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# Success of post-fire plant recovery strategies varies with shifting fire seasonality

Ryan Tangney [1,2,3 ✉], Ruby Paroissien [1], Tom D. Le Breton [1], Alexandria Thomsen [1], Chantelle A. T. Doyle[1], Mercedes Ondik[1], Russell G. Miller[2,4], Ben P. Miller [2,5] & Mark K. J. Ooi [1,6]

Wildfires are increasing in size and severity and fire seasons are lengthening, largely driven by climate and land-use change. Many plant species from fire-prone ecosystems are adapted to specific fire regimes corresponding to historical conditions and shifts beyond these bounds may have severe impacts on vegetation recovery and long-term species persistence. Here, we conduct a meta-analysis of field-based studies across different vegetation types and climate regions to investigate how post-fire plant recruitment, reproduction and survival are affected by fires that occur outside of the historical fire season. We find that fires outside of the historical fire season may lead to decreased post-fire recruitment, particularly in obligate seeding species. Conversely, we find a general increase in post-fire survival in resprouting species. Our results highlight the trade-offs that exist when considering the effects of changes in the seasonal timing of fire, an already present aspect of climate-related fire regime change.

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[1] Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney 2052 NSW, Australia. [2] Kings Park Science, Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, 1 Kattidj Close, Kings Park 6005 WA, Australia. [3] School of Agriculture and Environment, The University of Western Australia, Crawley 6009 WA, Australia. [4] Environmental and Conservation Sciences, Murdoch University, Murdoch 6150 WA, Australia. [5] School of Biological Sciences, University of Western Australia, Crawley 6009 WA, Australia. [6] New South Wales Bushfire Risk Management Research Hub, Wollongong, NSW, Australia. ✉email: R.Tangney@unsw.edu.au

Global fire regimes are shifting[1,2], driven by a combination of climate change and other anthropogenic pressures including accelerated land-use change[3,4]. In the last five years, megafires have burnt at unprecedented scales and intensities across many continents[5–7], commonly starting and ending outside the historical fire season[8–10]. This shift is frequently driven by early onset drought conditions, resulting in fuels that are dry enough to burn[6,7]. Fire regime elements include season, intensity, severity and fire return interval[11]. Within fire-prone ecosystems, plants are broadly adapted to relatively stable fire regimes[12] shaped by long term climate trends[13]. Therefore, substantial or prolonged modifications to fire regimes may affect plant life-cycles, with differential impacts likely dependent on plant functional type[14,15].

The frequency and extent of wildfires is influenced by the intersection of climate, weather, ignitions and landscape fuels[13], and their temporal variation drives patterns of fire season timing and length. In some ecosystems, the conditions conducive to wildfires can occur at any time, while in others they are predictable and typically persist for just a few to several months (e.g., Mediterranean climate regions within California[3,6,10] and Australia[5,7]). However, as a result of decreased rainfall and the increased frequency of severe fire weather associated with climate change[1], the length of fire seasons are extending in many regions[3,4], which is driving a substantial increase in the amount of vegetation burnt outside the historically predominate fire seasons[1].

Both the short-term characteristics of fire events and long-term, interval-related elements of fire regimes can shape species distributions. The characteristics of individual fire events can filter plant functional types in the short-term, leading to local mortality or recruitment failures[14–18], while the overall fire regime can impart selective pressures on species and traits within ecosystems over generations[14,19–21]. Research on how fire season influences fundamental life-cycle stages is surprisingly limited[22–24] and often focuses on the local scale. Fire seasonality is a component of the fire regime[25] and shapes plant responses to fire[26,27]. How plants respond to fire season variation is linked to seasonal phenological cycles of growth, dormancy, flowering, and reproduction[22], meaning that when fire occurs during vulnerable phenological stages, post-fire population recovery responses can be negatively impacted[22]. Whether these effects can have significant measurable influence over functional population processes is yet to be examined at a broad scale but is essential for informed interpretation of how local-scale outcomes are related to landscape-scale distributions. How plant species and their populations respond to shifts in fire seasonality is likely to differ between plant functional types and the environmental conditions in which species persist[28–30]. Identifying similar patterns across functional groups or ecosystems in different regions can allow greater predictive power beyond single-species studies. Fundamental to species resilience in fire-prone ecosystems is the development of traits to support population persistence that ensure survival, recruitment and reproduction following fire[15] and we hypothesise that different fire response traits may be differently affected by changes in the seasonal timing of fire.

There are two broad mechanisms by which plant populations recover following fire in fire-prone ecosystems: resprouting from protected buds and recruitment from seeds[31]. Some species use a combination of both resprouting and recruitment from seeds. For species that respond to fire by resprouting[31], the timing of fire relative to their active growing season may impact energy storage, resprouting vigour and survival[22]. Other elements of the fire regime, such as fire intervals, may also deplete their ability to resprout[32], potentially by interacting with season. Some resprouting species can also reproduce via fire-stimulated flowering (also known as post-fire flowering, PFF) to help ensure long-term population persistence[33]. In some fire-prone ecosystems, fire-stimulated flowering is the dominant fire response type[34]. The timing of fire relative to the peak flowering season may impact the flowering intensity and reproductive output[35].

