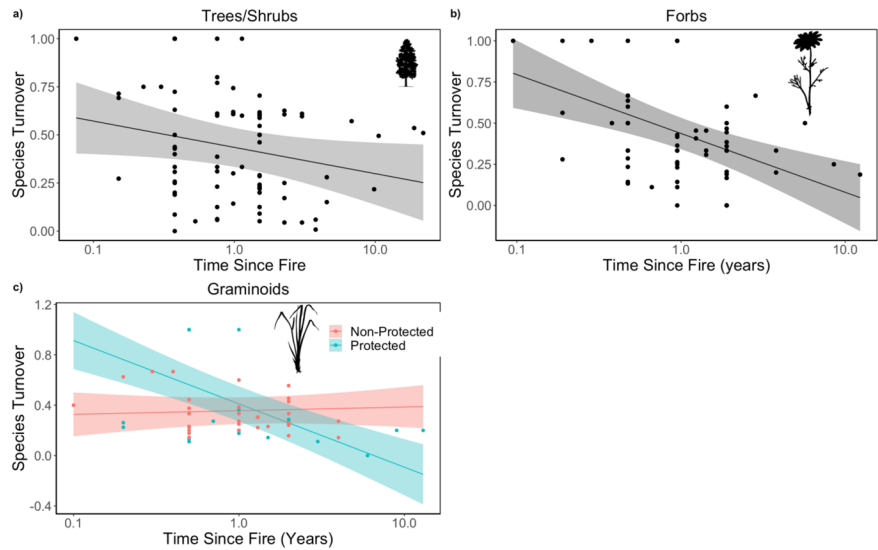
Models of turnover in species composition of tree/shrub, forb and graminoid communities between burnt and unburnt plots consistently had good explanatory power, which (except for forbs) was higher than equivalent models of relative species richness (trees/shrubs: 32.99 %, forbs: 27.60%, and graminoids: 64.95%). Dissimilarity in species composition of tree/shrub and forb communities was initially marked (Table 3; Fig3a, 3b). Composition of forb communities had returned to that of pre-fire communities approximately ten years after a fire (Fig. 3b), the composition of tree and shrub communities remained dissimilar to that of pre-fire communities ten years after the fire event (Fig. 3a).

Within protected areas graminoid communities exhibited marked turnover immediately following fire events, but these communities resembled pre-fire communities ten years after the fire event (Table 3; Fig. 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. 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 that lacked predictors (AICc 78.14).

**Table 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                                      | Life Forms                               | Life Forms                                    |
|------------|-------------------------------------------------|------------------------------------------|-----------------------------------------------|
| Predictors | Trees/Shrubs<br>Parameter estimate<br>(95 % CI) | Forbs<br>Parameter estimate<br>(95 % CI) | Graminoids<br>Parameter estimate<br>(95 % CI) |

|                                                                | Life Forms              | Life Forms              | Life Forms              |
|----------------------------------------------------------------|-------------------------|-------------------------|-------------------------|
| <i>Time Since Fire (ln transformed)</i>                        | -0.059 (-0.117, -0.001) | -0.155 (-0.235, -0.076) | -0.102 (-0.160, -0.044) |
| <i>Protection Status (Non-protected)</i>                       | —                       | —                       | -0.027 (-0.141, 0.084)  |
| <i>Time Since Fire (ln): Protection Status (Non-Protected)</i> | —                       | —                       | 0.115 (0.051, 0.176)    |
| <b>Model Explanatory Power (<math>D^2</math>)</b>              | <b>32.99 %</b>          | <b>27.60 %</b>          | <b>64.95 %</b>          |



**Fig 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 points represents the no. of sites. The X axis is plotted on a log scale. The shaded area represents the 95% confidence interval.

## 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 and 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.

### 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).

### 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 fire occurs (Eklund et al., 2022; Kearney et al., 2020). Indeed, there is concern that fire suppression in protected areas can result in 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 a stabilising influence that can limit the magnitude of fire induced changes in plant communities. Species richness of trees/shrubs increased (by ~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 in 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 condition for 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), that enables faster recovery.

### 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 these 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 forest, 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.

### 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 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 for any recovery in graminoids 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 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 are 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 increasing probability that fires will 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).

