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RESEARCH REVIEW

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# Natural hazard threats to pollinators and pollination

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## Abstract

Natural hazards are naturally occurring physical events that can impact human welfare both directly and indirectly, via shocks to ecosystems and the services they provide. Animal-mediated pollination is critical for sustaining agricultural economies and biodiversity, yet stands to lose both from present exposure to natural hazards, and future climate-driven shifts in their distribution, frequency, and intensity. In contrast to the depth of knowledge available for anthropogenic-related threats, our understanding of how naturally occurring extreme events impact pollinators and pollination has not yet been synthesized. We performed a systematic review and meta-analysis to examine the potential impacts of natural hazards on pollinators and pollination in natural and cultivated systems. From a total of 117 studies (74% of which were observational), we found evidence of community and population-level impacts to plants and pollinators from seven hazard types, including climatological (extreme heat, fire, drought), hydrological (flooding), meteorological (hurricanes), and geophysical (volcanic activity, tsunamis). Plant and pollinator response depended on the type of natural hazard and level of biological organization observed; 19% of cases reported no significant impact, whereas the majority of hazards held consistent negative impacts. However, the effects of fire were mixed, but taxa specific; meta-analysis revealed that bee abundance and species richness tended to increase in response to fire, differing significantly from the mainly negative response of Lepidoptera. Building from this synthesis, we highlight important future directions for pollination-focused natural hazard research, including the need to: (a) advance climate change research beyond static "mean-level" changes by better incorporating "shock" events; (b) identify impacts at higher levels of organization, including ecological networks and co-evolutionary history; and (c) address the notable gap in crop pollination services research—particularly in developing regions of the world. We conclude by discussing implications for safeguarding pollination services in the face of global climate change.

KEYWORDS

disturbance, ecosystem service, extreme event, extreme weather, natural hazard, pollination, resilience, vulnerability

## 1 | INTRODUCTION

The role of natural disturbances in structuring species composition, interactions, diversity, and landscape dynamics has a rich history (Sousa, 1984; Spiller, Schoener, & Piovia-Scott, 2018; Turner, 2010). Natural hazards are unique as discrete biophysical events, capable of producing damage to the physical and social space in which they occur. Although anthropocentric by definition, hazards such as drought, hurricanes, and earthquakes constantly reshape the biosphere. Beyond their initial occurrence, the impacts of such hazards may further extend across time, especially where exposure is continuous or repeated (Alcántara-Ayala, 2002). These events can be "extreme" in both their impact (e.g., statistically unusual precipitation), and in the response of ecosystems (e.g., statistically unusual primary productivity; Smith, 2011). In particular, climate change is set to alter the distribution, frequency, and intensity of several natural hazards (Easterling et al., 2000; van Aalst, 2006), threatening the survival of species and stability of ecosystems, particularly if interactions between species are disrupted (Aslan, Zavaleta, Tershy, & Croll, 2013; Hegland, Nielsen, Lázaro, Bjerknes, & Totland, 2009; Memmott, Craze, Waser, & Price, 2007; Tylianakis, Didham, Bascompte, & Wardle, 2008).

Animal-mediated pollination, one such interaction, is essential for the reproductive success of 87% of angiosperms (Ollerton, Winfree, & Tarrant, 2011), including many valuable crops that support nutritious and diverse diets (Eilers, Kremen, Greenleaf, Garber, & Klein, 2011; Klein et al., 2007). Two impacts of climate change on pollination have received considerable attention: (a) phenological disruption of plant–pollinator mutualisms (i.e., temporal decoupling; Bartomeus et al., 2011; Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013; Iler, Høoye, Inouye, & Schmidt, 2013) and (b) climate-driven range shifts (i.e., spatial decoupling; Herrera, Ploquin, Rodríguez-Pérez, & Obeso, 2014; Kerr et al., 2015; Sirois-Delisle & Kerr, 2018; Wilson et al., 2005). However, it remains unclear whether and to what extent natural hazards may affect pollinators and pollination, and what role climate change could play in exacerbating any such effect. In addition to climate-driven shifts in phenology and range, understanding the influence of natural hazards on pollination will provide unique insights into the stability of this critical mutualism (or lack thereof) in a time of rapid global change.

Natural hazards could disrupt pollination mutualisms by affecting plants, pollinators, or their interactions (Figure 1). Impacts to plants or pollinators could manifest across several levels of biological organization; from individual physiological responses (Scaven & Rafferty, 2013) and shifts in the taxonomic, functional, and phylogenetic composition of communities (Gámez-Virués et al., 2015; Harrison, Gibbs, & Winfree, 2018; Ponisio, M'Gonigle, & Kremen, 2016), to the rewiring of plant–pollinator networks (Burkle & Alarcon, 2011). While the impacts of anthropogenic drivers on pollinators and pollination (e.g., pesticide use, habitat conversion, and the spread of disease and invasive species) have received considerable attention (Potts et al., 2016; Winfree, Aguilar, Vazquez, LeBuhn, & Aizen, 2009), knowledge has yet to be synthesized on natural hazard impacts, including the biological factors responsible for modulating vulnerability or resilience in the face of exposure.

