

## Fire effects on pollination and plant reproduction: a quantitative review

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- **Background and Aims** Fire may favour plant flowering by opening up the vegetation and increasing abiotic resource availability. Increased floral display size can attract more pollinators and increase absolute fruit and seed production immediately after a fire. However, anthropogenic increases in fire frequency may alter these responses. We aim to assess the effects of fire on the pollination and reproductive success of plants at the global scale.
- **Methods** We performed a systematic literature review and meta-analyses to examine overall fire effects as well as different fire parameters on pollination and on plant reproduction. We also explored to what extent the responses vary among pollinators, pollination vectors, plant regeneration strategies, compatibility systems, vegetation types and biomes.
- **Key Results** Most studies were conducted in fire-prone ecosystems. Overall, single fires increased pollination and plant reproduction but this effect was overridden by recurrent fires. Floral visitation rates of pollinators were enhanced immediately following a wildfire, and especially in bee-pollinated plants. Fire increased the absolute production of fruits or seeds but not fruit or seed set. The reproductive benefits were mostly observed in wind-pollinated (graminoids), herbaceous and resprouter species. Finally, fire effects on pollination were positively correlated with fire effects on plant reproductive success.
- **Conclusions** Fire has a central role in pollination and plant sexual reproduction in fire-prone ecosystems. The increase in the absolute production of fruits and seeds suggests that fire benefits to plant reproduction are probably driven by increased abiotic resources and the consequent floral display size. However, reproduction efficiency, as measured by fruit or seed set, does not increase with fire. In contrast, when assessed on the same plant simultaneously, fire effects on pollination are translated into reproduction. Increased fire frequency due to anthropogenic changes can alter the nature of the response to fire.

**Key words:** Angiosperms, anthropic changes in fire regime, fire ecology, flowering plants, meta-analysis, plant fitness, plant–pollinator interaction, plant sexual reproduction, reproductive success.

### INTRODUCTION

Fire is a significant ecological and evolutionary factor that shapes biodiversity in many terrestrial ecosystems (Bowman *et al.*, 2009; Pausas and Keeley, 2009, 2023). It occurs in almost every biome although with different regimes (Archibald *et al.*, 2013). Anthropogenic influences on fire occurrence have been increasing over the last two centuries, with wildfires increasing in extent and severity, and fire seasons lengthening in many regions worldwide (Moritz *et al.*, 2012; Jolly *et al.*, 2015; Bowman *et al.*, 2020). Projections indicate a further significant global expansion of fire-prone areas due to a warming climate in future decades (Senande-Rivera *et al.*, 2022). These changes may have immediate impacts on both ecosystems (Kelly *et al.*, 2020) and societies (Pausas and Leverkus, 2023).

The ecological effects of fire on biotas are heterogeneous, as their response varies among species and depends on complex biotic interactions (Dafni *et al.*, 2012; Viljur *et al.*, 2022). While the regenerative response of many key plant species has been well documented or inferred from their life-history traits, less research has been performed about fire effects on plant–animal interactions such as pollination (Brown *et al.*, 2016; García *et al.*, 2018; Teixido *et al.*, 2022; Ballarin *et al.*, 2023). However, interactions between plants and pollinators are of crucial importance in re-establishing community structure, community functioning and the services that fire-prone ecosystems provide to humankind (Pausas and Keeley, 2019; da Silva Goldas *et al.*, 2022a).

Animal pollination is a vital ecosystem process for the sexual reproduction of most flowering plants (Rodger *et al.*, 2021) as

it not only allows seed formation but also helps maintain or increase genetic diversity, decreasing the likelihood of inbreeding depression (Wilcock and Neiland, 2002). Following a fire, most insect pollinators, and especially bees, increase their diversity and abundance (Carbone *et al.*, 2019; Nicholson and Egan, 2020). However, this is not the case in habitat-specialist Lepidoptera species (de Andrade *et al.*, 2017; Carbone *et al.*, 2019; Mason *et al.*, 2021). The observed overall resilience of pollinator activity to fire is supported by their flying ability, and nesting and feeding habits (Kral *et al.*, 2017; Pausas and Parr, 2018), along with the high availability of flowers and low competition levels in early post-fire habitats (Adedoja *et al.*, 2022; da Silva Goldas *et al.*, 2022b). The extent to which the increase in richness and abundance of floral visitors following a fire leads to a higher quantity or quality of pollination and, subsequently, enhanced plant reproductive success has only been assessed at the local level (Ne'eman and Dafni, 1999; Ne'eman *et al.*, 2000; Potts *et al.*, 2001; García *et al.*, 2018; Nicholson and Egan, 2020).

Many plant species exhibit a quick and synchronized flowering peak after a fire, generating high floral display sizes (i.e. increased number of open flowers per plant) due to the release of competition and increased availability of nutrients and light (Pyke, 2017; Burkle *et al.*, 2019; Wagenius *et al.*, 2020). As a result, these conditions often attract more pollinators and increase flower visitation, potentially enhancing pollination efficiency and plant fitness (Potts *et al.*, 2001; Burkle and Irwin, 2010). A higher ratio of fruit : flower or seed : ovule (hereafter fruit set or seed set, respectively) can indicate enhanced pollination efficiency, regardless of the size of the floral display (Dafni *et al.*, 2005). Nevertheless, a significant post-fire flowering peak may also reduce pollination efficiency because of increased geitonogamy (i.e. pollination among flowers within the same plant), which may reduce fruit and seed set in strict self-incompatible species or mostly outcrossing species (Goulson, 2000; LoPresti *et al.*, 2018; Marquez *et al.*, 2019; Wagenius *et al.*, 2020; Richardson and Wagenius, 2022). Consequently, the reproductive outcomes can vary depending on the mating behaviour and/or compatibility systems of plants (Ne'eman *et al.*, 2000).

Fire can also impact plant reproduction by altering abiotic resource availability. Post-fire conditions typically lead to a temporal increase in light and soil nutrients (e.g. Certini, 2005; Giorgis *et al.*, 2021), which can enhance sexual plant reproduction. Specifically, the absolute number of fruits or seeds per plant can be higher due to direct bottom-up effects (abiotic resource pulse) by producing a larger number of flowers after a fire (Muñoz *et al.*, 2005; Richardson *et al.*, 2023). However, human-induced frequent fires may cause erosion and depletion of soil nutrients (Certini, 2005; Pellegrini *et al.*, 2015, 2020), negatively affecting the reproduction of plant species capable of regenerating after a fire (Noble and Slatyer, 1980; Knox and Morrison, 2005; Tulloch *et al.*, 2016; Carbone and Aguilar, 2017). In addition, fire-induced changes in soil nutrients often vary across different vegetation types and biomes (Pellegrini *et al.*, 2018). Therefore, different reproductive effects are expected under different fire types (wildfires, prescribed fires) and ecosystems (e.g. tropical, mediterranean).

The response of plant sexual reproduction to fire can vary depending on certain life-history attributes (Noble and Slatyer, 1980; Poorter *et al.*, 2023). Self-incompatible (SI) plants are

highly dependent on pollinators for sexual reproduction, while self-compatible (SC) plants are less dependent on pollinators, as they can self-pollinate via autogamy or geitonogamy. If pollinator visitation to flowers increases early after a fire, this could be beneficial for the reproduction of these two plant groups. In addition, the replacement of functionally similar pollinators can offer reproductive resilience to plants after a fire (Potts *et al.*, 2001; García *et al.*, 2018). However, if fire benefits pollinator species that promote intra-plant pollination (geitonogamy) or reduce the activity of highly effective pollinators, it can drastically reduce fruit or seed set more in SI than in SC species (e.g. Ne'eman *et al.*, 2000). In contrast, autonomous selfing or wind-pollinated species (such as graminoids), which do not depend on pollinators, may exhibit fire-stimulated reproduction in open habitats due to abiotic factors (Linder *et al.*, 2018; Fidelis *et al.*, 2022; Pilon *et al.*, 2023).

