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META-ANALYSIS



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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 & Fensham, 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, shortlived, 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

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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

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(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 km^2 , 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; mixedseverity 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 stepchange 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 metaanalytic 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 metaanalytic 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 crownfire 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 shortterm 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 α = 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-test=0.317, p=0.751, df=1509), diversity (t-test=-0.522, p=0.602, df=502), and fitness (t-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 α = 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 α =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 [\leq 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 α =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 '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, lowseverity 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 NUEY- Global Ecology

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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BIOSKETCH

Roger Grau-Andrés: I study plant community responses to global changes (e.g. altered precipitation regimes, increased fire severity) and land management, and how that may affect ecosystem functioning. I am also interested in the study of plant traits and plant elementomes and their relationship to ecosystem functioning.

Bruno Moreira: I study fire ecology and plant evolution mainly in fire-prone Mediterranean ecosystems. My work focuses on traits related to plant persistence in fire-prone ecosystems, particularly post-fire regeneration strategies (germination and resprout) and plant flammability traits. Webpage: https://sites.google.com/site/brjmoreira/Home.

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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SUPPORTING INFORMATION – Appendix S1



Figure S1. PRISMA flowchart detailing the identification of studies via databases and backward and forward searches, and their subsequent screening. Backward and forward searches were performed on seven highly cited articles (Enright et al., 2014; Fairman et al., 2016; Hart et al., 2019; Johnstone & Chapin, 2006; Peterson & Reich, 2008; Schimmel & Granstrom, 1996; Uys et al., 2004) and on three recent reviews (Halofsky et al., 2020; Nolan et al., 2021; Prichard et al., 2017).

		(a)	Abundance	(b) Diversity	(c) Fitness
com.	frequency	-	(541, 99) +++	(251, 61) -	(82, 35) нон
FR	(a) Abundance (b) Di frequency (541, 99) \mapsto (251, (210, 45) (210, 45) (211, 6) (211, 6) (211, 6) (211, 6) (222, 5) (667, 125) \mapsto (108, 20) (9, 4) (242, 5) (667, 125) \mapsto (242, 5) (166, 2) (166, 2) (166, 2) (166, 2) (166, 2) (167, 2) (21, 7) \mapsto (21, 7) \mapsto ((210, 45)	(218, 70) + + +		
e	prescribed	-	(495, 86) ⊢0⊣	(188, 40) ⊢O⊣	(99, 39)
Typ	(a) Abundance (a) Abundance (b) (a) (a) Abundance (b) (b) (a) (b) (b) (b) (b) (b) (b) (b) (b) (b) (b	(271, 64) + + +	(201, 64) +		
ne	l long	-	(404, 93) HOH	(119, 32)0	(96, 33)
Ē	l short	-	(413, 85) ++++	(83, 20) -	(120, 40) ⊷
R	l no-fire	- (29, 6	š) I——o———i	(9, 4) - 0	(6, 4) - 0
st. F	surface	-	(581, 98) +	(242, 54)	(89, 38) 0
Climate Habitat Life form Hist. FR Time Type FR com.	l crown	-	(667, 125) ⊢ €⊣	(166, 37) ⊢O→	(163, 46) +
E	l bryophyte	-	(51, 16) - 0	(7, 3)	(3, 2) - 0
e foi	herb	-	(336, 84) ⊢O⊣	(124, 32) +0+	(26, 13) ⊷0⊶
Life	woody	-	(798, 193) 🛏	(120, 33) ⊢0⊣	(245, 81) +++
	forest-broadleaf	-	(289, 66) ⊢O ⊣	(93, 24) ⊢O →	(85, 31) ю
	forest-conifer	-	(545, 94)	(167, 34) HO-1	(95, 29) ⊷⊷
itat	forest-mixed	-	(81, 17) 🛏 🗕 🛶	(21, 7) •	└──● (41, 6)
Hab	grassland	-	(94, 15) - 0	(48, 14) - 0	(22, 9) ⊢
	shrubland	-	(146, 27) ⊷o ⊶i	(24, 7) ⊷−−−	(27, 11)0
	woodland	-	(184, 33)	(85, 21) imo	(26, 14) ⊷0−−−
	l arid	-	(90, 17) i=0	(59, 9) - 0	(24, 8)
te	cold	-	(375, 68)	(97, 21) -0	(88, 26) 🛏 🛏
ima	temperate-dry	-	(457, 68) ⊷	(171, 35) ⊷0→	(38, 16) +
Ü	temperate-nodry	-	(358, 80) ⊢o⊣	(101, 28) —0—1	(132, 41) юн
	l tropical	- (1	13, 23) 🛏 🕶 া	(33, 13)	(17, 11)0
	Overall	-	(1395, 256) H	(461, 105) +++	(300, 103) +++
		L_		J	╎└──┬──┬──┼──┬─┘
		-2.0	-1.0 0.0	-3 -2 -1 0 1	-5 -3 -1 0 1 2
				Effect size (Hedges' d)	