We address this knowledge gap through systematic review, and where possible meta-analysis, of the scientific literature on the effects of extreme events and natural hazardous phenomenon on pollinators and the pollination of wild and crop plants. Our specific objectives were to (a) characterize the attributes of studies in terms

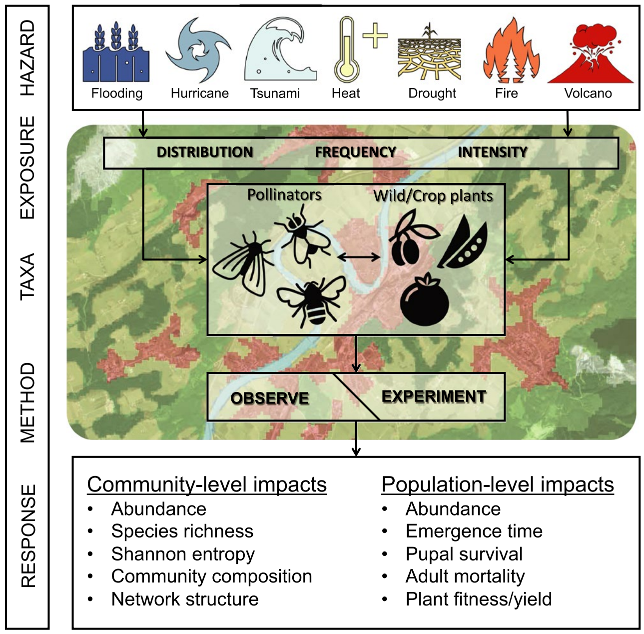


**FIGURE 1** Conceptual approach to the study of natural hazard impacts on pollinators and plant pollination. These impacts can be measured via observational studies that record changes resulting from natural events, or via experimental approaches that manipulate abiotic conditions in order to simulate natural hazard exposure. Our systematic literature review revealed that both approaches have commonly been used to record a variety of plant and pollinator responses at community and population levels; some examples of which are listed

of geographic focus, methodological approach, hazard type considered, and taxa observed; (b) score the impacts (positive/negative/no change) of natural hazards on different types of responses by plants and pollinators; (c) synthesize overall effect sizes for these responses via meta-analysis, where sufficient data are available; and (d) identify biases in the evidence base and highlight future research needs. We discuss the implications of our review in light of the value and challenge of moving pollination research forward toward accounting for natural hazard-based impacts—especially within context of climate change.

## 2 | METHODS

### 2.1 | Systematic literature review

We investigated a comprehensive range of hazard types, including those not moderated by climate change (e.g., volcanoes, earthquakes, asteroid impact), since no previous review of hazard impacts on pollination exists. To identify published studies of how pollinators and pollination respond to natural hazards, we conducted three separate searches. First, we searched Google Scholar using a systematic combination of keywords (e.g., polinat* AND hurricane; for full list see Table S1). Second, we conducted a Web of Science search of articles up to January 31, 2019, using four separate search terms that focused on broad taxonomic groups of pollinators (Table S1). Third, from the studies these searches yielded, we reviewed references and cited articles, including the bibliography of the IPBES pollination assessment report (IPBES, 2016).

We developed and applied a set of ex ante coding classifications based on our conceptual framework (Figure 1). We classified articles based on natural hazard type, publication year, study location, methodological approach (experimental, observational), focal mutualist (plant, pollinator, or both), pollinator taxa considered (bees, wasps, flies, lepidopteran, mammals), level of biological organization (community, population, individual), and whether studies measured crop pollination as an ecosystem service. We relied on author's interpretation of what constitutes a natural hazard type, and included both simulated and naturally occurring impacts.

We identified a total of 139 articles from 68 different journals. Our process for article inclusion followed PRISMA guidelines for systematic reviews (Moher, Liberati, Tetzlaff, Altman, & PRISMA Group, 2009; Figure S1). We focused on publications that provide empirical results and therefore excluded conceptual and review papers ($N = 4$). We excluded several publications ($N = 10$) because they did not explicitly investigate the effects of a natural hazard event (e.g., research conducted in floodplain forests). We excluded studies ($N = 8$) that did not explicitly investigate how natural hazards impact plants, pollinators, or specific aspects of pollination (e.g., research on the response of arthropods broadly to fire without mention of pollination). For a complete list of publications, including those which were excluded, see Appendix A.

For the remaining 117 studies, we recorded each reported response variable and whether natural hazards caused a positive, negative, or no change. The outcome of this change of sign depended on the response measured, and we provide illustrative examples and references for each (Table S2). For other responses (e.g., community composition, network structure), a change of sign did not apply, and for these we noted whether the response was significantly different or not. Many papers used multiple metrics to characterize responses (e.g., abundance, species richness, and Shannon entropy). We coded each of these separately for pollinators and plants. Population-level studies reported various types of responses (e.g., pupal survival, emergence time, seed set, flower size). For pollinators, we binned these into a "population effect" category, whereas for plants we distinguished between "floral traits" or "reproductive success" metrics (see Table S2 for a list of variables in each category). Due to a wide variety of methods and designs that often featured limited replication, a formal meta-analysis was not possible for many hazards (see below). Instead, we evaluated observed responses of plants and pollinators using a vote-counting methodology (Hedges & Olkin, 1985)—that is, whether the outcome in the response to the hazard was significantly positive or negative. This vote-counting approach allowed us to code studies consistently in order to examine hazard effects in a semi-quantitative way, in lieu of the ability to formally meta-analyze most hazards.

