

Community Responses to Fire: A Global Meta-Analysis Unravels the Contrasting Responses of Fauna to Fire

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Abstract: Globally, wildfires and prescribed fires are becoming more prevalent and are known to affect plant and animals in diverse ecosystems. Understanding the responses of animal communities to fire is a central issue in conservation and a panacea to predicting how fire regimes may affect communities and food webs. Here, a global meta-analysis of 2581 observations extracted from 208 empirical studies were used to investigate the effect of fire on aboveground and belowground fauna (e.g., bacteria, fungi, small mammals, arthropods). Overall, results revealed that fire had a negative effect on biomass, abundance, richness, evenness, and diversity of all faunas. Similarly, when considering wildfires and prescribed fires the data revealed that both fire regimes have negative effects on fauna. Similarly, fire had negative impacts on aboveground and aboveground fauna across most biomes and continents of the world. Moreover, there was little evidence of changes in pH, moisture and soil depth on soil organisms suggesting that other factors may drive community changes following a fire disturbance. Future research in fire ecology should consider the effects of fire across several species and across larger geospatial scales. In addition, fire effects on faunal community structure must be studied under contrasting global fire regimes and in light of the effects of climate change.

Keywords: prescribed; wildfire; invertebrates; vertebrates; belowground; aboveground



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1. Introduction

Fires are a natural part of ecological function in many parts of the world, and are widely acknowledged as a disturbance that can affect the ecological function of soil, flora and fauna in various ecosystems [1–6]. In recent decades, the incidence of fires has burgeoned due to anthropogenic mediated land use changes [7,8] and natural environmental factors such as prolonged summer droughts [9], lightning strikes [10,11], high combustibility of vegetation [12], increased net primary productivity [13], prolonged fire seasons [14,15], and a rapidly changing climate [16,17]. The increase in fire frequency has put fire regimes at the vanguard of global change, because fires can cause positive feedback loops that potentially compound global climate change [18].

Fire prevalence and its associated effects can vary across biomes and geographical regions. The effects of fire on soil and organisms have been extensively examined for many biomes such as savannahs [2,19], boreal forests in North America [20,21] and grasslands [22,23]. While the role of fire on organisms at a global scale has been extensively addressed [24,25], more studies are needed to fully understand the role of fire in shaping organism population dynamics in different biomes [25]. For instance, fires can drive the distribution and function of savannah biomes [26]. Researchers have demonstrated that fire can change tree community structure and can maintain savannah biomes [27]. Similarly, varying abiotic conditions (e.g., moisture, pH) also shape biomes. For example, in Africa, low rainfall deterministically results in savannah biomes whilst high rainfall shapes forests [28]. Consolidative studies that quantify fire effects on a range of organisms, with a broad geographical scope (that includes ecoregions and ecosystem types worldwide)

and that account for specific characteristics of these fire events (e.g., wildfires versus prescribed fires), are still lacking, even though such work is fundamental to gaining a better understanding of the environmental effects of fires globally.

Several researchers have documented the effects of fire on plant communities and have revealed the links between plants and animals after a fire disturbance [5,12]. Much of these works have revealed that fire can have positive, negative, and neutral effects on soils, organisms and plants [29,30]. For instance, some researchers have demonstrated that fire of varying intensities and degrees destroy vegetation and change soil physical, chemical, and biological properties potentially leading to reductions in soil quality [31]. Elsewhere fires are documented to increase soil pH and available nutrients [32], reduce soil moisture, and reduce organic soil carbon (C) and nitrogen (N) [33]. It is plausible that the changes in soil quality may subsequently impact organisms in a particular ecosystem. Given that fires of varying degrees can affect variety of soil, faunal and floral components in an environment, it is imperative to understand the effects of fire types (prescribed versus wildfires) on ecosystem structure, function, and dynamics globally.

Prescribed fire is increasingly used as a sporadic disturbance agent that simulates natural disturbance regimes. This management strategy is designed to clear vegetation, encourage regeneration of trees, improve pastures for foraging, reduce wildfire hazards [34,35], and more controversially, promote the conservation of biodiversity [36,37]. The latter suggestion that prescribed fires can promote conservation and biodiversity is predicated on two seminal hypotheses. The first hypothesis, the Intermediate Disturbance Hypothesis posits that species diversity will be highest in ecosystems that are subject to moderate levels of disturbance, and suggest that the habitat heterogeneity created by such disturbance serves as a precursor for biodiversity increases [38]. Findings of the Intermediate disturbance hypothesis are widely supported in the literature [25]. The second hypothesis, the Patch Mosaic Burn Hypothesis asserts that fires are an effective way to create habitat heterogeneity, because they create a mosaic of burned and unburned patches across space and time [39], which potentially creates habitat differences that can support a suite of organisms with different life history traits. The Intermediate Disturbance Hypothesis and Patch Mosaic Burn Hypothesis suggest that pyrodiversity (the spatial and temporal variability in fire effects) results in increases in biodiversity [40,41]. While these concepts broadly encapsulate the basis for the management of vegetation and biodiversity supporting evidence is contradictory (e.g., [42–45]) and confined to a limited range of taxonomic groups [46] with divergent life histories.

Responses of fauna to fire are mediated by a combination of their life history traits and the characteristics of the fire regimes that they are exposed to (reviewed by Robinson et al. [47]). Life history traits that often mediate the effects of fires are reproduction mode (e.g., parthenogenesis), dispersal ability, morphological adaptations, and body size [48–50]. Specifically, some traits include morphological adaptations to detect fire, including smoke-detecting antennae in cerambycid beetles [51], chemo-reception and visual perception of smoke in reed frogs [52], and infrared radiation sensors in buprestid beetles [53,54]. Moreover, some organisms are good dispersers and can often disperse away from the fire, while others can burrow into the soil [55,56], while some can recover quickly after a fire due to their ability to reproduce via parthenogenesis (e.g., Collembola; [50]). Postfire, faunal population responses will likely vary among species with different behaviors or life history traits that allow them to persist through fire. For instance, some animals live in burrows and are thus protected from direct contact with fires. Some animals quickly disperse and recolonize sites after fire. A recent study showed that fire increases abundance and richness of insect and bird pollinators globally, but short fire intervals only affect a select group of Lepidoptera (butterflies and moths) [57]. Because many insects are good flyers, they are able to recolonize or forage in burnt areas as soon as flowers are available [58,59]. In addition, ground-dwelling arthropods that survive the fire, as well as those that are eusocial may benefit in burned environments due to lower competition for floral resources and lower predation risk [60,61]. In addition, omnivorous fauna tend to recolonize burned sites

faster than organisms that depend on nectar (e.g., pollinators), as the latter need specific floral resources that may not be readily available immediately following a fire [59,62]. Belowground (organisms that spend copious amounts of time underground) organisms such as bacteria that are below the soil surface are potentially more protected from fire, and they will often recover more rapidly after fire than fungi [30,63]. Contrariwise, aboveground organisms (organisms that spend much of their life on the surface of the soil) such as red foxes, spotted owls and grasshoppers are not affected by fires [64,65], possibly owing to their ability to disperse.

Fires can have acute and chronic effects on organisms in terrestrial biomes. Acutely, fires can result in carbon monoxide poisoning, respiratory impairment, neurological impairment, respiratory and cardiovascular disease, oxidative stress, and immunosuppression, physical injury, or deaths of organisms. For instance, small mammals that dwell in highly flammable Australian alpine habitats are highly susceptible to fires and have been documented to die during a fire and immediately following a fire [50,51]. In the long-term fire may also have prolonged indirect effects on organisms by changing patterns of vegetation succession and the subsequent occurrence of key plants and landscape structure, which may increase the influence of biotic factors such as predation [66,67]. Concurrently, changes in organism abundance and diversity during and after a fire may change trophic interactions [41,68] in different biomes and alter the resilience of entire communities and ecosystems postfire. Because faunal communities can be differentially affected by fires, some faunal communities can be useful proxies in developing fire regimes appropriate to the maintenance of biodiversity [69–71]. However, before considering using organisms as proxies of fire effects on an ecosystem, there is a need to understand how specific group of organisms will react to fire effects.