Furthermore, the strategies by which plants regenerate after the fire, such as resprouting from buds (resprouters) or recruitment from seeds protected in the soil or in the canopy (seeders), can condition their reproductive responses (Lamont and Wiens, 2003; Tangney *et al.*, 2022). Seeders, which typically have a single cohort after a fire with synchronized reproductive cycles, are likely to maximize sexual reproduction during inter-fire periods (Pausas and Keeley, 2014). Thus, seeders can exhibit higher fecundity due to increased floral display after fire (Lamont and Wiens, 2003; Turner *et al.*, 2023). In contrast, the sexual reproduction of woody resprouters may be compromised because of their higher allocation to growth than reproduction after disturbance (Clarke *et al.*, 2013). However, recurrent fires may benefit precocious species that resprout rapidly and flower profusely early in post-fire habitats, such as geophytes, forbs and some shrubs (e.g. Diadema *et al.*, 2007; Giorgis *et al.*, 2021; Zirondi *et al.*, 2021). Considering the wide range of plant traits and ecological strategies, synthesizing current knowledge regarding the effect of fire on the pollination process and sexual reproductive success of flowering plants globally poses a challenge.

Our study aims to review existing knowledge on the effects of fire on the pollination process and reproductive success of flowering plants. Our hypothesis is that fire, by opening up the vegetation and increasing abiotic resource availability, favours flowering and pollinator activity and thus plant reproductive success. This effect should especially benefit plants that regenerate quickly after fire (resprouters) in fire-prone ecosystems. Specifically, we predict higher pollination and higher reproductive output (number of fruits or seeds) immediately after the fire in fire-prone ecosystems such as savannas and mediterranean-type ecosystems. However, this increased reproduction should not necessarily imply an increase in reproduction efficiency. Finally, increased fire frequency induced by human activities will deplete soil properties and degrade the ecosystem, which may limit flowering production, decreasing pollination and plant fitness. To test these predictions, we conducted a systematic literature review and hierarchical meta-analyses of available studies worldwide. Specifically, we performed two meta-analyses to examine how (1) pollination and (2) plant sexual reproduction respond to overall fire effects as well as to different fire parameters (fire frequency, post-fire time, fire type). This allowed us to examine to what extent the responses vary among pollinator groups, traits of plants including life forms, pollination vector, compatibility system

and regeneration strategy, and habitat characteristics such as vegetation type and biome.

## MATERIALS AND METHODS

### Literature search and inclusion criteria

We performed literature searches in Scopus (<https://www.scopus.com>), covering English, French, Spanish and Portuguese languages. We employed three different keyword combinations to retrieve relevant studies related to fire effects on the pollination process and on plant reproduction (Supplementary Information Table S1). The first search aimed to gather studies assessing the impact of fire on the pollination process. The second search focused on retrieving studies assessing fire effects on plant reproductive success. The third search targeted studies that simultaneously assessed both pollination and plant reproductive success responses to fire on the same plant species. For this search we pooled the two previous keyword strings into one (see Table S1). These searches yielded a total of 3299 articles (Fig. S1). We verified that these searches include studies cited in previous reviews on this topic such as Winfree *et al.* (2009), McKechnie and Sargent (2013), Carbone *et al.* (2019), Nicholson and Egan (2020), Giorgis *et al.* (2021), Mason *et al.* (2021) and Tangney *et al.* (2022).

For pollination studies, we included articles that specifically evaluated response variables related to the pollination process on plant species (e.g. proportion of pollinated flowers, amount of pollen deposited on the stigma, pollinator visits to flowers). We only included studies that used proper methodologies to accurately quantify plant–pollinator interactions. Studies that measured the abundance of insects potentially acting as pollinators using various types of traps were excluded.

For studies assessing plant sexual reproduction, we specifically selected articles that examined variables related to the female reproductive success of Angiosperm species (Gymnosperms were excluded). This involved quantifying the absolute number of fruits or seeds per plant or per unit area, and the probability of setting fruits and seeds (i.e. fruit set and seed set). While the absolute number of fruits or seeds offers a general indication of a direct pulse of abiotic resources, fruit or seed set provide a measure of reproductive efficiency, as fruit and seed production are relativized by the size of the floral display and ovule availability, respectively. In addition, to a lesser extent, we also included the number of fruiting/seeding plants, ramets or branches. We excluded variables such as the number of flowers, flowering branches per plant or the number of flowering individuals, as these indicators primarily reflect the allocation of resources to flowering prior to the processes of pollination and fertilization.

For both meta-analyses (pollination and plant reproductive success), we assessed the effects of fire by comparing data between burned (treatment) and unburned conditions (control). The unburned condition could refer to sites that had not experienced recent fires or sites in a pre-fire condition. We also included studies examining a post-fire chronosequence or a gradient of fire frequency/severity, without necessarily having an unburned control condition. These types of studies allow for the evaluation of fire effects on the pollination process and plant

reproductive success by examining changes over time or across different fire regimes.

To calculate the effect sizes for our analysis, we extracted two types of data from the literature. (1) For comparisons between burned and unburned conditions, we extracted the mean, standard deviation (or any other dispersion measure) and sample size for each condition. (2) For correlation data, such as post-fire chronosequence, we extracted the correlation coefficient (or convertible measures) and sample size. Data extraction was performed from the text, tables or plots of the literature, as needed. For extracting data from graphs, we used the *metaDigitise* R package (Pick *et al.*, 2019). An individual effect was considered when data were reported from different studies, different plant species or pollinator groups, different fire parameters or regions/sites with a spatially replicated design that compared fire effects. By contrast, when a study reported repeated measures over time for the same species, or when pseudoreplication was identified, we condensed the effects into a single effect from the same study. We excluded studies that reported the combined effects of fire with other disturbances (e.g. grazing, logging) as they did not provide independent data on fire effects.

### Moderator variables

We evaluated several moderator variables related to the characteristics of the studies. Regarding the parameters of the fire and based on the information provided by each study, we included two levels of fire frequency: ‘once burned’ or ‘recurrent burns’. ‘Once burned’ refers to studies reporting the effect of a single fire at a site, without the occurrence of any previous fires or where previous fire history is not considered. ‘Recurrent burns’ indicate studies assessing sites that exhibited more than one fire event in a certain temporal range, thus determining a shorter interval between fires. We also characterize the post-fire time, as the time elapsed since the last fire event, where ‘early’ refers to assessments conducted within 3 years after the fire and ‘late’ more than 3 years. In the case of chronosequences, we calculated an average post-fire time across the gradient that was included in one of the previous categories. Finally, we classified fire type as wildfire or prescribed fire. For the pollination meta-analysis, we considered the type of response variable measured (visitation frequency, proportion of pollinated flowers or pollen loads), and the taxonomic groups of the pollinators that interact with the flowers (vertebrates, beetles, flies, bees, wasps, butterflies or multiple insects). When pollination was measured on specific plant species, we categorized their life form (forbs, geophytes, shrubs) and compatibility system (SC, SI).

For the plant reproduction meta-analysis, we classified the reproductive success depending on the response variables assessed: (1) fruit set or seed set and (2) the absolute number of fruits or seeds produced. We also classified the pollination vector of plants (vertebrates, bees, wasps, beetles, Lepidoptera, flies, multiple insects or wind); their life form (tree, shrub, perennial forb, annual forb, geophyte, graminoid or liana); their post-fire regeneration strategy (seeder, resprouter or facultative – i.e. species that regenerate both by resprouting and by seeding); their compatibility system (SC, SI); and their pollination specialization systems (specialist or generalist; considering one or multiple insect orders that were reported as pollinators, respectively).

