

META-ANALYSIS

Global plant responses to intensified fire regimes

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Abstract

Aim: Global change factors, such as warming, heatwaves, droughts and land-use changes, are intensifying fire regimes (defined here as increasing frequency or severity of fires) in many ecosystems worldwide. A large body of local-scale research has shown that such intensified fire regimes can greatly impact on ecosystem structure and function through altering plant communities. Here, we aim to find general patterns of plant responses to intensified fire regimes across climates, habitats and fire regimes at the global scale.

Location: Worldwide.

Time period: Studies published 1962–2023.

Major taxa studied: Woody plants, herbs and bryophytes.

Methods: We carried out a global systematic review and meta-analysis of the response of plant abundance, diversity and fitness to increased fire frequency or severity. To assess the context dependency of those responses, we tested the effect of the following variables: fire regime component (fire frequency or severity), time since the last fire, fire type (wildfire or prescribed fire), historical fire regime type (surface or crown fire), plant life form (woody plant, herb or bryophyte), habitat type and climate. **Results:** Intensified fire regimes reduced overall plant abundance (Hedges' $d = -0.24$), diversity ($d = -0.27$), and fitness ($d = -0.69$). Generally, adverse effects of intensified fire regimes on plants were stronger due to increased severity than frequency, in wildfires compared to prescribed fires, and at shorter times since fire. Adverse effects were also stronger for woody plants than for herbs, and in conifer and mixed forests than in open ecosystems (e.g. grasslands and shrublands).

Main conclusions: Intensified fire regimes can substantially alter plant communities in many ecosystems worldwide. Plant responses are influenced by the specific fire regime component that is changing and by the biotic and abiotic conditions.

1 | INTRODUCTION

Fire is a natural and essential process that has shaped many ecosystems over geological time scales (Pausas & Keeley, 2009). As a result, plants are adapted to the historical fire regime, which encompasses

the characteristic fire activity (i.e. frequency, severity, extent and seasonality) that prevails in their area of distribution. However, fire regimes are shifting abruptly due to global change (Pausas & Keeley, 2021; Pellegrini et al., 2021; Turner et al., 2019). Land-use changes such as the abandonment of agriculture and livestock

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grazing, as well as fire suppression policies, have increased plant biomass loads and continuity in many regions (Bowman et al., 2011; Dara et al., 2020; Moreira et al., 2011). Moreover, climate change, characterized by warmer temperatures, increased frequency and intensity of heatwaves, and prolonged droughts, is increasing the weather and fuel conditions conducive to fire (Abatzoglou et al., 2019; Berg et al., 2017; Jones et al., 2022). Furthermore, the expansion of the wildland–urban interface in many ecosystems, including roads in tropical and boreal forests, is raising the number of fire ignitions (Jones et al., 2022; Radeloff et al., 2018). As a result of all these factors, many ecosystems are undergoing a perturbation of their fire regime (*sensu* Keeley & Pausas, 2019). We refer to this perturbation as intensification of the fire regime because frequency, severity and size of fires are moving towards the high extreme of their historical range of variability (Canadell et al., 2021; Pausas & Keeley, 2021; Senande-Rivera et al., 2022; Whitman et al., 2022). Given that plant species and communities are adapted to historical fire regimes (Keeley et al., 2011), such intensification of the fire regime can substantially alter plant communities, and the structure and functioning of ecosystems (Karavani et al., 2018; Keeley & Pausas, 2019; Nolan et al., 2021; Whitman et al., 2019). Here, we aim to summarize plant responses to intensified fire regimes across climates, habitats and fire regimes at the global scale.

The frequency and severity of fires are crucial components of fire regimes that greatly influence plant populations and communities. Increased fire frequency (i.e. the shortening of fire-free intervals) can select for the individuals that are most suited to the novel fire regime (Guiote & Pausas, 2023). However, strong or abrupt increases in fire frequency may prevent plants from refilling their seed bank (limiting postfire recruitment) or their carbon and nutrient reserves (limiting postfire resprouting), thus decreasing the resilience of fire-adapted plants (Enright et al., 2015; Hoffmann et al., 2012; Zedler, 1995). More severe fires can also damage key plant organs such as basal and epicormic buds, secondary meristems, seeds and the hydraulic system, hindering post-fire survival and regeneration (Pausas & Paula, 2020; Schimmel & Granström, 1996). As such, both increased fire frequency and severity have been observed to reduce the abundance of key species in several habitats including grasslands (Gomes et al., 2018; Wright & Fenham, 2016), broadleaf forests (Etchells et al., 2020; Fairman et al., 2016), conifer forests (Schimmel & Granström, 1996; Turner et al., 2019) and shrublands (Foster et al., 2018; Talluto & Suding, 2008). Negative impacts on plant diversity have also been reported with increased fire frequency and severity (Cavender-Bares & Reich, 2012; Collins & Calabrese, 2012; DeSiervo et al., 2015). Therefore, as climatic and environmental changes escalate, intensified fire regimes (i.e. increased frequency or severity of fires) are expected to have an increasing adverse impact on plant communities worldwide.

Plant responses to intensified fire regimes are complex and can be influenced by the different variables associated with the fire regime. The specific component of the intensified fire regime (i.e. fire frequency or severity) is a key driver of plant responses (Alba et al., 2015; Giorgis et al., 2021; Keeley et al., 2005) because

different species or populations have different fire-adaptive traits to cope with each component of the fire regime (Johnstone et al., 2016; Keeley & Pausas, 2022). The broad type of historical fire regime may be associated with the fire regime component being intensified: in crown-fire regimes the intensification is mainly related to an increase in fire frequency (e.g. warmer and drier conditions in North American boreal forests), while in surface-fire regimes it is typically related to an increase in fire severity (e.g. greater fuel accumulation in North American Ponderosa pine forests that facilitates crown fires; Covington & Moore, 1994; Enright et al., 2015). Effects of intensified fire regimes inferred from studies using prescribed fires (burns) may differ from those using wildfires, as wildfires are typically larger and more severe (Alba et al., 2015). Moreover, time since the last fire can influence the observed fire effects (Alba et al., 2015; Eales et al., 2018) and mediate the response of different plant types, because the rate at which different plants respond to disturbances varies widely (Keeley et al., 2005). For example, short-lived, resource-acquisitive plants such as graminoids and forbs generally recover faster from fire than long-lived, resource-conservative shrubs and trees that often take longer to restore their biomass (Díaz et al., 2016; Willms et al., 2017).

Plant community composition and the environmental context can also mediate plant responses to intensified fire regimes (Pellegrini et al., 2021). Crucially, the life form of a plant may influence its responses due to differences in traits (Keeley & Pausas, 2022; Pekin et al., 2012). For example, compared to herbaceous plants, woody plants take longer to develop fire-coping mechanisms (e.g. reach sexual maturity, accumulate a reliable seedbank, grow a thick bark), and thus may be more susceptible to shortening fire-free intervals (Enright et al., 2015; Pausas & Paula, 2020; Willms et al., 2017). Conversely, woody species may have higher potential to survive low-intensity fires. Meanwhile, some bryophytes are capable of quickly colonizing bare ground after a high-severity fire due to their high dispersal capacity (Maltby et al., 1990). Plant responses may also depend on the type of habitat, such as forest, shrubland or grassland, because the different biotic and abiotic conditions (e.g. soil thermal and moisture dynamics, soil fertility, light and nutrient availability and herbivory pressure) impact post-fire regeneration (Alba et al., 2015; Foster et al., 2018; Pausas & Bond, 2020; Pellegrini et al., 2021). Similarly, post-fire plant recovery can also be driven by differences in large-scale abiotic conditions associated with broad climate types (e.g. temperature, water and light availability) (DeSiervo et al., 2015; Giorgis et al., 2021; Nolan et al., 2021).

While research on plant responses to intensified fire regimes has grown substantially over the past two decades (Giorgis et al., 2021), it has mainly focused on local and regional scales. Thus, we lack a global view of the effects of the ongoing intensification of fire regimes, and the context-dependency of those effects. Moreover, most quantitative research syntheses examining fire effects on plants at continental or global scales have focused on the effects of fire *per se* (i.e. burnt vs. unburnt comparisons) rather than on the effects of changes in fire regime (Alba et al., 2015; Eales et al., 2018; Giorgis et al., 2021; Willms et al., 2017). Only the synthesis by

Tangney et al. (2022) has addressed plant responses to altered fire regimes at the global scale but focusing exclusively on fire seasonality. To date, no study has investigated plant responses to increased fire frequency and severity across the diversity of climates, habitats and fire regimes worldwide.

In this study, we carried out a global systematic review and meta-analysis to examine the impact of intensified fire regimes on plant abundance, diversity and fitness. Our hypothesis is that, at the global scale, the intensification of fire regimes, that is, the increase in frequency or severity of fires, should negatively affect plants and thus modify their abundance, diversity or fitness, although the two components (severity and frequency) may be relevant in different ecological conditions. Specifically, we tested the following predictions: (1) Intensified fire regimes reduce overall plant abundance, diversity or fitness, because many plants may be unable to recover from fire regimes that are at the extreme or outside of their historical range (Enright et al., 2015; Johnstone et al., 2016; Keeley & Pausas, 2019). (2a) Increased fire severity has greater effects than increased fire frequency in forests, as potential step-changes in fire regime type (e.g. from surface to crown fires) can overwhelm plant responses (Fernández-García et al., 2020; Keeley & Pausas, 2019); meanwhile, (2b) increased fire frequency has greater effects on woody than on herbaceous plants because the former have lower growth rates and are thus more sensitive to shorter fire-free intervals (Díaz et al., 2016; Knapp et al., 2015). (3) Increased fire severity has greater effects at short time scales (early post-fire) as the effect may fade with time (Giorgis et al., 2021), and this should be especially evident for woody vegetation due to their slower growth (Keeley et al., 2005; Willms et al., 2017). (4) Intensified wildfire regimes have greater effects on plants in wildfire studies compared to prescribed fire studies, because fire severity and extent are usually greater in wildfires (Alba et al., 2015; Allen et al., 2016). (5) Forests are more sensitive to intensified fire regimes than open-canopy ecosystems (e.g. grasslands, shrublands) as the latter are historically more fire prone (Dantas et al., 2016; Karavani et al., 2018; Pausas & Bond, 2020). (6) Effects of intensified fire regimes are stronger (more negative) in ecosystems from arid and cold climates than in temperate and tropical climates because plant recovery rates in the former are more resource-limited (Fernández-García et al., 2020; Giorgis et al., 2021; Pellegrini et al., 2021). By addressing these predictions, we aimed to improve our understanding of the resilience of plant communities to the intensification of fire regimes, and the context-dependency of the fire effects across global environmental gradients.