Although several studies have examined the effects of fire on animal and plant communities in individual ecosystems [72–74], there is a need for more data on the global effect of fires on organisms because data are only available for a few species. In addition, studies that present a global view of fire types (prescribed burning versus wildfire) and the associated effect of aboveground and belowground (living in the soil) organisms are scanty. Here, I conducted a global meta-analysis of the literature to figure out the extent to which organism biomasses, abundances, and diversity are affected by fire disturbances. Given the contrasting studies that document the effect of fires on organisms, I aimed to answer the following questions: (1) to what extent does fire disturbance affect aboveground and belowground organisms? (2) how do contrasting fire types (prescribed vs. wildfire) and fire intensities affect organisms? (3) how do fire effects vary across biomes and continental scales? (4) how do key abiotic factors such as moisture, pH, and sampling depth influence belowground organism responses to fire? Two hypotheses were tested: (A) aboveground organisms will be negatively affected to a greater extent than belowground organism as the former tend to have the ability to move and to other habitats compared to their underground counterparts, and (B) Abiotic factors (i.e., pH, sampling depth and depth) should have differential effects on organisms (see Table 1 for expectations). In addressing the preceding questions and hypothesis, I discuss the underlying mechanisms driving organism response to fires. Knowledge gaps in the literature and recommended research priorities for understanding the consequences of fire regimes on organisms and ecosystem function are also discussed.

Table 1. Tabular summary of the study questions, hypotheses, and expectations. See methods (Section 2.3) for statistical descriptions used to address questions in this meta-analysis.

	Expectations
<p>Question 1: to what extent does fire disturbance affect aboveground and belowground organisms?</p> <p>Hypothesis A: <i>aboveground organisms will be negatively affected to a greater extent than belowground organism as the latter tend to have the ability to move and to other habitats compared to their underground counterparts</i></p>	<ul style="list-style-type: none"> • Effects of fire on belowground > than aboveground • The effects on above ground and belowground will be taxon specific
<p>Question 2: how do contrasting fire types of intensities affect organisms?</p>	<ul style="list-style-type: none"> • High fire intensities should result in negative effects
<p>Question 3: how do fire effects vary across biomes and continental scales?</p>	<ul style="list-style-type: none"> • No specific expectations
<p>Questions 4: how do key abiotic factors such as moisture, pH, and sampling depth influence below-ground organism responses to fire?</p> <p>Hypothesis B: <i>Abiotic factors should have differential effects on organisms</i></p>	<ul style="list-style-type: none"> • Fire decreases moisture which decreases fauna • Fire effects on organism less pronounced at higher depths • Fire increases pH (liming effect) which increases nutrients and possibly increase organism recovery

2. Methods

2.1. Article Search

I developed an a priori systematic search and screening protocol to find articles that investigated the effects of fires on all fauna available in the literature. I used the free software "Publish or Perish" [75] to locate articles from 1900 to 2021 in English. I conducted the search in October 2021. I used the following search terms to locate articles on fire impacts on animals: ("fire*" OR "wildfire*" OR "burn*" OR "pyrogenic*" OR "organic matter*") AND ("function*" OR "response*" OR "measure*" OR "abundance*" OR "biomas*" OR "diversity*") AND ("belowground*" OR "aboveground*" OR "*organism*" OR "microorganisms*" OR "soil microbe*" OR "soil biota*" OR "soil animal*" OR "soil biodiversity*" OR "soil fauna*" OR "soil flora*" OR "arthropod*" OR "spider*" OR "invertebrate*" OR "snail*" OR "slug*" OR "earthworm*" OR "nematode*" OR "*protozoa*" OR "bacteria*" OR "fungi*" OR "acari*" OR "*worm*" OR "collembola*" OR "dipluran*" OR "proturan*" OR "symphytan*" OR "archaea*" OR "pauropoda*" OR "arachnid*" OR "enchytraeid*" OR "microbe*" OR "crustacea*" OR "beetle*" OR "hexapoda*" OR "hymenoptera*" OR "ant*" OR "termite*" OR "myriapod*" OR "mollusc*" OR "mollusk*" OR "periwinkle*" OR "isopod*" OR "amphipod*" OR "polychaet*" OR "gammarid*" OR "reptile*" OR "amphibians*" OR "salamanders*" OR "frogs*" OR "herpetofauna*" OR "insect*" OR "turtle*" OR "snake*" OR "vertebrate*" OR "small mammal*" OR "rodent*" OR "mole*" OR "rats*" OR "mice*" OR "squirrels*" OR "hamster*" OR "porcupine*" OR "tardigrade*" OR "rotifer*" OR "archaea*" OR "scorpion*"). The search string was created to include three main elements of my primary question (linked by the Boolean operator 'AND'; [76,77]). Additionally, these complex group of keywords were added to avoid the inclusion of the considerable number of studies reporting general information on fire occurrence with no associated measured effects of fire reported.

2.2. Inclusion Criteria and Screening

The initial search identified over 900 articles that potentially investigated fire impacts on organisms. I removed duplicate articles and then conducted three screening steps to locate articles that included information on fire effects on fauna (See Table S1 in Supplementary Information). I performed forward (papers that cited each selected paper) and backward (papers cited by each selected paper) searches on all identified articles to obtain additional data. The forward and backward searches yielded an additional 500 papers. After applying the same criteria for inclusion (detailed below) to these studies, I ultimately included 50 studies in the final analyses (Table S1). Initially, I screened articles based on titles, then abstracts, and finally screened the full text of all remaining articles. A single article could contribute multiple impact measurements to the database. Using the Population, Intervention, Control, and Outcome framework inclusion criteria (PICO; [78]) and the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA; [76]), the following a priori acceptance criteria were used for studies to be included in the meta-analysis: (1) studies must measure the response of one or more organisms to fire (*Population*); (2) all articles had to include replicate plots or study sites where fire effects were recorded (*Intervention*) (3) studies must compare the response(s) of said soil organism(s) between either burned and no burned, or pre-fire and post-fire areas (*Control*); (4) measured response variables must include either biomass, abundance, richness (e.g., number of species, number of operational taxonomic units), evenness or diversity indices (*Outcome*; See Table 2), (5) studies must report mean responses, standard deviation or standard error, and sample size. After considering the above criteria I included 208 studies from different biomes of the world in my final analyses (see Figure 1 and Supplementary File for all data included in the final meta-analyses).

Table 2. Summary of the broad categories of response variables of studies in the meta-analysis, and the specific description of response variables that comprise them.

