**Functional Ecology** 

DOI: 10.1111/1365-2435.14197

## REVIEW

Fire as a Dynamic Ecological and Evolutionary Force

# Increasing prevalence of severe fires change the structure of arthropod communities: Evidence from a meta-analysis

Blyssalyn V. Bieber<sup>1</sup> | Dhaval K. Vyas<sup>1</sup> | Amanda M. Koltz<sup>2</sup> | Laura A. Burkle<sup>3</sup> | Kiaryce S. Bey<sup>1</sup> | Claire Guzinski<sup>1</sup> | Shannon M. Murphy<sup>1</sup> | Mayra C. Vidal<sup>4</sup>

<sup>1</sup>Department of Biological Sciences, University of Denver, Denver, Colorado, USA

<sup>2</sup>Department of Integrative Biology, University of Texas at Austin, Austin, Texas, USA

<sup>3</sup>Department of Ecology, Montana State University, Bozeman, Montana, USA

<sup>4</sup>Biology Department, University of Massachusetts, Boston, Massachusetts, USA

Correspondence Mayra C. Vidal Email: mayra.cadorinvidal@umb.edu

Funding information University of Denver

Handling Editor: Joseph K. Bailey

### Abstract

- 1. Animal ecology and evolution are shaped by environmental perturbations, which are undergoing unprecedented alterations due to climate change. Fire is one such perturbation that causes significant disruption by causing mortality and altering habitats and resources for animals. Fire regimes are changing on a global scale, but the effects of these changes on animal communities are poorly understood. Arthropods are one of the most ubiquitous and diverse animal taxa on the planet and their populations are sensitive to environmental change. Given their wide-ranging impacts on ecosystem functioning, a better understanding of arthropod responses to changing fire regimes is critical and may also provide more general insights into how other groups might respond to fire.
- 2. Here, we provide a comprehensive meta-analytical assessment of how fire influences the arthropod community across habitats and functional groups. Using data from 130 peer-reviewed papers across the globe, we tested how a variety of fire characteristics, including management regime, severity and time-sincefire affect arthropod populations and communities across habitats.
- 3. Our results show that arthropod communities display substantial variation in response to fire and that community-level responses are most likely to be detected within the first year. Responses also vary depending on fire characteristics and habitat. Specifically, while community metrics such as diversity were increased by low severity fires, they were reduced by high severity fires. Likewise, evenness increased after prescribed burns but was reduced after wildfire. Measures of arthropod community structure decreased following fires in deserts and forests.
- 4. Across the entire arthropod community, fire also had variable effects on community diversity. Fire tended to have a negative effect size on arthropods across life stages, but responses did vary among groups. Nearly all functional groups exhibited a negative response to fire with the exception of herbivores, for which abundance, diversity and richness increased after fire.

Blyssalyn V. Bieber and Dhaval K. Vyas co-first authors.

Shannon M. Murphy and Mayra C. Vidal co-last authors.

© 2022 The Authors. Functional Ecology © 2022 British Ecological Society.

5. Our results suggest that the increasing prevalence of high-severity wildfires are changing the structure of arthropod communities. Given their ubiquitous presence and diverse roles in terrestrial ecosystems, these community changes are likely to affect ecosystem functioning in various ways, including through increased herbivory.

### KEYWORDS

abundance, burn, climate change, diversity, environmental disturbance, fire regime, fire severity, insect

### 1 | INTRODUCTION

Climate change has altered wildfire regimes by increasing the size, frequency and severity of wildfires (IPCC, Core Writing Team, 2014). Animal communities have experienced substantial direct and indirect effects of these increases in wildfires (Burkle et al., 2019; Koltz et al., 2018; Pressler et al., 2018). One animal group of particular interest is arthropods because they have the highest biodiversity globally and are sentinels of climate change-induced shifts in disturbance regimes (Høye et al., 2021). Arthropods have gained increased attention because of precipitous declines in their abundance and biodiversity, particularly among insects (Van Klink et al., 2020; Wagner et al., 2021). However, we know little about how changes in fire regimes differentially affect diverse arthropod taxa. A better understanding of responses across taxa and functional groups is necessary, because variation in responses (e.g., increasing vs. decreasing) to novel fire regimes may lead to changes in the ecosystem services provided by arthropods. Given the important role that these invertebrates play in influencing the ecology, ecosystem services, and economies of ecosystems globally, it is critical that we develop a better understanding of how fire disturbance influences the structure and function of arthropod communities.

Fires have direct mortality impacts on arthropods, but these disturbances can also indirectly influence arthropods through shortand long-term changes to their habitats and food resources (Koltz et al., 2018). For example, Kim and Holt (2012) found that insect herbivores were more affected by the indirect effects of fire, rather than the direct effects of fire due to mortality, and that these indirect effects were mediated through changes in habitat structure. How a fire may influence the arthropod community, therefore, depends on the habitat in which it occurs and on the specific characteristics of the fire itself. In particular, fire severity and frequency both influence the extent of direct (i.e., mortality) and indirect (e.g., via changes in habitat and food resources) effects of fire on arthropods. These same fire characteristics, combined with the amount of time elapsed since a fire event, can influence community recovery from fire. Previous work suggests that increased fire severity may negatively influence some arthropod groups, due to both higher mortality from severe fire events and the corresponding loss of habitat and resources immediately following high severity fire (Certini et al., 2021; Koltz et al., 2018). For this reason, wildfires may have stronger effects on arthropods compared

to prescribed fires because wildfires tend to be more severe (Hiers et al., 2020). Arthropods may also have differential responses to fire between habitat types due to variation in fire severity. For instance, fire severity can be higher in forests compared to grasslands because fuel loads are often higher in forests (Hurteau & Brooks, 2011). Different habitats are also subject to often unique suites of management – including grazing in grasslands and logging in forests—that may interact with fire to influence arthropods.

Effects of fire on arthropods also vary depending upon the life history strategies of different groups and which life stages are exposed to fire. For example, some pyrophilic species of flat bugs and beetles are attracted to areas that recently burned and their increased survival and reproduction in these burned areas led to increases in abundance and richness following fire disturbance (Heikkala et al., 2016, 2017). Responses by other groups, like pollinators, are strongly dependent on time-since-fire, peaking in abundance and diversity soon after fire and decreasing with declining floral resources as succession proceeds (Carbone et al., 2019; Potts et al., 2003). Previous meta-analyses investigating the effects of fire on insects have largely focused on abundance and richness measures of specific functional groups (e.g., Carbone et al., 2019 on pollinators and Pressler et al., 2018 on detritivores) or a few key insect taxa, such as certain families of Hymenoptera, Lepidoptera, and ground dwelling Coleoptera (Carbone et al., 2019; Mason Jr. et al., 2021). These meta-analyses have shown that pollinator abundance and richness can be positively affected by fire in some circumstances. However, by focusing on certain groups and metrics, it is unclear how entire arthropod communities may be affected by fire. Previous studies have also focused on adult responses to fire, while the effects of fire on different life stages within groups remain largely unexplored. Yet, developing a better understanding of fire effects on arthropods across life stages is important, because some life stages may be more sensitive than others. For example, for holometabolous insects, some life stages (e.g., larva) are less mobile than others (e.g., adult), hampering their capability to disperse and escape a fire event. Conversely, some stages of development may be more resilient to threats from fire, such as subterranean life stages of pupating insects. Thus, considering all groups of arthropods across life stages is critical because taxa have previously been shown to display differing responses to fire (Mason Jr. et al., 2021; Moretti et al., 2006; Nicholson & Egan, 2020).