Figure S2. Response of plant abundance (a), diversity (b), and fitness (c) to intensified fire regimes across moderator categories and overall, for data excluding imputed standard deviations. 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', to fire type; 'Time', to time since the last fire; and 'Hist. FR', to type of historical fire regime. Time since fire was only examined in fire severity studies (not for fire frequency).

Figure S3. Response of plant abundance (a), diversity (b), and fitness (c) to intensified fire regimes across moderator categories, for each of the two historical fire regime types (i.e., surface fires or crown fires). 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. Overall effects are provided in Figure 2 (see 'Hist. FR').

Figure S4. Funnel plots of effective sample size against residuals of overall meta-analysis models of plant abundance, diversity, and fitness. P-values refer to the intercept of Egger regressions including meta-analytic residuals as the response variable and effective sample size as the explanatory variable. The grey vertical line indicates the average of the residuals.

Figure S5. Location of studies in areas of high concentration of studies: western US (a), Iberian Peninsula (b), and south-eastern Australia (c). Climate zones follow the Köppen-Geiger classification system (Peel *et al.*, 2007).

Table S1. Word strings used to search peer-reviewed articles relevant to vegetation responses to fire regimes in the databases Scopus and Web of Science, and the number of records those searches returned. Search fields 'TITLE-ABS-KEY' (Scopus) and 'TS' (Web of Science) include title, abstract, and keywords. Search operators 'W/3' (Scopus) and 'NEAR/3' (Web of Science) return results where words at either side of the operator are spaced up to three words away from each other. Asterisks include all possible terminations of the search term. Note that searches in both databases were performed in English and Spanish.

Database	Search string	Num.
Scopus	TITLE ((wildfire OR fire OR burn*) AND ((plant OR vegetation OR flora	1742
	OR understor* OR overstor* OR forest* OR woodland OR rainforest OR	
	shrub* OR heath* OR chaparral OR cerrado OR grass* OR savanna* OR	
	prairie OR wetland OR tundra OR tree OR seed* OR woody OR graminoid OR	
	forb OR herb* OR bryophyte OR moss) AND (regeneration OR response OR	
	recovery OR recruitment OR regrowth OR surviv* OR resilience OR	
	germination OR resprout* OR abundance OR cover OR mortality OR richness	
	OR diversity OR biodiversity))) AND TITLE-ABS-KEY ((fire OR burn* OR	
	wildfire*) W/3 (sever* OR frequen* OR intens* OR regime OR interval))	
Web of	TI = ((wildfire OR fire OR burn*) AND ((plant OR vegetation OR flora OR	1668
Science	understor* OR overstor* OR forest* OR woodland OR rainforest OR shrub*	
	OR heath* OR chaparral OR cerrado OR grass* OR savanna* OR prairie OR	
	wetland OR tundra OR tree OR seed* OR woody OR graminoid OR forb OR	
	herb* OR bryophyte OR moss) AND (regeneration OR response OR recovery	
	OR recruitment OR regrowth OR surviv* OR resilience OR germination OR	
	resprout* OR abundance OR cover OR mortality OR richness OR diversity OR	
	biodiversity))) AND TS = ((fire OR burn* OR wildfire*) NEAR/3 (sever*	
	OR frequen* OR intens* OR regime OR interval))	
Scopus	TITLE-ABS-KEY((fuego OR quema OR incendio) AND (severidad OR	28
	frecuencia OR intensidad OR régimen OR intervalo)) AND (LIMIT-TO(
	LANGUAGE, "Spanish"))	
Web of	TS = ((fuego OR quema OR incendio) AND (severidad OR frecuencia OR	1
Science	intensidad OR régimen OR intervalo))	