2 | METHODS

2.1 | Literature search and compilation of data set

We followed the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) to complete this review (O'Dea et al., 2021; Page et al., 2021). We searched peer-reviewed research

articles and book chapters in the databases Scopus and Web of Science using word combinations in English and Spanish related to fire regimes and vegetation responses in titles, abstracts and keywords. All searches were carried out on 15 February 2023, and yielded 1779 publications (for complete search strings see Table S1 in Supporting Information). We screened titles and abstracts with the help of the *revtools* package (Westgate, 2019) in R software version 4.1.1 (R Core Team, 2021), and selected 593 publications for full-text screening.

We then selected the publications that met the following criteria: (1) the study focused on vegetation responses to variation in fire severity, or fire frequency (we did not consider fire extent, seasonality, or simply burnt vs. unburnt comparisons); (2) vegetation response could be interpreted as positive or negative (e.g. compositional change was excluded); (3) fire regime comparisons were not obviously confounded with other factors such as seasonality, ecosystem type or management interventions; (4) the study was directly relevant to natural ecosystems and was based on wildfires or prescribed fires in any season (small-scale experimental fires were excluded because of their highly artificial settings); (5) the study was based on original data (reviews and simulation studies were excluded) and on (6) current fire regimes (paleo- and dendro-ecological studies were excluded); and (7) they included information to calculate an effect size based on Hedges' *d* (i.e. mean, standard deviation and number of observations of paired treatment groups) or to estimate *d* (correlation coefficients or *F*-tests and number of observations) (Borenstein, 2009; Lajeunesse, 2013). A total of 273 publications met these criteria.

To further improve the literature search, on 19 February 2023, we performed backward and forward searches on the seven most highly-cited publications among our selected publications, plus in three recent relevant reviews (Foo et al., 2021). This resulted in 1865 new publications, from which we selected 121 that met the criteria described above. Thus, the total number of publications considered was 394. The PRISMA flowchart (Figure S1) and list of the data sources (Appendix 1) provide more details on the database.

2.2 | Effect sizes

To standardize results across studies, we used Hedges' *d* (sometimes called Hedges' *g*), which is a bias-corrected effect size based on the standardized mean difference between control and treatment groups (Rosenberg et al., 2013). To do this, we first extracted from figures, tables and text the mean, standard deviation and number of observations of vegetation response metrics for lower ('control') and higher ('treatment') fire frequency or fire severity. If a study reported more than two fire regime levels (e.g. low, moderate and high), we only considered the lowest and highest levels. Studies included a range of metrics for fire severity (e.g. soil heating, litter consumption, char height, canopy scorch) and, in a few cases, they provided fire intensity data. We grouped all these metrics together and used the term 'fire severity'. In our data set, the higher treatment

(most intense fire regime) was generally associated with greater fire frequency or severity than the historical norm or towards the high end of the historical variability. This was explicitly stated or implicit in most studies (e.g. Bret-Harte et al., 2013; Etchells et al., 2020; Fernández-García et al., 2020; Grau-Andrés et al., 2019; Ibáñez et al., 2022; Turner et al., 2019; Whitman et al., 2019). Although for some studies the intensified fire regime may have been well within the historical variability, by considering both frequency and severity we explored the intensification of fire regimes in many environments, in line with global change projections (Abatzoglou et al., 2019; Jones et al., 2022; Pausas & Keeley, 2021; Senande-Rivera et al., 2022).

We used *metaDigitise* (Pick et al., 2019) to extract data from boxplots, *WebPlotDigitizer* (Rohatgi, 2022) for scatterplots and *ImageJ* (Rasband, 1997) for other plot types. Then, we calculated Hedges' *d* and its variance following Borenstein (2009). When primary data for calculating *d* was not reported, we estimated it from secondary data (e.g. frequency tables, *F*-ratios, *t*-tests) using conversion formulas in Borenstein (2009) and Lajeunesse (2013), and the online effect size calculator (Wilson, 2001). While most selected studies reported results for discrete fire regime levels (e.g. high and low fire severity), some (76 studies) reported results over continuous fire regime variables (e.g. a gradient of soil heating). In these cases, we first computed Pearson's *r* and then converted it to Hedges' *d* following Borenstein (2009). Effect sizes standardize responses of plants under more intense fire regimes relative to those under less intense fire regimes. Therefore, a positive effect size indicates a positive response to an intensified fire regime (e.g. an increase in plant abundance with fire severity), while a negative effect size indicates the opposite.

Standard deviations (or data to estimate them) were not available for 35 studies. To avoid lowering the sample size that would likely increase publication bias (Kambach et al., 2020), we imputed the missing standard deviations following Lajeunesse (2013). To do this, we first computed coefficients of variation (i.e. standard deviation to mean ratios) of complete-case studies included in the data set. Because the coefficient of variation can vary widely across environmental and experimental settings, we modelled coefficients of variation by fitting linear mixed effects models (function 'lme' in the package *nlme*; Pinheiro et al., 2022) including fire type (prescribed fire or wildfire), number of observations, plant life form, climate zone and time since fire as explanatory variables (see next section for details of each variable). Study ID was included as a random effect to account for non-independence. We fitted separate models for each of our three response variables (i.e. abundance, diversity and fitness; see below). Reduced models including only statistically significant ($p < 0.05$) explanatory variables were then used to estimate coefficients of variation. Finally, modelled coefficients of variation were multiplied by the reported means to obtain imputed standard deviations for the studies for which it was not available. Results of meta-analyses excluding effect sizes computed using imputed data are also provided.

Pseudo-replication (non-independent data due to, e.g. high spatial autocorrelation) was detected in 27 studies. Using an artificially

high number of observations wrongly reduces effect size variance and can ultimately bias meta-analysis through inflated effect size precision. To address this, in studies with pseudo-replicated data, we computed the variance of Hedges' *d* using the lower number of observations at the reported true replicate level (e.g. at the plot rather than at the individual level), which results in a more conservative variance estimate (Eales et al., 2018). Five remote sensing studies on large wildfires reported very high sample sizes based on the total number of pixels retrieved. Given the high spatial correlation of these data, we reduced the sample size by simulating an increase of the pixel size to 4 km², which we estimated to be large enough to be spatially independent in the context of large wildfires. Although our approach is somewhat arbitrary, it led to conservative sample sizes (median sample size was reduced from 441 to 18), coherent with similar remote sensing studies.

2.3 | Response and moderator variables

We classified plant responses into three categories termed 'abundance' (including plant frequency, density, cover, size, biomass and recovery), 'diversity' (including taxonomic and functional richness, Shannon-Wiener and inverse Simpson diversity indices, Pielou's evenness, beta-diversity), and 'fitness' (including fitness components and other related variables, e.g. survival, growth rate, photosynthetic and other fluxes, reproductive output, nutrient content). The number of effect sizes and studies for each metric, within the three plant response categories, is provided in Table S2. For each effect size, we recorded information of variables that may affect vegetation responses to altered fire regimes (i.e. moderator variables). These variables were fire type (wildfire and prescribed fires), fire regime component (fire severity and fire frequency), the type of historical fire regime (surface fires, crown fires or non-fire prone), plant life form (bryophytes, herbs and woody vegetation), habitat type (broadleaf forest, conifer forest, mixed forest, grassland, shrubland and woodland), climate (arid, cold, temperate with a dry season, temperate without a dry season and tropical), and time since the last fire (short, i.e. 24 months or less, and long, i.e. longer than 24 months; Giorgis et al., 2021). The type of historical fire regime was based on the prevailing fire regime for the ecosystem in question; mixed-severity fire regimes were included in the crown-fire type. Climate types were defined following the Köppen-Geiger classification system (Peel et al., 2007) and assigned to each location with the help of the R package *kgc* (Bryant et al., 2017). We chose a 24-month cutpoint for short versus long time since fire because the vegetation is most dynamic during the first 2 years post-fire (Giorgis et al., 2021; Grau-Andrés et al., 2017; Velle et al., 2014), although we acknowledge there is large variation, for example, among habitats and plant life forms. Time since fire was only considered when studying fire severity (and not for fire frequency to avoid confounding effects).

Given that switching from surface fire to crown fire is one of the most abrupt fire regime changes currently occurring in many landscapes (Keeley & Pausas, 2019; Pausas & Keeley, 2014a), we

specifically identified effect sizes related to surface-to-crown fire regime changes. For this, we considered studies where such step-change was possible, that is, in forests where low- and high-fire severity levels could be associated with surface and crown fires, respectively. We selected studies in which fire regime type was clearly stated or could be confidently inferred from site description and fire effects (e.g. post-fire tree mortality). Thus, this is a special case of increasing fire severity.

2.4 | Meta-analysis

We carried out all data analyses and plotting using R software version 4.1.1. Meta-analyses were performed by fitting multivariate mixed-effects linear models, as implemented in the function 'rma.mv' from the package *metafor* (Viechtbauer, 2010). We fitted separate models for each of the three response variables (i.e. abundance, diversity and fitness). We identified extremely influential observations using the function 'cooks.distance.rma.mv' in *metafor*. As a result, we removed three effect sizes in the abundance data set, two effect sizes in the diversity data set and two effect sizes in the fitness data set. Given that most studies contributed with more than one effect size (e.g. for different taxa, sites), to account for non-independence of effect sizes, all models incorporated as a random factor the effect size identity (a unique identifier for each effect size) nested within study identity (Cornwall et al., 2022; Giorgis et al., 2021). We ran the models without the intercept to test effect size differences from zero, and to estimate the mean effect size for each moderator level. Mean effect sizes were considered significantly different from zero if their 95% confidence intervals did not include zero. For each response variable, we first fitted a global model including Hedges' d and its variance without moderator variables, to test the overall effect of intensified fire regimes on vegetation. We then fitted models that included one moderator (i.e. fire regime component, fire type, time since the last fire, historical fire regime type, plant life form, habitat or climate) to test how the different moderator variables affect plant responses. To gain further insights into the effect of key fire-related moderators (fire regime component, fire type, time since the last fire and historical fire regime type), we tested these moderators for data subsets of other moderators. Finally, to assess the effect of step-changes in fire behaviour, we analysed plant responses to increased fire severity associated with a change from surface to crown fire.