In this paper, we address the above knowledge gaps through a global meta-analysis to provide a comprehensive review of arthropod responses to fire across the entire arthropod community. We investigated how the diverse natural histories of arthropods influence their responses to fire, and we also considered how different fire characteristics are associated with a given response type. Susceptibility to fire may depend on the arthropod functional group, as some groups benefit from resource flushes available after fire events, whereas others experience resource losses. Similarly, arthropods have distinct life stages that are unequal in their vulnerability to fire due to different habitats and thus exposure to fire (e.g., underground vs. aboveground; Koltz et al., 2018); therefore, we investigated fire impacts across life stages. Variation in abiotic and biotic conditions within different habitats suggests responses to fire may vary according to habitat types as well, so we also examined how habitat type mediates arthropod responses to fire. Previous meta-analyses have focused primarily on terrestrial systems where fires occur (e.g., forests and grasslands), but here we expand our analyses to include the impacts on less-studied habitats as well, such as streams, wetlands, and agricultural fields. Finally, fire impacts vary based on fire severity and time since fire, so we measured the roles played by these variables.

Here, we provide an exploratory analysis of how fire impacts all arthropod taxa and functional groups for which there are published studies available, including those groups for which responses to fire are relatively understudied. Moreover, by including several global regions, we are able to examine generalities of arthropod responses to fire across various systems. We address the following questions: (1) How are functional groups and life stages differently affected by fires? (2) Do fires have different impacts on arthropod communities depending on the habitat? (3) Do the impacts of fires on arthropods vary by fire severity, time since fire, or type of fire (prescribed vs wildfire)? Our study provides a novel and general perspective of how increasing severity of fires, a major consequence of global change, will affect some of the planet's most ubiquitous animals.

### 2 | MATERIALS AND METHODS

### 2.1 | Literature survey

We compiled papers from five databases, including Biological Abstracts, Web of Science Core Collection, Academic Search Complete, Agricultural & Environmental Science Collection (ProQuest), and GreenFILE. We searched the databases on December 10 and 11, 2020 using variations of the keywords ((burn\* OR prescribe\* OR control\* OR fire\* OR wildfire\* OR pyro\*) AND (intens\* OR sever\*)) AND (insect\* OR arthropod\* OR spider\* OR bee\* OR parasitoid\* OR pollinat\* OR hexapod\*). When searching these databases, we selected the option to search for papers that were in English, and while this is commonly done in many meta-analyses, we recognize that this method can produce bias in results (Konno et al., 2020). We then supplemented these results with several other

studies that had been cited in a recent review paper on the effects of fire on insects (Koltz et al., 2018). The first search produced 4479 studies. We did an initial screening of these studies to remove papers that were non-empirical papers, including reviews or modelling studies, or those that did not include response variables related to an arthropod. Of the remaining 831 studies, each was evaluated for suitability by at least two authors. During this process, we kept studies that were relevant to arthropod responses to fire, reported some measure of variance (or provided raw data from which we could calculate variance), included an unburned control treatment. and did not have confounding variables that made it impossible to determine the effect of fire (e.g., if grazing only happened in the fire treatment but not in the control; if a confounding variable was found in both the fire treatment and the control, we retained those studies in the dataset and recorded the confounding variable). The response variables that we were interested in studying were directly related to the focal arthropod of the study and not proxies related to that arthropod's impact on their host plant or environment. For example, Murphy et al. (2018) measured percent herbivore damage; although this is a proxy for herbivore abundance, it is not a direct measure of abundance, so we did not include it in our analysis. Studies that reported raw data were included if we could calculate the mean and variance ourselves or if the authors were able to provide the missing information. After this second screening, 130 studies remained.

Within each of these studies, we extracted data from the text, tables or figures into individual cases for each taxonomic group or organism that was independently measured. For data reported in figures, we used PlotDigitizer® (Huwaldt, 2020) to extract data to measure the means and standard error or standard deviation. For each paper, we attempted to record additional moderators that could influence the effect of fire on our response variables; these moderators included geographic region (country), taxa, functional group, life stage, whether the arthropod species was generalist versus specialist, dispersal ability, subterranean life stage, habitat type, fire type (wildfire vs. prescribed), time since fire for both the burned and unburned plots, and fire severity (as assessed by the authors, only 32% of cases reported any measure of severity). Fire type was primarily categorized into wildfire or prescribed, but some studies spanned areas that were both wildfire and prescribed fire and were thus classified as "mixed". Some experiments were conducted in a laboratory and were classified as "lab" and many studies did not report the fire type and those were classified as NA. While fire frequency is an important attribute of fires, we instead analysed time since fire because authors were more likely to publish dates of fires than how often a fire occurred in their study sites.

We classified arthropods into functional groups based on the arthropod's feeding habit or ecosystem service; for instance, herbivores were arthropods that fed on vegetative plant parts, whereas pollinators were arthropods that provided pollination service. We categorized arthropods as pollinators based on (1) the authors' designation of the arthropod as a pollinator, or (2) the historical documentation of the taxa as pollinators (e.g., butterflies and bees). For Lepidoptera, our classification approach meant that adults were considered as pollinators and larvae as herbivores. Time since fire was binned into categories for analysis ranging from <0.5, 0.5–1, 1–5, and >5 years. Some unburned plots had been burned many years before or had an unknown burn history, but we deferred to the classifications made by the authors. Most papers did not include all of these moderators.

When organizing the data from each study, we considered the control variable to be either from unburned or pre-burned plots; studies had to report results from one of these controls to be included. If results from both pre-burn and unburned areas were reported, we used data from unburned plots as the control to avoid differences between fire treatment and control due to temporal factors. Whether the control treatment was considered unburned depended on the habitat type and history of the land. For example, when comparing habitats, a forest that burned over 50 years ago could be used as a control (e.g., Malison & Baxter, 2010), but 4 years since the last burn might have been sufficient for a grassland control (e.g., Anderson et al., 1989). We did not include a cut-off for the time since fire for unburned controls because of this extreme variation in intervals between burn events across habitats.