Species unable to resprout and thus typically killed by fire, termed obligate seeders, often maintain long-lived, fire-tolerant seed banks within soils or canopy-stored woody fruit (serotiny) that allow for post-fire germination and recruitment[36]. As adult plants of obligate seeding species are typically killed by fire, they rely solely on regeneration from seeds to persist[37]. Often, seeds of obligate seeders from fire-prone ecosystems have dormancy breaking and germination stimulation cues associated with fire. These fire cues lead to obligate seeding species frequently recruiting in even-aged cohorts in the first few years after fire[31]. Yet, due to their sometimes-complex dormancy and germination requirements, seasonal changes in fire may lead to mismatches between dormancy release cues and germination stimulation cues, resulting in delayed emergence, loss of seedling vigour, or ultimately reduced or failed recruitment[24].

To understand how changes in fire season impacts plant population persistence in fire-prone ecosystems, we asked the fundamental question: How do changes in fire season affect post-fire plant survival, recruitment and reproductive output in fire-prone ecosystems? To test this, we conducted a systematic meta-analysis, collating evidence from English-language articles spanning, Europe, North and Central and South America, Australia and South Africa (as well as single articles from Asia, the Middle East). We examined how reproduction, recruitment and survival of plant species are affected by changes in fire season. We explicitly tested whether their response is differentially affected by fires that occur outside the historical fire season or at different times within their historical fire season. We also examined how different plant functional groups within a range of climate and vegetation types respond to fires outside the historical fire season. Changes in the seasonal timing of fire are hypothesised to have the greatest impact on plant responses that are integrally linked to seasonally varying environmental cues, such as flowering phenology[33] and reproduction[33]; resprouting function[22]; and seed dormancy and germination dynamics[24].

## Results and discussion

**Fires out of their historical temporal range affect plant species recruitment.** Across our analysis, the modelled effects of fires outside the historical fire season resulted in significantly reduced recruitment compared to fires that occurred within the historical season (Hedges' $g$: mean $= -3.03$, 95%; CI $= -4.58$; $-1.47$), whereas fires occurring outside the historical fire season had no significant impact on reproduction (Hedges' $g$: mean $= -0.04$; CI $= -1.51$; 0.60; Fig. 1a). Conversely, fires outside their historical season resulted in higher survival (Hedges' $g$: mean $= 2.89$, CI $= 1.94$; 3.84; Fig. 1a). Negative recruitment effects were most evident in hot desert climates (Hedges' $g$: mean $= -1.66$, CI $= -2.59$; $-0.73$), woodland-type vegetation (Hedges' $g$: mean $= -2.13$, CI $= -2.76$; $-1.49$) and obligate seeder species (Hedges' $g$: mean $= -1.69$, CI $= -2.51$; $-0.88$, Fig. 2a).