We used funnel plots and Egger's regressions to examine publication bias (Nakagawa et al., 2022). To do this, we used the meta-analytic residuals of the overall models (adequate for models with dependency structures such as ours, and for accounting for data heterogeneity; Leal et al., 2022; Nakagawa et al., 2022; Nakagawa & Santos, 2012). We plotted, for each response variable, the meta-analytic residuals against sample size, and ran linear regressions with the meta-analytic residuals as the response variable and sample size as the explanatory variable. To calculate sample size, rather than

simply adding up sample sizes of treatment and control groups, we used the 'effective sample size', as it accounts for unbalanced sampling designs (following Nakagawa et al., 2022).

3 | RESULTS

3.1 | Data sets of effects of intensified fire regime on vegetation

We computed 2363 effect sizes of plant responses to intensified fire regimes from 394 studies. The country where most studies were performed was the United States (151 studies), followed by Australia (68), Spain (30), Canada (22), South Africa (16), Brazil (15) and Argentina (10) (Figure 1). The most studied response variable was abundance (1514 effect sizes), followed by diversity (506), and fitness (343) (Figure 2). Regarding fire regime components, there were more effect sizes on fire severity than on fire frequency (1377 and 986, respectively). More studies focused on wildfires (1499 effect sizes) than on prescribed fires (861). Total effect sizes from long- and short-time since fire studies were similar (662 and 649, respectively; note that time since fire was not considered for fire frequency). Historical fire regimes consisting of surface fires and of crown fires were similarly represented (1004 and 1079 effect sizes, respectively), while only 12 studies (62 effect sizes) were carried out in non-fire-prone ecosystems.

3.2 | Overall plant responses to intensified fire regimes (Figure 2)

Intensified fire regimes significantly reduced plant abundance, diversity and fitness (Figure 2, Tables S3–S5; see Figure S2 for results excluding imputed data). Within each response variable, the different metrics analysed showed broadly similar responses (Table S2). There was some variation in magnitude among metrics, most notably among the main abundance metrics, that is, frequency or density (Hedges' $d = -0.314$, 95% CI = $-0.456, -0.171$) and cover ($d = -0.062$, CI = $-0.220, 0.097$).

Most moderator variables significantly affected plant responses. Fire severity and frequency reduced plant abundance, while only fire severity reduced plant diversity and fitness. In studies on wildfires, intensified fire regimes significantly decreased plant abundance, diversity and fitness, but not on prescribed fires. Moderator analyses testing the effect of time since fire showed that increased fire severity reduced plant abundance in the short term (i.e. ≤ 2 -year post-fire), and plant diversity and fitness in both the long and short time. In surface-fire regimes, intensified fire regimes reduced plant abundance and diversity, while in crown-fire regimes, they reduced plant abundance and fitness. Regarding plant life form, intensified fire regimes significantly reduced abundance and fitness of woody plants but had no effect on diversity of bryophytes and herbs. Analyses including habitat type as

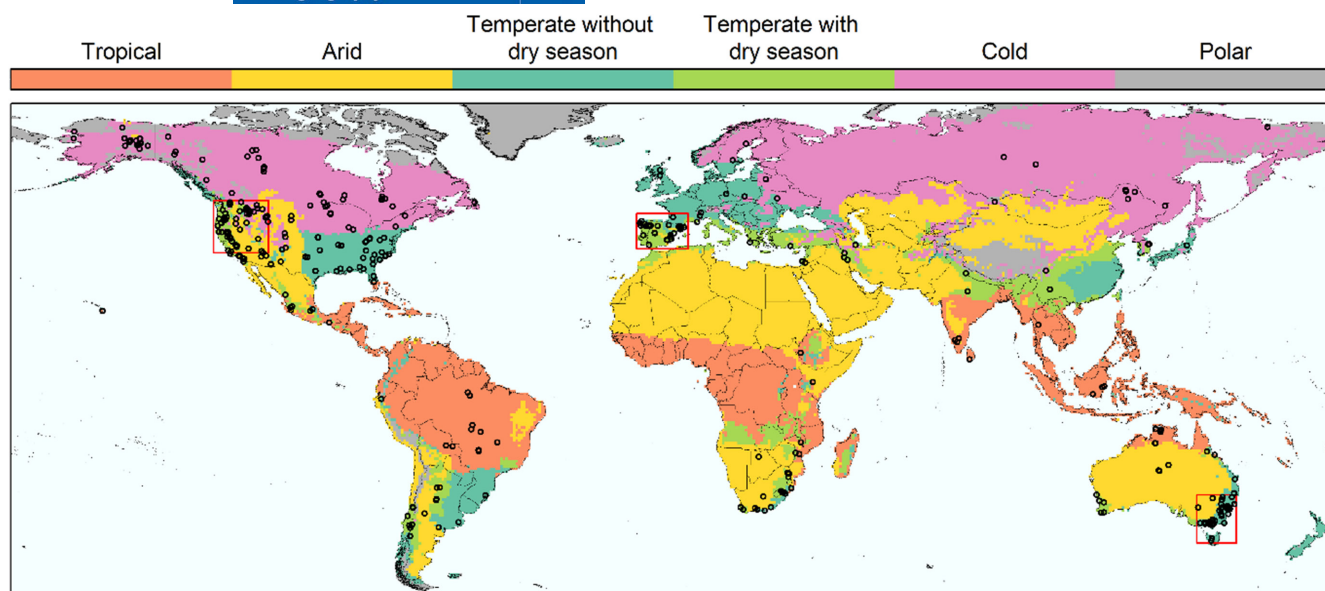


FIGURE 1 Locations of studies included in the meta-analyses (circles). Climate zones follow the Köppen-Geiger classification system (Peel et al., 2007). Areas with a high concentration of studies (in red rectangles) are detailed in Figure S5.

moderator showed that significant negative effects of intensified fire regimes on plant abundance, diversity and fitness were generally most evident in conifer and mixed forests. Intensified fire regimes impaired plants most strongly in cold climates, temperate climates with a dry season and tropical climates; but diversity was less affected than abundance and fitness (Figure 2).

3.3 | Plant responses by fire moderators (Figures 3–5)

The response of plant abundance to intensified fire regimes was mediated by the fire regime component (i.e. increased fire frequency or severity) across moderator variables (Figure 3a). This was most evident when considering the historical fire regime type, as plant abundance was significantly reduced by intensified fire severity (but not frequency) in surface-fire ecosystems, and by intensified fire frequency (but not severity) in crown-fire ecosystems. Surface-fire ecosystems were mostly grasslands and woodlands, while crown-fire ecosystems were shrublands and conifer forests (Figure S3). Further, woody plant abundance was reduced by increased fire frequency, but not by increased severity. Regarding plant diversity, it was reduced by increased fire severity in surface-fire regimes, wildfire studies, mixed forests, woodlands, cold climates and temperate climates with a dry season, while increased fire frequency had no effect (Figure 3b). Conversely, diversity of woody vegetation was reduced by higher fire frequency, not higher fire severity. For plant fitness, the greater effect of fire severity compared to fire frequency on decreasing fitness was consistent across most moderator categories (Figure 3c).

Fire type (i.e. prescribed or wildfire) mediated the effect of intensified fire regimes on plant abundance, because negative effects in surface- and crown-fire regimes, and in most habitats and climates,

occurred for wildfires, but not for prescribed fires (Figure 4a). Similarly, plant diversity in surface-fire regimes, woody plants, and in some habitats and climates was significantly reduced by intensified fire regimes in wildfire studies only (Figure 4b). Plant fitness was also significantly reduced by intensified fire regimes in wildfire studies (but not in prescribed fire studies) in surface- and crown-fire regimes, woody plants, conifer and mixed forests, and temperate climates with a dry season (Figure 4c). However, in shrublands and in tropical climates, intensified fire regimes significantly impaired plant fitness in prescribed fire studies, but not in wildfires.

Shorter time since fire led to stronger negative effects of increased fire severity on plant abundance and diversity across several moderators (Figure 5a,b). As such, we observed significant short-term effects (but not long-term effects) on plant abundance in studies focused on wildfires, surface-fire historical regimes, herbaceous, conifer forests, mixed forests and grasslands, and arid, cold and temperate climates without a dry season (Figure 5a). Similarly, plant diversity was reduced in the short term (but not in the long term) in wildfires, surface-fire regimes, bryophytes, shrublands, and cold and temperate climates without a dry season (Figure 5b). Conversely, for plant fitness we found significant negative effects of increased fire severity in both the short and the long term (Figure 5c). For example, plant fitness in prescribed fire studies, in non-fire-prone ecosystems, and of woody plants was reduced in both the short and the long term. In crown-fire ecosystems and conifer forests, intensified fire regimes impaired plant fitness in the long term, but not in the short term.