Table S2. Meta-analytical models output of plant responses to intensified fire regimes for the main metrics within each response variable (abundance, diversity, and fitness). Recovery metrics are based on a baseline level (e.g., delta-NDVI); flux metrics are rates of fluid exchange (e.g., photosynthetic rates, transpiration); diversity metrics were transformed, if necessary, so that larger values indicate greater evenness (e.g., for Simpson's dominance index, the sign of the effect size was changed). k is the number of effect sizes, n is the number of studies, and P is the p-value from statistical testing of differences from zero.

Response variables and metrics	k	п	Hedges' d (95% CI)	Р
Abundance	1510	280	-0.244 (-0.353, -0.135)	< 0.001
Density and frequency	613	162	-0.314 (-0.456, -0.171)	< 0.001
Cover	573	106	-0.062 (-0.220, 0.097)	0.446
Size and biomass	186	66	-0.205 (-0.422, 0.013)	0.066
Recovery	70	17	-0.942 (-1.400, -0.483)	< 0.001
Diversity	505	117	-0.268 (-0.478, -0.059)	0.012
Richness	308	102	-0.280 (-0.502, -0.059)	0.013
Shannon and Simpson	107	47	-0.344 (-0.624, -0.064)	0.016
Evenness	38	19	-0.226 (-0.577, 0.126)	0.208
Beta-diversity	27	8	-0.246 (-0.728, 0.235)	0.316
Fitness	342	110	-0.686 (-1.015, -0.358)	< 0.001
Survival	169	59	-0.948 (-1.360, -0.537)	< 0.001
Growth	76	27	-0.404 (-0.893 , 0.085)	0.106
Flux	40	11	-0.198 (-1.139, 0.743)	0.680
Reproductive effort	23	9	-0.580 (-1.262, 0.101)	0.095
Nutrient content	18	8	-0.216 (-1.277, 0.845)	0.690

Table S3. Meta-analytical models output of plant abundance responses to intensified fire regimes. For each moderator category, k is the number of effect sizes, n is the number of studies, P are statistical differences from zero, and Q_M and Q_E are Q-statistics from Wald-type chi-square tests that assess residual heterogeneity (Q_E , for the overall model) and the effect of moderators (Q_M , for models including moderator variables). This information is displayed graphically in Figure 2a of the manuscript.

Moderators	Category	k	п	Hedges' d (95% CI)	Р	$\mathbf{Q}_{\mathbf{M}}$ or $\mathbf{Q}_{\mathbf{E}}\left(\mathbf{P}\right)$	
Fire regime	frequency	605	111	-0.267 (-0.435, -0.099)	0.002		
component	severity	905	174	-0.229 (-0.368, -0.090)	< 0.001	$Q_{\rm M} = 19.3 \ (<0.001)$	
	prescribed	530	94	-0.176 (-0.363, 0.012)	0.067	0 = 10.7 (-0.001)	
Fire type	wildfire	979	185	-0.278 (-0.413, -0.143)	< 0.001	$Q_{\rm M} = 19.7 (<0.001)$	
Time since	long	431	102	-0.057 (-0.248, 0.135)	0.563	0 10.1 (.0.001)	
last fire	short	430	94	-0.415 (-0.616, -0.214)	< 0.001	$Q_{\rm M} = 18.1 \; (< 0.001)$	
	no-fire	46	8	-0.344 (-1.026, 0.337)	0.322		
Historical	surface	621	108	-0.231 (-0.403, -0.058)	0.009	$Q_{\rm M} = 15.2 \ (0.002)$	
me regime	crown	714	135	-0.218 (-0.375, -0.061)	0.007		
	bryophyte	56	19	0.387 (0.028, 0.747)	0.035	Q _M = 29.9 (0.001)	
Plant life	herb	376	96	-0.089 (-0.255, 0.077)	0.293		
IOIIII	woody	843	209	-0.287 (-0.412, -0.162)	< 0.001		
	forest-broadleaf	299	68	-0.123 (-0.346, 0.101)	0.282		
	forest-conifer	594	105	-0.295 (-0.468, -0.121)	0.001		
TT 1	forest-mixed	83	18	-0.632 (-1.073, -0.190)	0.005		
Habitat	grassland	127	21	-0.247 (-0.623, 0.129)	0.198	$Q_{\rm M} = 23.2 \ (0.001)$	
	shrubland	151	28	-0.177 (-0.521, 0.167)	0.313		
	woodland	200	36	-0.136 (-0.429, 0.158)	0.365		
	arid	100	19	-0.227 (-0.637, 0.183)	0.277		
	cold	393	71	-0.263 (-0.481, -0.044)	0.019		
Climate	temperate-dry	490	74	-0.252 (-0.455, -0.049)	0.015	$Q_M = 22.1 \ (0.001)$	
	temperate-nodry	407	91	-0.149 (-0.344, 0.047)	0.136		
	tropical	118	25	-0.531 (-0.913, -0.149)	0.006		
Overall	Overall	1510	280	-0.244 (-0.353, -0.135)	< 0.001	Q _E = 12615 (<0.001)	