### 2.2 | Meta-analysis

Meta-analysis was conducted based on the literature assembled from the systematic review (Appendix A). This literature was screened to extract all suitable studies and data. A detailed description of the data extraction, statistical analysis, and validation protocols conducted for the meta-analysis is provided in supplemental methods (Appendix B). A list of included publications (11 total), extracted values (33 total), and calculated effect sizes are also provided (Appendix C). Fire was the only natural hazard for which an adequate number of studies were identified to facilitate meta-analysis. Of the numerous outcome variables measured in the literature (Table S2), the availability of suitable quantitative data was almost entirely restricted to two; fire effects on pollinator abundance and species richness. This outcome data were mainly extracted in the form of a mean (±SE or SD) for abundance and species richness in burnt versus a non-burnt time period or control site. Sufficient data existed to analyze fire outcome measures for three individual pollinator taxa; bees, beetles, and Lepidoptera.

Meta-analysis was conducted using the "metafor" package (Viechtbauer, 2010) in R 3.5.1. We used as a measure of effect size the standardized mean difference (Hedges' $d$; Hedges & Olkin, 1985) in abundance and species richness between burnt and non-burnt time periods/sites. Two models were fitted for the meta-analysis: first, a global model to estimate heterogeneity and an overall mean effect size (±95% confidence interval) pooled across all outcome measures and pollinator groups; and second, a multivariate moderator model to explicitly consider the interaction between the two outcome measures and "pollinator taxa" as a fixed effect (i.e., "moderator").

## 3 | RESULTS

### 3.1 | Systematic literature review

We identified 117 scientific articles published in 68 different journals dating from 1979 to 2018 that were of direct relevance to natural hazards, pollinators, and pollination (Figure 2)—64% of which were published in the last 10 years. Research took place in 45 countries (Figure 2), but with a geographic bias toward economically developed regions; especially North America (41%) and Europe (32%). We identified studies that focused on seven natural hazards across four hazard categories, including climatological (extreme heat, fire, drought), hydrological (flooding), meteorological (hurricanes), and geophysical (volcanic activity, tsunamis; Figure 2). These studies were largely observational (74%), rather than experimental (26%). For pollinators, the majority of research focused on community-level responses (61%), whereas the opposite is true for plants (62% population-level responses; Figure S2). Few studies (5%) examined how the effects of natural hazards could disrupt crop pollination services.

Research was not evenly distributed across pollinator groups, with many impacts recorded for bees (63), followed by Lepidoptera (28), flies (9), wasps (8), birds (7), beetles (6), and bats (4; Figure S3). We recorded 269 unique responses (184 pollinator, 79 plant, and

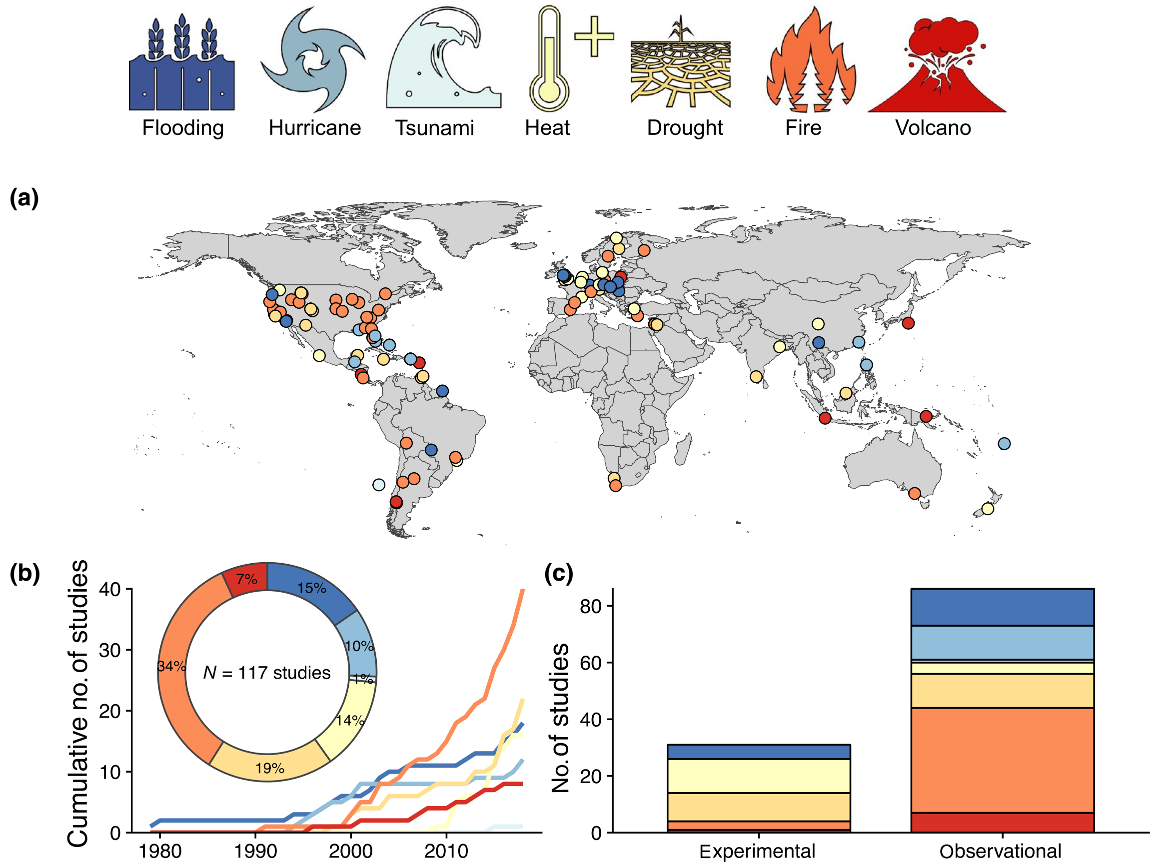


**FIGURE 2** Our systematic review yielded research on seven natural hazard types across four categories: climatological (extreme heat, fire, drought), hydrological (flooding), meteorological (hurricanes), and geophysical (volcanic activity, tsunamis). The distribution of these studies in space (a), time (b), and methodological approach (c) varied according to hazard type