Recruitment processes within the plant life cycle, including dormancy and germination, are uniquely temperature and moisture dependant[38]. Thus, changes in the season of fire can alter how seeds receive the cues required to initiate germination, and, in some cases, changes in fire season lead to mismatched dormancy and germination cues, resulting in delayed or failed emergence[39,40]. Reduced recruitment following fires out of the historical range may also be a result of a reduction in the availability or survival of seed banks[41]. This reduction could be
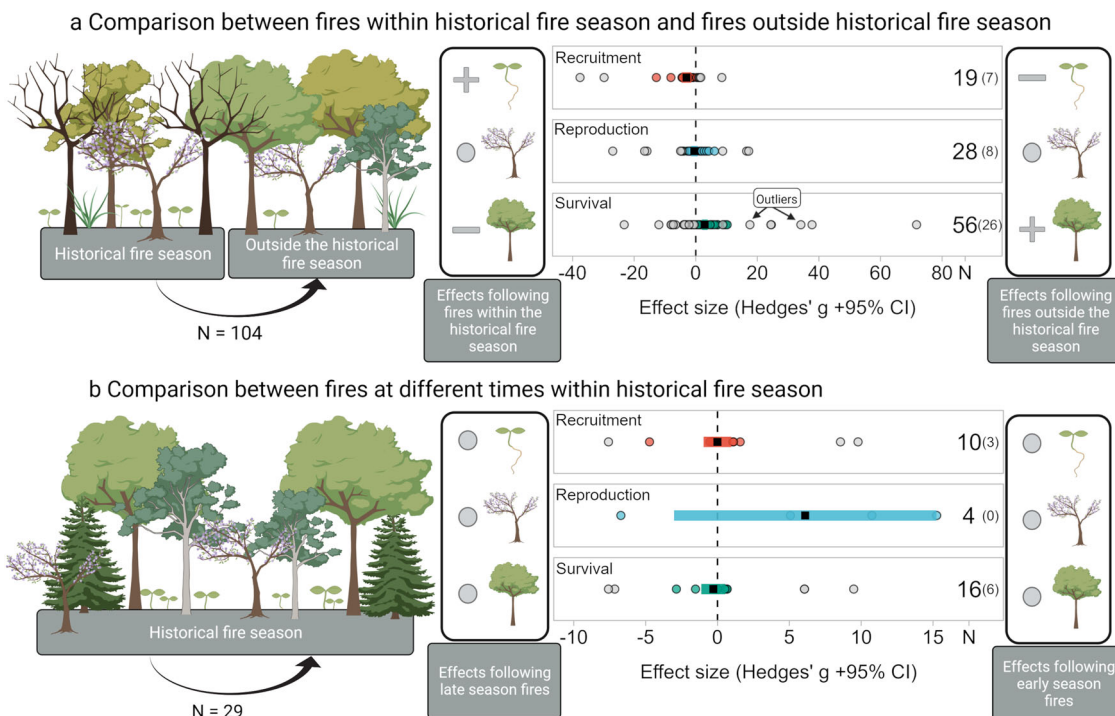
**Fig. 1 Success of post-fire plant recovery strategies varies with shifting fire seasonality.** Conceptual design and pooled results of meta-analysis for paired comparisons **a** Comparison between fires occurring within the historical fire season and fires occurring outside the fire season. **b** Comparison between fires occurring early and late season fire in the historical fire season. Modelled mean effects and 95% confidence intervals around the mean presented, coloured points represent studies within 95% CI of pooled effect size estimate and non-coloured points have been identified as outliers and excluded from analysis. Negative Hedges' g-values represent increased effects following fires in the historical fire seasons (in **a**) or late season fires (in **b**) relative to fires outside historical fire seasons early season fires, respectively. Positive Hedges' g-values represent increased effects following fires outside historical fire seasons (in **a**) or early season fires (in **b**) relative to fires in the historical fire seasons late season fires, respectively. N represents the number of paired comparisons (i.e., sample size) within each topic group, numbers within parenthesis adjacent to N numbers indicate number of outliers that were identified within each analysis. Conceptual diagrams created with BioRender.com.

driven by increased seed bank mortality during fires (due to increased seed moisture[23]), a loss in seed viability between fire and the subsequent germination period[17], reduced opportunity for germination[17] or increased pre-germination seed predation[41]. Given that seedling recruitment is essential for the persistence of obligate seeders following lethal fires, reductions in the recruitment processes (germination, emergence and establishment) have the potential to cause the abrupt local loss of obligate seeding species.

Reduced recruitment as a result of changes in fire season is supported by previous work describing the theoretical framework of plant response to fire seasonality. Miller, Tangney[22] and Keith, Dunker[42] collectively identified eight mechanisms which can impact how plants respond to out of season fires, and seven of these theoretical mechanisms are directly associated with recruitment processes.

On average, there was a neutral effect on reproduction by fires outside their historical season (Fig. 1a). However, results within subgroups varied widely. For instance, the mean pooled effect size corresponding to the impact on reproduction within grassland vegetation types varied from a lower estimate of −2.16, to an upper estimate of 0.69 (Fig. 2b), however, upper effect sizes sourced from studies extended up to an estimated hedge's g of between 16 and 17 (Fig. 2b). Grasslands are frequently comprised of a proportionally large number of post-fire flowering species[34], which are inherently resprouting species. These same grasslands may be under the influence of short fire intervals (e.g., 1–4 years between fires[26]), and therefore, reproduction in PFF species in grasslands may be less contingent on the timing of fire and more

influenced by variables not captured by this analysis, such as, local differences in environmental conditions that impact post-fire reproduction success[43].

On average, survival increased following fires outside their historical seasons (Fig. 1a). Studies from four out of five tested climate regions showed significantly higher survival following fires outside compared to within their historical seasons, and post-fire survival of resprouting species was significantly higher for the same comparison (Fig. 2c). These responses may be correlated with a decrease in fire severity during fires outside the historical fire season, leading to higher plant survival[44,45]. Higher plant survival outside of the historical fire season may also be because many plant species may be in their resistant (dormant) state at this time owing to temperature- or moisture-limited growing phenology[22,46]. That is, some resprouting species may be actively growing during the historical fire season where this aligns to the growing season. Resprouting plants that experience high severity fire during or shortly after their growing season may suffer increased mortality and resprouting failure as their carbohydrate reserves are depleted and their ability to resprout is limited[22]. Thus, the combined effect of higher severity fires occurring during periods when resprouting plants are actively growing may explain why there is increased mortality following fires within the historical fire season.