Information about these plant traits was extracted from the same study or from other published sources. Regarding habitat characteristics, we considered the vegetation type (forest, grassland, shrubland or savanna) and the biome (following Olson *et al.*, 2001). Finally, because some studies assessed fire effects through different sampling designs and scales, we classified as ‘regional’ those studies that utilized sites as true spatial replicates (i.e. where the sample size corresponded to the number of sites per condition) and as ‘local’ those evaluating fire effects on plant reproduction without spatial replicates (i.e. where the sample size corresponded to the number of plants measured within one site per condition; see Quinn and Keough, 2002).

### Meta-analysis

We used Hedges’  $d$ , the standardized unbiased mean difference, as the effect size measure across all studies, which has the advantage of being unbiased by a small sample size (Gurevitch *et al.*, 2001). For most of the studies, Hedges’  $d$  was calculated straightforwardly from the mean values, standard deviations and sample sizes of pollination or plant reproduction variables in each of the two contrasting fire conditions: the treatment (burned, of any type) and the control (unburned, long time since last fire, or mature habitat). In studies that provided correlational data (e.g. post-fire time or fire frequency gradients), we calculated Pearson’s correlation coefficient  $r$  (Rosenberg *et al.*, 2013) and transformed it into Hedges’  $d$  following Borenstein *et al.* (2009). Negative values of  $d$  imply a decrease in the mean value of the pollination or plant reproduction responses in burned conditions, whereas a positive  $d$  value means an increased response in recently burned compared to the unburned conditions or to the late post-fire conditions.

We performed hierarchical mixed effects meta-analyses for each response variable (pollination and plant reproduction). The inverse variance-weighted models included fixed (moderators, see below) and random effects to estimate the differences across studies. These assume that effects do not share a common mean effect but that there is random variation among them, in addition to within-study variation (Borenstein *et al.*, 2009). These models also took into account the hierarchical dependence in our data due to cases where multiple data points (effect sizes) were obtained from the same study. For that, a study-level random effect was included as a nesting factor (Stevens and Taylor, 2009). These analyses were performed with the *metafor* R package (v.4.3.0) using the restricted maximum likelihood (REML) method (R Core Team, 2023; Viechtbauer, 2010). The respective plots were performed with the *orchaRd* R package (Nakagawa *et al.*, 2021). An effect of fire was considered significant if the 95 % confidence intervals (CIs) of the effect size ( $d$ ) did not overlap zero (Rosenberg *et al.*, 2013). Datasets used in the meta-analyses and the R scripts are found in Carbone *et al.* (2023).

The heterogeneity of effect sizes was assessed with  $Q$  statistics, which are weighted sums of squares tested against a  $\chi^2$  distribution (Hedges and Olkin, 1985). We examined the  $P$  values of  $Q_{\text{between}}$  ( $Q_b$ ) statistics that describe the variation in effect sizes that can be attributed to differences among categories of each moderator variable. A significant  $P$  value related to  $Q_b$  indicates that categories being compared have different responses to fire. We tested the following categorical moderator variables in

relation to fire characteristics: fire frequency, post-fire time and fire type; in relation to pollination moderators: pollinator taxa, plant life form and compatibility system; regarding plant reproduction moderators: reproductive success variable, life form, pollination vector, compatibility system, pollination specialization and post-fire regeneration strategy; and finally for habitat predictors: vegetation type and biomes (see Supplementary Information Table S2). We also included the overall fire effect across all studies independent of the moderators.

Phylogenetically independent meta-analysis was performed to explore to what extent the evolutionary relatedness among plant species affects their reproductive response to fire. For this, we generated a phylogenetic tree of the plant species included in our analysis with the *U.PhyloMaker* R package (Jin and Qian, 2023). We then calculated one effect size for each plant species by condensing multiple data points (186 total plant species and effect sizes). We used the *phyloMeta* software (Lajeunesse, 2009) to calculate the overall effect size of a phylogenetically independent meta-analysis. The output of this phylogenetic meta-analysis was compared to the standard (non-phylogenetic) meta-analysis (using the same dataset) with Akaike’s information criterion (AIC). Phylogeny effects on pollination meta-analysis were not tested because most (>50 %) of the effect sizes were measured at the plant community scale (grouping multiple plant species).

Finally, to assess the potential influence of wind-pollinated species on the overall effect size of plant reproductive response to fire, we conducted a sensitivity analysis. This analysis involved recalculating the overall effect size after excluding the individual effects of anemophilous plant species, primarily from the families Poaceae and Cyperaceae.

### Publication bias

We assessed the occurrence of publication bias (i.e. studies showing significant results have a higher probability of being published) with Kendall’s rank correlations of effect sizes and standard errors across the studies (Begg, 1994). Significant  $P$  values indicate potential publication bias, whereby studies with small sample size (large standard errors) are only published if they showed large effect sizes. In addition, we also performed the *trim and fill* method, which is used as a sensitivity analysis that estimates how the overall effect size would change if missing studies were incorporated (Jennions and Møller, 2002). Finally, we calculated the fail-safe number using the Rosenberg (2005) approach for pollination and plant reproduction datasets. This metric estimates the number of non-significant, unpublished studies that would need to be incorporated to the database to nullify the overall effect (Rosenberg, 2005). A fail-safe number higher than  $5N + 10$  (where  $N$  is the number of studies) indicates that the results are robust regardless of publication bias.

## RESULTS

### Fire and pollination

We identified 40 studies across 10 countries that met our inclusion criteria (Fig. 1; Supplementary Information Fig. S1); they yielded 125 effect sizes for pollination. Visitation frequency of

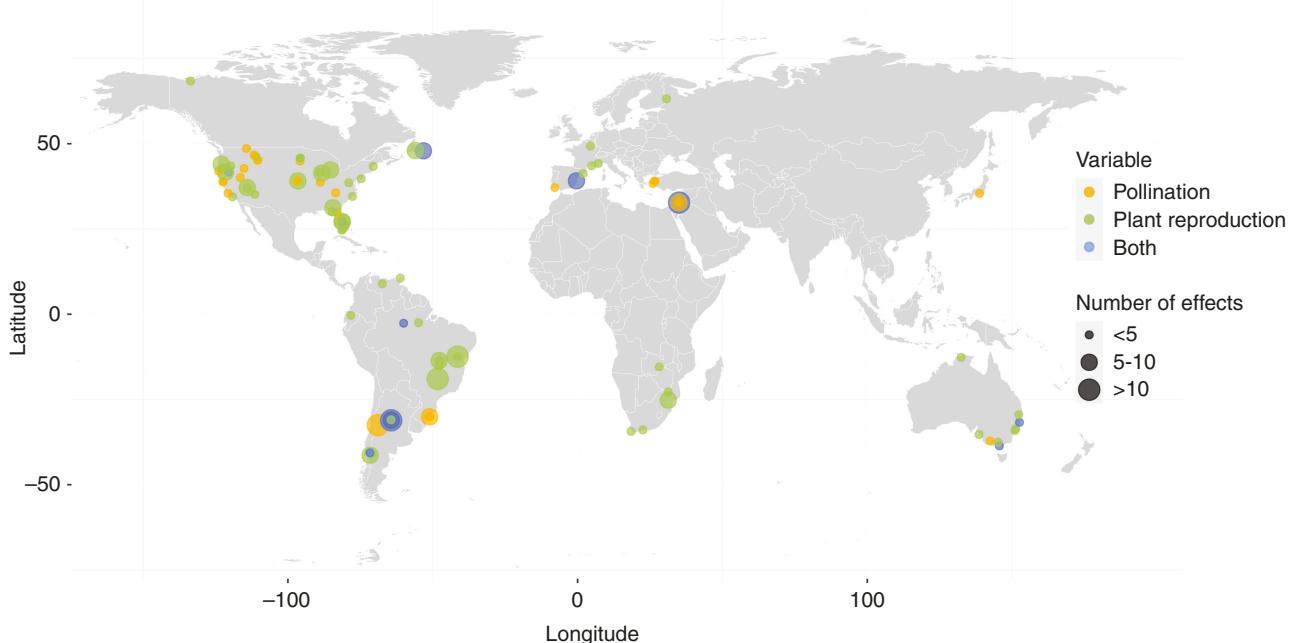


FIG. 1. Distribution of studies evaluating fire effects on pollination and plant reproductive success. Studies reporting data on pollination, plant reproduction and both simultaneously are indicated with different colours. The number of effects per study is indicated with different circle sizes.

pollinators to flowers was the most reported response variable, while the proportion of pollinated flowers and pollen loads had lower representation (see  $n$  values in Fig. 2). Most of the studies evaluated fire effects at the level of the plant community (53.6 % of the effect sizes), by comparing once burned vs. unburned conditions, for wildfire effects and mainly focused on insect pollination, especially bees.