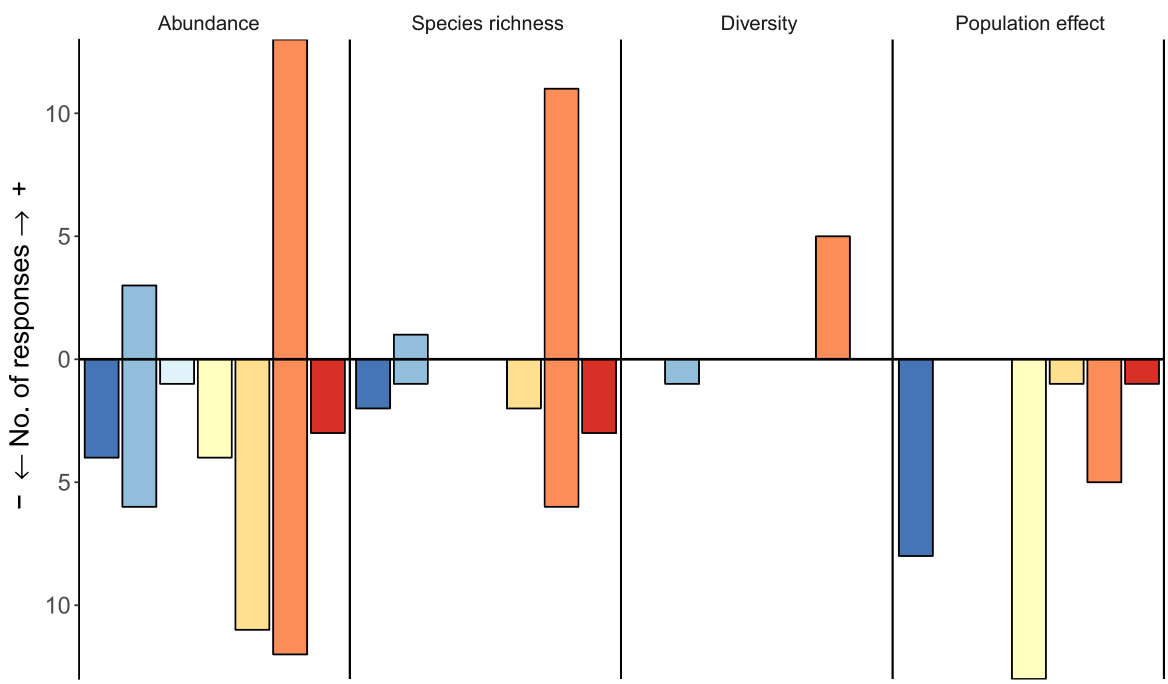


**FIGURE 3** Natural hazard impacts on different pollinator responses. The number of statistically significant positive or negative responses varied according to natural hazard type. Population effects included responses such as pupal or adult survival, emergence time, and foraging activity (for a full list, see Table S2)

6 plant–pollinator network), with 19% of all responses reporting no significant impact on plants or pollinators. Studies tended to report impacts to pollinators in terms of abundance (41% of responses), species richness (19%), and various population-level effects (19%), whereas impacts to plants were measured in terms of reproductive success (39%), floral traits (27%), and species richness (11%).