In general, natural plant populations maintain substantial levels of genetic diversity which provides a source for adaptive capacity, allowing them to adapt to changes in their environment, which may potentially include changes in fire season[47]. Phenotypic plasticity within populations can also provide avenues
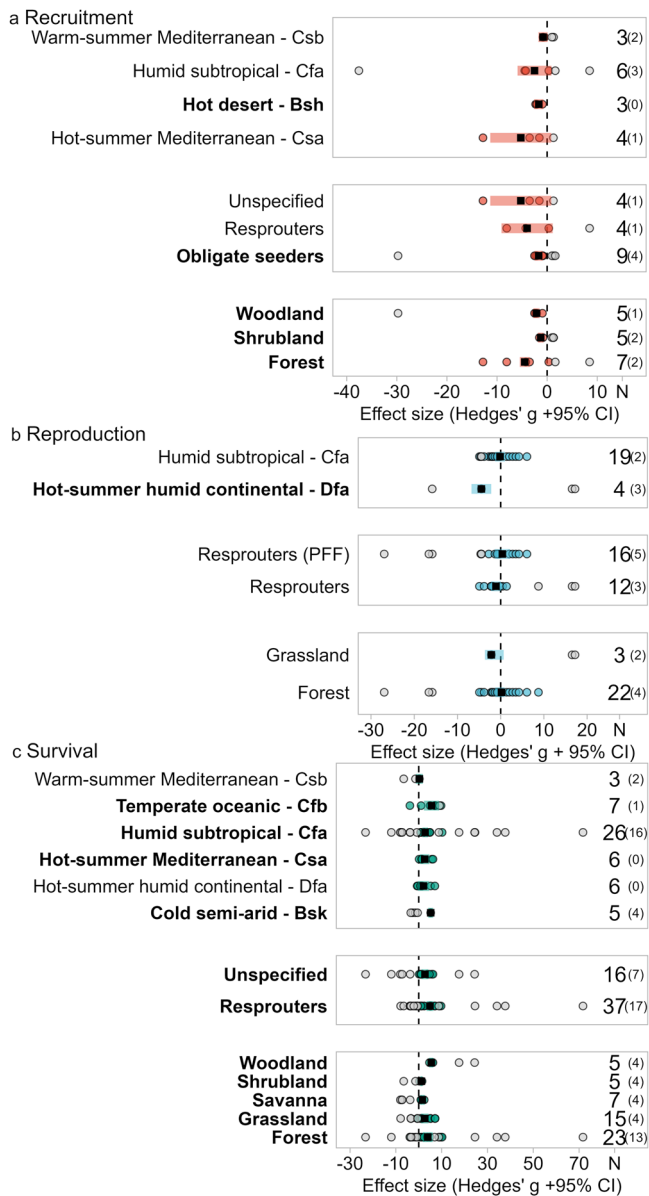
**Fig. 2 Fires out of their historical temporal range affect plant species recruitment.** Results of subgroup meta-analysis investigating the effects of climate type, plant functional group and vegetation type for comparisons of **a** recruitment **b** reproduction and **c** survival between fires within the historical fire season and fires outside the historical fire season. Modelled mean effects and 95% confidence intervals around the mean presented. Negative Hedges' $g$-values represent increased effects following fires in historical fire seasons relative to fires outside historical fire seasons. Positive Hedges' $g$-values represent increased effects following fires outside historical fire seasons relative to fires in historical fire seasons, coloured points represent studies within 95% CI of pooled effect size estimate and non-coloured points have been identified as outliers and excluded from analysis. $N$ represents the sample size in each of the subgroup comparisons, numbers within parenthesis adjacent to N numbers indicate number of outliers that were identified within each analysis. Bold text indicates subgroups with significant effects. Studies where species responses were reported without reporting response traits we characterised as "unspecified".

for quick adaptation to changing conditions, for example, flowering phenology has been demonstrated in several studies to be highly plastic in response to warming, resulting in plants flowering earlier and, in some cases, flowering longer[48]. However,

the ability of species and plant populations to adapt to changes in fire season may be dependent on whether fire seasons shift slowly via gradual changes in the timing of fire, or rapidly via extreme out-of-season fires[47]. Obligate seeding species are particularly vulnerable to abrupt changes in fire regimes[14] as they maintain long-lived seed banks either in the soil or within woody fruits in the canopy of adult plants and are often unable to recruit between fire events[49]. Therefore, abrupt shifts in the recurrent seasonal timing of fire may outpace the adaptive capacity of long-lived obligate seeding species.

**Early season fires have a neutral affect on post-fire recruitment, reproduction and survival.** Changes in the timing of fires within the historical fire season had a muted effect on recruitment, reproduction and survival (Fig. 1b). The mean pooled effect size for reproduction was higher following early season fires compared to late season fires; although it was not significant, and the sample size was small ($N = 4$ pairwise comparisons; Fig. 1b). Reduced reproduction in late season fires may be due to the direct effect of fire occurring during flower or ovule development and interrupting subsequent seed production[50], a correlation with generally higher fire severity in late season fires, or a mismatch between the timing of late season fire and post-fire flowering cues. Fewer available flowers following fire can result in fewer seeds produced, which may have flow-on effects for post-fire recruitment in subsequent years[51].