General Response Variable	Specific Response Variable
Abundance	representation of number of organisms
	Number of Individual per unit area/volume (e.g., ind.m ⁻² , individual.core ⁻¹ , individual. gram of soil ⁻¹ , nematodes. cm ⁻³)
	Colony Forming Units (CFU) Spores per unit of soil
Biomass	total mass of organisms in an area, habitat, or region dry weight (mg.g ⁻¹ , ug ergosterol/g, PLFA/Kg, ug/g dry soil, mg)
Richness	number of species in a community (number of species or genera, families, OTUs, morphospecies, groups) Shannon-Wiener diversity index
Diversity	Simpson Diversity Index McIntosh index
Evenness	Pielou's evenness, Simpson's equitability, Shannon evenness

2.3. Data Extraction

I extracted 20 pieces of data from each publication. The data extracted related to study characteristics (e.g., publication year, biome, taxon) or quantitative measurements (e.g., mean richness, sample size, and standard deviation). I documented the article's first author, publication year, country, fire intensity, type of fire, and whether fauna occurred aboveground or belowground. When authors documented explicitly how they determined the fire intensities and their associated classes [low (light), moderate, severe], I included these in the data extraction. When documenting biomes, I listed plantations and agricultural land as disparate biomes because these landscapes experience different management practices and thus the use of fire and pesticides may potentially shape the flora and faunal communities in these ecosystems. I used broad taxonomic classifications based on other systematic reviews in ecology (amphibians [$N = 16$], reptiles [$N = 41$], avian [$N = 61$],

arthropods [$N = 1181$], small mammals [$N = 61$], mollusks [$N = 33$], nematodes [$N = 84$], annelids [$N = 16$], microbes [$N = 328$], bacteria [$N = 295$] and fungi [$N = 465$]). Annelids, some arthropods, fungi, microbes, bacteria, and nematodes were considered belowground taxa whereas amphibians, some arthropods, birds, mammals, molluscs, and reptiles were considered aboveground organisms. Many of the studies only measured ‘microbes’ as a group using methods that do not discriminate between organisms (e.g., using chloroform fumigation), as such I considered ‘microbial’ responses separately from other animal groups in the analyses. In addition, I also collected abiotic variables (moisture, depth, and pH) from each of the studies. After literature sources were compiled, I extracted data from text, tables, or graphs. If the data were not reported in numbers, they were extracted from published diagrams using PlotDigitizer Version 3 (<http://plotdigitizer.sourceforge.net>, accessed 14 December 2022; [79]). I extracted any data that presented the central tendency (mean or median if no mean was presented) in response to fire exposure. If the study was an experimental manipulation, I extracted data from the treatments containing the manipulation and the control. If a study evaluated multiple treatments (e.g., two fire regimes such as low severity fires and high severity fires), I extracted all the data contained in the paper. If the authors described multiple experiments for a given response that were independent of each other, e.g., conducted over two distinct time periods, or if the authors reported results of a pilot study as well as the main study, I included records from each experiment.

The literature search yielded studies with a range of response variables. I only included response variables most strongly related to abundance, biomass, richness, diversity, and evenness (see Table 2 for detailed descriptions) and grouped different specific response variables into representative broad categories.

2.4. Effect Size Calculation and Analysis

Because studies extracted often used different approaches to measure and gather abundance, biomass, and diversity data, I used the Hedges’ g as a measure of effect size to estimate the differences between experimental treatments (i.e., exposed to prescribed and wildfires) and control groups (no fire exposure). Hedges’ g effect size and variance were calculated for each observation within the global dataset (k observations in total) to estimate the differences in the response variable between control and experimental treatment. Hedges’ g , which is the bias corrected standardized mean difference (SMD) between the treatment and control groups [80,81], weighs cases by their sample size and the inverse of their variance [82]. Overall, for all responses, effect sizes for each individual record were calculated using Hedges’ g , which is essentially Cohen’s d multiplied by a correction factor [82].

$$\text{Hedges' } g = \frac{F_t - F_c}{SD_p} \times J$$

where F_t and F_c are the treatment and control fire treatment groups, respectively. The correction for bias of small sample sizes, is denoted by J , which was estimated as:

$$J = 1 - \frac{3}{4(n_t - n_c - 2) - 1}$$

SD_p , which denotes the pooled standard deviation was enumerated as follows:

$$SD_p = \sqrt{\frac{(n_t - 1) \times SD_t^2 + (n_c - 1) \times SD_c^2}{n_t + n_c - 2}}$$

where n is the sample size and SD is the standard deviation of the treated and control groups. Given that Hedges’ g requires a pooled standard deviation estimate, if a study reported standard error (SE), I converted it to standard deviation (SD) using $SD = SE \times \sqrt{n}$. If a study reported 95% confidence intervals (CI), I assumed a normal distribution and

converted it SD using the formula $SD = CI \times \frac{\sqrt{n}}{1.96}$ (converting reported results to one-way 95% CIs where necessary). Because there can be inequalities in study variances, effect sizes (V_d) were weighted using the inverse of the sampling variance for each effect site as:

$$V_d = \frac{n_t + n_c}{n_t n_c} + \frac{g^2}{2(n_t n_c)}$$

Because the sign of Hedges' g tells the direction of the effect, a negative value of Hedges' g indicates that fire has a negative effect on the specific response considered. Hedges' g values of less than ± 0.2 represent small effects, values between ± 0.2 and ± 0.5 represent moderate effects, with values greater than ± 0.5 suggesting large effects [83].

All meta-analysis computations were done in R (version 4.1.2, Vienna, Austria) [84], using the metafor package [85]. All statistical models were performed using the 'rma.mv' function of the metafor package in R. The 'rma.mv' function, which uses a Wald-type test to determine statistical difference among tested groups [85], is often useful for global meta-analyses [86]. Mixed effects models were run that included the study identification number (i.e., the ID of the study as reported in the dataset) and the response (abundance, biomass, diversity, evenness, richness) as random effects to account for heterogeneity and non-independence of results. Effect sizes (Hedges' g) for each of the models including categorical fixed factors were considered to be statistically significant if their 95% confidence interval (CI) did not overlap with zero and if their p values were less than 0.05.

To examine the effects of pH, moisture and soil depth a meta-regression was performed using the 'lmer' function from the lme4 library to perform mixed-effect regression analyses [87]. These 'lmer' function was selected because it assume that the sampling variances are not known [88].

2.5. Publication Bias

An intrinsic problem in any systematic quantitative review is the possibility of publication bias, that is, studies showing significant results have a higher probability of being published. As such, potential publication bias was assessed using Egger's regression test [89]. Potential publication bias was determined when groups studied showed evidence of funnel plot asymmetry ($p \leq 0.05$). When potential bias was detected, I examined the data for potential outliers by looking at the effect sizes with standardized residual values exceeding the absolute value of three [85] using the standard function in R. Potential outliers were removed to adjust for publication bias. For all the analyses adjusting for publication bias did not change the interpretation of the analyses (based on comparing fitted random-effects models with and without the influence of the potential outliers). In addition, I performed a "trim-and-fill" method [90,91], which is used as a sensitivity analysis that recalculates the estimated mean effect size; this provides an estimate of how the overall effect size would change if missing studies were incorporated [92,93]. The mean effect size estimate for the data before trim-and-fill was identical to the estimate after trim-and-fill. Overall, the sensitivity analyses showed that the results of the models were robust against publication bias.