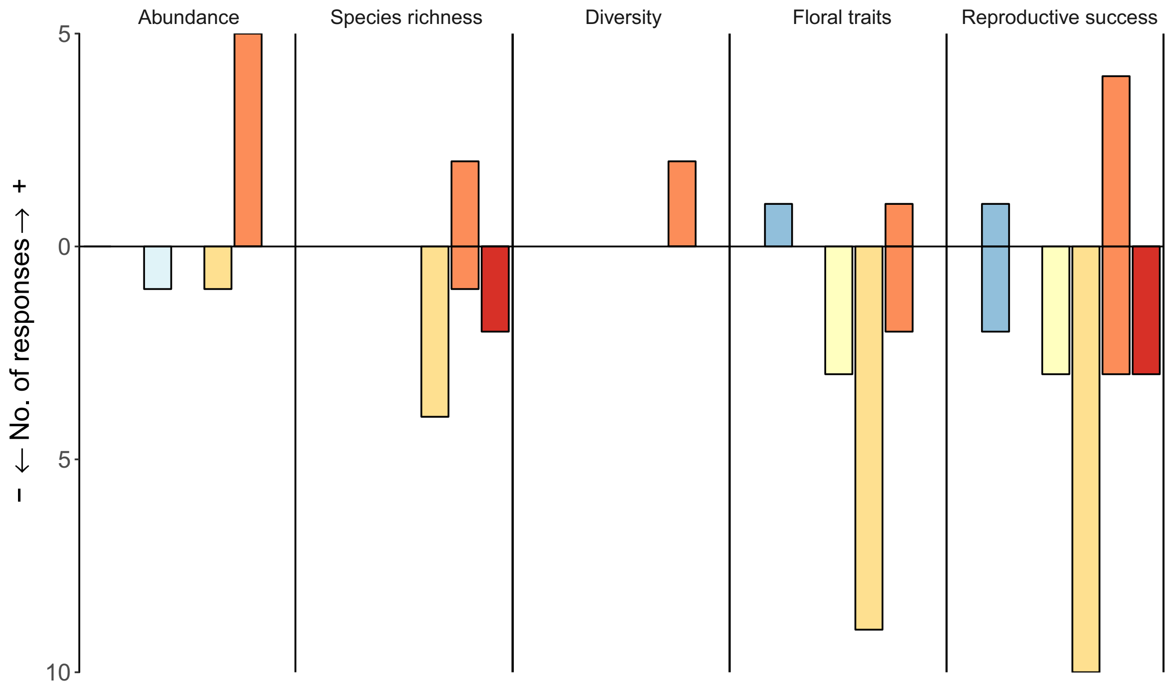


**FIGURE 4** Natural hazard impacts on different plant responses. The number of statistically significant positive or negative responses varied according to natural hazard type. Floral traits and reproductive success effects included responses such as flower morphology and phenology, fruit set, and seed set (for a full list see Table S2)

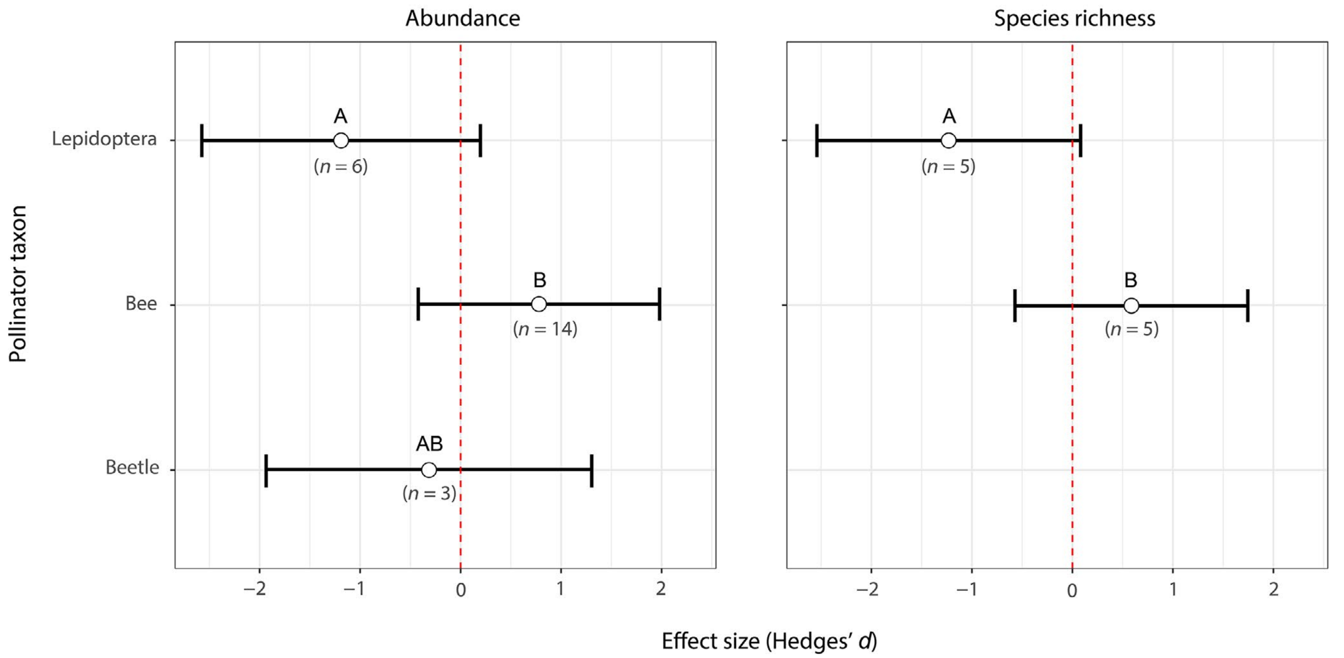


**FIGURE 5** Meta-analysis of the effect of fire on pollinator abundance and species richness (Hedges' *d*/standardized mean difference ± 95% CI). Positive values denote an increase in abundance or species richness in burnt versus unburnt times/sites, whereas negative values denote a decrease. Pollinator taxa which do not share a letter differ significantly from each other according to adjusted post hoc comparisons (abundance) or test of the overall model moderator (species richness). Beetles were not included in the analysis of species richness due to lack of available data (see Appendix B, Supplementary Materials)

Whether plants or pollinators responded positively or negatively varied according to the type of hazard and response considered. For plants and pollinators, we identified consistently negative impacts resulting from flooding, drought, extreme heat, volcanic activity, and tsunamis, whereas responses were mixed for hurricane and fire (Figures 3 and 4). We also identified hazard-driven shifts in community composition resulting from fire (14 pollinator and two plant responses), drought (one pollinator response), and flooding (four pollinator responses), as well as no detected effect on community composition for fire (three responses) and hurricanes (one response). A detailed description of focal taxa, methodological approach, and responses for individual hazard types is provided in Appendix D.