Table S4. Meta-analytical models output of plant diversity responses to intensified fire regimes. For each moderator category, k is the number of effect sizes, n is the number of studies, P are statistical differences from zero, and Q_M and Q_E are Q-statistics from Wald-type chi-square tests that assess residual heterogeneity (Q_E , for the overall model) and the effect of moderators (Q_M , for models including moderator variables). This information is displayed graphically in Figure 2b of the manuscript.

Moderators	Category	k	п	Hedges' d (95% CI)	Р	$\mathbf{Q}_{\mathbf{M}}$ or $\mathbf{Q}_{\mathbf{E}}\left(\mathbf{P}\right)$
Fire regime	frequency	276	69	-0.059 (-0.313, 0.195)	0.609	0 14.0 (0.001)
component	severity	229	50	-0.543 (-0.826, -0.260)	< 0.001	$Q_{\rm M} = 14.2 \ (0.001)$
	prescribed	202	46	-0.024 (-0.355, 0.306)	0.905	0 0 0 (0 011)
Fire type	wildfire	301	70	-0.409 (-0.677, -0.141)	< 0.001	$Q_{\rm M} = 9.0 \ (0.011)$
Time since	long	132	36	-0.430 (-0.857, -0.003)	0.059	
last fire	short	89	23	-0.619 (-1.089, -0.150)	< 0.001	$Q_{\rm M} = 6.8 \ (0.033)$
	no-fire	9	4	0.203 (-0.997, 1.402)	0.750	
Historical	surface	263	62	-0.315 (-0.613, -0.016)	0.046	$Q_{\rm M} = 5.1 \ (0.166)$
file legime	crown	186	39	-0.161 (-0.536, 0.214)	0.280	
	bryophyte	9	4	-0.05 (-0.855, 0.755)	0.842	$Q_{\rm M} = 2.3 \; (0.515)$
Plant life	herb	127	33	-0.048 (-0.273, 0.176)	0.605	
IOIIII	woody	120	33	-0.175 (-0.405, 0.056)	< 0.001	
	forest-broadleaf	94	25	-0.186 (-0.623, 0.251)	0.330	Q _M = 13.0 (0.043)
	forest-conifer	189	37	-0.139 (-0.501, 0.224)	0.462	
TT 1	forest-mixed	25	8	-1.108 (-1.790, -0.425)	0.003	
Habitat	grassland	53	16	-0.217 (-0.801, 0.367)	0.497	
	shrubland	24	7	-0.488 (-1.310, 0.334)	0.239	
	woodland	97	26	-0.238 (-0.691, 0.215)	0.326	
	arid	59	9	0.105 (-0.615, 0.825)	0.813	Q _M = 10.0 (0.074)
	cold	97	21	-0.289 (-0.779, 0.200)	0.256	
Climate	temperate-dry	192	37	-0.328 (-0.684, 0.027)	0.068	
	temperate-nodry	122	37	-0.137 (-0.50, 0.227)	0.473	
	tropical	35	14	-0.755 (-1.417, -0.093)	0.036	
Overall	Overall	505	117	-0.268 (-0.478, -0.059)	< 0.001	$Q_E = 4593 \; (<0.001)$

Table S5. Meta-analytical models output of plant fitness responses to intensified fire regimes. For each moderator category, k is the number of effect sizes, n is the number of studies, P are statistical differences from zero, and Q_M and Q_E are Q-statistics from Wald-type chi-square tests that assess residual heterogeneity (Q_E , for the overall model) and the effect of moderators (Q_M , for models including moderator variables). This information is graphically displayed in Figure 2c of the manuscript.