3.4 | Surface-to-crown fires (Figure 6)

Increased fire severity leading to step-changes in fire behaviour (i.e. surface-to-crown fires) had no overall effect on plant

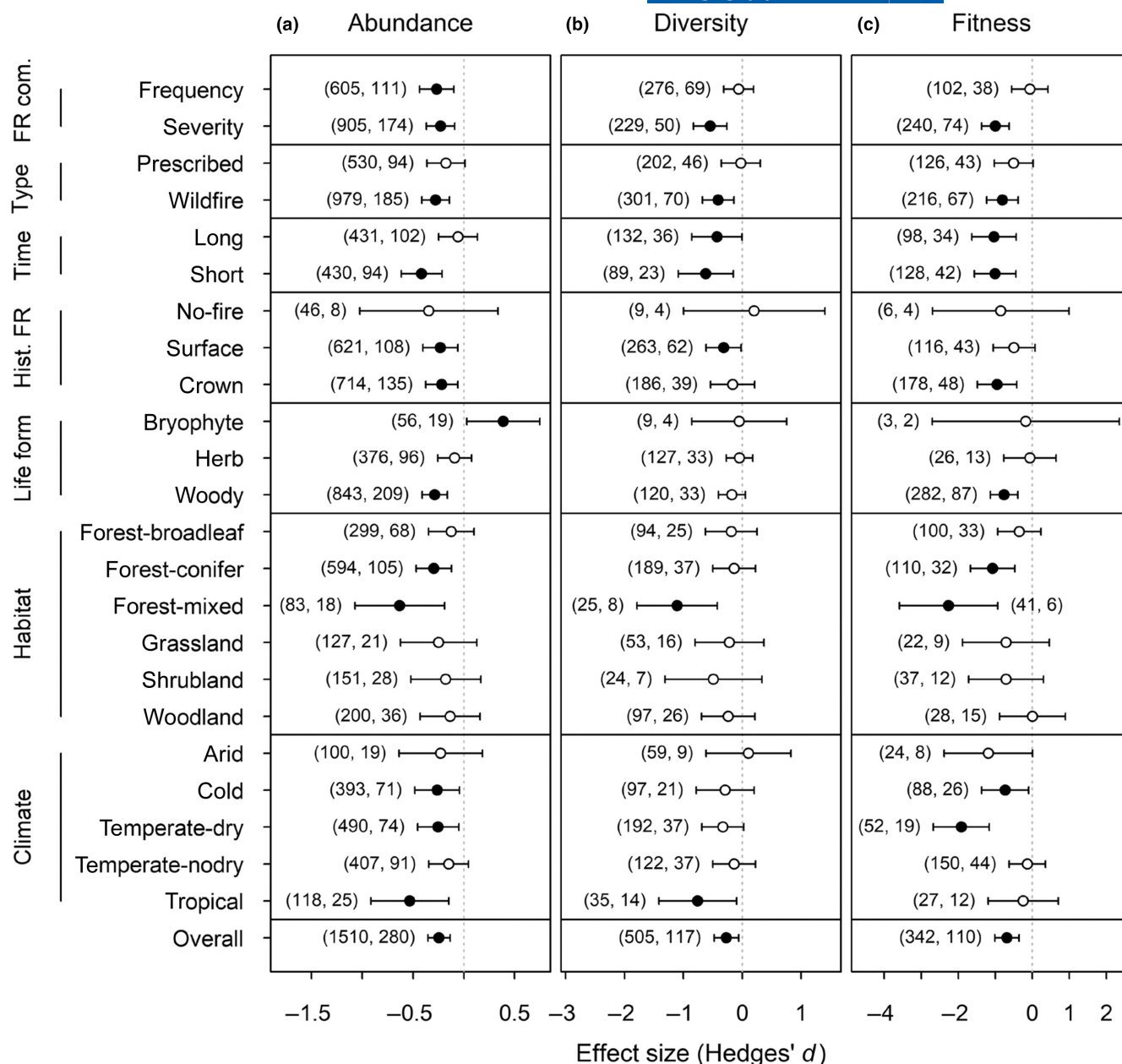


FIGURE 2 Response of plant abundance (a), diversity (b) and fitness (c) to intensified fire regimes across moderator categories and overall. Circles are effect size estimates and whiskers are 95% confidence intervals. Open circles indicate that estimates are not statistically significantly different from zero at $\alpha=0.05$, while filled symbols indicate significant differences. In parentheses, number of effects sizes, followed by number of studies. 'FR com.' refers to fire regime component; 'Type' refers to fire type; 'Time' refers to time since the last fire; and 'Hist. FR' refers to type of historical fire regime. Time since fire was only examined in fire severity studies (not for fire frequency). Statistical information on the models underpinning this Figure 2 is given in [Tables S3–S5](#).

abundance ($d=-0.129$, 95% CI= -0.340 to 0.082) and diversity ($d=-0.162$, 95% CI= -0.551 to 0.226), but significantly reduced fitness ($d=-1.473$, 95% CI= -2.407 to -0.539 ; [Figure 6](#)). Nevertheless, plant abundance and diversity were significantly reduced by this step-change in mixed forests, while diversity of herbaceous plants decreased. Plant fitness was significantly reduced in crown-fire regimes, woody plants, conifer forests, and in temperate climates with a dry season.

3.5 | Publication bias

Funnel plots showed that data of plant abundance, diversity and fitness were reasonably symmetrical ([Figure S4](#)). The intercepts of modified Egger's regressions did not significantly differ from zero for abundance ($t\text{-test}=0.317$, $p=0.751$, $df=1509$), diversity ($t\text{-test}=-0.522$, $p=0.602$, $df=502$), and fitness ($t\text{-test}=-0.579$, $p=0.563$, $df=340$). Thus, there was no indication of publication bias.

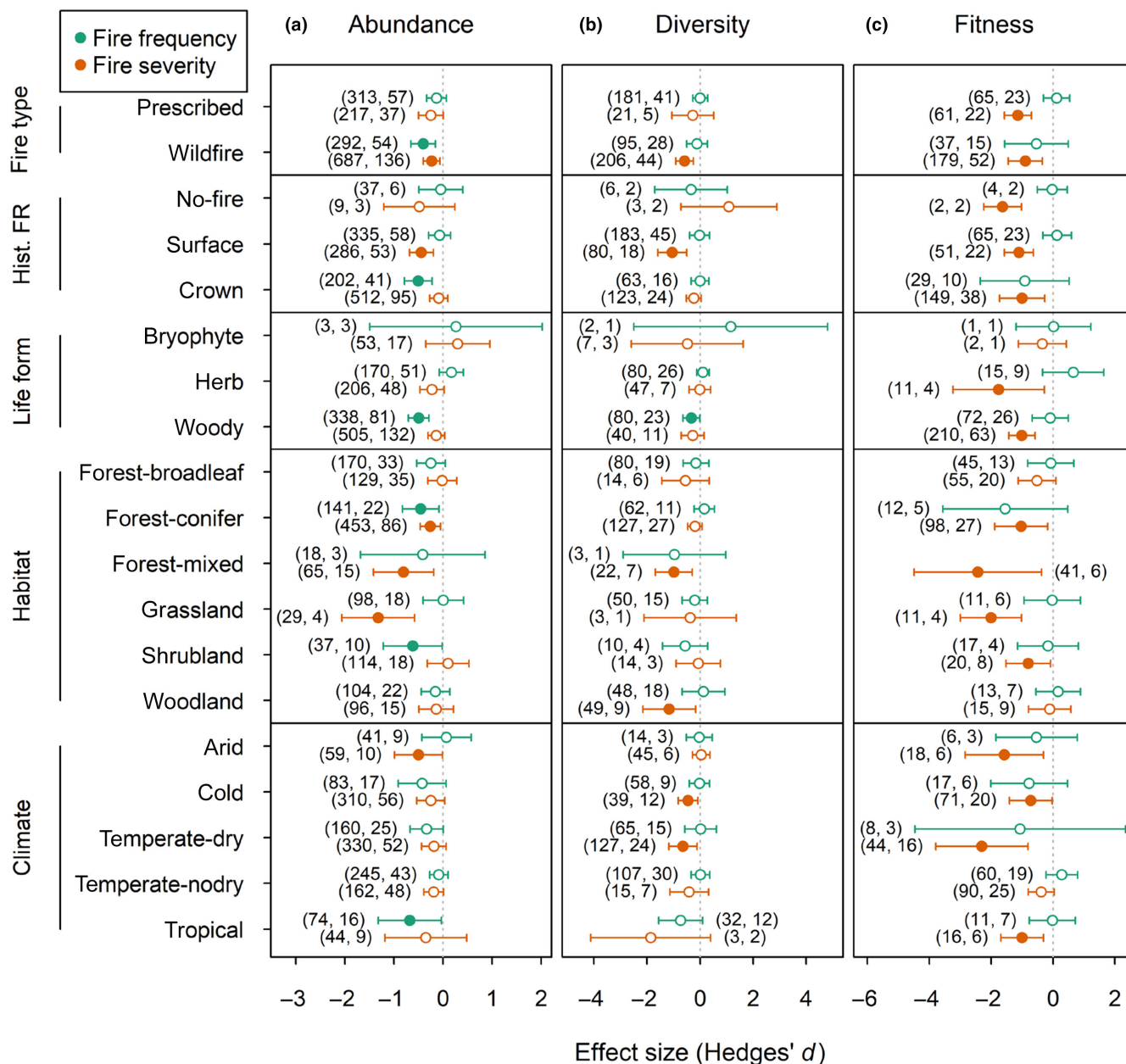


FIGURE 3 Response of plant abundance (a), diversity (b) and fitness (c) to intensified fire regimes across moderator categories, for each of two fire regime components (i.e. increased fire frequency or increased fire severity). Symbols are effect size estimates and whiskers are 95% confidence intervals. Open symbols indicate that estimates are not statistically significantly different from zero at $\alpha = 0.05$, while filled circles indicate significant differences. In parenthesis, number of effects sizes, followed by number of studies; when these values are low, results should be interpreted with care. 'Hist. FR' refers to type of historical fire regime. Overall effects are provided in Figure 2 (see 'FR com.').