### 3.2 | Meta-analysis

The global analysis indicated no overall positive or negative effect in pollinator response to fire (Hedges' $d = 0.095 \pm 1.206$ CI, $N = 33$ from 11 studies), as pooled across all outcome measures (abundance and species richness) and pollinator taxa (bees, beetles, and Lepidoptera). However, subsequent analysis of moderators revealed a significant interaction between "outcome" and "pollinator taxa" ($Q_M = 13.131$, $df = 5$, $p = .022$). Thus, while no overall positive or negative effect of fire was found for the individual pollinator groups (95% CIs intersect zero in Figure 5), there were significant differences between groups in terms of how fire affected abundance ($Q_M = 12.294$, $df = 3$, $p = .006$) and species richness ($Q_M = 9.966$, $df = 3$, $p = .007$; Figure 5). Bee abundance and species richness generally tended to increase in response to fire, in contrast to the more negative response of Lepidoptera, and neutral response of beetles (Figure 5).

## 4 | DISCUSSION

Taken together, our findings show that the response of pollinators and pollination to natural hazards depends on the type of disturbance and level of biological organization observed and that different pollinator taxa can respond very differently to the same hazard. For example, we found that while drought, flooding, extreme heat, volcanic activity, and tsunamis consistently held significant negative impacts, both plant and pollinator responses to fire and hurricanes were mixed. This mixed response to fire could be largely disaggregated by pollinator group; positive responses were more commonly seen for bees, more neutral responses for beetles, and more negative responses for Lepidoptera. Moreover, we found that studies that examined community-level responses, such as species richness or abundance, reported more mixed responses when compared to studies that focused on population-level impacts. Although some of these investigated hazards are entirely geophysical (e.g., volcanic activity), climate change has already begun to modify the majority of natural hazards we recorded, such as by increasing their distribution, frequency, and/or intensity (van Aalst, 2006), as well as exposure to interactive effects from co-occurring hazards (e.g., extreme heat, droughts, fire). These growing threats emphasize the need to better understand the links between global change, natural hazards, and biotic interactions such as pollination.

### 4.1 | Response of pollinators and pollination to natural hazards

We found more research on the response of pollinators (in particular bees) than plants to natural hazards. For pollinators, research largely focused on community-level impacts, whereas plant research focused on population-level responses. This disparity echoes long-standing trends in pollination ecology (Knight et al., 2018), where plant-focused research tends to observe physiological or reproductive effects of single populations while pollinator-focused research observes larger biodiversity trends. The level of biological organization investigated depended on hazard type. Authors recorded more extreme heat impacts on population-level responses, such as plant outcrossing rates (Bishop, Jones, OSullivan, & Potts, 2017; Kay & Picklum, 2013), nectar volume (Takkis, Tscheulin, Tsalkatis, & Petanidou, 2015), or larval survival (Bauerfeind & Fischer, 2014). For pollinators, research tended to examine how fire and drought shaped the abundance (Campbell, Hanula, & Waldrop, 2007; Minckley, Roulston, & Williams, 2013), diversity (Hoiss, Krauss, & Steffan-Dewenter, 2015; Kambach, Guerra, Beck, Hensen, & Schleuning, 2013), and composition of communities (Burkle & Runyon, 2016; Lazarina et al., 2017; Love & Cane, 2016). Although the majority of plant and pollinator responses to natural hazards were negative, many studies of fire (and to a lesser extent hurricanes) reported increases in the abundance, richness, diversity or reproductive success of species, or other beneficial population effects.

Fire in particular is notable for its mixed impacts. In many ecosystems, fires are the most common disturbance (Bowman et al., 2009) and actively shape the ecology and evolution of plant and pollinator communities (Bond, Woodward, & Midgley, 2005; Burkle, Myers, & Belote, 2015; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). On the one hand, fire can negatively affect plants and pollinators by altering seed germination patterns (Pausas & Keeley, 2014) and mortality rates (Ne'eman, Dafni, & Potss, 2000; Thom, Daniels, Kobziar, & Colburn, 2015). However, fires can also create early successional habitats with greater availability of abiotic resources important for understory plant reproduction (Certini, 2005), such as light and soil nutrients (Potts, Dafni, & Ne'Eman, 2001; Swanson et al., 2011; Van Nuland et al., 2013). Post-fire flushes of floral resources have also been linked with increases in pollinator activity, abundance, and diversity (Mola & Williams, 2018). As such, moderate fire severities can even promote the diversity of many pollinator guilds at local to landscape scales (Lazarina et al., 2019)—although such disturbance–abundance relationships may sharply decline beyond an intermediate optimum.

Our conducted meta-analysis provided an overall assessment of fire effects on pollinators and contributes to recent efforts to synthesize this topic (Carbone, Tavella, Pausas, & Aguilar, 2019). A number of explanations may be offered toward the finding that bee abundance and species richness generally responded favorably to fire, in comparison to the neutral response of beetles, and mainly negative response of Lepidoptera. Perhaps, the most likely relate to heterogeneity between pollinator taxa in terms of the life-history traits of body size, nesting preference, and dispersal and recolonization ability (Lazarina et al., 2016; Mateos, Santos, & Pujade-Villar, 2011). Fires are known to change the availability of nesting resources (e.g., bare soil or course woody debris) with benefits for many (Heil & Burkle, 2018; Potts et al., 2005), but not all species (Grundel et al., 2016). One plausible scenario underlying these findings is that bee nesting behavior (such as ground and cavity nesting) allows for greater persistence during fires, which could also be coupled with quicker rates of recolonization into post-fire landscapes. Future work will ultimately be required to test such mechanisms, and to separate the relative importance of in situ persistence versus recolonization. The timing and duration of any such studies are, however, a consideration of critical importance, as highlighted by Potts et al. (2003), whom showed that bee communities declined immediately after fire, but recovered quickly within 2 years.