### 2.2 | Data survey and extraction

To calculate effect sizes for the meta-analysis, we used standard mean difference (SMD). We decided to use this effect size measurement because our cases included means with zero or negative values, which precluded using other types of effect size calculations. The most common response variables that we recorded were population and community level measures (e.g., abundance, species richness, density, evenness, biomass) with fewer measures related to individuals (e.g., body size, growth rate, development time). When a study included development time of the insect, we switched the treatment and control, since shorter development time is often associated with greater fitness (Price et al., 1980). Although the 130 studies yielded a total of 3783 cases for inclusion in the analysis, close to half of these cases were repeated measures in a time series of both unburned and burned sites, compared different treatment means to the same control mean, or measured multiple response variables for the same taxon. To avoid pseudoreplication for each of these instances, we used the same case ID within the time series, the same control group for multiple entries, or for a taxon with multiple measurements (following Nakagawa et al., 2017). If a study had both time series and used the same control treatment across multiple treatments, we used the same case ID numbers only within the time series. Thus, from the 130 papers, there were 1925 independent cases included in the analysis.

### 2.3 | Statistical analysis

For our statistical analysis, we used multilevel error meta-analysis, with case identity nested in publication identity as a random factor,

the moderators as fixed effects, and standardized mean difference (SMD) as the response variable. We included the variation from each effect size as our weight in the model. Although we show in the figures, we did not describe the results of moderator levels with six or fewer effect sizes because such small sample sizes can cause imprecision in the analysis using random models (Borenstein et al., 2009; Murphy et al., 2017). We analysed the response variables, functional groups, degree of dietary specialization, life stages, habitat types, taxa, fire severities, time since fire and fire types (wildfire, prescribed, lab, or mixed) as individual moderators. We then tested for the effect of fire on different response variables within the various functional groups, life stages, habitat types, fire severity, time since fire and fire type. Similarly, we investigated the potential for different effects of fire on the taxon within life stages. The estimates and confidence intervals used in our figures were obtained from models including a -1 term to compare the main effects with a zero intercept. We tested for publication bias using Rosenberg's fail-safe number (Rosenberg, 2005) and tested asymmetry of effect sizes (egger's test) by using a *rma.mv* model with the function "mod = vi" for the whole dataset and for each subset. We calculated heterogeneity as  $l^2$  using the function *mlm.variance.distribution* from the package DEMETAR (Harrer et al., 2019). We removed effect sizes that were extremely high given the distribution of the data (higher than 1000, or lower than -1000), because these studies could have incorrectly skewed the results. These removed effect sizes accounted for 0.66% of all data points (n = 25 effect sizes). We performed the models using the METAFOR package with rma.mv function (Viechtbauer, 2010). We performed all statistical tests in R environment 4.0.3 (R Core Team, 2020).

We also conducted sensitivity analyses, whereby we first removed cases that considered other variables along with fire (e.g., confounding variables such as logging, thinning, herbicide use, etc.) and re-ran the overall model to see if those additional variables influenced the results. Lastly, we re-ran the analysis after removing papers that had more than 100 data points to ensure that these few papers (n = 9) were not biasing our results.

### 3 | RESULTS

### 3.1 | Literature review results

The studies in our analysis were published between 1962–2020, with 89% of the studies published since 2000 (Figure S1), indicating that the publication rate has increased over time. However, of all the studies identified that were related to arthropods and fire (n = 831), the proportion we were able to include in our meta-analysis (those that included means and variance) was relatively constant for each decade (16%) and did not increase over time. Just over half of the total number of studies were from North America (52% of the studies; Figure S2) with the United States representing the most studies of any country (46% of the studies). Studies from Europe (18%), Oceania (10%) and South America (9%) were also relatively common

compared to Central America, Africa, Middle East, and Asia (all <5% of studies), which may be due to bias in searching for only English language papers (Konno et al., 2020). Most studies had relatively poor replication. Moreover, many studies had different numbers of replicates for different response variables; in terms of the maximum number of replicates employed in a given study, over half of the studies had 9 or fewer replicates for their control and fire treatments (Figure S3). Interestingly, fire treatments (median replication n = 8).

# 3.2 | Data heterogeneity, asymmetry, and sensitivity analyses

We obtained 3783 data points from 130 papers (Figure 1, see Figure S4 for histogram of effect sizes and funnel plot and Data S1 for the list of papers used in the meta-analysis; Dataset available in Bieber et al., 2022). Before conducting the analysis, we removed 25 data points that had extremely high effect size values (higher than 1000, or lower than -1000). The overall model without considering any moderator was heterogeneous ( $I^2 = 79.65\%$ ,  $Q_F = 16,426.82$ , df = 3755, p < 0.0001), and the effect size did not show a clear overall effect of fire on arthropods (Estimate = 0.027, 95% CI = -0.093, 0.147, z-test = 0.44, p = 0.661). The heterogeneity shown by the  $I^2$  statistics in our meta-analysis is slightly below the mean value found in most ecological meta-analyses (91.7% according to Senior et al., 2016); 34.4% of the heterogeneity can be attributed to withinstudies heterogeneity and 45.4% to between-studies heterogeneity. All subsequent models performed to analyse the effects of moderators showed significant  $Q_{\rm F}$ , and  $l^2$  ranged from 68.6% to 90.1%.

We tested for the influence of different response variables, functional groups, degree of specialization, habitat types, taxa, fire severities, time since fire and fire types to explain the heterogeneity in the data by including these variables as moderators in our models. We found that fire severity did not account for heterogeneity in the data ( $Q_M = 5.5$ , df = 3, p = 0.139), nor did fire type ( $Q_M = 0.37$ , df = 3, p = 0.946), habitat type ( $Q_M = 2.77, df = 10, p = 0.973$ ), life stage (QM = 1.89, df = 4, p = 0.594) or country of origin ( $Q_M = 36.13$ , df = 28, p = 0.139). The variables that accounted for portions of heterogeneity in the dataset were response variable (i.e., abundance, richness, diversity;  $Q_M = 91.59$ , df = 7, p < 0.0001), functional groups ( $Q_M = 12.28$ , df = 5, p = 0.031), taxon ( $Q_M = 67.99$ , df = 33, p = 0.0003), diet breadth ( $Q_M = 4.08$ , df = 1, p = 0.043), and time since fire ( $Q_M$  = 19.33, df = 3, p = 0.0002). Considering response variables, we found that biomass and evenness were overall reduced by fire. For functional groups, fire had a positive effect size for only herbivores. For taxon, fire decreased oribatid mites, while Diptera and Coleoptera increased. For time-since-fire, the heterogeneity of this moderator can be explained by the bin from 0-0.5 yearsince-fire having a negative effect size relative to the 0.5-1 year bin. Specialists, more than generalists, showed an increase in all response variables pooled together following a fire; however, this subset of data had very low sample size (Figure 1).

The meta-analysis data were asymmetric (egger's test: z = 3.69, p = 0.0002, Figure S4), even though we did not encounter publication bias based on Rosenberg's test of fail-safe number (n = 447,697, p < 0.0001, above 5 N +10 of 18,965). The correlation between standard error and effect size was indicative of small-study effect (i.e., studies with low sample size having high effect sizes, Figure S4). To explore the effect of publication bias shown by the asymmetry of our dataset, we followed the approach by Nakagawa et al. (2022). More specifically, we used a model that included as moderators the variance and the factors that contributed the most to heterogeneity (response variables and time since fire, see above; n = 3446 effect sizes). We found that the model with the variance had an overall effect size of 0.003 (95% CI = -0.133, 0.143), whereas the same model not accounting for the small-study effect (without the variance) had an effect size of 0.09 (95% CI = -0.042, 0.222). This shows that the publication bias can potentially change the effect sizes in our model; thus, we performed a posteriori sensitivity analysis including the variance as a moderator in all cases where there was a significant asymmetry.