4 | DISCUSSION

We found global evidence that increasing frequency or severity of fires towards historical extreme values (intensified fire regimes) has an overall negative effect on plant abundance, diversity and fitness (Figure 2). Negative plant responses are observed at high fire severity or intensity, when the heat of the fire surpasses bark capacity to protect the cambium and transport tissues (i.e. not reaching the fire resistance threshold; Hoffmann et al., 2012), or when vegetative regenerative structures (i.e. buds) or seeds are damaged, affecting

resprouting and recruiting abilities (Schimmel & Granström, 1996; Wright & Fensham, 2016). Moreover, increased fire frequency can also impede postfire resprouting and recruiting through exhausting bud reserves (Clarke et al., 2013) and preventing the accumulation of a soil or canopy seed bank (e.g. immaturity risk, Keeley & Pausas, 2022; Zedler, 1995), leading to abrupt post-fire vegetation changes (Etchells et al., 2020; Turner et al., 2019). Although fire is a natural process in many ecosystems, our findings indicate that the intensification of fire regimes has, on average, negative ecological consequences (Enright et al., 2015; Johnstone et al., 2016; Keeley

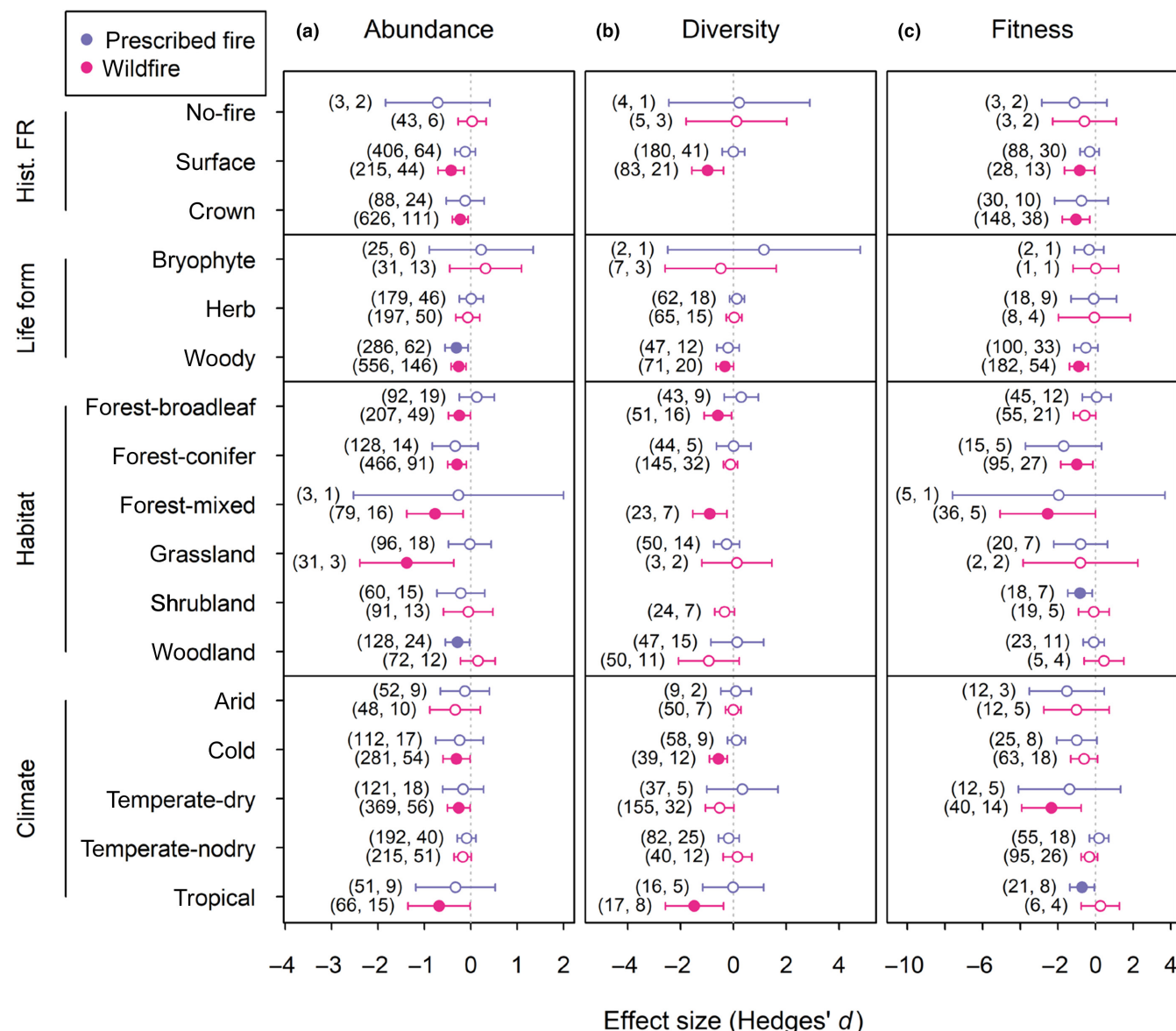


FIGURE 4 Response of plant abundance (a), diversity (b) and fitness (c) to intensified fire regimes across moderator categories, for each of two fire types (i.e. prescribed fires or wildfires). Symbols are effect size estimates and whiskers are 95% confidence intervals. Open symbols indicate that estimates are not statistically significantly different from zero at $\alpha=0.05$, while filled symbols indicate significant differences. In parenthesis, number of effects sizes, followed by number of studies; when these values are low, results should be interpreted with care. 'Hist. FR' refers to type of historical fire regime. Overall effects are provided in Figure 2 (see 'Type').

& Pausas, 2019). However, the overall effects of this intensification were relatively minor, at least for the studied fire regime changes, as the magnitude of d for abundance (0.24), diversity (0.27) and fitness (0.69) indicate small (0.2) to medium (0.5) effects (Cohen, 1988).

The extent of negative plant responses varied across moderator variables, with only about a quarter of tests yielding significant negative responses (Figures 3–5). This variability in the resilience of ecosystems is likely due to differences in their previous fire history and the degree of intensification tested compared to historical variability. There was also variability among the response variables, with plant abundance being reduced by both increased fire severity and frequency, while plant diversity and fitness were unaffected by increased fire frequency (Figure 2). This limited

effect of increased fire frequency on plant diversity and fitness could result from negative plant responses being balanced by positive ones. For example, increased fire frequency often impairs the abundance of dominant species, preventing competitive exclusion of other species, and could thus contribute to the observed no effect on diversity (Miller & Safford, 2020; Velle et al., 2014). Similarly, although increased fire frequency can have direct negative effects on plant function, it can also enhance growth rates or reproductive output through rejuvenating plant communities or improving soil nutrient availability (Green et al., 2010; Hobbs & Gimingham, 1984), which on average could lead to a neutral effect on fitness. Overall, our findings point to more negative plant responses to increased fire severity (47% of the tests in Figure 3)

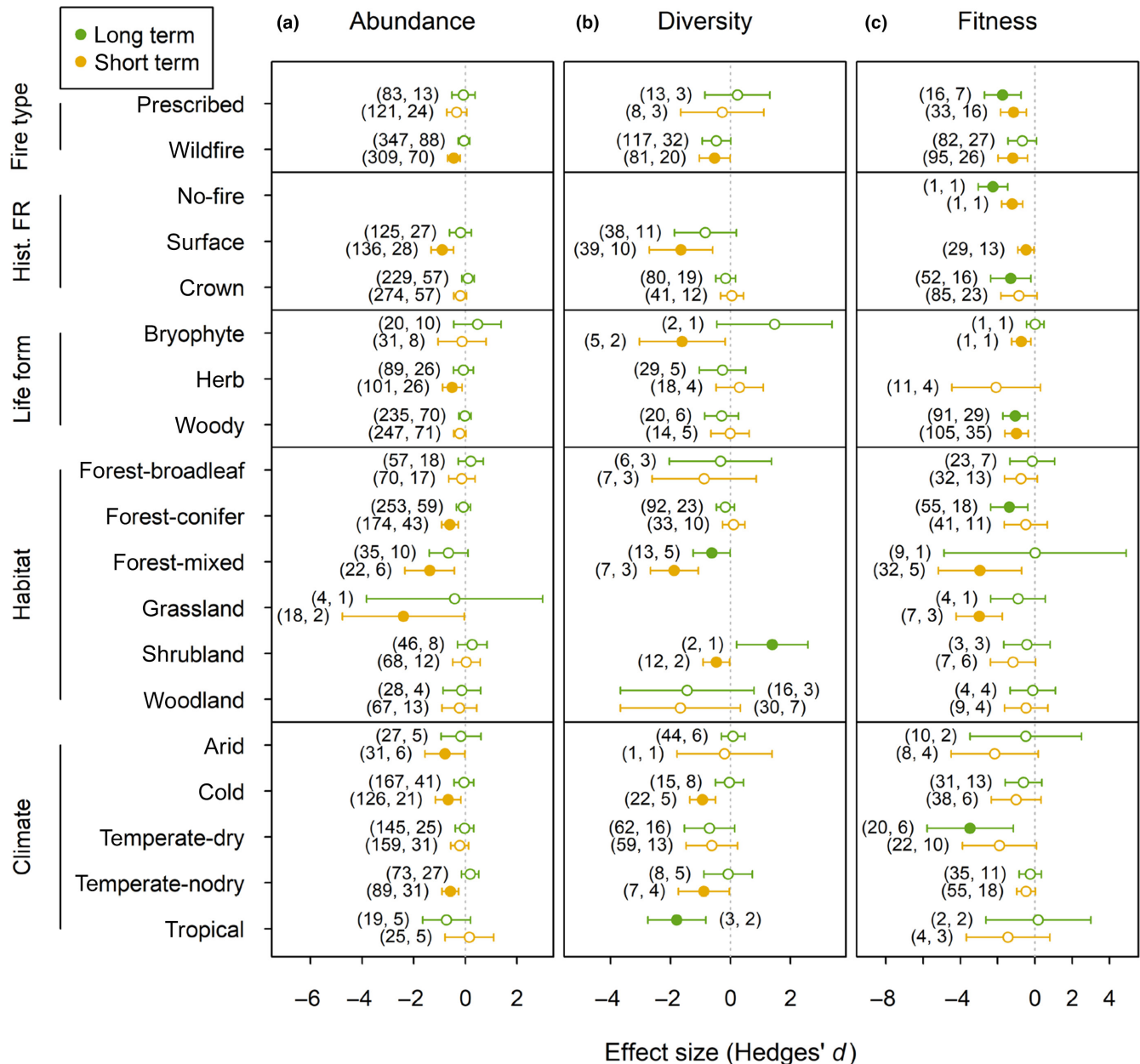


FIGURE 5 Response of plant abundance (a), diversity (b) and fitness (c) to intensified fire regimes across moderator categories, for each of two levels of time since the last fire (i.e. long-term >24 months, or short-term ≤24 months). Symbols are effect size estimates and whiskers are 95% confidence intervals. Open symbols indicate that estimates are not statistically significantly different from zero at $\alpha=0.05$, while filled symbols indicate significant differences. In parenthesis, number of effect sizes, followed by number of studies; when these values are low, results should be interpreted with care. 'Hist. FR' refers to type of historical fire regime. Overall effects are provided in Figure 2 (see 'Time'). These results exclude fire frequency studies, as time since fire was only analysed in fire severity studies.

than to increased fire frequency (8% of the tests), particularly for diversity and fitness indicators.