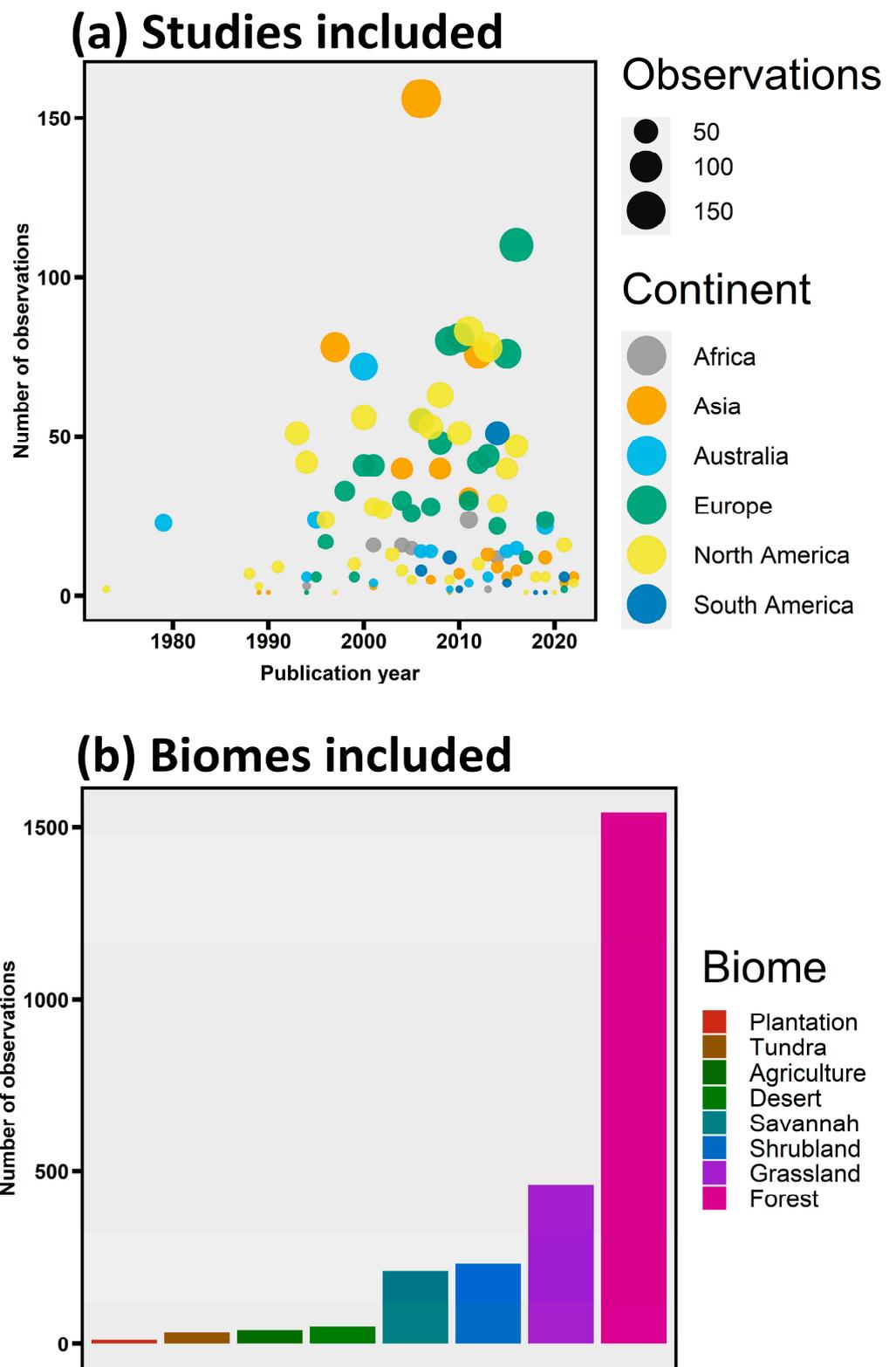


Figure 1. The locations of study sites (N = 208) that met all selection criteria and were used for meta-analysis. Classification of biomes is based on Olson et al. [94].

2.6. Distribution of Data in the Literature

Most studies included in the meta-analysis focused on bacteria, fungi, microbes, and arthropods, whereas a much smaller percentage focused on nematodes, annelids and molluscs. No studies looked at Archaea alone but presumably these were all included in microbial biomass estimates. Fewer studies considered vertebrates compared to invertebrates, with the bulk of studies focusing on small mammals and birds; with fewer studies documenting fire effects on amphibians and reptiles. Studies investigating abundance and richness were more common than studies examining aspects of diversity and evenness. While studies were distributed across different biomes, most studies were conducted in forests, shrublands and grasslands with fewer studies in the tundra. Studies investigating wildfires were more ubiquitous compared to prescribed fires. Sampling methods varied widely across all studies (see Supplementary Addendum; Table S5).

3. Results

3.1. Effect of Fire on Aboveground and Belowground Fauna (Question 1)

Generally, results revealed that the effect of fires varies in aboveground and belowground organisms (Figures 2 and 3; Supplementary Tables S2 and S3). Amphibian abundance and richness was positively affected by fire (effects ranged from moderate to large). Small mammal abundance and richness was not affected by fire. Bird biomass and diversity were not affected by fire while fire had moderate positive effects on abundance and richness of birds. Arthropod biomass and diversity were not affected by fire, while evenness and richness were also positively affected by fire. While arthropod biomass (aboveground) and diversity (aboveground and belowground) were not affected fire had small negative effects on abundance of arthropods. Regarding reptiles, fire had no effect on abundance and diversity of reptiles but had a small positive effect on richness of reptiles. Fire had strong negative effects on abundance and richness of molluscs.

Regarding belowground fauna, annelids, arthropods, bacteria, fungi, and nematodes were all negatively affected by fires, with the exception of microbes that were only affected negatively in biomass and positively in richness only (Figure 3; Tables S2 and S3). Fire had no effect on abundance, diversity, and evenness in microbes. In addition, fire had no effects on biomass in nematodes and richness in bacteria.

Summarizing data across all groups (Figure 4; Tables S2 and S3), revealed that fire exposure has moderately significant negative effects on abundance, biomass, diversity, evenness, and richness. Strikingly, negative fire effects were more pronounced in belowground animals compared to aboveground animals (Figures 2, 3 and 5; Table S4), contrary to the a priori expectations (**Hypothesis A**).