We performed two sensitivity analyses, one removing cases that included confounding variables, and another removing studies that had more than 100 effect sizes. The overall effect size without confounding cases (n = 614 or 16% of all effect sizes) is 0.028 (95% Cl = -0.100, 0.157), very similar to the effect size with these data points. Similarly, the model without studies with more than 100 effect sizes (n = 1248, or 33%) resulted in an effect size of 0.033 (95% Cl = -0.098, 0.165). Thus, as the effect sizes from these sensitivity analyses were similar to the model using all data, we conducted the rest of the analysis using the whole dataset.

### 3.3 | Effects of fire on arthropod functional groups

We investigated how response variables differed across functional groups, finding that arthropod herbivores displayed the most varied responses to fire irrespective of elements of fire regime ( $Q_M = 157.21$ , df = 8, p < 0.0001,  $l^2 = 84.92\%$ ), followed by detritivores ( $Q_M = 53.35$ , df = 7, p < 0.0001,  $I^2 = 68.62\%$ ), pollinators ( $Q_M = 28.05$ , df = 5, p < 0.0001,  $l^2 = 77.09\%$ ), and omnivores  $(Q_{M} = 12.23, df = 5, p = 0.03, l^{2} = 75.19\%)$ . The dataset of predators ( $Q_M = 13.31$ , df = 8, p = 0.102,  $l^2 = 69.97\%$ ) showed that the response variable as a moderator did not contribute to explain the heterogeneity in this subset of data. Fire reduced herbivore biomass (z = -3.06, p = 0.002), density (z = -1.97, p = 0.048), and evenness (z = -5.08, p < 0.0001), but increased herbivore abundance (z = 2.4, p < 0.0001)p = 0.016), diversity (z = 2.72, p = 0.007), and richness (z = 6.10, p < 0.0001). Predators and detritivores experienced null or negative impacts from fire, which tended to reduce measures of arthropod community diversity (detritivore: z = -2.73, p = 0.006) and evenness (detritivore: z = -6.72, P < 0.0001; predator: z = -2.57, p = 0.01; Figure 2). Pollinator diversity was also reduced by fire (z = -2.14, p = 0.032), but pollinator abundance, density, and richness each showed no overall effect from fire. However, pollinators were the



FIGURE 1 Number of effect sizes for each response or moderator variable used in our analysis.

group with the lowest sample size analysed here and only pollinator abundance (n = 194) and richness (n = 27) had large enough sample sizes (e.g., >25, Gurevitch et al., 2018) to make reliable conclusions. Therefore, our results for pollinators should be interpreted with caution. Omnivores were the only group for which fire reduced the growth of individuals (z = -2.67, p = 0.007).

The dataset with omnivores showed publication bias from both the Rosenberg's fail-safe number (p = 0.063) and the Egger's test (p < 0.0001). The subsets with herbivores and pollinators were also asymmetric, whereas predators and detritivores were not asymmetric, based on Egger's test with alpha value at 0.01. When exploring how the asymmetry could have influenced the results using variance as a moderator, the differences we found were that herbivore abundance (estimate = -0.002, 95% CI = -0.281, 0.276) and diversity (estimate = 0.252, 95% CI = -0.194, 0.697) were not significantly different from zero, whereas for omnivores, abundance had a negative effect size due to fire (estimate = -0.55, 95% CI = -0.875, -0.217). All other results remained the same.

## 3.4 | Effects of fire on arthropods life stages

Fire can also affect different life stages in variable ways, especially when arthropods in particular life stages are more mobile than

evenness (n=7) diversity (n=10) richness (n=73) growth (n=8) detritivore abundance (n=250)density (n=76) mass or size (n=4) biomass (n=8) evenness (n=13) density (n=28) arowth (n=6) herbivore mass or size (n=8) abundance (n=456) diversity (n=31) richness (n=54) growth (n=10) evenness (n=3) diversity (n=3) omnivore abundance (n=194) richness (n=6) density (n=49) diversity (n=6) density (n=6) pollinator richness (n=27) abundance (n=194) biomass (n=4) evenness (n=15) mass or size (n=13) dispersal (n=5) predator diversity (n=28) abundance (n=331) density (n=82) richness (n=55) \_3 \_2 2 Effect size (Estimate)

FIGURE 2 The effects of fire on various response variables categorized by arthropod functional group with sample sizes for each effect size given in parentheses. Dots represent the estimate of the variables based on the multi-level model and lines represent the 95% confidence interval of the model. Variables that do not vary significantly from zero are shown in black, significantly negative effect sizes are in orange, and significantly positive effect sizes in blue.

others. For those studies that reported the focal life stage, the vast majority investigated the impact of fire on adults, while many fewer included data on immature arthropods (Figure 1). The life stages that can be considered immobile were rarely analysed: eggs were included in just two papers, while insect pupae (i.e., life stage between immatures and adults of holometabolous insects) lacked any representation. When analysing the life stages that had good representation in our dataset, we found that both adults ( $Q_M = 51.08$ , df = 8, p < 0.0001,  $l^2 = 79.35\%$ ) and immatures ( $Q_M = 16.96$ , df = 5, p = 0.005,  $l^2 = 72.96\%$ ) showed variable responses to fire.

Fire reduced both adult and immature arthropods biomass (adults: z = -3.27, p = 0.001, immatures: z = -3.23, p = 0.001; Figure 3a). Immature arthropod growth was also reduced by fire (z = -2.26, p = 0.024, Figure 3a). For adults, we also found that fire reduced species richness (z = -2.35, p = 0.019) and evenness (z = -4.77, p < 0.0001; Figure 3a). The only response variable measured for eggs was abundance, thus we did not analyse how fire affects different egg responses. Our dataset included only two arthropod orders (Lepidoptera and Hemiptera) whose egg stages were investigated for their response to fire, but only the hemipteran showed greater abundance of eggs after fires (z = 2.53, p = 0.0115; Figure 3b). When analysed by taxon, we found no clear effect of fire among any order for adult and immature stages (Figure 3b).

The subset of the adult life stage was asymmetric (z = 5.93, p < 0.0001), whereas the immature life stage subset was not (z = 0.71, p = 0.4). When exploring the effect of this asymmetry on the model

using adult life stage data, we found that adult diversity also had a negative effect with fire (estimate = -0.4, 95% CI = -0.587, -0.205), whereas the other results followed the same pattern as before.