This greater effect of fire severity was especially evident in mixed forests, but was also apparent in grasslands (Figure 3), which does not support our second prediction of greater negative effects of increased fire severity than of increased fire frequency in forests. Additionally, we found weak support for our prediction that those greater negative effects are related to step-changes in fire behaviour, as switching from surface to crown fires reduced plant abundance, diversity or fitness in mixed or conifer forests,

but these effects were not widespread (Figure 6). Nevertheless, our finding that, in surface-fire regimes, plant abundance, diversity and fitness were reduced by increased fire severity but not by increased fire frequency (Figure 3) supports ecological theory positing that historical fire regimes consisting of frequent, low-severity fires are sensitive to increases in severity but resilient to increases in frequency (Keeley & Pausas, 2022). Also consistent with our second prediction, we found that increased fire frequency impaired abundance and diversity of woody plants but not of herbaceous plants (Figure 3). This is likely due to the generally low

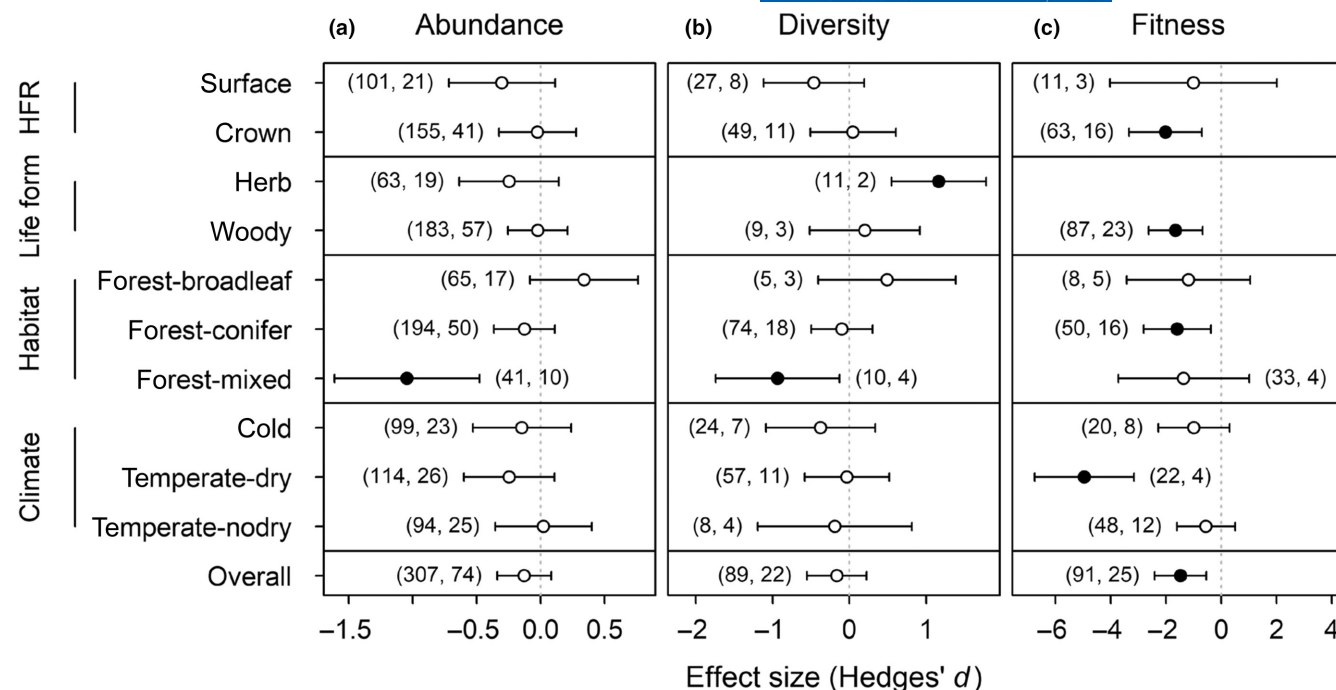


FIGURE 6 Response of plant abundance (a), diversity (b) and fitness (c) in forests and woodlands to increased fire severity leading to a step-change in fire regime type (i.e. surface-to-crown fires), across moderator categories and overall. Circles are effect size estimates and whiskers are 95% confidence intervals. Open circles indicate that estimates are not statistically significantly different from zero at $\alpha=0.05$, while filled circles indicate significant differences. In parenthesis, number of effects sizes, followed by number of studies. 'HFR' refers to the historical fire regime. Crown HFR include mixed-severity fires.

growth rates of woody plants, which require longer fire-free intervals than herbaceous plants to mature and develop fire-coping mechanisms (Díaz et al., 2016; Knapp et al., 2015; Zedler, 1995). As a result, woody plants may be more sensitive than herbs to increased fire frequency.

Increased fire severity reduced plant abundance at early post-fire stages, but the effect decreased with time (after 2 years post-fire), in line with our third prediction (Figure 2). However, increased fire severity reduced the short-term abundance of herbs but not woody plants, contrary to our expectation that woody plants would be more sensitive than herbs in the short term (Figure 5). Although herbaceous vegetation is usually more resource-acquisitive and has higher growth rates than woody vegetation, the latter is more likely to have fire-adaptive traits to survive direct fire effects (e.g. thick bark, growth in height; Pausas & Keeley, 2014b; Pekin et al., 2012). Therefore, the set of traits that confers quicker recovery from fire may depend on the environmental context. Overall, our results indicate that short-term responses to increased fire severity at the global scale do not differ substantially between herbaceous and woody vegetation.

For a few moderator categories, we detected significant effects of increased fire severity in the long term, but not in the short term (Figure 5). Among these, we found long-term reduced plant fitness in crown-fire regimes and in conifer forests. These long-term effects could be due to indirect fire severity effects on plants (e.g. through post-fire microclimate, soil conditions, competitive interactions, phenological mismatch with pollinators), which take longer to affect plant communities than direct fire effects,

and thus ultimately alter plant communities in the long term (Bowd et al., 2022; Ibáñez et al., 2022). Taken together, our findings illustrate that plant responses to disturbances, including to altered fire regimes, are temporally complex and, in some cases, may become stronger with time (Komatsu et al., 2019; Pellegrini et al., 2021).

Plant abundance and diversity were significantly reduced by intensified fire regimes in wildfire studies, but not in studies using prescribed fires (Figure 2), and this was consistent across many moderator categories (Figure 4). This was expected (fourth prediction) as severity and area burnt are generally much greater in wildfires than in prescribed fires (Allen et al., 2016). Therefore, the higher fire severity in wildfires may further impair plant regeneration through damage to vegetative structures and seeds, and the higher fire extent may limit regeneration from seed sources outside the fire area (Alba et al., 2015; Johnstone et al., 2016). Our results suggest that the effect of intensified fire regimes in prescribed fire studies are mild compared to those in wildfire studies.

Our finding that plant abundance, diversity and fitness were overall most strongly affected by intensified fire regimes in conifer and mixed forests supports our fifth prediction that forests are particularly sensitive to changes in fire regime (Figure 2). These results are broadly consistent with theory predicting that plants in less fire-prone ecosystems, such as forests, have less fire-adaptive traits and are thus more sensitive to fire than shrublands and grasslands (Karavani et al., 2018; Pausas & Bond, 2020). The lack of effects of intensified fire regimes in broadleaf forests could be due to the high fire resilience of Australian eucalypt forests (Foster et al., 2018), as

these highly fire-prone ecosystems comprised most of the broadleaf forest data in our study. In contrast to our results, some previous studies at the local scale suggest that shrublands and grasslands are more sensitive than forests to fire (Alba et al., 2015) and to increased fire frequency (Foster et al., 2018; Pellegrini et al., 2021). This emphasizes the importance of meta-analysis in searching for general ecological patterns and points out the dangers of extrapolating from single studies.

We found that plant abundance and fitness were reduced by intensified fire regimes in cold climates and in temperate climates with a dry season (Figure 2). While significant effects were also found in tropical climates, our results partly agree with our sixth prediction that ecosystems in drier and colder climates are particularly sensitive to fire effects. Moisture limitation, which can hinder post-fire plant recovery, may be behind this pattern (Giorgis et al., 2021; Pellegrini et al., 2021). Furthermore, in drier climates, compound disturbances (i.e. fire followed by drought) that further impair plant recovery may have also contributed to the observed greater fire effect compared to other climates (Nolan et al., 2021; Whitman et al., 2019). Similarly, plants may be particularly sensitive to intensified fire regimes in cold climates where fires are not historically common and plant recovery is limited by low temperatures (Sundqvist et al., 2020). Furthermore, given that nutrient limitation is prevalent across much of the boreal region that comprises the cold climate (Sponseller et al., 2016), low nutrient availability could also hinder post-fire recovery. Conversely, plant diversity was only reduced in tropical climates. This is in agreement with the sensitivity of some tropical forests (rainforests) to fire (Cochrane, 2003; Jones et al., 2022) but not with the resilience of tropical savannas to fire (Pausas & Bond, 2020). Overall, our results point to substantial negative effects of intensified fire regimes on plant abundance and fitness in ecosystems of dry and cold climates, and on plant diversity in tropical forests.

One of the limitations of this study is that it was not possible to measure how extreme the intensified regimes ('treatments') were compared with the historic variability. This is because of the lack of sufficient information on the historic variability of fire regimes for each study. Furthermore, for non-fire-prone ecosystems, the very few data available and their high variability precluded us from being able to confidently assess effects of intensified fire regimes (Figure 2). Finally, studies on fire effects are not homogeneously distributed across the globe. The high concentration of studies in some regions (e.g. western United States, south-eastern Australia, southern Europe) highlights that some other environments are underrepresented. Although we made an effort to compile as many studies as possible (Figure S1), our results are spatially biased by the current research available.