Despite small sample sizes for many subgroup comparisons, including an insufficient number of studies describing the effects of fire season on reproduction (i.e., <3), there were no significant effects on recruitment across any of the subgroups (Fig. 3a). In the case of Setterfield[52], recruitment following fires in tropical eucalypt savannas were similar despite changes in fire season; however, there was a delay in seedling emergence until the following year. As seeds have seasonal dormancy and germination requirements (acknowledging some seeds may cycle through dormancy[51]), timing of fire relative to these dormancy states may be critical to stimulate germination during the non-dormant phase[24,40]. Plant survival was higher in early season fires compared to late season fires in studies which did not specify fire-response type ('unspecified', Fig. 3b). Early season fires in many ecosystems tend to be lower in intensity and severity[53], thus allowing higher plant survival.

The tropical savannas of Australia present an example of consistent widespread early season burning. Early season burning is undertaken as part of an annual fire management programme and incidentally contributes to the income of regional landowners[54]. The foundation of the programme aims to reduce large scale, high intensity, late season fires, which results in lower annual carbon emissions by reducing the total amount of biomass consumed by late season fires. In addition, plant survival in these systems may derive a benefit from early season fires owing to reduced fire intensity as less grassy understorey biomass is available[53]. However, as noted by Prior, Williams[55], in systems that are subjected to annual burning regimes, survival of young trees is critically important; yet in some cases, younger age classes suffer high mortality during fire regardless of fire severity or season[55].

Notwithstanding the strength of evidence from individual case studies, there remains a fundamental need for further research into the effects of changes in fire season to adequately assess the risks posed under future fire regimes. Specifically, there is a need for a greater understanding of how changes in the timing of fire within historical fire seasons may impact plant populations across a broader scope of climate, vegetation types and functional groups, evident from the small sample sizes in this study. Future

Fig. 4 Plant response interactions with characteristics of fire and fire regimes. The response of plants to fires in different seasons may be influenced by interactions with fire severity, intensity, and time since previous fire. To assess how impactful these interactions were on plant responses, we recorded all mentions of these fire metrics from each of the sampled articles. No fire metrics were recorded within 38 of the 53 target articles. Of the 53 articles only 26 mentioned time since previous fire and only one article [109] used time since previous fire in their experimental design. A total of 18 metrics were reported from the 53 articles and despite their similarities, no consistent metric was found to allow for comparisons between articles.
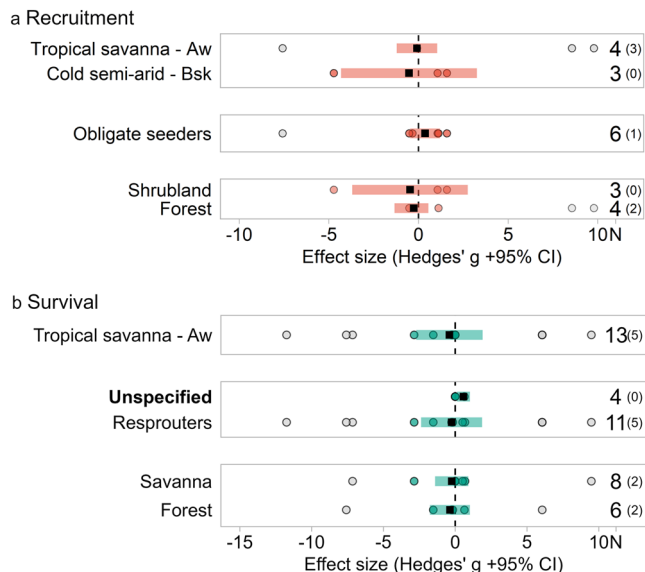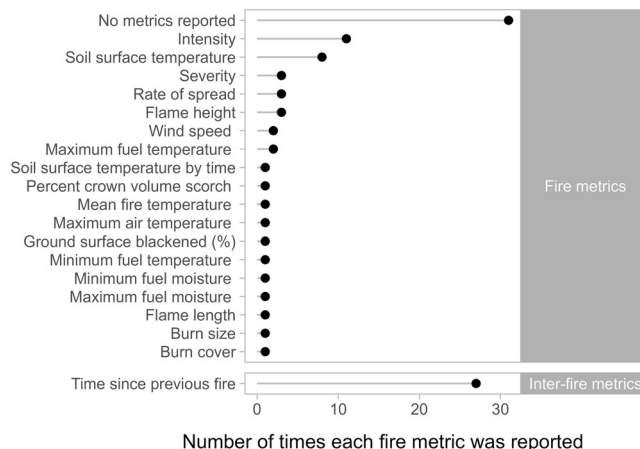