The overall weighted-mean effect size of fire on pollination across all studies was significantly positive (Fig. 2A; Supplementary Information Table S2), implying that, on average, fire increased pollination. Importantly, the positive effects of fire on pollination were observed after a single fire event whereas no increments were observed after recurrent fires (Fig. 2C). Pollination was higher at the early post-fire age (i.e. <3 years), and after wildfires (Fig. 2D, E).

Fire effects on pollination differed depending on the pollinator group (Supplementary Information Table S3). Pollination by bees, either alone or forming multiple-order insect assemblages, presented the highest positive response to fire (Fig. 2F; Table S2). In contrast, fire had no significant effects on pollination by beetles and butterflies, although these had a low sample size, as in flies, vertebrates and wasps (Fig. 2F). When pollination was assessed on specific plant species (46.4 % of the effects), fire had no effect on pollination regardless of their life form or their compatibility system (Table S2). Pollination in forests (Fig. 2G) and in biomes such as mediterranean and temperate showed positive responses to fire, contrary to pollination in the desert and xeric biomes that showed a negative trend (Table S2).

#### Fire and plant reproductive success

We recorded 80 studies across 16 countries that quantified fire effects on sexual plant reproduction in the last four

decades (Fig. 1; Supplementary Information Fig. S1). We obtained 290 individual effect sizes, representing the responses of 186 plant species grouped in 57 Angiosperm families (Table S5). Poaceae, Asteraceae and Fabaceae were the most well represented families, accounting for 38.6 % of the effects. Almost all of the responses found were from native plant species (only nine effect sizes from alien species), of which 26.6% were endemisms. Most studies analysed the reproductive response to fire by assessing the absolute number of fruits or seeds (68.6 % of the effect sizes); a lower proportion of studies evaluated fruit or seed set (31.4 %; Fig. S2). Fire effects were predominantly assessed during the early post-fire stages (73.4 % of the effects at post-fire age <3 years), and most of them compared once burned vs. unburned conditions produced by prescribed fires (Fig. S3). Regarding the characteristics of the studied plants, most of the effects were for plants pollinated by animals (39.3 % of the effect sizes), represented mainly by melitophilous plants (29.8 %), and secondly for anemophilous plants (29%). One-third of these plant species were perennial forbs, followed by shrubs (27 %) and graminoids (26 %), and two-thirds used resprouting as the post-fire regeneration strategy (Fig. S2). The majority of studies were conducted in fire-prone habitats (48 % of the effects in grasslands, and 27 % in shrublands) from tropical/subtropical or temperate biomes.

The overall fire effect on plant reproduction was positive and different from zero (Fig. 3A; Supplementary Information Table S2). The variability of fire effects was largely explained by the type of response variable used as a proxy of plant reproductive success. Fire showed positive and significant effects only when assessing reproduction as total fruit or seed number, whereas no fire effects were observed on fruit set or seed set (Fig. 3B; Tables S2 and S3). Fire effects on reproduction were only positive after a single burn and no effects were

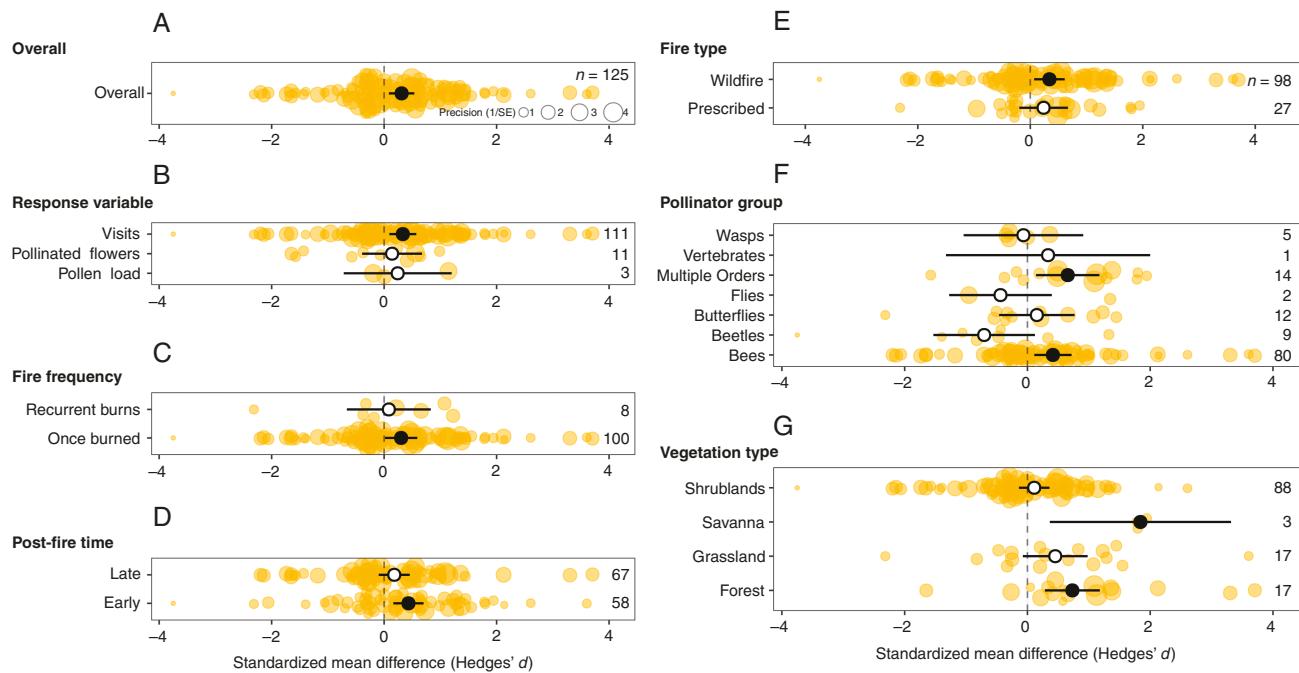


FIG. 2. Effect of fire on the pollination process. The weighted-mean effect sizes and 95% bias-corrected confidence intervals of overall (A), pollination variables (B), fire frequency (C), post-fire time (D), fire type (E), pollinator group (F) and vegetation type (G). Mean estimates with confidence intervals that do not overlap the vertical dotted line ( $Hedge's\ d = 0$ ) have a significant positive effect (black circles). White circles indicate non-significant effects. Sample sizes ( $n$ ) for each category are shown on the right side of the panels. The size of each individual effect is proportional to its weight or contribution to the overall mean calculation ( $1/s.e.$ ). Full statistical information is provided in Tables S2 and S3.

found after recurrent fires (Fig. 3C). Plant reproduction was higher at the late post-fire age than at the early one, although at an early age was the trend marginally positive (Fig. 3D; Table S2). Only prescribed fires increased plant reproduction as no effects were observed after wildfires (Fig. 3E). These reproductive differences regarding fire parameter effects were only positive and significant when testing the total number of fruits or seeds, and no effects were found when assessing fruit or seed set (Fig. S4). Reproduction of plants pollinated by animals showed no significant fire effects, regardless of the group, while wind-pollinated plants increased their reproduction after fire (Fig. 3F). Graminoids and perennial forbs showed increased reproductive success after fire, while no fire effects were observed in trees, shrubs and geophytes (Fig. 3G). The reproduction of non-woody species was only higher in early post-fire stages; however, long-lived woody species were not affected by fire in either early or late post-fire stages (Fig. S5). In relation to the post-fire regeneration strategy, sexual reproduction was positively affected by fire in resprouters but negatively affected in seeders (Fig. 3H). As previously observed, the positive response of resprouters was only higher after fire when measuring reproduction as total fruit or seed number, while no fire effects were found on fruit or seed set (Fig. S6).