Moderators	Category	k	п	Hedges' d (95% CI)	Р	$\mathbf{Q}_{\mathbf{M}}$ or $\mathbf{Q}_{\mathbf{E}}\left(\mathbf{P}\right)$	
Fire regime	frequency	102	38	-0.066 (-0.553, 0.421)	0.790		
component	severity	240	74	-0.995 (-1.366, -0.625)	< 0.001	$Q_{\rm M} = 28.3 \ (<0.001)$	
	prescribed	126	43	-0.502 (-1.026, 0.022)	0.061		
Fire type	wildfire	216	67	-0.806 (-1.230, -0.383)	< 0.001	$Q_{\rm M} = 1/.5 \; (<0.001)$	
Time since	long	98	34	-1.034 (-1.636, -0.432)	0.001	0 17.0 (0.001)	
last fire	short	128	42	-1.004 (-1.567, -0.441)	< 0.001	$Q_{\rm M} = 17.8 (< 0.001)$	
	no-fire	6	4	-0.85 (-2.693, 0.992)	0.366		
Historical	surface	116	43	-0.494 (-1.060, 0.072)	0.087	$Q_{\rm M} = 15.9 \ (0.001)$	
fire regime	crown	178	48	-0.951 (-1.484, -0.417)	< 0.001		
	bryophyte	3	2	-0.177 (-2.704, 2.349)	0.891	$Q_{\rm M} = 17.6 \ (0.001)$	
Plant life	herb	26	13	-0.062 (-0.770, 0.645)	0.863		
Iorm	woody	282	87	-0.759 (-1.131, -0.387)	< 0.001		
	forest-broadleaf	100	33	-0.348 (-0.932, 0.237)	0.244	Q _M = 28.3 (<0.001)	
	forest-conifer	110	32	-1.073 (-1.669, -0.476)	< 0.001		
	forest-mixed	41	6	-2.263 (-3.589, -0.937)	0.001		
Habitat	grassland	22	9	-0.710 (-1.882, 0.463)	0.235		
	shrubland	37	12	-0.709 (-1.716, 0.298)	0.168		
	woodland	28	15	0.006 (-0.880, 0.892)	0.990		
	arid	24	8	-1.187 (-2.382, 0.007)	0.051	Q _M = 34.5 (<0.001)	
	cold	88	26	-0.734 (-1.367, -0.101)	0.023		
Climate	temperate-dry	52	19	-1.918 (-2.67, -1.165)	< 0.001		
	temperate-nodry	150	44	-0.134 (-0.623, 0.355)	0.592		
	tropical	27	12	-0.244 (-1.190, 0.701)	0.613		
Overall	Overall	342	110	-0.686 (-1.015, -0.358)	< 0.001	$Q_E = 3604 \; (< 0.001)$	

Supplementary references

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APPENDIX 1 – DATA SOURCES

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LIST OF ITEMS IN THE SUPPORTING INFORMATION

Appendix S1

- 1. Figure S1. PRISMA flowchart
- 2. Figure S2. Results for data excluding imputed standard deviations.
- 3. Figure S3. Moderator analyses for historical fire regime types.
- 4. Figure S4. Funnel plots of sample size versus meta-analytical residuals.
- 5. Figure S5. Location of studies in areas of high concentration of studies.
- 6. Table S1. Word strings used to search databases Scopus and Web of Science.
- 7. Table S2. Meta-analysis results for metrics within each response variable.
- 8. Table S3. Meta-analysis results for plant abundance.
- 9. Table S4. Meta-analysis results for plant diversity.
- 10. Table S5. Meta-analysis results for plant fitness.