### 3.5 | Habitat type affects the impact of fire

Diverse abiotic and biotic factors within a habitat can influence how fire affects arthropods and the bottom-up and top-down selective pressures that affect fitness and community metrics (Vidal & Murphy, 2018). While most of the response variables did not differ significantly across different habitats, some decreased following fires in desert and forest habitats ( $Q_M = 157.12$ , df = 38, p < 0.0001,  $l^2 = 80.81\%$ ). Species richness (z = -2.85, p = 0.004) and diversity (z = -2.57, p = 0.010) were both reduced by fires in deserts (Figure 4). For forest dwelling arthropods, fire reduced biomass (z = -2.83, p = 0.005) and species evenness (z = -2.22, p = 0.026;Figure 4). Arthropod richness was marginally increased after fire in forests (z = 1.99, p = 0.049), however, this result was not robust to publication bias (estimate = 0.096, 95% CI = -0.087, 0.279). Additionally, when we consider variance in the model to account for asymmetry, we found that fire reduced evenness in grasslands (estimate = -0.823, 95% CI = -1.633, -0.013) and richness in savannas (estimate = -0.695, 95% CI = -1.328, -0.062) and in scrub habitats (estimate = -0.597, 95% CI = -1.161, -0.033). The results with diversity and richness in deserts, and biomass and evenness in forests remained significant.



FIGURE 3 (a) The effects of fire on various response variables categorized by life stage (adult and immature) with sample sizes for each effect size given in parentheses. (b) The effects of fire on different taxa categorized by life stage with sample sizes for each effect size given in parentheses. Dots represent the estimate of the variables based on the multilevel model and lines represent the 95% confidence interval of the model. Variables that do not vary significantly from zero are shown in black, significantly negative effect sizes are in orange and significantly positive effect sizes in blue

FIGURE 4 The effects of fire on various response variables categorized by habitat with sample sizes for each effect size given in parentheses. Dots represent the estimate of the variables based on the multi-level model and lines represent the 95% confidence interval of the model. Variables that do not vary significantly from zero are shown in black, significantly negative effect sizes are in orange, and significantly positive effect sizes in blue



# 3.6 | The effect of fire type, fire severity, and time since fire on arthropods

Prescribed and wildfires had contrasting effects on arthropods  $(Q_{\rm M} = 116.45, df = 23, p < 0.0001, l^2 = 81.26\%)$ , with positive effect

sizes only observed with prescribed fires (Figure 5a). Prescribed fires increased arthropod evenness (z = 5.1, p < 0.0001), but reduced biomass (z = -2.54, p = 0.012). Wildfires only reduced species evenness (z = -3.31, p = 0.0009). However, burn severity was a significant factor that influenced arthropod responses





છ

 $(Q_{M} = 162.99, df = 16, p < 0.0001, I^{2} = 90.1\%$ ; Figure 5b). High severity fire reduced arthropod richness (z = -2.64, p = 0.008) and diversity (z = -3.40, p = 0.0006). Conversely, low severity fires resulted in increased evenness (z = 5.13, p < 0.0001), and diversity (z = 3.23, p = 0.012). We also tested if prescribed and wildfires could have variable effects on arthropods depending on habitat type and fire severity; however, we found no consistent effects of prescribed and wildfire across either of these variables (Figures S5 and S6). All subsets of data for fire severity and type of fire were asymmetric (Egger's test with p < 0.0001), except for wildfire (z = -1.56, p = 0.12). The model including variance as a moderator showed the same pattern as without it for fire type, except for reduced richness with prescribed fire (estimate = -0.24, 95% CI = -0.421, -0.051). For fire severity, when considering publication bias, richness was not significantly negative with high severity fire (estimate = -0.39, 95% CI = −0.081, 0.03).

Habitats undergo significant changes following burns, so arthropod response and recovery are dependent on the amount of time that has passed since a fire impacted the region. We found the most significant effects to be when less than 1 year had passed since the burn, with impacts varying depending on the response variable ( $Q_M = 363.19$ , df = 32, p < 0.0001,  $l^2 = 79.77\%$ ; Figure 5c). Considering the effects of variables that had more than 10 effect sizes, we found that immediately after a burn (<0.5 year), evenness (z = 3.1, p = 0.002) and diversity (z = 2.44, p = 0.015) increased, but richness (z = -3.87, p < 0.0001) and biomass (z = -2.5, p = 0.012) decreased. Studies examining the impact of fire between 0.5 and 1 year following a burn found decreases in species density (z = -4.16, p < 0.0001), whereas these fires resulted in increasing species abundance (z = 3.45, p = 0.0005). Arthropod abundance again increased 1–5 years after a fire (z = 2.95, p = 0.003), and beyond 5 years, fires increased species richness (z = 2.45, p = 0.023), but decreased species evenness (z = -8.98), p < 0.0001).

Data used to test time-since-fire were asymmetric (Egger's test with p < 0.0001). Considering the effect of publication bias in our model, the differences from the model without variance were that immediately after a fire, abundance was reduced (estimate = 0.24, 95% CI = -0.427, -0.062). Between 1 and 5 years after a fire, abundance was not significantly different from zero anymore (estimate = 0.128, 95% CI = -0.023, 0.279), whereas evenness was reduced (estimate = -0.35, 95% CI = -0.612, -0.088). After more than 5 years, fire led to reduced diversity (estimate = -0.256, 95%) CI = -0.505, -0.007), whereas richness was not different from zero (estimate = 0.15, 95% CI = -0.042, 0.351). These results indicate that the analysis of time-since-fire is prone to type I and type II errors. However, these differences with the models considering asymmetry all occurred when the effect sizes and their confidence intervals were close to zero, following Cohen's definition of small effect size (<0.3, Cohen, 1988); effect sizes that are considered moderate or high (0.5 and >0.8, respectively) tended to be robust to asymmetry.

# 4 | DISCUSSION

Fire is a significant abiotic force that shapes arthropod populations and communities. We found that arthropods display substantial variation in their responses to fire and that community-level responses are most likely to be detected within the first year following a fire. Notably, community metrics of diversity were increased by low severity fires and reduced by high severity fires, which suggests that the increasing prevalence of high-severity wildfires are likely detrimental for arthropods in the face of global change. Further, evenness increased after prescribed burns, but was reduced after wildfires, which demonstrates that the type of fire has important impacts on community structure and diversity; differences in evenness may be due to increased severity, temperature, and/or extent of wildfires compared to prescribed burns. Overall, when there was a significant effect of fire on a functional group, the response tended to be negative, except for herbivores which increased in richness, abundance, and evenness. When considering the impacts of fire on community structure, we show that species richness and evenness were often reduced by fire, potentially indicating a shift towards communities dominated by few abundant species. This pattern was more apparent in deserts and forests, such that burned desert habitats experienced reduced arthropod richness and diversity, while burned forest habitats showed reduced evenness and biomass.

# 4.1 | Responses to fire differed among functional groups

Arthropod communities showed high variability in their responses to fire based on the functional group. Herbivorous arthropods represented the majority of effect sizes and the only group for which fire increased abundance, richness, and diversity of herbivores. These findings suggest that fire may drive increases in herbivore populations and consequently, in rates of herbivory, thereby exacerbating other similar global change-induced increases in herbivore impacts (e.g., Meineke et al., 2019).