Fire did not affect any reproductive variable of SI species. However, for SC species, fire had contrasting effects on reproduction, depending on the type of response variable assessed: fire had negative effects on fruit or seed set (Fig. 4A), but positive effects on total fruit and seed production (Fig. 4B). Reproduction of plant species with specialist or generalist

pollination systems were not affected by fire (Supplementary Information Table S2). For habitat characteristics, reproduction of grassland plant species was positively affected by fire (Fig. 4C), and plants from cold-climate biomes such as temperate and boreal ecosystems showed the highest positive reproductive responses (Table S2).

The mean effect size of the phylogenetically independent meta-analysis showed a similar positive fire effect compared to the mixed-effects hierarchical meta-analysis, which also presented the best fit (Supplementary Information Table S4). Such a result revealed that our datasets were not subject to the influence of phylogenetic bias. On the other hand, when wind-pollinated species were excluded from the hierarchical meta-analysis (i.e. 84 effect sizes of plant species within 10 families, Poaceae being the most abundant), the mean effect size also continued to be positive although slightly lower than the overall effect for all Angiosperms, and the positive fire effect on fruit or seed number also persisted (Fig. S7).

When the spatial scales of the studies were considered, fire had positive effects on plant reproduction in studies at local scales but no effect in studies at regional scales (Supplementary Information Fig. S8).

#### *Fire, pollination and plant reproductive success*

Only 13 studies assessed the effects of fire simultaneously on both pollination and reproductive success on the same plant species and sites (17 effect sizes, 15 species). There was a positive and significant relationship between fire effects

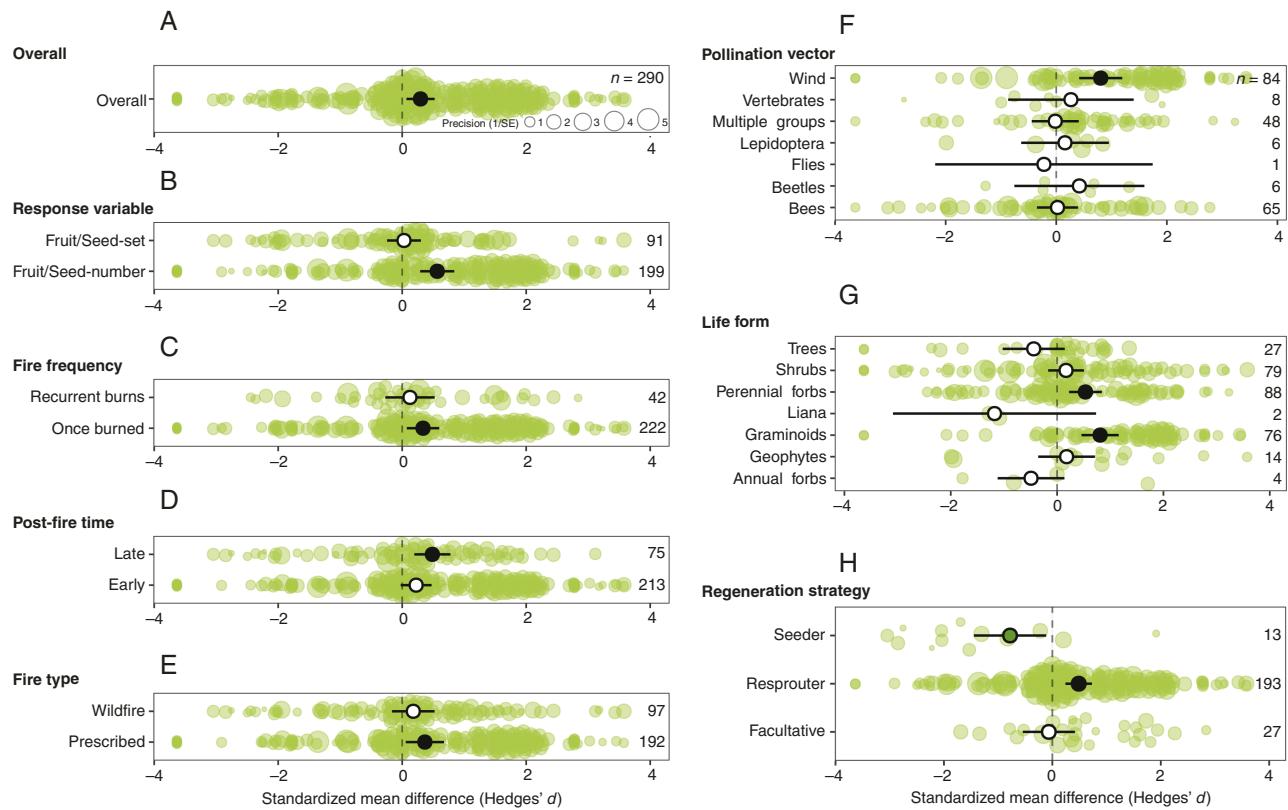


FIG. 3. Effect of fire on plant reproductive success. The weighted-mean effect sizes and 95% bias-corrected confidence intervals of overall (A), reproduction variables (B), fire frequency (C), post-fire time (D), fire type (E), pollination vector (F), life form (G) and post-fire regeneration strategy (H). Mean estimates with confidence intervals that do not overlap the vertical dotted line (Hedge's  $d = 0$ ) have a significant positive (black circles) or negative (green circles) effect. White circles indicate non-significant effects. Sample sizes ( $n$ ) for each category are shown on the right side of the panels. The size of each individual effect is proportional to its weight or contribution to the overall mean calculation (1/s.e.). Full statistical information is provided in Tables S2 and S3.

on pollination and on plant reproductive success (Pearson's  $r = 0.489$ ,  $P = 0.046$ ; Fig. 5). This result implies that negative (or positive) fire effects on pollination are similarly translated into negative (or positive) effects on sexual plant reproduction. In other words, reduced plant reproduction as measured by fruit or seed set would be mostly due to the negative effects observed in the pollination process.

#### Publication bias

Rank correlation tests of funnel plot asymmetry (Supplementary Information Fig. S9) indicate that our datasets did not exhibit evidence of publication bias (Kendall's  $\tau_{\text{pollination}} = 0.0312$ ,  $P = 0.606$ ; Kendall's  $\tau_{\text{plant reproduction}} = -0.053$ ,  $P = 0.179$ ); that is, there is no relationship between effect size and standard error. The unbiased overall effect size after incorporating all potentially non-significant missing studies was 0.467 ( $P < 0.0001$ , CI = 0.267–0.667) for the pollination meta-analysis and 0.4601 ( $P < 0.0001$ , CI = 0.305–0.615) for plant reproduction meta-analysis, which does not differ from the outputs of our original analysis. In addition, the fail-safe numbers were 1215 and 7401 for the pollination and plant reproduction datasets, respectively, which are greater than  $5N + 10$  and evidenced that the results are robust regardless of publication bias.