5 | CONCLUSIONS

Previous broad-scale research has demonstrated that shifts in fire seasonality due to global change can fundamentally alter plant

communities (Tangney et al., 2022). Our global meta-analysis shows that the overall effect of increasing fire severity or fire frequency, which are occurring in many ecosystems and are projected to intensify, reduces plant abundance, diversity and fitness, although the magnitude of the effect is limited and the specific effect depends on other factors. It also shows the importance of considering the different fire regime components (frequency, severity, type) for understanding the effects of fire in ecosystems (Keeley & Pausas, 2022). While spatial variations in fire activity enhance diversity in both plants and animals (Moritz et al., 2023; Pausas & Ribeiro, 2017), this is not necessarily true for temporal variations, as organisms are adapted to the historical fire regime in a given area. Instead, the observed overall reduction in diversity suggests that some ecosystems may become less diverse in the future if fire regimes keep intensifying. Our results also indicate that woody plants are more sensitive to intensified fire regimes than non-woody plants, which suggests that ecosystems dominated by woody plants may be particularly vulnerable to altered fire regimes (Giorgis et al., 2021). The fact that this was not observed in the short term may indicate that some time is required for differences between life forms to become perceptible. Overall, our study demonstrates that intensified fire regimes can alter plant responses in many ecosystems worldwide, and that the magnitude and key drivers of those fire effects are context dependent.

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CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are available in Dryad (<https://doi.org/10.5061/dryad.0vt4b8h6j>).

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REFERENCES

- Abatzoglou, J. T., Williams, A. P., & Barbero, R. (2019). Global emergence of anthropogenic climate change in fire weather indices. *Geophysical Research Letters*, 46, 326–336.
- Alba, C., Skálová, H., McGregor, K. F., D'Antonio, C., & Pyšek, P. (2015). Native and exotic plant species respond differently to wildfire and prescribed fire as revealed by meta-analysis. *Journal of Vegetation Science*, 26, 102–113.
- Allen, K. A., Denelle, P., Ruiz, F. M. S., Santana, V. M., & Marrs, R. H. (2016). Prescribed moorland burning meets good practice guidelines: A monitoring case study using aerial photography in the Peak District, UK. *Ecological Indicators*, 62, 76–85.

- Berg, A., Sheffield, J., & Milly, P. C. D. (2017). Divergent surface and total soil moisture projections under global warming: Future soil moisture changes in coupled model intercomparison project phase 5. *Geophysical Research Letters*, 44, 236–244.
- Borenstein, M. (2009). *Effect sizes for continuous data. The handbook of research synthesis and meta-analysis* (H., Cooper, L., Hedges, & J., Valentine, pp. 221–235). Russell Sage Foundation.
- Bowd, E. J., Egidi, E., Lindenmayer, D. B., Wardle, D. A., Kardol, P., Cary, G. J., & Foster, C. (2022). Direct and indirect effects of fire on microbial communities in a pyrodiverse dry-sclerophyll forest. *Journal of Ecology*, 110, 1687–1703.
- Bowman, D. M. J. S., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. A., D'Antonio, C. M., DeFries, R., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Mack, M., Moritz, M. A., Pyne, S., Roos, C. I., Scott, A. C., Sodhi, N. S., & Swetnam, T. W. (2011). The human dimension of fire regimes on Earth: The human dimension of fire regimes on Earth. *Journal of Biogeography*, 38, 2223–2236.
- Bret-Harte, M. S., Mack, M. C., Shaver, G. R., Huebner, D. C., Johnston, M., Mojica, C. A., Pizano, C., & Reiskind, J. A. (2013). The response of Arctic vegetation and soils following an unusually severe tundra fire. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 368, 20120490.
- Bryant, C., Wheeler, N. R., Rubel, F., & French, R. H. (2017). *kgc: Koeppen-Geiger climatic zones*.
- Canadell, J. G., Meyer, C. P., Cook, G. D., Dowdy, A., Briggs, P. R., Knauer, J., Pepler, A., & Haverd, V. (2021). Multi-decadal increase of forest burned area in Australia is linked to climate change. *Nature Communications*, 12, 6921.
- Cavender-Bares, J., & Reich, P. B. (2012). Shocks to the system: Community assembly of the oak savanna in a 40-year fire frequency experiment. *Ecology*, 93, S52–S69.
- Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright, N. J., & Knox, K. J. E. (2013). Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist*, 197, 19–35.
- Cochrane, M. A. (2003). Fire science for rainforests. *Nature*, 421, 913–919.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Routledge.
- Collins, S. L., & Calabrese, L. B. (2012). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, 23, 563–575.
- Cornwall, C. E., Harvey, B. P., Comeau, S., Cornwall, D. L., Hall-Spencer, J. M., Peña, V., Wada, S., & Porzio, L. (2022). Understanding coralline algal responses to ocean acidification: Meta-analysis and synthesis. *Global Change Biology*, 28, 362–374.
- Covington, W. W., & Moore, M. M. (1994). Southwestern ponderosa forest structure: Changes since euro-American settlement. *Journal of Forestry*, 92, 39–47.
- Dantas, V. d. L., Hirota, M., Oliveira, R. S., & Pausas, J. G. (2016). Disturbance maintains alternative biome states. *Ecology Letters*, 19, 12–19.
- Dara, A., Baumann, M., Hölzel, N., Hostert, P., Kamp, J., Müller, D., Ullrich, B., & Kuemmerle, T. (2020). Post-soviet land-use change affected fire regimes on the Eurasian steppes. *Ecosystems*, 23, 943–956.
- DeSiervo, M. H., Jules, E. S., & Safford, H. D. (2015). Disturbance response across a productivity gradient: Postfire vegetation in serpentine and nonserpentine forests. *Ecosphere*, 6, 1–19.
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171.
- Eales, J., Haddaway, N. R., Bernes, C., Cooke, S. J., Jonsson, B. G., Kouki, J., Petukofsky, G., & Taylor, J. J. (2018). What is the effect of prescribed burning in temperate and boreal forest on biodiversity, beyond pyrophilous and saproxylic species? A systematic review. *Environmental Evidence*, 7, 19.
- Enright, N. J., Fontaine, J. B., Bowman, D. M., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*, 13, 265–272.
- Etchells, H., O'Donnell, A. J., Lachlan McCaw, W., & Grierson, P. F. (2020). Fire severity impacts on tree mortality and post-fire recruitment in tall eucalypt forests of southwest Australia. *Forest Ecology and Management*, 459, 117850.
- Fairman, T. A., Nitschke, C. R., & Bennett, L. T. (2016). Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. *International Journal of Wildland Fire*, 25, 831.
- Fernández-García, V., Marcos, E., Fulé, P. Z., Reyes, O., Santana, V. M., & Calvo, L. (2020). Fire regimes shape diversity and traits of vegetation under different climatic conditions. *Science of the Total Environment*, 716, 137137.
- Foo, Y. Z., O'Dea, R. E., Koricheva, J., Nakagawa, S., & Lagsiz, M. (2021). A practical guide to question formation, systematic searching and study screening for literature reviews in ecology and evolution. *Methods in Ecology and Evolution*, 12, 1705–1720.
- Foster, C. N., Barton, P. S., MacGregor, C. I., Catford, J. A., Blanchard, W., & Lindenmayer, D. B. (2018). Effects of fire regime on plant species richness and composition differ among forest, woodland and heath vegetation. *Applied Vegetation Science*, 21, 132–143.
- Giorgis, M. A., Zeballos, S. R., Carbone, L., Zimmermann, H., von Wehrden, H., Aguilar, R., Ferreras, A. E., Tecco, P. A., Kowaljew, E., Barri, F., Gurvich, D. E., Villagra, P., & Jaureguiberry, P. (2021). A review of fire effects across South American ecosystems: The role of climate and time since fire. *Fire Ecology*, 17, 11.
- Gomes, L., Miranda, H. S., & Bustamante, M. M. d. C. (2018). How can we advance the knowledge on the behavior and effects of fire in the Cerrado biome? *Forest Ecology and Management*, 417, 281–290.
- Grau-Andrés, R., Davies, G. M., Waldron, S., Scott, E. M., & Gray, A. (2019). Increased fire severity alters initial vegetation regeneration across Calluna-dominated ecosystems. *Journal of Environmental Management*, 231, 1004–1011.
- Grau-Andrés, R., Gray, A., & Davies, G. M. (2017). *Sphagnum* abundance and photosynthetic capacity show rapid short-term recovery following managed burning. *Plant Ecology and Diversity*, 10, 353–359.
- Green, S. R., Arthur, M. A., & Blankenship, B. A. (2010). Oak and red maple seedling survival and growth following periodic prescribed fire on xeric ridgetops on the Cumberland Plateau. *Forest Ecology and Management*, 259, 2256–2266.
- Guiote, C., & Pausas, J. G. (2023). Fire favors sexual precocity in a Mediterranean pine. *Oikos*, 2023, e09373.
- Hobbs, R. J., & Gimingham, C. H. (1984). Studies on fire in Scottish heathland communities II. Post-fire vegetation development. *The Journal of Ecology*, 72, 585.
- Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O. L., Haridasan, M., & Franco, A. C. (2012). Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*, 15, 759–768.
- Ibáñez, T. S., Wardle, D. A., Gundale, M. J., & Nilsson, M.-C. (2022). Effects of soil abiotic and biotic factors on tree seedling regeneration following a boreal forest wildfire. *Ecosystems*, 25, 471–487.
- Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14, 369–378.
- Jones, M. W., Abatzoglou, J. T., Veraverbeke, S., Andela, N., Lasslop, G., Forkel, M., Smith, A. J. P., Burton, C., Betts, R. A., van der