Pollinators are another arthropod group that is likely sensitive to fire, because of supposed mortality of low-mobility larval or juvenile stages (potential negative effects) and typical post-fire increases in floral resource availability (potential positive effects). However, in contrast to findings from other recent meta-analyses (Carbone et al., 2019; Mason Jr. et al., 2021), we did not find that fire increased any response variable for pollinators. The reduction in diversity of pollinators we found could result in potential negative effects at the ecosystem level; however, we have only six effect sizes so that precludes reliable conclusions about ecosystem effects from our result. The lack of a potential positive effect of fire on pollinators in our study could be explained by several important differences in our analyses compared to those used by previous researchers. First, the pollinator group had relatively few data-points in our meta-analysis (Figure 1), which may partly be explained by our avoidance of non-peer reviewed literature (grey literature), unlike Mason Jr. et al. (2021). Second, we excluded non-insect pollinators (e.g., bats) and did not use search terms in our literature search that focused on specific taxa, as done by Carbone et al., 2019. Third, for studies to be included in our analysis, the response variable had to be a direct measure related to the focal arthropod's fitness or population/community level measures that included means and variance. For instance, we did not include papers that measured beta-diversity, whereas these types of papers were included in Carbone et al. (2019). Lastly, our assignment of functional groups was primarily based on information provided by study authors, so some pollinators may not have been designated as such. Even with these narrower guidelines for which studies were included in our analyses, we were able to obtain a number of effect sizes close to Carbone et al. (2019) (342 vs 237 in our study).

The negative associations between fire and community metrics for both predators and detritivores align with previously published pyroentomological studies for these groups. In particular, fire reduced predator evenness, consistent with the expectation that higher trophic levels will be negatively affected by global changes due to their proportionally lower abundances and their dependency on lower trophic levels (Price et al., 2011; Stireman & Singer, 2018). If higher trophic levels are negatively affected by fire, this may lead to enemy release scenarios depending on the identity of the predator species being absent or at lower abundances after fire. The reduction in predator evenness that we found suggests that fire events may skew the relative abundances in favour of predatory species that can either survive the fire event or quickly take advantage of the resources available following a burn. For example, Thompson et al. (2022) observed both positive and negative impacts from fires on predatory and parasitic Dipterans and Hymenopterans, however fire-adapted species tended to be less negatively impacted. The cumulative effect of fire on predator evenness may alter predator-prey interactions and top-down pressures on lower trophic levels.

Reductions in detritivore diversity due to fire aligns with previous work showing that detritivores are particularly sensitive to environmental change, including a recent meta-analysis that found fire reduces the richness and abundance of soil arthropods (Pressler et al., 2018). Detritivore sensitivity to fire may be explained by their poor dispersal abilities (e.g., Lehmitz et al., 2012) limiting recolonization of burned areas and from the short- and long-term changes to the quantity and quality of available litter resources and habitat after fires. Thus, the reduction in population and community metrics of detritivores shown in this meta-analysis and others could result in reduced ecosystem services, such as nutrient cycling.

# 4.2 | The influence of fire severity, time since fire and management on arthropods

Ecological impacts of fire are influenced by management strategies and time since fire. We found that prescribed fires increased species evenness. In comparison, evenness was reduced after wildfires; however, this result suffers from low replication (n = 7 effect sizes). Similarly, the

strongest effect of time since fire occurred on evenness, in which there was a positive effect size less than 1 year after fire, but negative effect size after more than 5 years since the fire event. The sample size in these cases was moderate (>20 effect sizes). This result suggests that immediately after a fire, the arthropod community is more even with different species similarly being affected by the fire event. However, after the community has time to re-establish, some species may dominate the community, thereby reducing evenness.

We found that high severity fires decreased richness and diversity in communities whereas low severity fires increased diversity and evenness in arthropod communities. This result is fairly intuitive given that areas affected by high severity burns take longer to recover their aboveground and belowground resources, which are necessary for higher trophic levels to rebound. Overall, few studies actually reported the severity of the fire they studied, which limits our ability to generalize how arthropods respond to changing fire regimes. A major hindrance in synthesizing literature on the ecological effects of fire is that unlike some other major environmental disturbances (e.g., hurricanes, tornadoes) that are categorized using an accepted scale, measures of fire severity vary widely. Even with some proposed scales for fire severity, few studies followed a standardized scale or reported severity using a difference Normalized Burn Ratio (dNBR), as used by the monitoring Trends in Burn Severity (MTBS), an interagency programme in the United States. This lack of consistency leads to arbitrary assessments of fire severity across studies even when it is reported, thereby reducing our ability to assess its impact on arthropods. Thus, our understanding of how fire severity can influence communities would be greatly improved by the development of more standardized metrics.

# 4.3 | Geographic, taxonomic, and life stage representation

We reviewed 130 studies spanning 58 years, a period that showed a trend of increasing attention to how fire impacts arthropods. Our analysis included global representation from fire-affected ecosystems. However, over half of our data were from North America, indicating that this region may disproportionately shape our understanding of the effects of fire on arthropod communities. In addition, while arthropods are a highly diverse taxon, we found a skewed representation across taxonomic orders, suggesting that just a few groups contribute to most of our understanding of the impacts of fires on arthropods. In fact, coleopterans along with hymenopterans (75% being ants) accounted for the same number of effect sizes as did all other arthropod taxa combined. When the arthropod life stage was considered within studies, we found both adult and immature life stages responded negatively to fire. However, overall there was a disproportionate focus on abundances of adult arthropods and very little data on responses of other life stages (e.g., eggs, larvae, pupae) or on other metrics of fitness (e.g., growth, body mass). Thus, knowledge gaps remain regarding how fire may affect the fitness and various life stages of different arthropod groups, especially less mobile stages (e.g., eggs and pupae).

### 4.4 | Challenges and future directions

We initially wanted to fill knowledge gaps from a recent review (Koltz et al., 2018) that highlighted the lack of information reported on the relationship between fire and arthropod life stage, functional group, diet breadth (i.e., dietary generalist vs. specialist), dispersal ability and subterranean life stage. While we were able to analyse how the life stage and functional group mitigate arthropod responses to fire, we encountered challenges when trying to analyse how diet breadth, dispersal ability, and subterranean life stages are affected by fire. Koltz et al. (2018) suggested that a more generalized diet breadth, greater dispersal ability, and/or subterranean life stages may increase an arthropod's ability to survive, escape, or repopulate a high-severity fire area. Unfortunately, these attributes were only infrequently reported. Further, when multiple taxa were collected in a single trap or data were lumped into a single taxonomic group (e.g., beetles), functional group, and distinction of generalists or specialists was difficult to establish. Importantly, most studies also neglected to mention what life stage (immobile or mobile) or whether their focal organism occupied subterranean habitats during the fire, and this information is unfortunately impossible to determine post-hoc for outside readers especially when species were lumped by higher-order taxon, functional group or community. To be able to make predictions about how fire will impact species, future studies should report diet breadth, dispersal ability and subterranean life stages of their organisms at the time of the fire whenever possible.