## DISCUSSION

Our meta-analyses comprehensively assessed the global current scientific evidence about the effects of fire on the pollination process and sexual reproductive success of wild flowering plants across different fire-prone ecosystems. The overall mean fire effects on both pollination and sexual plant reproduction were positive. However, two important aspects must be underlined: (1) positive effects were observed in studies assessing single fire events, not in those considering recurrent fires with a short fire interval, and (2) increased reproduction was evidenced when assessed as an absolute value, whereas no effects were observed when assessing the probability of setting fruits and seeds. We only found negative effects on the reproduction of seeders and in fruit or seed set of SC species.

#### Fire promotes pollination under specific conditions

Our results demonstrate that floral visitation rates of pollinators are notably enhanced immediately following a single fire (<3 years since the burn), for wildfires, in forests, and in temperate and mediterranean ecosystems. This trend is probably driven by the common early post-fire response in many plants, characterized by increased floral displays at early post-fire times which offer more conspicuous visual cues and floral rewards, thereby attracting more pollinators. Our findings are

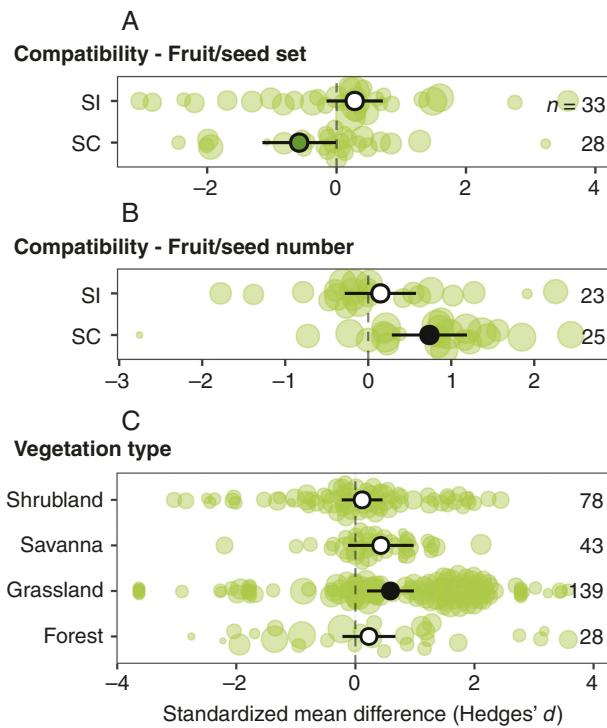


FIG. 4. Effect of fire on fruit set or seed set (A) and on fruit or seed number (B) for self-incompatible (SI) and self-compatible (SC) plant species; and effect of fire on reproductive success of plant species in different vegetation types (C). Mean estimates with confidence intervals that do not overlap the vertical dotted line (Hedge's  $d = 0$ ) have a significant positive (black circles) or negative (green circles) effect. White circles indicate non-significant effects. Sample sizes ( $n$ ) for each category are shown on the right side of the panels. The size of each individual effect is proportional to its weight or contribution to the overall mean calculation (1/s.e.).

in accordance with previous evidence that have demonstrated an overall positive response to fire across various animal guilds that potentially act as pollinators (Winfree *et al.*, 2009; Van Nuland *et al.*, 2013; Carbone *et al.*, 2019; Nicholson and Egan, 2020; Mason *et al.*, 2021). Pollination in fire-prone ecosystems such as grasslands is highly resilient to fire effects (da Silva Goldas *et al.*, 2022a). However, not all fires are beneficial nor do all groups of pollinators show positive responses. The few studies ( $n = 8$ ) that assessed the effects of recurrent fires with short fire intervals suggest that, on average, pollination levels are not different from those in unburned conditions (Fig. 2C). Because of the small sample size, care should be taken with this result.

Different pollinator groups show contrasting responses to fire. Pollination by bee species notably increases early after a fire, but when pollination involves other groups, fire effects can either be neutral or even turn negative, as has been observed for flies, beetles, butterflies and moths (García *et al.*, 2018; Banza *et al.*, 2019, 2021; Carbone *et al.*, 2019). Overall, it is not surprising that an increase in the most common and diverse pollinator group (Hymenoptera) results in higher levels of pollination following a fire. In particular, social bees can show high floral visitation rates in burned sites because colonies with a larger number of individuals forage more intensively on the floral resources than solitary species (Ne'eman *et al.*, 2000; Mola and

Williams, 2018; Carbone *et al.*, 2019). A greater number of pollinators interacting with flowers after a fire may potentially translate into an increased pollen load on stigmas and a higher proportion of pollinated flowers. Although a very few studies have examined pollination at the individual flower level (i.e. pollen load; Fig. 2B), they suggest that the efficiency of pollen transfer may not be enhanced by fire (Banza *et al.*, 2021).

Our review suggests positive short-term effects of single fires based mainly on historical or natural fire regimes in fire-prone ecosystems. However, these results may change with the effect of anthropogenic perturbations in fire regimes (Keeley and Pausas, 2019). Recent human increases in fire frequency, severity or extension may negatively impact on fire-regime-adapted species in fire-prone ecosystems or most importantly in fire-sensitive ecosystems (e.g. tropical rain forests; Fidelis, 2020; Kelly *et al.*, 2020). Nonetheless, few studies have documented the consequences of anthropogenic fires on pollination and on plant sexual reproduction in non-fire-prone ecosystems (but see de Andrade *et al.*, 2017). Interactions with other anthropogenic drivers with typically negative impacts on plant pollination and reproduction, such as grazing (Wentao *et al.*, 2023), habitat fragmentation (Aguilar *et al.*, 2006; R. Aguilar *et al.*, unpubl. res.), urbanization (Liang *et al.*, 2023) and climate change effects (Anderson, 2016), can change the nature of fire responses. Thus, interacting effects and changing fire regimes may limit the reproductive benefits of fire (Tulloch *et al.*, 2016; Beck *et al.*, 2023) or, more critically, disrupt ecological processes on which conservation and management decisions are based.

#### Fire enhances plant reproduction via abiotic resources

The different methods used to measure plant reproductive output are crucial for understanding the potential mechanisms of reproductive responses. When assessing reproduction in absolute terms such as the number of fruits or seeds produced per plant, reproductive output increases in post-fire conditions. However, when accounting for the likelihood that a flower/ovule becomes a fruit/seed (i.e. fruit or seed set; Fig. 3B), we found no fire effect. This suggests that the post-fire abiotic environment provides better conditions (open habitat, nutrients, light) for flowering and fruiting, but not necessarily for a higher efficiency in sexual reproduction (LoPresti *et al.*, 2018; Richardson *et al.*, 2023). Therefore, while both abiotic resources and pollination peak immediately after a fire, the pulse of abiotic resources appears to have greater relevance in plant reproduction. In addition, fire cues (e.g. chemical products of the combustion) may also stimulate flowering (Keeley, 1993; Lamont and Downes, 2011). The increase of reproduction observed in anemophilous and graminoid species, such as grasses and sedges (Fig. 3F, G), which are prevalent in fire-prone ecosystems and do not rely on animals for pollination (Stephens *et al.*, 2023), support the positive fire effect through abiotic resources, smoke or both. The opening of the vegetation by fire may increase the chance of wind-pollination in grasses (Fig. 3) as wind is able to move pollen grains more efficiently in open habitats. Thus, wind-pollination, together with other life-history traits of grasses such as below-ground bud banks, rhizomatous growth and the C4 photosynthetic pathway