Fig. 3 Early season fires increase post-fire reproduction relative to late season fires. Results of subgroup meta-analysis investigating the effects of climate type, plant functional group and vegetation type for comparisons of a recruitment and b survival between early and late season fires. Modelled mean effects and 95% confidence intervals around the mean presented. Negative Hedges' g-values represent increased effects of late season fires relative to early season fires. Positive Hedges' g-values represent increased effects of early season fires relative to late season fires, coloured points represent studies within 95% CI of pooled effect size estimate and non-coloured points have been identified as outliers and excluded from analysis. N represents the sample size in each of the subgroup comparisons, numbers within parenthesis adjacent to N numbers indicate number of outliers that were identified within each analysis. Bold text indicates subgroups with significant effects. Comparison sample size for reproduction was too small (<3) and therefore was not included in this subgroup analysis. Studies where species responses were reported without reporting response traits we characterised as "unspecified".

research into the effects of changes in the seasonal timing of fire should endeavour to assess interactions with other fire regime elements, especially fire severity, and strive for consistent metrics, including documenting underlying fire history (e.g., fire intervals) and spatial measures of fire severity (linked with plot-based measurements). Furthermore, while we were able to show the immediate impacts of changes in fire season (~1-year post-fire), we critically need robust and well-designed studies that attempt to separate immediate fire effects from on-going climate and compound disturbance effects to assess the long-term response of plant populations to changes in fire season.

## Conclusion
Changes in the seasonal timing of fire can have significant effects on plant reproduction, survival and recruitment in fire-prone ecosystems. Our results indicate that post-fire recruitment is, on average, reduced by fires outside their historical temporal range, with the effect being particularly notable for obligate seeding species, which wholly rely on post-fire recruitment for population recovery. Conversely, survival of resprouting species is, on average, higher under the same changes in fire timing. Therefore, there is an inherent trade-off between the success of these key post-fire recovery strategies, with the potential to impact species composition under persistent changes in fire seasonality. Climate change is shifting the timing and length of global fire seasons[56–58], and the findings of this meta-analysis indicate that

such shifts may have broad and interacting effects across many regions and across a range of major plant functional types.

## Methods
**Literature search**. We identified relevant literature using keyword searches of Web of Science and Scopus databases in September 2020 and September 2021. We targeted all available papers published before September 2021. We conducted one search for each of the key responses, (1) Fire AND season AND plant recruitment, resulting in 550 papers, of which 370 were unique. (2) Fire AND season AND plant reproduction, resulting in 329 papers, of which 245 were unique; and (3) Fire AND season AND plant survival, resulting in 426 papers, of which 291 were unique. We also included 90 papers identified in a previous publication[22]. Combined, 996 papers were identified for screening. The first screening determined if each paper was relevant to the topic, through the reading of the title and abstract; 667 were removed at this stage. The remaining 329 were thoroughly examined, of which 277 were excluded based on criteria outlined below, leaving 52 articles included in this meta-analysis[19,43,50,52,55,59–105], which produced a data set of 133 pairwise comparisons. PRIMSA diagram included as Supplementary Fig. 1.

To be included in this analysis, studies needed to (1) measure plant species response following fire in the field; (2) have comparisons between at least two different fires in two different months measured once following fire at similar post-fire ages (Supplementary Fig. 2); (3) report on plant survival, reproduction or recruitment (articles that measured diversity, richness or evenness were discarded); and (4) contain data on means (or pairwise F-statistics reported within ANOVA tables), estimation of variation (including standard deviation or standard error > 0) and a clearly defined and stated sample size for each experimental group. Reported statistics were extracted from each relevant paper, either from text and tables or from figures using the 'metadigitise' package[106] within the R statistical programme[107]. From each of the papers, we also extracted secondary characteristics that we aimed to examine as correlates of plant response to fire season. These included fire metrics (e.g., fire severity, fire intensity, flame height or soil temperature; Fig. 4) and inter-fire metrics (e.g., time since last fire; Fig. 4), historical fire season, climate type, vegetation type and functional plant groups. Due to limited and inconsistent reporting of fire and inter-fire metrics (Fig. 4), these potential correlates of fire season effects were unable to be included in further analysis. Historical fire season, climate type, vegetation type and functional plant groups were sufficiently represented in the literature to be included further in the analysis.

Historical fire season was defined as a period of the year that historically had the highest level of fire activity and was either defined within the paper itself or derived from a combination of secondary literature associated with the target region or local reviews on fire season (e.g., Knapp, Estes[26]).

For comparisons between the historical and non-historical season fires, we classed fires that occurred within the historical season as the control group, and

fires that occurred during the non-historical fire season as the treatment group. Where there were multiple treatment group (non-historical season) fires (e.g., spring and autumn fires) compared to a single historical season fire (e.g., summer), we split the N of the historical season fire to avoid double counting of control groups[108]. For each pairwise comparison we did not separate whether non-historical season fires occurred before or after the historical fire season.

For comparisons between two different periods within the historical fire season, the control group was defined as the period of the year that is driest (lowest rainfall and/or highest temperature). This is because drier periods are more likely to result in relatively higher burnt area than wetter time periods, defined here as the treatment group[13], thus, having a larger effect on plant responses across ecosystems.