In addition to the limitations associated with the specific moderators described above, many studies were omitted from our analyses because they did not report any measure of variance (e.g., standard error) within the text or in their figures, and raw data were not available to directly calculate means and variance. Further, some studies that reported variance failed to specify if their variance measure corresponded with the control or the experimental treatment (e.g., in some data tables there was only one column for variance even though there were multiple treatments) while others did not indicate if the reported variance was the standard deviation or standard error. While these additional data on how fire affects arthropods would have been helpful, these studies had to be excluded from our analysis; to increase the number of studies in future meta-analyses, it is imperative that researchers report both the mean and a measure of variance in their studies, or make their data available so that calculations could be performed. We also frequently struggled to determine the sample sizes for replication of both the control and fire treatments and appreciated authors who included that information clearly in the methods or table/figure captions. An additional problem with replication is that >50% of the studies in our meta-analysis included fewer than 10 replicates in either the control or fire treatment and more worryingly 21% of the studies had sample sizes between 1-4. These sample sizes are small enough to cause concern about the power of some studies to detect an effect of fire.

### 4.5 | Conclusions

Altered fire regimes are an anticipated result of global climate change. Our meta-analysis highlights the negative relationship between arthropod communities and increasing fire severity. Even a year after a burn, the effects of fire were associated with modified community dynamics that favoured a few abundant species. Furthermore, while fires occur in a number of different types of ecosystems, we found that arthropod community responses to fire varied by habitat type. We also highlight important knowledge gaps that have hindered our ability to make predictions about how fire will impact arthropod species in the future. One existing challenge in understanding the global implications of fire on arthropods is that North American studies are overrepresented within the pyroentomological literature. Given that fire regimes are changing in ecosystems on nearly every continent, additional studies are needed from underrepresented regions that are increasingly being affected by fire. While the plight of larger wildlife species often attracts most of our attention, arthropods are the most ubiquitous terrestrial animals in several ecosystems; thus, they should gain more attention when assessing the impact of fire on wildlife. With our analysis, we show that high severity wildfires present a serious threat to some arthropod communities whose demise is likely to have broader implications on ecosystem functioning.

### AUTHOR CONTRIBUTIONS

Shannon M. Murphy, Blyssalyn V. Bieber, Dhaval K. Vyas and Mayra C. Vidal conceived the ideas and designed the methodology; Blyssalyn V. Bieber, Dhaval K. Vyas, Shannon M. Murphy, Claire Guzinski, and Kiaryce S. Bey collected the data; Mayra C. Vidal and Laura A. Burkle double checked the data; Mayra C. Vidal performed the meta-analysis; Mayra C. Vidal, Dhaval K. Vyas, Blyssalyn V. Bieber, and Shannon M. Murphy analysed the data; Blyssalyn V. Bieber, Dhaval K. Vyas, Amanda M. Koltz, Laura A. Burkle, Claire Guzinski, Shannon M. Murphy and Mayra C. Vidal wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### ACKNOWLEDGEMENTS

We thank Fernanda Santos, Jennifer Schweitzer, and Joe Bailey for their invitation to this special review and comments on a previous manuscript draft. We thank Meg Eastwood, the University of Denver Science Librarian, for help with the database searches. We thank Adrian Carper for comments on a previous version of the manuscript.

#### CONFLICT OF INTEREST

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data are available from Dryad Data Repository https://doi. org.10.5061/dryad.np5hqbzxb (Bieber et al., 2022).

#### ORCID

Dhaval K. Vyas <sup>(b)</sup> https://orcid.org/0000-0002-6038-606X Amanda M. Koltz <sup>(b)</sup> https://orcid.org/0000-0002-7341-4306 Laura A. Burkle <sup>(b)</sup> https://orcid.org/0000-0002-8413-1627 Shannon M. Murphy <sup>(b)</sup> https://orcid.org/0000-0002-5746-6536 Mayra C. Vidal <sup>(b)</sup> https://orcid.org/0000-0003-3374-8050

### REFERENCES

- Anderson, R. C., Leahy, T., & Dhillion, S. S. (1989). Numbers and biomass of selected insect groups on burned and unburned sand prairie. American Midland Naturalist, 122(1), 151–162. https://doi. org/10.2307/2425692
- Bieber, B. V., Vyas, D. K., Koltz, A. M., Burkle, L. A., Bey, K. S., Guzinski, C., Murphy, S. M., & Vidal, M. C. (2022). Data from: Increasing prevalence of severe fires change the structure of arthropod communities: Evidence from a meta-analysis. *Dryad Data Repository*. https:// doi.org/10.5061/dryad.np5hqbzxb
- Borenstein, M., Hedges, L. V., Higgins, J. P. T., & Rothstein, H. R. (2009). Introduction to meta-analysis. John Wiley & Sons, Ltd.
- Burkle, L. A., Simanonok, M. P., Durney, J. S., Myers, J. A., & Belote, R. T. (2019). Wildfires influence abundance, diversity, intraspecific and interspecific variation of native bees and flowering plants across burned and unburned landscapes. *Frontiers in Ecology and Evolution*, 7, 252. https://doi.org/10.3389/fevo.2019.00252
- Carbone, L. M., Tavella, J., Pausas, J. G., & Aguilar, R. (2019). A global synthesis of fire effects on pollinators. *Global Ecology and Biogeography*, 28(10), 1487–1498. https://doi.org/10.1111/geb.12939
- Certini, G., Moya, D., Lucas-Borja, M. E., & Mastrolonardo, G. (2021). The impact of fire on soil-dwelling biota: A review. *Forest Ecology and Management*, 488, 118989. https://doi.org/10.1016/j.foreco.2021.118989
- Cohen, J. (1988). Statistical power analysis for the behavioral sciences (2nd ed.). Lawrence Erlbaum.
- Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Metaanalysis and the science of research synthesis. *Nature*, 555, 175– 182. https://doi.org/10.1038/nature25753
- Harrer, M., Cuijpers, P., Furukawa, T. & Ebert, D. D. (2019). dmetar: Companion R package for the guide 'Doing Meta-Analysis in R'. R package version 0.0.9000. http://dmetar.protectlab.org/
- Heikkala, O., Martikainen, P., & Kouki, J. (2016). Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. *Biological Conservation*, 194, 39–47. https://doi. org/10.1016/j.biocon.2015.12.002
- Heikkala, O., Martikainen, P., & Kouki, J. (2017). Prescribed burning is an effective and quick method to conserve rare pyrophilous forestdwelling flat bugs. *Insect Conservation and Diversity*, 10, 32–41. https://doi.org/10.1111/icad.12195
- Hiers, J. K., O'Brien, J. J., Varner, J. M., Butler, B. W., Dickinson, M., Furman, J., Gallagher, M., Godwin, D., Goodrick, S. L., Hood, S. M., Hudak, A., Kobziar, L. N., Linn, R., Loudermilk, E. L., McCaffrey, S., Robertson, K., Rowell, E. M., Skowronski, N., Watts, A. C., & Yedinak, K. M. (2020). Prescribed fire science: the case for a refined research agenda. *Fire Ecology*, *16*, 11. https://doi.org/10.1186/s42408-020-0070-8
- Høye, T. T., Loboda, S., Koltz, A. M., Gillespie, M. A. K., Bowden, J. J., & Schmidt, N. M. (2021). Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. Proceedings of the National Academy of Sciences of the United States of America, 118, e2002557117. https://doi.org/10.1073/ pnas.2002557117
- Hurteau, M. D., & Brooks, M. L. (2011). Short- and long-term effects of fire on carbon in US dry temperate forest systems. *Bioscience*, 61, 139–146. https://doi.org/10.1525/bio.2011.61.2.9
- Huwaldt, J. A. (2020). PlotDigitizer (version 2.6.9) [computer software]. plotdigitizer.sourceforge.net.