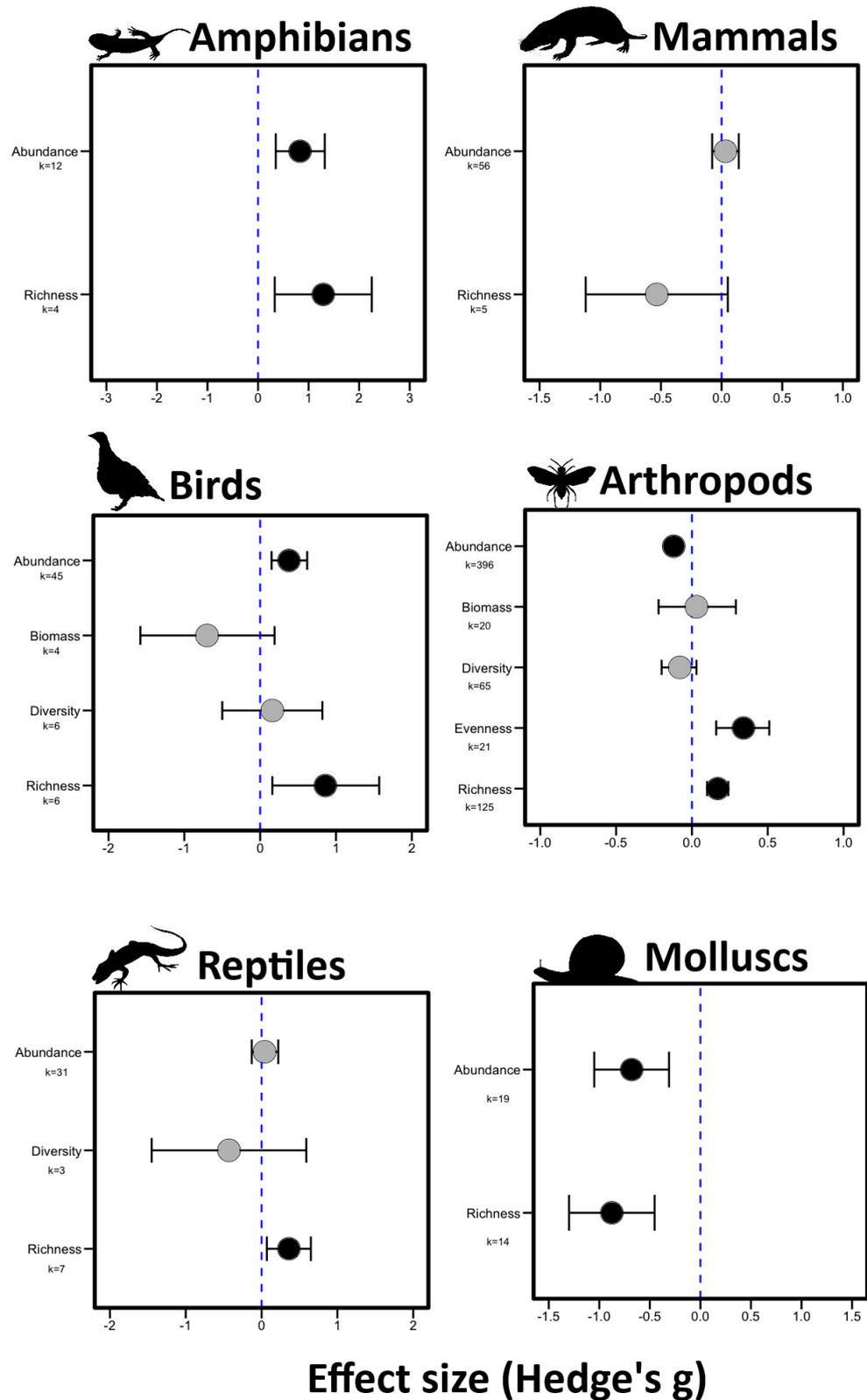


Figure 2. Effect of fire on abundance, biomass, diversity, evenness, and richness of aboveground faunal groups. The x-axis shows overall effect size (Hedges' g). k is the number of observations included in each analysis. Circles denote the hedges' g value and lines denote the 95% confidence intervals (CI) for each Hedges' g value. Black circles represent significant effects whilst grey circles show no significant effects the Hedges' g value.

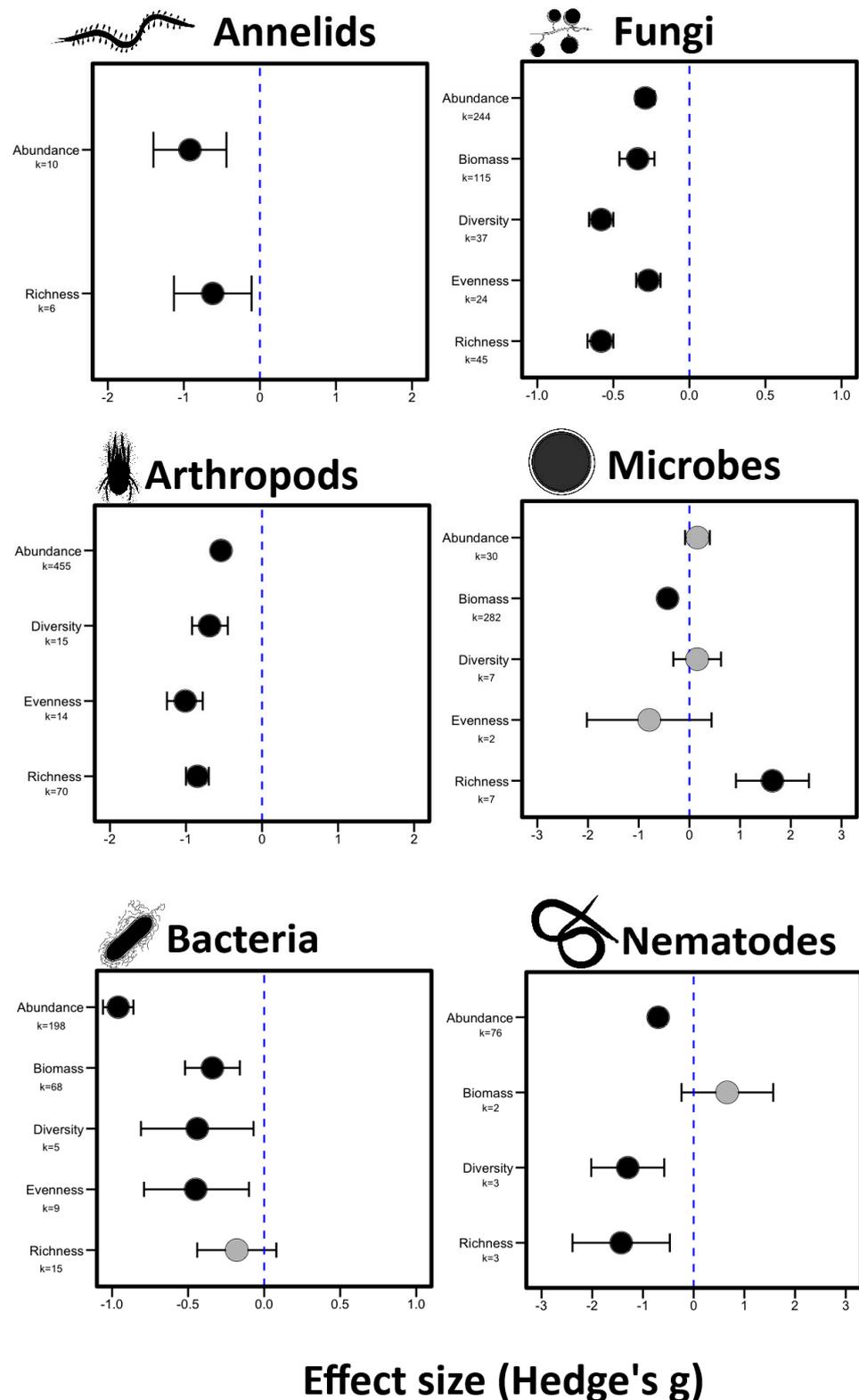


Figure 3. Effect of fire on abundance, biomass, diversity, evenness, and richness of belowground faunal groups. The x-axis shows overall effect size (Hedges' g). k is the number of observations included in each analysis. Circles denote the Hedges' g value and lines denote the 95% confidence intervals (CI) for each Hedges' g value. Black circles represent significant effects whilst grey circles show no significant effects the Hedges' g value.

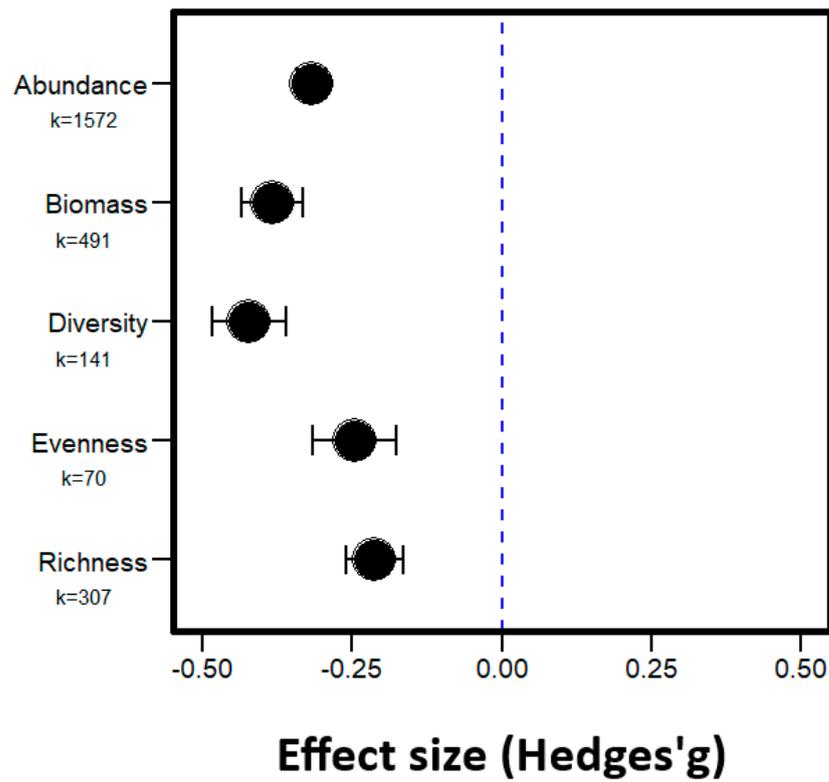


Figure 4. Overall effect of fire on abundance, biomass, diversity, evenness, and richness of all faunal groups. The x-axis shows overall effect size (Hedges' g). k is the number of observations included in each analysis. Circles denote the Hedges' g value and lines denote the 95% confidence intervals (CI) for each Hedges' g value. Black circles represent significant effects whilst grey circles show no significant effects the Hedges' g value.