**Categorisation of effect size**. We created pairwise comparisons to examine the effects of fire season across two levels of inference: (1) between historical and non-historical fire seasons, and (2) between two different periods within the historical fire season (e.g., early and late season fires, Fig. 1a, b). For each pairwise comparison, Hedges' *g* was calculated, along with an estimated standard error and 95% confidence bounds around the mean effect using the "esc" package[109] within the R statistical programme[110].

We categorised the effect size measures from each article into three different topics based on the ecological process examined: (1) post-fire recruitment (measured by seedling density, seedling abundance, or germination %); (2) post-fire reproduction (measured by number of flowering stems, % of individuals flowering, or flowering density); and (3) post-fire plant survival (measured by survival %, plant density or number of resprouting stems).

**Random effects model and subgroup analysis**. We implemented three random effects models over each of the three topics of interest (i.e., recruitment, reproduction and survival). We chose a random effects model because we believe that there will be no single fixed effect size[111]. Instead, we assumed that effect size will differ between climate types, vegetation communities and plant functional groups. Therefore, a random effects model was deemed most appropriate and allowed us to investigate any drivers of differences in effect size between studies[108]. Using the 'meta' package in R, we implemented the meta-analysis using the "metagen()" function, applying the inverse variance method[111] paired with the Hartung-Knapp method to refine the variance estimate around the mean treatment estimate[110]. This was implemented only when Hartung-Knapp confidence intervals were narrower than CIs from classic random effects models that used DerSimonian-Laird estimations[111]. As part of a conservative approach, we excluded outliers from this analysis. To identify outliers, we used the 'dmetar' package[112] within the R statistical programme[107]. We defined outliers as pairwise comparisons where the 95% confidence interval of the effect size from the individual study is beyond the bounds of the 95% confidence interval of the pooled effect size[112]. We report pooled effects without the influence of outliers[112].

To further understand differences within and between fire seasons for each topic, we assigned each pairwise comparison to a subgroup based on the climate type and vegetation type of the study ecosystem and the plant functional group to which each species belongs that was reported within the comparisons. Using the calculated effect sizes for each pairwise comparison and assigned subgroups, we conducted a subgroup analysis which examines the variance within topics based on similar subgroup characteristics (e.g., climate type, vegetation type and functional group). Subgroup analysis was conducted using the 'update.meta' function in the 'meta' package[110] in R[107] and where there were less than subgroups with <3 pairwise comparisons were discarded from further analysis. All analyses are visualised using ggplot2[113] in R[107].

Below, we briefly explain the variables used to define subgroups and the role they play in defining ecosystem characteristics and plant responses to fire.

**Climate Type**. Climate plays an integral role in defining the fire season of many ecosystems[56,114,115]. Climate type, defined by the Köppen climate classifications, allows us to analyse how differences in climate regime may influence plant responses to changes in seasonal timing of fire[7]. Specifically, we can gain insights into how plant responses vary between seasonal climates (e.g., hot-summer Mediterranean climate (Csa)) and aseasonal climates (e.g., humid subtropical climate (Cfa))[116]. For each article, climate type was extracted directly from the paper or derived from location data using the Köppen climate map provided by Peel, Finlayson[117].

Of the 53 articles we examined, 18 described research conducted in humid subtropical climates (Cfa), eight in Tropical savanna with dry-winter climates (Aw), six in Oceanic climates (Cfb), five in Hot-summer Mediterranean climates (Csa) and five in Cold semi-arid (BSk) climates. The other 11 articles were comprised of research from Hot-summer humid continental climates (Dfa, three articles), Hot semi-arid (Bsh, two articles), Warm-summer Mediterranean (Csb, two articles), Warm-summer humid continental (Dfb, two articles), Subtropical highland (Cwb, one article), and Warm dry-winter continental (Dwa, one article) climates.

**Vegetation type**. Vegetation type can be broadly described as forest, woodland, savanna, shrubland or grassland, and reflects variation in local geological and climate interactions that define the extent of distinct ecosystems. Vegetation type influences the fuel dynamics and fire regime of an ecosystem[118], and thus, the typical fire severity (e.g., stand-replacing versus surface fire), season, interval and extent. For example, dry forests may be characterised by surface and low severity fire regimes, whereas shrublands typically experience canopy (stand-replacing) fire regimes[118–120]. Including vegetation type in this analysis allows us to evaluate the sensitivity of different ecosystems to fire seasonality effects and provides a means to indirectly assess potentially interacting fire metrics inconsistently reported in the literature (e.g., fire severity). All papers defined the vegetation type of their study region.

From the 53 articles we examined, 51 articles focused on a single vegetation type, while two articles included plant responses from multiple vegetation types[99,104]. Forest was the most frequently studied vegetation type (21 articles), followed by savanna and grassland-type vegetation (13 and 10 articles, respectively) while the last 12 articles examined seasonal responses to fire in Woodlands (8), Shrublands (four) and Wetlands (one).