As a whole, it is clear that fire-induced community-level changes depend on fire attributes (distribution, frequency, intensity), as well as the life history of organisms responding to fire, and that the effects of fire disturbance as such are variable (Brown, York, Christie, & McCarthy, 2017; Carbone et al., 2019).

### 4.2 | Crop pollination services: A critical research gap

Despite the vital function that pollinators perform in agricultural ecosystems (Garibaldi et al., 2013), too few studies (5% of literature) were identified in order to draw firm conclusions concerning natural hazard effects on crop pollination services. Crop pollination can be measured as a biophysical supply (e.g., crop visitation rate) or as material benefits (e.g., improved crop production; Ricketts et al., 2016). Natural hazards can disturb both these factors, complicating efforts to measure potential changes because of the need to disentangle hazard impacts to pollinators from impacts to crops. For instance, if crop production decreases following an extreme heat event, is this due to pollination limitation or reduction in photosynthetic ability?

Experimental approaches can help to untangle how pollination services respond to natural hazards. Bishop, Jones, Lukac, and Potts (2016) combined pollinator exclusion experiments and bean plants exposed to different temperature regimes. They found yield loss due to heat stress was six times greater in plants excluded from pollinators compared to those with bumblebee pollination, suggesting that yields of sufficiently pollinated crops may be more resistant to extreme weather events. Generally, there is a categorical lack of studies examining the effect of natural hazards on pollination services, and so we have to rely on the basic literature to make inferences, despite several key limitations in this evidence base.

### 4.3 | Biases, limitations, and caveats

Our findings highlight several important biases. First, observational studies were three times more common than experimental work. Observing in situ impacts of natural hazards is, largely out of necessity, opportunistic. Opportunistic studies generally arose when research was initiated post-hazard ("first responder research," e.g., Piessens, Adriaens, Jacquemyn, & Honnay, 2009; Woyke & Gabka, 2011) or when hazards interrupted ongoing research ("lemonade research," e.g., Mola & Williams, 2018; Rathcke, 2000). Unlike typical observational research, which trades experimental control for understanding of processes at larger spatial and temporal scales, these opportunistic studies were often short-lived and lacked replication, possibly limiting their ability to detect any real differences resulting from many hazardous events. However, experimental studies of hazards likewise possess drawbacks, such as in the challenge to realistically simulate the distribution, frequency, and intensity of natural events. As such, observational and experimental approaches each possess their merits, and their complementary application will no doubt continue to provide valuable insight.

The unpredictability of natural hazards is linked to a second important bias: our knowledge of natural hazard impacts on pollination includes only a subset of natural hazards. We used 15 hazard-related search terms (Table S1), yet found research into only seven hazard types. Hazards with more frequent return intervals (e.g., fire, drought, flooding) comprise a disproportionate number of total recorded responses. Furthermore, while climatological studies on the effects of fire and drought were the most numerous and rapidly growing (in terms of accumulated number of pollination-related studies—Figure 2), this knowledge base is generally at odds with global trends in natural disaster occurrence, where meteorological hazards (i.e., floods and storms) constitute the most frequent and fastest growing type of disaster (Keiler, 2013).

Finally, observational or experimental approaches were applied to hazard types unevenly. The majority of extreme heat research is experimental, whereas research into the impacts of fire, flooding, and hurricanes is largely observational. Of course, some of these limitations are to be expected given the rare, punctuated, and dangerous nature of extreme events. Nonetheless, these biases point toward important considerations and implications for future study of natural hazard impacts.

## 5 | OUTLOOK AND FUTURE DIRECTIONS

Against the backdrop of ongoing climate change, natural hazard research has attracted attention across several domains of ecology, including food webs (Spiller et al., 2018), succession (Schowalter, Willig, & Presley, 2017), and plant–herbivore interactions (Fagan & Bishop, 2000). Yet our understanding of pollination impacts is only just emerging. Thus, as a call to expand this knowledge base, we highlight three future directions for natural hazard research: (a) carefully quantifying and contextualizing the exposure to extreme events; (b) quantifying natural hazard impacts at higher levels of organization, including ecological networks and evolutionary history; and (c) elaborating the connection between exposure to hazards and impacts on crop pollination services.

### 5.1 | Quantifying exposure

Extreme events are challenging to study, not only because of their rarity but also because the "extremeness" of an event is relative to historic disturbance records and what the ecosystem and its species have experienced previously (Smith, 2011). This context dependency makes it critical to accurately quantify hazard exposure (a product of distribution, frequency, and intensity; Figure 1). We found that although some studies measured the intensity of hazard exposure (e.g., km/hr, °C), many relied on categorical distinctions (e.g., un/flooded, un/burnt, with/out water). However, the distribution (spatial occurrence and scale) and frequency of natural hazards can also structure communities. Indeed while some studies have sought to explore multiple components of exposure (Carbone & Aguilar, 2017; Lazarina et al., 2016; Ponisio, Wilkin, et al., 2016), potential additive and interactive impacts remain in much need of examination. Moreover, few studies have explicitly identified whether observed exposure was statistically extreme, and even fewer placed these events in context of historic or future climate patterns. Better quantifying hazard exposure (and in particular the intensity and duration of extreme events) will equip ecologists with clear information on the relationship between exposure and impacts (Jentsch, Kreyling, & Beierkuhnlein, 2007), as an aid to future predictability and evidence-based management.