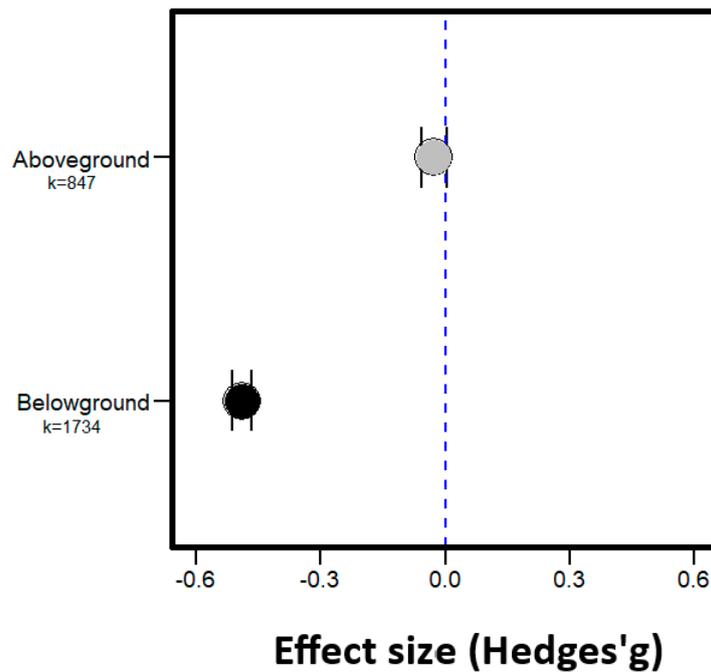


Figure 5. Effects of fire on aboveground and belowground fauna. Circles denote the Hedges' g value and lines denote the 95% confidence intervals (CI) for each Hedges' g value. Black circles are significant effects whilst grey circles show no significant effects.

3.2. Effect of Fire Types and Intensity on Organisms (Question 2)

Overall, fire regimes of varying intensity negatively impacted organisms (Figure 6). Different fire types had significantly different effects on all organisms. Both wildfire and prescribed fire had negative influence on terrestrial organisms. The greatest effect of fire on organisms was apparent in areas with severe fires with light fire having small negative effects on organisms. Moderate fires did not seem to influence organisms.

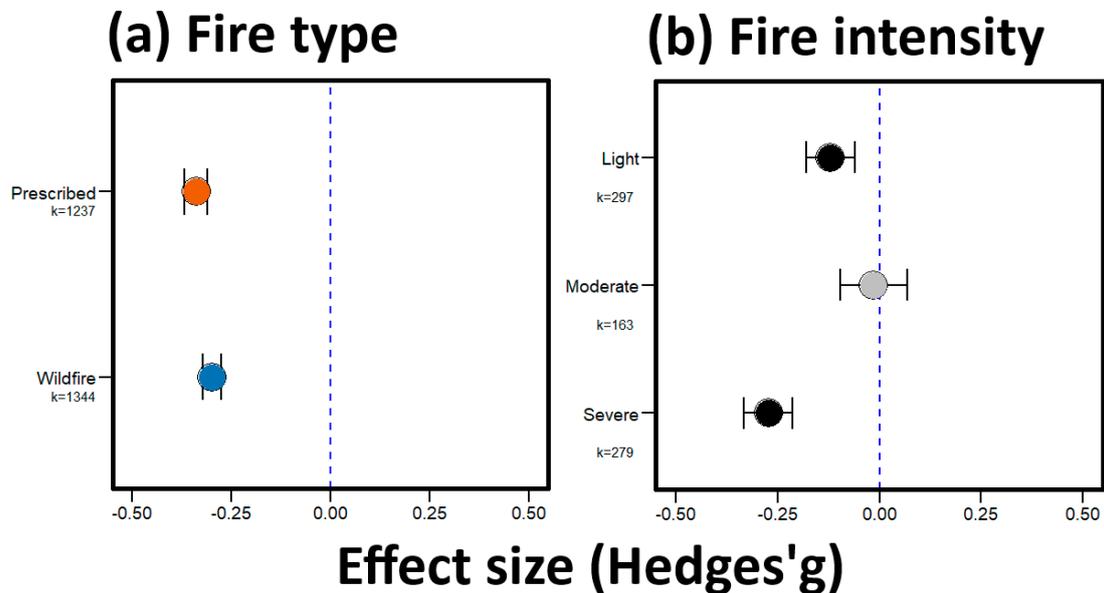


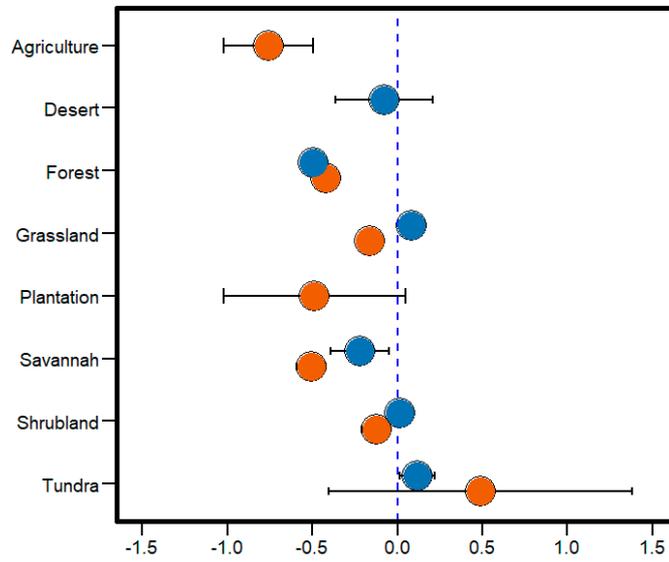
Figure 6. Overall effect of fire regimes (a) prescribed vs. wildfire (b) Fire intensity. The x-axis shows overall effect size (Hedges' g). k is the number of observations included in each analysis. Circles denote the Hedges' g value and lines denote the 95% confidence intervals. In (b), Black circles are significant effects whilst grey circles show no significant effects.

3.3. Global Effect of Fires across Biomes and Continents (Question 3)

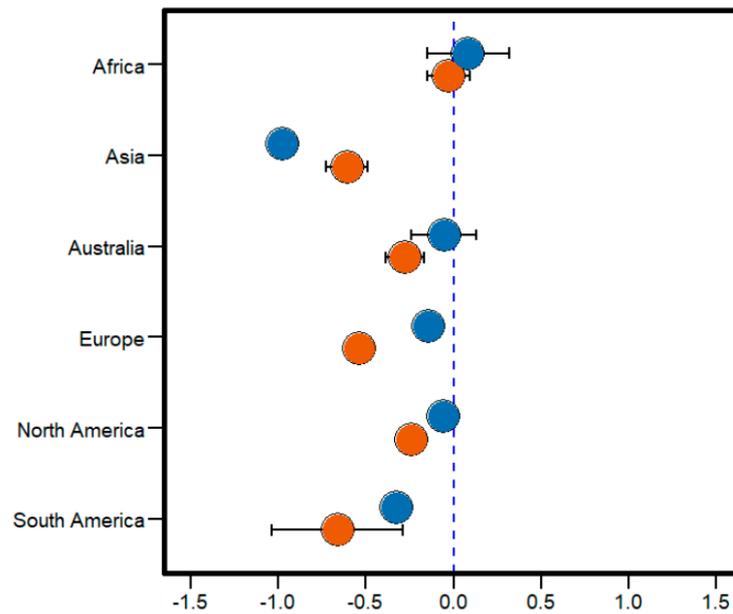
Fire effects on animals differed across biomes and continents (Figure 7 and Table S4). Prescribed fires had negative effects on agricultural land, forests, grassland, savannah, and shrubland biomes. Conversely, wildfire affected organisms negatively in only forest and savannah biomes with marginal positive effects in Tundra and Grassland biomes. Negative fire effects were apparent across all continents with the exception of Africa where prescribed and wildfire did not have significant effects on fauna.