**Functional group**. Many plant species that inhabit fire-prone ecosystems have developed traits that support recruitment, reproduction and survival under historical fire regimes[15,29,31]. Adaptive traits influence how plants respond and recover following fire[15]. The distribution of these fire-adapted traits within and between ecosystems is driven, at least in part, by the long-term characteristics of the fire regime[29,120,121]. Thus, we hypothesise that different traits may be differently affected by changes in the seasonal timing of fire. In this analysis, we focused on three functional traits best represented in the literature relating to recruitment, reproduction and survival. These traits were post-fire resprouting, obligate seeding (synonymous with fire-killed or post-fire non-sprouting) and fire induced flowering (post-fire flowering, PFF[29]).

Six articles compared the response of multiple functional groups to changes in fire season, with the remaining 47 articles focused solely on individual functional groups. The most common functional group analysed in our data set was resprouting plants, occurring in 29 articles. The other two functional groups had equal representation with ten articles examining both obligate seeding species and ten articles examining post-fire flowering species. In ten articles, responses of obligate seeding and resprouting species were combined, thus representing a collective response to changes in fire season.

**The data set, publication bias and p-hacking**. From the 53 reviewed articles, the resulting data set contained[122] pairwise comparisons, with effect sizes (Hedges' *g*) ranging from −37 to 80. Using a random effects model resulted in a global mean, excluding outliers, reported in Hedges' *g* of 0.3505 (95% CI: 0.0005; 0.7005, *P*-value = 0.04). These data comprise research from six continents, including a large representation from North America, Australia, Mediterranean Europe and South Africa, and across 10 climate regions, including 42 comparisons from humid subtropical (Cfa) climate regions.

Data were dominated by comparisons between historical fire season and fires outside the historical fire season (*N* = 104). From these 104 pairwise comparisons, articles that examined the effects of fire season on plant survival were most frequent (*N* = 56 comparisons), followed by comparisons that examined reproduction (*N* = 29), and least represented were papers that examined how changes in fire season impact recruitment (*N* = 19). There were 29 pairwise comparisons between fires at different times within the historical fire seasons with a large proportion of these comparisons (*N* = 12, ~40%) coming from climates with predictable seasonal rainfall, e.g., tropical savannas (Aw).

For each of the three topics (i.e., survival, reproduction and recruitment), we assessed each set of responses for publication bias and p-hacking. Tests for publication bias assume that studies that report low effect size (Hedges' *g* ~ 0) are less likely to be published compared to papers with large effect sizes[123]. However, publication bias may also arise as a result of P-hacking, where researchers selectively collect data or apply statistical analyses until nonsignificant results become significant, thus resulting in *P*-values close to significance thresholds (e.g., *P*-value = 0.05)[124]. Publication bias was assessed by visually identifying asymmetry in funnel plots and applying Egger's regressions[125]. Egger's regression is a linear regression model that tests for asymmetry in the data set, using the standardised effect score as the response variable, and the inverse standard error for each study as the predictor variable[125]. An intercept overlapping zero suggests that there is no significant asymmetry. Egger's test and funnel plots were constructed using the 'meta' package[110] within *R* statistical programme[107]. P-hacking was tested using the *P*-curve technique within the 'dmetar' package[112] in R[107]. The *P*-curve can provide evidence of P-hacking if there is an overrepresented and skewed proportion of *P*-values close to 0.05[126].

There was no evidence of asymmetry for any of the three groups (recruitment: Egger test: *t* = −1.62, *P* = 0.11; reproduction: Egger test: *t* = 0.71, *P* = 0.48; or survival: Egger test: *t* = 1.41, *P* = 0.13) and no evidence of P-hacking from any of the groups. All three *P*-curves displayed strong left-skewness (recruitment: 58.62 % of comparisons are *P* < 0.025; reproduction: 53.12% of comparisons are *P* < 0.025; and survival: 72.22% of comparisons are *P* < 0.025; Power Estimate ranged from

97–99%). Combined, the *P*-curve analysis and the Egger's regression show no evidence of publication bias or *P*-hacking.

**Reporting summary**. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

Data used, generated or analysed during this study are available for download from Dryad Digital Repository (https://doi.org/10.5061/dryad.7sqv9s4t5)[122]. All data is presented in tabulated comma delimited format accompanied by a html file which describes each data file including metadata of each column.

## Code availability

All R script and Rmarkdown outputs generated during analysed this study are available for download (https://doi.org/10.5061/dryad.7sqv9s4t5) from Dryad Digital Repository[122]. Within the Markdown.html file are descriptions of all packages used within R statistical programme and their version numbers used for this analysis. No custom functions were created for this analysis.

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## Author contributions

R.T., R.P., T.D.L.B., A.T., C.A.T.D., M.O. extracted and compiled the data from literature. R.T. designed the collection criteria and methodology. R.T. analysed the data and R.T. led the writing of the manuscript. R.T., R.G.M., B.P.M. and M.K.J.O. conceived the ideas, helped develop the contextual framework and designed methodology.

## Competing interests

The authors declare no competing interest.

## Additional information

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**Correspondence** and requests for materials should be addressed to Ryan Tangney.

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