- IPCC, Core Writing Team. (2014). Climate change 2014: Synthesis report, Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.
- Kim, T. N., & Holt, R. D. (2012). The direct and indirect effects of fire on the assembly of insect herbivore communities: examples from the Florida scrub habitat. *Oecologia*, 168, 997-1012. https://doi. org/10.1007/s00442-011-2130-x
- Koltz, A. M., Burkle, L. A., Pressler, Y., Dell, J. E., Vidal, M. C., Richards, L. A., & Murphy, S. M. (2018). Global change and the importance of fire for the ecology and evolution of insects. *Current Opinion in Insect Science*, 29, 110–116. https://doi.org/10.1016/j.cois.2018.07.015
- Konno, K., Akasaka, M., Koshida, C., Katayama, N., Osada, N., Spake, R., & Amano, T. (2020). Ignoring non-English-language studies may bias ecological meta-analyses. *Ecology and Evolution*, 10, 6373– 6384. https://doi.org/10.1002/ece3.6368
- Lehmitz, R., Russell, D., Hohberg, K., Christian, A., & Xylander, W. E. (2012). Active dispersal of oribatid mites into young soils. *Applied Soil Ecology*, 55, 10–19. https://doi.org/10.1016/j.apsoil.2011.12.003
- Malison, R. L., & Baxter, C. V. (2010). Effect of wildfire of varying severity on benthic stream insect assemblages and emergence. Journal of the North American Benthological Society, 29(4), 1324–1338. https:// doi.org/10.1899/09-022.1
- Mason, S. C., Jr., Shirey, V., Ponisio, L. C., & Gelhaus, J. K. (2021). Responses from bees, butterflies, and ground beetles to different fire and site characteristics: A global meta-analysis. *Biological Conservation*, 261, 109265. https://doi.org/10.1016/j.biocon.2021.109265
- Meineke, E. K., Classen, A. T., Sanders, N. J., & Jonathan Davies, T. (2019). Herbarium specimens reveal increasing herbivory over the past century. *Journal of Ecology*, 107(1), 105–117. https://doi. org/10.1111/1365-2745.13057
- Moretti, M., Duelli, P., & Obrist, M. K. (2006). Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. *Oecologia*, 149, 312–327. https://doi.org/10.1007/s0044 2-006-0450-z
- Murphy, S. M., Vidal, M. C., Hallagan, C. J., Barnes, E. E., & Broder, E. D. (2017). A slow-growth high-mortality meta-analysis for insects: a comment on Chen and Chen. *Journal of Insect Science*, 25, 352–354. https://doi.org/10.1111/1744-7917.12459
- Murphy, S. M., Vidal, M. C., Smith, T. P., Hallagan, C. J., Broder, E. D., Roland, D., & Cepero, L. C. (2018). Forest fire severity affects host plant quality and insect herbivore damage. *Frontiers in Ecology* and Evolution., 6(135), 1–11. https://doi.org/10.3389/fevo.2018. 00135
- Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, 13(1), 4–21. https://doi.org/10.1111/2041-210X.13724
- Nakagawa, S., Noble, D. W. A., Senior, A. M., & Lagisz, M. (2017). Meta-evaluation of meta-analysis: Ten appraisal questions for biologists. *BMC Biology*, 15(18), 1–14. https://doi.org/10.1186/ s12915-017-0357-7
- Nicholson, C. C., & Egan, P. A. (2020). Natural hazard threats to pollinators and pollination. *Global Change Biology*, 26, 380–391. https:// doi.org/10.1111/gcb.14840
- Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., & Wilmer, P. (2003). Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos*, 101(1), 103–112. https://doi.org/10.1034/j.1600-0706.2003.12186.x
- Pressler, Y., Moore, J. C., & Cotrufo, M. F. (2018). Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos*, 00, 1–19. https://doi. org/10.1111/oik.05738
- Price, P. W., Bouton, C. E., Gross, P., Mcpheron, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among 3 trophic levels-Influence of plants on interactions between insect herbivores and

- Price, P. W., Denno, R. F., Eubanks, M. D., Finke, D. L., & Kaplan, I. (2011). Insect ecology: behavior, populations and communities. Cambridge University Press.
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org
- Rosenberg, M. S. (2005). The file-drawer problem revisited: A general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, *59*, 464–468. https://doi.org/10.1554/04-602
- Senior, A. M., Grueber, C. E., Kamiya, T., Lagisz, M., O'dwyer, K., Santos, E. S., & Nakagawa, S. (2016). Heterogeneity in ecological and evolutionary meta-analyses: Its magnitude and implications. *Ecology*, 97(12), 3293–3299. https://doi.org/10.1002/ecy.1591
- Stireman, J. O., & Singer, M. S. (2018). Tri-trophic niches of insect herbivores in an era of rapid environmental change. *Current Opinion in Insect Science*, 29, 117–125. https://doi.org/10.1016/j.cois.2018.07.008
- Thompson, H. M., Lesser, M. R., Myers, L., & Mihuc, T. B. (2022). Insect community response following wildfire in an Eastern North American pine barrens. *Forests*, 13, 66. https://doi.org/10.3390/f13010066
- Van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., & Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, 368(6489), 417–420. https://doi.org/10.1126/science.aax9931
- Vidal, M. C., & Murphy, S. M. (2018). Bottom-up vs. top-down effects on terrestrial insect herbivores: A meta-analysis. *Ecology Letters*, 21(1), 138–150. https://doi.org/10.1111/ele.12874

Viechtbauer, W. (2010). Conducting meta-analyses in R with the meta-

Functional Ecology

2109

- for package. Journal of Statistical Software, 36(3), 1–48. https://doi. org/10.18637/jss.v036.i03
- Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. Proceedings of the National Academy of Sciences of the United States of America, 118(2), e2023989118. https://doi.org/10.1073/ pnas.2023989118

### SUPPORTING INFORMATION

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

How to cite this article: Bieber, B. V., Vyas, D. K., Koltz, A. M., Burkle, L. A., Bey, K. S., Guzinski, C., Murphy, S. M., & Vidal, M. C. (2023). Increasing prevalence of severe fires change the structure of arthropod communities: Evidence from a meta-analysis. *Functional Ecology*, *37*, 2096–2109. https://doi.org/10.1111/1365-2435.14197