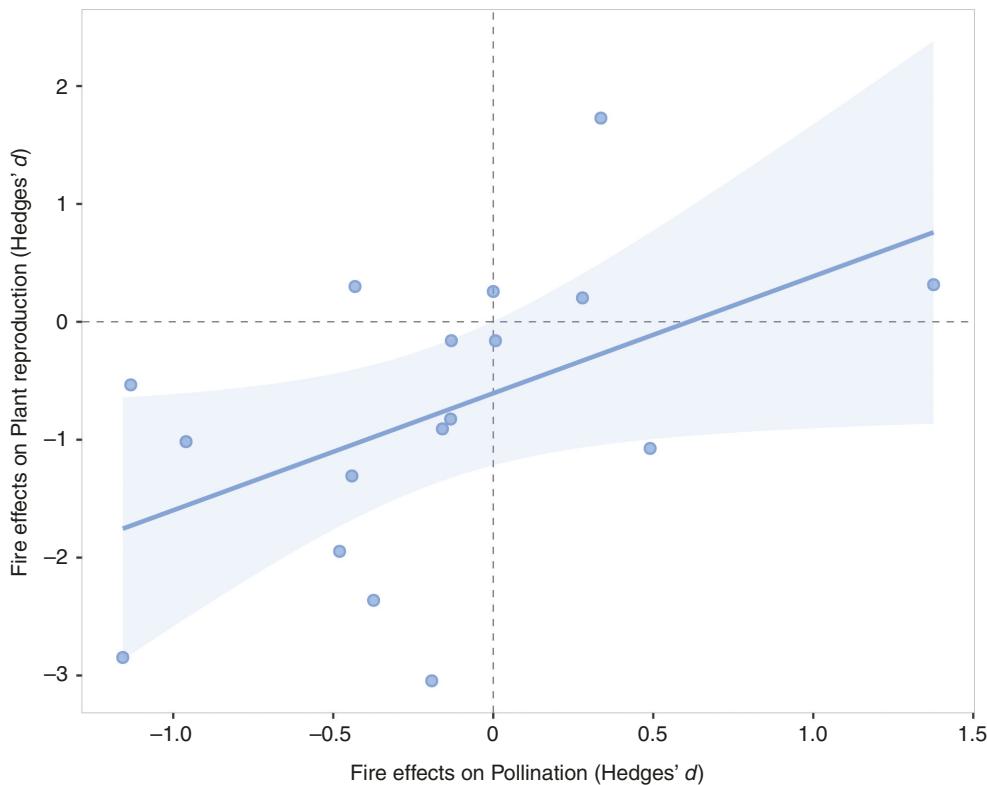


FIG. 5. Relationship between fire effects on pollination and on plant reproductive success (fruit set or seed set). Each point represents a unique plant species where fire effects were assessed simultaneously on both the pollination process and fruit set or seed set as a measure of female reproductive success. The relationship is positive and significant (Pearson's  $r = 0.489$ ,  $P = 0.046$ ,  $N = 17$  effect size pairs, representing 15 plant species from 13 studies).

(Keeley and Rundel, 2005; Pausas and Paula, 2020), may contribute to explain the reproductive success of this life form in fire-prone ecosystems.

In addition, perennial forbs were the life forms within dicots that experienced the most favourable reproductive benefits following a fire. Herbaceous species that resprout and quickly reach minimum reproductive sizes soon after the fire (Araújo *et al.*, 2013; Pilon *et al.*, 2021, 2023; Zirondi *et al.*, 2021) probably benefit from these nutrient-rich and low competitive environments, contributing to their enhanced reproductive output. The positive effect of fire on the reproductive fitness of grasses and forbs has been previously reported across various ecosystems (Giorgis *et al.*, 2021; Pilon *et al.*, 2021; Zirondi *et al.*, 2021; Fidelis *et al.*, 2022; Mndela *et al.*, 2023). In contrast, the reproduction of woody species such as trees and lianas, despite their potential ability to resprout, tends to be negatively affected in burned sites (this study; Clarke *et al.*, 2013). This can be attributed to their high investment in vegetative regrowth and the delayed flowering. As the succession progresses, competition among plants becomes more intense, and there may be a decline in abiotic resource availability (Nield *et al.*, 2016). All these findings support the notion that abiotic factors can be an important driver of plant reproductive responses after fire (Lybbert *et al.*, 2017).

Our findings show a significant reproductive increase after fire, at least when fire intervals are not very short. While over the short term (months or a few years), a single fire can stimulate soil fertility and plant reproduction, over the long term

(decades), a potential decline in soil nutrients after recurrent fires may suppress the effect on plant sexual reproduction (Pellegrini *et al.*, 2018, 2020). Based on our data, the average fire interval for studies reporting multiple fires was 5–6 years (s.d. = 6.7), with sites experiencing overly short intervals between burns (annual or biannual), which largely corresponded to prescribed fires (74%), being in non-forested (open) ecosystems. These overly frequent anthropogenic fires may override the benefit of intermediate- or low-frequency fires on plant reproduction or even cause negative effects (Tulloch *et al.*, 2016). On the other hand, the reproductive benefit was clear for plants growing in habitats subjected to prescribed fires, where most of these positive responses corresponded to studies evaluating reproductive output in absolute terms (78% of the effects), on graminoids (38%) and in grasslands (68%). In contrast, the neutral reproductive effects of wildfires were measured in a similar proportion for absolute and relative fitness, on shrubs in shrublands (55 %, Supplementary Information Fig. S3). Prescribed fires are usually low-intensity fires, which cause low plant mortality and little damage to plant tissues. Thus, prescribed fires allow rapid regeneration and promote the reproduction of highly resilient plants such as graminoids in open biomes. Our results reinforce the idea that fire is a key factor for maintaining biodiversity and conservation of grasslands and savannas (Pausas and Keeley, 2019). However, both fire-suppression policies and overly frequent prescribed burnings may disrupt the reproductive benefits of intermediate-frequency/intensity fires. Therefore, understanding plant–pollinator interactions and reproductive

ecology, along with fire parameters, is crucial to advance the conservation and management of fire-prone ecosystems.

The response to fire is frequently determined by the successional state where the species occur, with early-successional species often benefiting due to the presence of adaptive vital attributes (e.g. persistence, short lifespans, high growth rates) while late-successional species may be negatively impacted (Noble and Slatyer, 1980). Initially, we expected that plant reproduction would be enhanced primarily in the first years following a fire, driven by both increased abiotic resources and pollination levels. This pattern was verified for non-woody species (i.e. forbs, graminoids; *Supplementary Information Fig. S5*). In contrast, the reproductive success of woody plants was not affected by fire in either the early or late post-fire stages. Since our data primarily involve individual plants, fire effects on reproductive fitness could be influenced by plant conspecific density. It is likely that individual plants of forbs or small shrubs increase their conspecific density, mating opportunities and consequently their reproductive success, but species found at low population size due to low regeneration after fire may not change or reduce their reproductive success despite displaying higher individual flowering. Further research would require a detailed analysis of post-fire plant reproduction considering the post-fire changes in conspecific density.

#### *Fire can also affect plant reproduction via pollinators*

Studies that assessed plant reproduction through measurements of fruit set and seed set did not detect significant fire effects (*Fig. 3B*). The post-fire resilience of plant–pollinator interactions can explain the similar probability of setting fruits or seeds between burned and unburned conditions (Potts *et al.*, 2001; Carbone and Aguilar, 2017; García *et al.*, 2018). Nevertheless, other factors such as compatibility systems, life forms and pollination vectors of the plants may influence the overall impact of fire. Based on a small set of plant species where pollination and fruit set or seed set were measured simultaneously, we observed that the effects of fire on pollination are translated to plant reproduction: for the majority of cases when fire negatively affects pollination, plant reproduction is also reduced but in higher magnitude than pollination; and to a lesser extent when fire promotes pollination, fruit or seed set is also increased (*Fig. 5*). This relationship suggests that the effects of fire on plant reproduction are not only due to abiotic factors (high nutrient availability and low competition) but also to pollinators, as has been observed in several fire-prone environments (Ne'eman *et al.*, 2000; Carbone and Aguilar, 2017; García *et al.*, 2018; Carbone *et al.*, 2021; Richardson *et al.*, 2023). Thus, when pollination levels are low, the potential influence of abiotic resources may not be sufficient to offset plant reproduction due to pollen limitation.