### 5.2 | Quantifying impacts

Our review revealed that changes in species abundance and population-level effects—responses that react rapidly to perturbation (Hillebrand, Bennett, & Cadotte, 2008)—were commonly observed. In contrast, fewer studies examined changes to plant–pollinator interactions, or whether hazardous events leave a lasting signal on the co-evolutionary trajectory of plants and pollinators.

How natural disturbance regimes shape plant–pollinator networks is a rapidly developing field of study (Vázquez, Bluthgen, Cagnolo, & Chacoff, 2009), and including natural hazards as a driver should be an important component of this research program. We recorded seven studies that observed changes to plant–pollinator networks. Different network structural properties may offer different means to resist species loss, and understanding these dynamics can guide restoration efforts (Devoto, Bailey, Craze, & Memmott, 2012; Thébault & Fontaine, 2010). For example, if recently burned areas have reduced network modularity (Peralta, Stevani, Chacoff, Dorado, & Vázquez, 2017), this less compartmentalized network may exhibit greater fragility, as effects of other disturbances can spread faster across the entire community (Stouffer & Bascompte, 2011).

We did not find any studies that explored whether phylogenetic diversity was affected. Habitat alteration can erode phylogenetic diversity (Frishkoff et al., 2014) and reduce co-phylogenetic correspondence in plant–pollinator networks (Aizen et al., 2016). These changes in a community's evolutionary history can affect ecosystem functioning (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011; Naeem et al., 2016) or drive rapid evolutionary change (Galetti et al., 2013). It remains unknown how the separate or combined evolutionary history of plants and pollinators respond to extreme events. Whereas plant species which depend on more tightly co-evolved pollinator interactions may be expected to show low reproductive resilience to natural hazards, this need not always be the case, such as where pollinator replacement can to some extent mitigate this occurrence (García, Castellanos, & Pausas, 2018). Otherwise, preserving phylogenetically diverse species interactions is generally considered crucial for conservation, because of the capacity of these interactions to generate and maintain biodiversity at evolutionary timescales (Thompson, 2005).

### 5.3 | Connecting natural hazards, pollination, and people

Whether natural hazards translate into effects on pollinators and crop pollination services—and ultimately human well-being—depends on several biological and socioeconomic factors. The link between pollinator diversity and pollination services to crops can be shaped by the functional or taxonomic redundancy in the pollinating fauna (Garibaldi et al., 2015). If natural hazard exposure affects only specific pollinators, others may replace their ecological role with no observable effect on crop yield (i.e., bestow a rescue effect from pollination deficit). From a socioeconomic perspective, whether such effects on pollinators and their services are actually economically relevant will depend on a crop's pollinator dependency (e.g., high vs. low), the extent to which pollinator-dependent crops are cultivated per area (e.g., diversified vs. monoculture systems), and the vulnerability of farmers (i.e., smallholders vs. large-scale farmers).

How climate change will alter the provision of key agro-ecosystem services is a matter of major concern for smallholder farmers and developing regions (Egan & Price, 2017; Morton, 2007)—given the disproportionate threat to food security in these areas (Lipper et al., 2014), and that cultivation of pollinator-dependent crops is here higher (Aizen, Garibaldi, Cunningham, & Klein, 2009). Yet, as this and past studies demonstrate (Steward et al., 2014), pollination services research is strongly biased toward developed regions and large-scale production systems. Moving forward—and given that climate-driven natural hazards are only set to increase (Seneviratne et al., 2012)—addressing these considerable gaps in research, policy, and management will be vital in order to build effective strategies for disaster risk reduction and climate change adaptation. Fortunately, recognition of these needs does appear to be emerging at the political level—as evidenced in the UN FAO's "The State of the World's Biodiversity for Food and Agriculture" (Bélanger & Pilling, 2019), wherein, for instance, the government of Oman has noted increasing concern for crop yields owing to the effects of extreme heat on pollinators.

In contrast to the extent of peer-reviewed literature available for wild pollinators, natural hazard impacts on honey bees and managed pollinators are virtually restricted to gray and anecdotal evidence only. This disparity is, however, far from a reflection of economic importance. For instance, the high winds and flood waters associated with hurricane Irma in 2017 were estimated to have impacted 80% of Florida's bee colonies, causing a loss of 1%–1.5% of bees and shortages in crop pollination services (MacFawn, 2017). The dearth of scientific literature on natural hazard threats to managed pollinators suggests that this topic would in future benefit greatly from more formal analyses.

## 6 | CONCLUSIONS

Shifts in natural hazard regimes are likely to have some of the most profound impacts on ecological communities and the ecosystem services they provide (Turner, 2010). Meanwhile, economic and social costs associated with natural hazards are growing dramatically (Dilley et al., 2005). Given the predicted increase in frequency and severity of extreme events with global climate change (Seneviratne et al., 2012), we need to better understand how increasing exposure affects biodiversity and human livelihoods through shifts in the supply of critical ecosystem services such as pollination. Our understanding of natural hazard impacts on pollination is wanting, and current evidence is unable to guide conservation or climate adaptation efforts that aim to support pollinators and secure pollination for wild and crop plants. The development of evidence-based policy and management will necessitate addressing this research gap, particularly in less developed countries where climate change is expected to hold disproportionately large effects on food security. Building the capacity for conservation and climate adaptation will hence ultimately require knowing under what conditions ecological communities and ecosystem services are (or can be) rendered resilient to natural hazard events.

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## SUPPORTING INFORMATION

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

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