(a) Biomes



(b) Continents



Effect Sizes (Hedges'g)

Figure 7. Overall effect of fire on (a) biomes (b) continents of all faunal groups. Circles denote the Hedges' g value and lines denote the 95% confidence intervals (CI) for each Hedges' g value.

3.4. Relationship between Abiotic Factors and Fire Effects (Question 4)

Contrary to a priori expectations (**Hypothesis B**), moisture, pH and sampling depth were poor predictors of all four responses considered ($p > 0.05$) with one exception (Table 3), whereby moisture content has a negative effect on evenness.

Table 3. Results of regression analyses between effect size (dependent variable = Hedges' g) and three independent variables (log-transformed) extracted from the literature (moisture in %, pH, Depth in cm). Significant differences are highlighted in bold.

Response	Independent Variable	β	SE	Lower-95	Upper-95	R ²	p
Abundance							
	Moisture	322.00	276.73	−187.04	833.74	0.03	0.26
	pH	1846.00	3360.23	−4341.37	8842.58	0.03	0.58
	Depth	1717.50	17,212.01	−1437.74	4868.22	0.03	0.34
Biomass							
	Moisture	0.05	0.03	0.00	0.11	0.12	0.06
	pH	−0.20	0.22	−0.67	0.21	0.12	0.36
	Depth	0.18	0.09	0.00	0.36	0.12	0.05
Diversity							
	Moisture	0.00	0.04	−0.06	0.06	0.13	0.95
	pH	0.48	0.49	−0.37	1.03	0.13	0.41
	Depth	−0.16	0.22	−0.39	0.01	0.13	0.62
Evenness							
	Moisture	−0.08	0.02	−0.11	−0.05	0.72	0.03
	pH	−0.51	0.23	−0.85	−0.16	0.72	0.12
	Depth	0.63	0.36	0.10	1.15	0.72	1.00
Richness							
	Moisture	−0.03	0.06	−0.15	0.07	0.26	0.62
	pH	0.63	0.80	−1.52	1.88	0.26	0.44
	Depth	−0.27	0.16	−0.52	−0.02	0.26	0.20

4. Discussion

Organismal responses to fire have been extensively documented, but inconsistencies among studies have impeded our ability to draw general conclusions for the conservation and management of terrestrial biomes. Here, a meta-analysis of published data was conducted across several taxa in different geographic areas and across several biomes, with the broad aim to improve our ability to predict how fire frequency and severity will alter aboveground and belowground fauna. In summary, abundance, biomass, diversity, evenness, and richness declined following fires. These results were congruent with works documented by other researchers, that suggest fires may alter population dynamics of organisms [30,63]. Contrariwise, the results contradicted findings by other meta-analyses; these studies show positive and negative responses to fire, although looking at them globally, the effects seem neutral [25,65,95]. One key result of this metanalysis is that belowground faunas were more negatively affected by fires compared to their aboveground counterparts (as evidenced by differences in Hedges' g values). The negative responses of the fauna considered here can be explained by several factors. For instance, in belowground organisms burning of the soils can transfer heat to soil, which leads to microbial deaths [96]. Alternatively, declines in fungi and bacteria may arise from reduction in labile carbon. Post-fire declines in above- and belowground net primary productivity can also potentially decrease populations of organisms.

4.1. Belowground Fauna Are More Susceptible to Fire Than Aboveground Fauna

Negative effects of fire were apparent on all belowground organisms, suggesting that belowground fauna are susceptible to the impacts of prescribed and wildfires. These findings are congruent to those of other researchers [97,98]. Fire eradicates fungal and bacterial species that cannot withstand intense heat, reducing species richness to those species that can survive fire through fire-resistant propagules [99,100]. Considering the negative effects of fire on fungal populations, the results are consistent with studies that have demonstrated that fungal diversity decreases in ecosystems exposed to fire [63]. Evidence suggests that this is due to both the lower thermal tolerance of fungi, mycorrhizal fungi, and the mortality of plant hosts during fires [101–103]. Fire did not affect abundance, diversity and evenness of microbes affirming the notion that microbes, as a whole, are resistant to fire effects. It is worth noting that microbes may potentially consist of many organisms (e.g., bacteria, fungi, archaea, protozoa, nematodes) with varying resistance to fire and this may explain why there was no effect of fire on microbial diversity and abundance. However, microbial biomass did decrease in response to fires, an aspect that has been documented by other researchers [104,105]. The changes in the nutrient supply due to the loss of plant residues is proposed as the reason for microbial biomass reductions following a fire [102,106]. These findings suggest that fire may affect biomass, while abundance and diversity and evenness may not be affected substantially following a fire. Overall, the effect of fire on belowground diversity is strongly negative, but more research is needed to validate this negative effect across different taxa and ecosystems. Soil mesofauna (e.g., nematodes) and macrofauna (e.g., annelids and arthropods) and microorganisms all showed the negative effects of fires. The subtle differences among belowground taxa are due in part to differences in the morphologies, physiologies and ecologies of all organisms considered; these findings may explain the differences in fire effects observed across taxa [107]. For instance, some belowground species are generalists (omnivorous) though others are specialist feeders. In addition, some species are highly mobile while others (e.g., fungi) are relatively immobile [108].

Aboveground fauna appeared to be more resilient to the effects of fire exposure (Figure 2). This pattern has also been reported in different areas around the world. The resilience of aboveground fauna to fire effects is plausible because large, highly mobile arthropods and mammals can escape the negative effects of fire, compared to less mobile soil arthropods [57,109]. In addition, mobile arthropods, mammals and reptiles can take advantage of the usually high availability of plant biomass in early postfire succession [110,111]. With arthropods, Gongalsky et al. [112] suggests that reduced competition could explain increases in ground beetle richness (as seen in Figure 2). Arthropods are more agile than other invertebrates and can move around in search of more favorable conditions. The spatial heterogeneity of sites after a fire is an important control on arthropod community recovery with unburned sites generally having greater abundance and diversity of arthropods than burned sites [113]. Foraging behavior may also explain the low impacts of fires on arthropods and other aboveground organisms. Since omnivory is common among arthropods and many small mammals, these organisms still have many prey options available, which may allow for greater survival as prey resources become limiting after a fire [108]. Amphibians and reptiles were not affected by fire and in some cases their abundance and richness actually increased following a fire. Research on the effects of fire on herpetofauna by other researchers indicates that fire results in herpetofauna mortality, but has little effect on amphibian and reptile abundance, diversity, richness, and in some cases results in increases in abundance for some herpetofauna [95,114,115]. The reasons for the survival of herpetofauna remains an open research question but there are some possibilities that may explain these results. First, amphibians are known to dwell in moist environments, such as plant litter, that cannot sustain fire, or in underground refuges, such as small mammal tunnels [116], that would insulate them from fire [117]. Second, reptiles may seek refuge under objects such as rocks. Third, reduced litter following a fire may increase the amount of bare ground, and removal of the midstory within burned

forest resulted in more advantageous thermoregulatory conditions for lizards [110]. Of all the organisms considered mollusc (mostly snails) abundance and richness was negatively affected by fire to the greatest extent, contrary to findings by other researchers who have shown that prescribed fires (via the creation of novel microhabitats) can have positive effects on snail populations [118]. Negative effects of snail mortality after burning have been documented in field experiments [119] and studies [22]. The negative effects of fires on molluscs may be associated with high snail mortality which results from increased desiccation or food supply. Desiccation is recognized as the major cause of death after a fire as has been demonstrated by Ray and Bergey [119] where they showed that adding water in burnt areas increased survival of snails. Fires reduce leaf litter and exposes the soil, which consequently results in loss of leaf litter, increases in soil temperature and ultimately desiccation of snails [119].