- Werf, G. R., Sitch, S., Canadell, J. G., Santín, C., Kolden, C., Doerr, S. H., & Le Quére, C. (2022). Global and regional trends and drivers of fire under climate change. *Reviews of Geophysics*, 60, e2020RG000726.
- Kambach, S., Bruelheide, H., Gerstner, K., Gurevitch, J., Beckmann, M., & Seppelt, R. (2020). Consequences of multiple imputation of missing standard deviations and sample sizes in meta-analysis. *Ecology and Evolution*, 10, 11699–11712.
- Karavani, A., Boer, M. M., Baudena, M., Colinas, C., Díaz-Sierra, R., Pemán, J., de Luis, M., Enríquez-de-Salamanca, Á., & Resco de Dios, V. (2018). Fire-induced deforestation in drought-prone Mediterranean forests: Drivers and unknowns from leaves to communities. *Ecological Monographs*, 88, 141–169.
- Keeley, J. E., Fotheringham, C. J., & Baer-Keeley, M. (2005). Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecological Applications*, 15, 1515–1534.
- Keeley, J. E., & Pausas, J. G. (2019). Distinguishing disturbance from perturbations in fire-prone ecosystems. *International Journal of Wildland Fire*, 28, 282.
- Keeley, J. E., & Pausas, J. G. (2022). Evolutionary ecology of fire. *Annual Review of Ecology, Evolution, and Systematics*, 53, 203–225.
- Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16, 406–411.
- Knapp, B. O., Stephan, K., & Hubbart, J. A. (2015). Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. *Forest Ecology and Management*, 344, 95–109.
- Komatsu, K. J., Avolio, M. L., Lemoine, N. P., Isbell, F., Grman, E., Houseman, G. R., Koerner, S. E., Johnson, D. S., Wilcox, K. R., Alatalo, J. M., Anderson, J. P., Aerts, R., Baer, S. G., Baldwin, A. H., Bates, J., Beierkuhnlein, C., Belote, R. T., Blair, J., Bloor, J. M. G., ... Zhang, Y. (2019). Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 17867–17873.
- Lajeunesse, M. J. (2013). *Recovering missing or partial data from studies: A survey of conversions and imputations for meta-analysis. Handbook of meta-analysis in ecology and evolution* (J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.)), pp. 195–206. Princeton University Press.
- Leal, L. C., Nogueira, A., & Peixoto, P. E. C. (2022). Which traits optimize plant benefits? Meta-analysis on the effect of partner traits on the outcome of an ant-plant protective mutualism. *Journal of Ecology*, 111, 263–275.
- Maltby, E., Legg, C. J., & Proctor, M. C. F. (1990). The ecology of severe moorland fire on the North York moors: Effects of the 1976 fires, and subsequent surface and vegetation development. *The Journal of Ecology*, 78, 490.
- Miller, J. E. D., & Safford, H. D. (2020). Are plant community responses to wildfire contingent upon historical disturbance regimes? *Global Ecology and Biogeography*, 29, 1621–1633.
- Moreira, F., Viedma, O., Arianoutsou, M., Curt, T., Koutsias, N., Rigolot, E., Barbati, A., Corona, P., Vaz, P., Xanthopoulos, G., Mouillot, F., & Bilgili, E. (2011). Landscape–Wildfire interactions in southern Europe: Implications for landscape management. *Journal of Environmental Management*, 92, 2389–2402.
- Moritz, M. A., Batllori, E., & Bolker, B. M. (2023). The role of fire in terrestrial vertebrate richness patterns. *Ecology Letters*, 26, 563–574.
- Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, 13, 4–21.
- Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26, 1253–1274.
- Nolan, R. H., Collins, L., Leigh, A., Ooi, M. K. J., Curran, T. J., Fairman, T. A., Resco de Dios, V., & Bradstock, R. (2021). Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment*, 44, 3471–3489.
- O'Dea, R. E., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Gurevitch, J., Page, M. J., Stewart, G., Moher, D., & Nakagawa, S. (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: A PRISMA extension. *Biological Reviews*, 96, 1695–1722.
- Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L., Tetzlaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hróbjartsson, A., Lalu, M. M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., ... Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *BMJ*, 372, n71.
- Pausas, J. G., & Bond, W. J. (2020). Alternative biome states in terrestrial ecosystems. *Trends in Plant Science*, 25, 250–263.
- Pausas, J. G., & Keeley, J. E. (2009). A burning story: The role of fire in the history of life. *BioScience*, 59, 593–601.
- Pausas, J. G., & Keeley, J. E. (2014a). Abrupt climate-independent fire regime changes. *Ecosystems*, 17, 1109–1120.
- Pausas, J. G., & Keeley, J. E. (2014b). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist*, 204, 55–65.
- Pausas, J. G., & Keeley, J. E. (2021). Wildfires and global change. *Frontiers in Ecology and the Environment*, 19, 387–395.
- Pausas, J. G., & Paula, S. (2020). Grasses and fire: the importance of hiding buds: A response to Moore et al. (2019) 'Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses'. *New Phytologist*, 226, 957–959.
- Pausas, J. G., & Ribeiro, E. (2017). Fire and plant diversity at the global scale. *Global Ecology and Biogeography*, 26, 889–897.
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633–1644.
- Pekin, B. K., Wittkuhn, R. S., Boer, M. M., Macfarlane, C., & Grierson, P. F. (2012). Response of plant species and life form diversity to variable fire histories and biomass in the jarrah forest of south-west Australia. *Austral Ecology*, 37, 330–338.
- Pellegrini, A. F. A., Refsland, T., Averill, C., Terrer, C., Staver, A. C., Brockway, D. G., Caprio, A., Clatterbuck, W., Coetsee, C., Haywood, J. D., Hobbie, S. E., Hoffmann, W. A., Kush, J., Lewis, T., Moser, W. K., Overby, S. T., Patterson, W. A., Peay, K. G., Reich, P. B., ... Jackson, R. B. (2021). Decadal changes in fire frequencies shift tree communities and functional traits. *Nature Ecology & Evolution*, 5, 504–512.
- Pick, J. L., Nakagawa, S., & Noble, D. W. A. (2019). Reproducible, flexible and high throughput data extraction from primary literature: The metaDigitise R package. *Methods in Ecology and Evolution*, 10, 426–4315.
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2022). *nlme: Linear and nonlinear mixed effects models*.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Radeloff, V. C., Hesters, D. P., Kramer, H. A., Mockrin, M. H., Alexandre, P. M., Bar-Massada, A., Butsic, V., Hawbaker, T. J., Martinuzzi, S., Syphard, A. D., & Stewart, S. I. (2018). Rapid growth of the US wildland-urban interface raises wildfire risk. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 3314–3319.
- Rasband, W. S. (1997). ImageJ.
- Rohatgi, A. (2022). Webplotdigitizer: Version 4.6.
- Rosenberg, M. S., Rothstein, H. R., & Gurevitch, J. (2013). *Effect sizes: Conventional choices and calculations. Handbook of meta-analysis in ecology and evolution* (J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.)). Princeton University Press.
- Schimmel, J., & Granström, A. (1996). Fire severity and vegetation response in the boreal Swedish forest. *Ecology*, 77, 1436–1450.

- Senande-Rivera, M., Insua-Costa, D., & Miguez-Macho, G. (2022). Spatial and temporal expansion of global wildland fire activity in response to climate change. *Nature Communications*, 13, 1208.
- Sponseller, R. A., Gundale, M. J., Futter, M., Ring, E., Nordin, A., Näsholm, T., & Laudon, H. (2016). Nitrogen dynamics in managed boreal forests: Recent advances and future research directions. *Ambio*, 45, 175–187.
- Sundqvist, M. K., Sanders, N. J., Dorrepaal, E., Lindén, E., Metcalfe, D. B., Newman, G. S., Olofsson, J., Wardle, D. A., & Classen, A. T. (2020). Responses of tundra plant community carbon flux to experimental warming, dominant species removal and elevation. *Functional Ecology*, 34, 1497–1506.
- Talluto, M. V., & Suding, K. N. (2008). Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. *Landscape Ecology*, 23, 803–815.
- Tangney, R., Paroissien, R., Le Breton, T. D., Thomsen, A., Doyle, C. A. T., Ondik, M., Miller, R. G., Miller, B. P., & Ooi, M. K. J. (2022). Success of post-fire plant recovery strategies varies with shifting fire seasonality. *Communications Earth & Environment*, 3, 126.
- Turner, M. G., Brazionas, K. H., Hansen, W. D., & Harvey, B. J. (2019). Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 11319–11328.
- Velle, L. G., Nilsen, L. S., Norderhaug, A., & Vandvik, V. (2014). Does prescribed burning result in biotic homogenization of coastal heathlands? *Global Change Biology*, 20, 1429–1440.
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.
- Westgate, M. J. (2019). revtools: An R package to support article screening for evidence synthesis. *Research Synthesis Methods*, 10, 606–614.
- Whitman, E., Parisien, M.-A., Thompson, D. K., & Flannigan, M. D. (2019). Short-interval wildfire and drought overwhelm boreal forest resilience. *Scientific Reports*, 9, 18796.
- Whitman, E., Parks, S. A., Holsinger, L. M., & Parisien, M.-A. (2022). Climate-induced fire regime amplification in Alberta, Canada. *Environmental Research Letters*, 17, 055003.
- Willms, J., Bartuszevige, A., Schwilk, D. W., & Kennedy, P. L. (2017). The effects of thinning and burning on understory vegetation in North America: A meta-analysis. *Forest Ecology and Management*, 392, 184–194.
- Wilson, D. (2001). Practical meta-analysis effect size calculator [Online calculator].
- Wright, B. R., & Fensham, R. J. (2016). Relationships between fire severity and recruitment in arid grassland dominated by the obligate-seeding soft spinifex (*Triodia pungens*). *International Journal of Wildland Fire*, 25, 1264.

Zedler, P. H. (1995). *Fire frequency in southern California shrublands: Biological effects and management options. Brushfires in California wildlands: Ecology and resource management* (pp. 101–112). International Association of Wildland Fire.

BIOSKETCH

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Juli G. Pausas: My research focuses on the ecology and evolution of fire-prone ecosystems, and specifically on understanding the role of fire in shaping plant species, populations, communities and landscapes. Webpage: <https://www.uv.es/jgpausas/>.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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