### 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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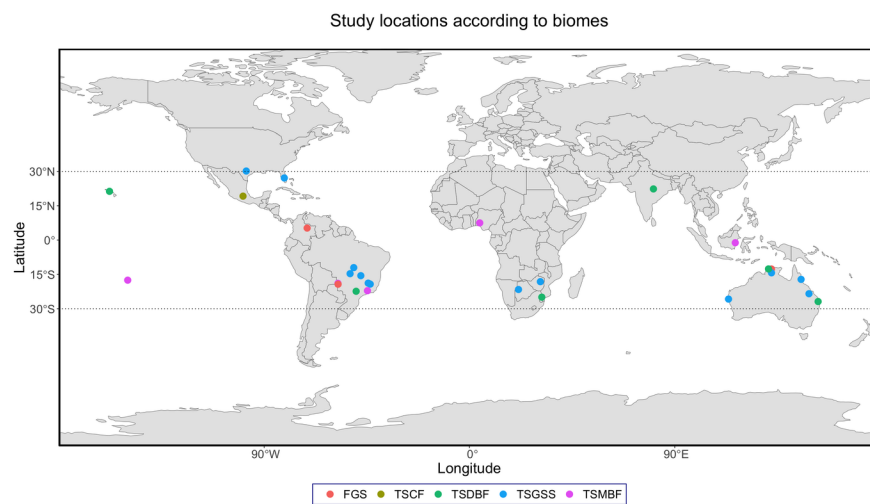
### Conflict of interest disclosure:

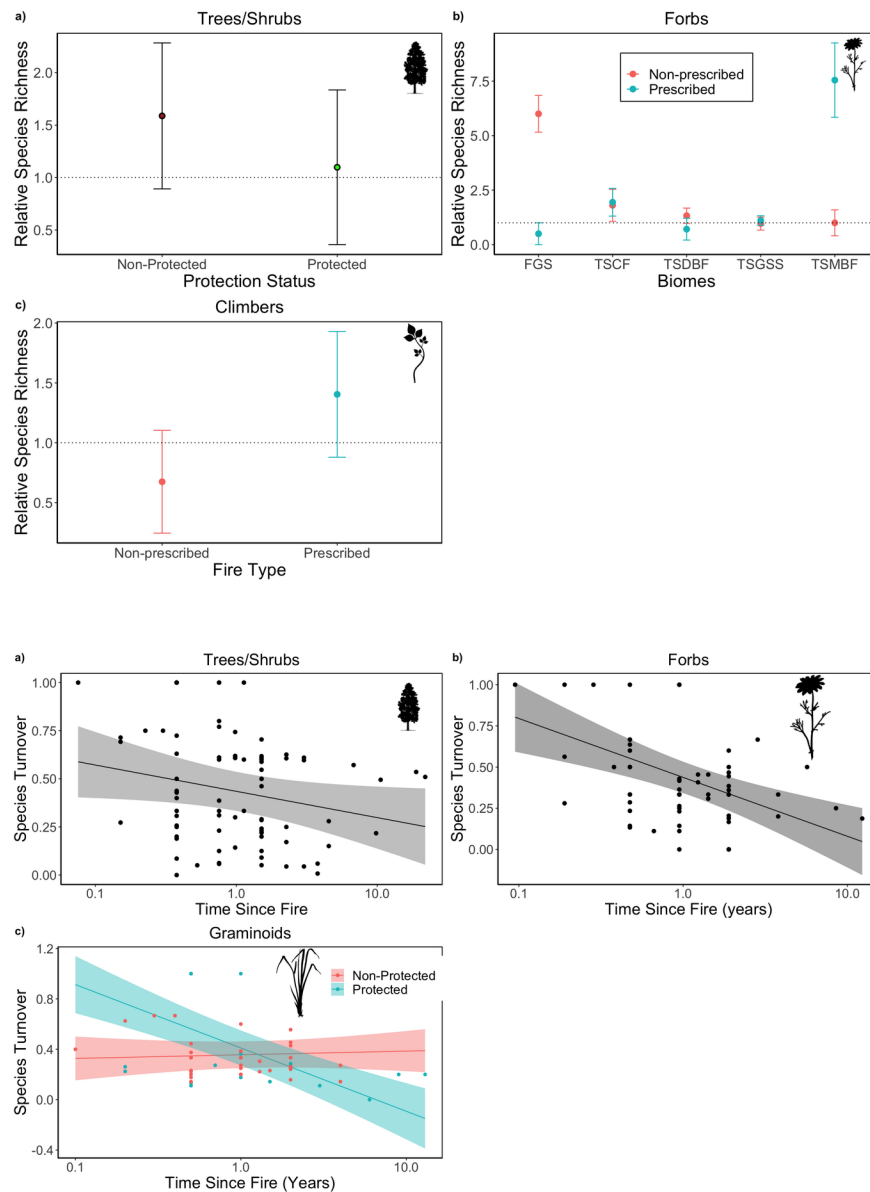
We have no conflicts of interest to disclose.

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### Author contributions:

**Dharma Sapkota:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **David P. Edwards :** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Visualization (supporting); Writing – review & editing (equal). **Mike Massam :** Formal analysis (supporting); Methodology (supporting); Visualization (supporting); Writing – review & editing (supporting). **Karl Evans :** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Methodology (equal); Supervision (equal); Visualization (supporting); Writing – review & editing (equal).





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