4.2. Fire Types and Intensities Negatively Affect Organisms

Prescribed fires and wildfires both had negative effects on all animal fauna. These findings support findings by researchers [5,106,119] whereby they showed that fauna decreased shortly after a fire. The declines under both fire types could be explained by hot temperatures that organisms cannot survive in. Consequently, because fire severity may be a crucial factor in explaining the survival and recovery rate of organisms, this factor should be considered when assessing fire effects on organisms. Strikingly, moderate fires had no effect on organisms in sharp contrast to some of the tenets of the Intermediate Disturbance Hypothesis [38]. It is not immediately apparent why moderate fires had no effect on diversity but there are some data from some biomes [42] that show that species populations are lowest at sites of moderate and high fire frequency. Fire frequency is probably the most influential factor related to fire effects at local and landscape scales [120]. However, effects of fire frequency and fire intensity can be difficult to tease apart. Of the extracted studies it was always difficult to get consistent reports of fire frequency and details on fire severity. Nonetheless, considering fire intensity and fire frequency is a requisite when one is considering the effects of fire on fauna. Similarly, some studies [121–123] suggest that winter prescribed burning can be efficacious for restoring grassland habitats compared to summer burning. As such, it may be useful to consider season in future meta-analyses on fire effects.

4.3. Fire Effects Are More Pronounced in Certain Biomes and Continents

Negative fire effects were apparent on agricultural land, grasslands, forests and savannahs possibly because these biomes, except for agricultural land, experience fire as fires are one of the main sources of disturbance in these landscapes [124]. Tundra fauna were not affected by fire. Recent studies on tundra biomes have shown that fires have no effects on lichens and fungi [125,126]. Negative fire effects on fauna were also observed across continents. Prescribed and wildfires had no effect on Africa. These results are surprising considering that 70% of the fires that occur in the world occur in Africa [127,128]. The findings may show how African fauna and flora are shaped by fires. Savannahs depend on lighting as a key management activity in many of the iconic protected areas of Africa. For instance, the Serengeti in Tanzania a famous wildlife tourist area has over of 50% of its grasslands burnt each year [129], yet it boasts the highest biodiversity on the continent.

In the current meta-analysis, I considered different type of forests as one amalgamated group. For example, boreal forests that have higher humidity and a historically longer fire durations were combined with temperate forests, which are drier and have a historically higher fire frequency. Analyzing forests separately (e.g., boreal forests versus temperate forests), may have given different results on the effects of fires on fauna in forests. However, the extracted studies did not allow for further divisions of forests into more specific classifications, which is something that should be implemented in the future when more studies have been conducted. The meta-analysis extraction showed that there are restrictions on the taxa studied by continent. For instance, fungi studies were highly restricted geographically,

while vertebrates showed the lowest number of studies, even though vertebrate groups are fundamental for controlling cascading effects across trophic levels. There is a need for more research on studies documenting the effects of fire on higher trophic levels

4.4. Abiotic Factors Do Not Predict Fire Effects Well

Soil moisture, pH and depth were poor predictors of responses of organism to fire. It is plausible that other physical, chemical, and biological mechanisms such as organic matter, soil texture, plant community composition, trophic interactions may have influenced the response of organisms to fire, but these variables were not measured or reported consistently across the literature and thus could not be included as moderators in my meta-analysis.

4.5. Future Research Needs in Fire Ecology

The global metanalysis revealed many striking patterns and revealed some major gaps that need to be filled in future research. First, the biotic mechanisms by which food webs are influenced by fire are scant in the literature. Second, novel approaches are needed to study the responses diverse fauna to fire in the context of climate changes. As with much of the literature on fire ecology (*sensu* [68]), there is a clear gap in our understanding of how multiple taxa and organisms at higher trophic levels may respond to fire [126,130]. It is necessary to consider taxa at higher trophic levels and how they interact with primary consumers, primary consumers and all food web components when developing the understanding of the effects of fire on ecosystem function because food web perspectives can be useful predictors of organism vulnerability to disturbances [131]. However, the literature search showed a general paucity of studies representing particular taxa. For instance, protozoa, nematodes and annelids, amphibians were fewer than microorganisms (bacteria, fungi,) and arthropods. Further, a copious number of the studies considered one type of organism and when they considered multiple organisms, they did not consolidate their findings into a food web perspective.

In this meta-analysis, I considered aboveground and belowground organisms in tandem something that is not often done by many authors. Future studies need to always consider aboveground and belowground effects of fire on fauna. An aboveground-belowground dichotomous study is a promising approach to improve our understanding of faunal responses to fire and consequences for ecosystem function and will be useful in postfire restoration efforts [132,133]. It is worth noting that many of the studies that were extracted only focused on organisms but did not simultaneously focus on the plant communities that were affected by the same fires. Future studies that concomitantly assess the links between animals and plant communities will be important in predicting organism susceptibility to disturbances. For instance, fungi (i.e., mycorrhizae) are always associated with plants [134], and fire effects on fungi like affect plants and vice versa. Similarly, many pollinators have a key association with angiosperm plants and are thus concurrently affected by fires [135].

In this meta-analysis studies extracted often only considered the effect of single fire events on organisms. Understanding the short-term implications of a single fire on aboveground and belowground communities is important as it can give glimpse of the short-term impacts immediately following the fire, however, there is need for researchers to transcend to more long-term studies. This is particularly important because fire frequency, severity, size and seasonal timing is stochastic in many ecosystems as a result of climate change [136]. Therefore, there is a need for authors to consider fire effects within several climate change scenarios. As with many disturbances (e.g., floods), fire regimes do not occur independently of other global changes, therefore a multipronged approach is needed to understand the combined effects of several disturbances on organisms.

Considering some of the gaps identified in the preceding text requires future research to move from single-population (i.e., autecological) perspectives of fire effects to the effects of fires at multiple trophic levels. Some of the immediate research needs are for researchers to: (1) incorporate multi- taxa studies that use a food web perspective, (2) consider using

biogeochemical tracers (e.g., stable isotope analyses; [137,138]) and niche analyses (e.g., hypervolumes; [139,140]) to trace the subtle and chronic impacts of fires on community interactions, (3) Identify biotic and/or abiotic mechanisms that are the most important drivers of faunal communities after a fire event, (4) Investigate how multiple fire events, rather than single fire events, potentially restructure aboveground and belowground communities, (5) Utilize both experimental (e.g., mesocosms), observational and modelling approaches to explore the interactive effects of fire with other land use changes, population growth and global climate change. (6) Include more studies on the effects of fire on fungi and lichens from understudied continents (e.g., Africa), and (7) Interdisciplinary work (e.g., using citizen science and traditional ecological knowledge; [141,142]) on the role of fire in shaping animal and plant communities

5. Conclusions

In conclusion, the meta-analyses presented an extensive global synthesis of empirical evidence across many animal groups and showed that some organisms are more resilient to fires than others. Given the ongoing global fire regime changes, it is imperative to monitor fire regimes across many ecosystems, as the results suggest that fire differentially affects belowground fauna and to a lesser extent aboveground fauna.

Supplementary Materials: The following supplementary files are available online at <https://www.mdpi.com/article/10.3390/earth3040063/s1>, Table S1: Modified Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA), Table S2: Overall effect of fire on abundance, biomass, diversity, evenness and richness of all faunal groups and aboveground animals, Table S3: Overall effect of fire on abundance, biomass, diversity, evenness and richness of all faunal groups and belowground animals, Table S4: Overall effect of fire by intensity and habitat on fauna. Analyses were conducted using a mixed-effects model, Table S5: Meta-analysis datasheet.

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