Fire can also affect the quality of pollination in addition to its quantity. Changes in pollinator assemblages as a result of fire are likely to have impacts on pollination quality and thus on plant reproduction (but see García *et al.*, 2018). Pollinators that forage on plants with larger floral displays in burned environments have the potential to increase selfing rates by visiting a greater number of flowers within the same plant (geitonogamy),

thereby reducing outcrossing opportunities (LoPresti *et al.*, 2018). This is supported by the lower overall effect size of fruit set and seed set in burned conditions compared to fruit/seed number (*Fig. 3B*). However, it is unexpected that the decrease in fruit or seed set occurs in SC but not in SI species (*Fig. 4A*). This suggests that a decrease in the quality of pollination is unlikely. Reduced fruit or seed set in SC species may also be a consequence of limited abiotic resources for complete fruit and seed development (Carbone & Aguilar, 2017). SC species had higher absolute fruit and seed production after the fire (*Fig. 4B*), indicating that floral displays were also greater in burned sites. Thus, to produce a similar proportion of fruits and seeds compared to unburned sites, many more fruits and seeds would need to be developed.

#### *Plant reproductive responses differ among post-fire regeneration strategies*

Plant species that regenerate via resprouting after a fire show a clear reproductive benefit. In that vein, the unexpected positive effect of fire in cold ecosystems such as boreal and temperate broadleaf and mixed forests (*Supplementary Information Table S2*) is probably due to the overrepresentation of resprouting shrub and perennial herb species from these biomes in our dataset. Post-fire flowering provides a fitness benefit in various herbaceous resprouting species, including tuberous and bulbous geophytes, lignotuberous shrubs and forbs, rhizomatous and bunch grasses, leaf succulents, and grass-trees (Lamont and Downes, 2011; Pyke, 2017; Keeley and Pausas, 2022). Species with below-ground organs that survive fire can increase their asexual reproduction due to the fast use and availability of stored assimilates. This scenario may also explain the increase of reproduction in absolute terms without an increase in reproduction efficiency, due to larger mating among related clonal ramets. Early post-fire flowering, higher mating opportunities and increased fecundity without the risks of recruitment failure appear to be a key fitness benefit for resprouting species (Lamont *et al.*, 2011; Keeley and Pausas, 2022). Our data provide support for certain plant groups such as graminoids and perennial forbs, but less evidence of this relationship in the case of geophytes. Further research is needed to gain a better understanding of the ecological and evolutionary dynamics of post-fire reproduction.

The main exception for the fire-driven reproductive benefits were obligate seeder species, which showed an unexpected overall negative reproductive response to fire (particularly for fruit or seed set). Regardless, fire kills the adults of obligate seeders, which then recruit massively from seed banks, and they only flower several years after the fire. Therefore, the life cycle of seeders is always determined by the fire (Pausas & Keeley, 2014). Based on the few studies ( $n = 13$ ) that have assessed this functional group in our dataset, one possible explanation of the negative fire effects is that reproduction of seeder species can be especially sensitive to the loss of effective specialist pollinators or to changes in pollinator assemblages, particularly regarding SI species (e.g. Ne'eman and Dafni, 1999; Ne'eman *et al.*, 2000; Potts *et al.*, 2001). Additional studies are required to determine whether this negative response is a widespread pattern or the result of research bias.

### Knowledge gaps and study limitations

We provided a comprehensive compilation of the available studies on pollination and reproduction of wild plants in fire-prone habitats. However, there are significant environmental and geographical gaps in the currently available published information, as most of the tropical regions (e.g. megadiverse Mesoamerica, Africa and southeast Asia), as well as some cold ecosystems (e.g. taiga, tundra), and deserts are clearly underrepresented biomes that require more study. In addition, the extremely low representation in our dataset of fire-sensitive ecosystems, such as tropical forests subject to anthropogenic fires, precludes extrapolations from fire-prone habitats. It is essential to conduct additional studies to understand the implications for conservation and post-fire restoration in environments undergoing anthropogenic changes in fire regimes. Furthermore, our database comprises a considerable number of records of endemic plant species (about one-quarter of the effect sizes), for which prescribed fire is employed as a management tool to promote their reproduction. Considering the high representation of resprouters, graminoids and perennial forbs in our sample of study species, it suggests that the majority of these species may be pyrophytic plants that typically benefit from fire. In that situation, fire is key to determine the reproductive dynamics which have potentially significant implications for biodiversity conservation and evolutionary ecology.

The discrepancies found between fire effects on pollination and reproduction for some parameters (i.e. post-fire age, fire type and pollinator group) are possibly due to the independent database used for each of the two meta-analyses performed. It is possible that different levels of analysis (mostly at the community level in pollination vs. population level in plant reproduction), study species (anemophilous graminoids present in reproduction vs. absent in pollination) and ecosystems (mostly mediterranean for pollination vs. tropical and subtropical grassland, savanna and shrublands for plant reproduction) contribute to the disparity of the response patterns between pollination and plant reproductive success. Measurements of the two processes simultaneously for the same plant species would provide a clearer causal inference on plant sexual reproduction.

It would be interesting to investigate the effect of fire on the floral display and its consequences on pollination and the reproductive success of plants with different life forms and post-fire regeneration strategies. Our databases are not sufficiently comparable between life forms to adequately address these relationships (i.e. there are almost no studies assessing fire effects on tree pollination). While herbaceous species typically increase floral display early after the fire (e.g. [Lamont and Downes, 2011; Pyke, 2017](#)), woody species may not do so. If that occurs, there would be a higher probability of an increase in geitonogamy in herbaceous plants than in woody plants. Fire effects may change plant mating patterns and their consequences may be more evident on the performance of the progeny than on fruit and seed production ([Aguilar et al., 2006, 2019; Fontenelle et al., 2020](#)).

Our synthesis contributes to the understanding of the effects of fire on pollination and plant reproduction at a global scale. These findings highlight the vital role of fire in facilitating

pollination and modulating sexual reproduction in plant species from fire-prone ecosystems. Enhanced pollination and seed production are likely to have cascading effects on consumers (e.g. predators of pollinators or of seeds, seed dispersers), potentially modifying the whole trophic chains in fire-prone landscapes. Given the current alterations in fire regimes caused by anthropogenic drivers, our study carries significant ecological and evolutionary implications for both pollinators and flowering plants.

### SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Fig. S1: PRISMA diagram. Figs S2 and S3: Flow diagram with the number of effects of the main moderator variables of plant reproduction meta-analysis. Fig. S4: Fire effects on plant reproduction for fire moderators differentiated by fruit or seed set and fruit or seed number. Fig. S5: Fire effects on sexual reproduction of woody and non-woody plant species at different post-fire times. Fig. S6: Fire effects on plant reproduction for species with different post-fire regeneration strategies differentiated by fruit or seed set and fruit or seed number. Fig. S7: Fire effect on reproduction of biotic pollination plants. Fig. S8: Fire effect on plant reproduction for studies at regional and local scales. Fig. S9: Trim and fill plots. Table S1: Bibliographic searches. Tables S2 and S3: Statistical information from the meta-analyses. Table S4: Results of the phylogenetically independent meta-analysis. Table S5: List of plant species included in the meta-analysis. Tables S6 and S7: List of studies included in the meta-analyses.

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### CONFLICT OF INTEREST

We have no conflicts of interest to declare.

### DATA AVAILABILITY

The data that support the results of this work are available at: <http://hdl.handle.net/11336/218595>

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