Journal of Animal Ecology

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Article type : Review

Handling Editor: Dr M. Noelia Barrios-Garcia

Predator responses to fire: a global systematic review and meta-analysis

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Abstract

1. Knowledge of how disturbances such as fire shape habitat structure and composition, and affect animal interactions, is fundamental to ecology and ecosystem management. Predators also exert strong effects on ecological communities, through top-down regulation of prey and competitors, which can result in trophic cascades. Despite their ubiquity, ecological

importance and potential to interact with fire, our general understanding of how predators respond to fire remains poor, hampering ecosystem management.

2. To address this important knowledge gap, we conducted a systematic review and meta-analysis of the effects of fire on terrestrial, vertebrate predators worldwide. We found 160 studies spanning 1978–2018. There were 36 studies with sufficient information for meta-analysis, from which we extracted 96 effect sizes (Hedge's *g*) for 67 predator species relating to changes in abundance indices, occupancy or resource selection in burned and unburned areas, or before and after fire.

3. Studies spanned geographic locations, taxonomic families, and study designs, but most were located in North America and Oceania (59% and 24%, respectively), and largely focussed on felids (24%) and canids (25%). Half (50%) of the studies reported responses to wildfire, and nearly one third concerned prescribed (management) fires.

4. There were no clear, general responses of predators to fire, nor relationships with geographic area, biome or life history traits (e.g. body mass, hunting strategy and diet). Responses varied considerably between species. Analysis of species for which at least three effect sizes had been reported in the literature revealed that red foxes (*Vulpes vulpes)* mostly responded positively to fire (e.g. higher abundance in burned compared to unburned areas) and eastern racers (*Coluber constrictor)* negatively, with variances overlapping zero only slightly for both species.

5. Our systematic review and meta-analysis revealed strong variation in predator responses to fire, and major geographic and taxonomic knowledge gaps. Varied responses of predator species to fire likely depend on ecosystem context. Consistent reporting of ongoing monitoring and management experiments is required to improve understanding of the mechanisms driving predator responses to fire, and any broader effects (e.g. trophic interactions). The divergent responses of species in our study suggest that adaptive, context-specific management of predator-fire relationships is required.

Introduction

Fire has shaped Earth's ecosystems for millennia through the combustion of vegetation (Bond & Keeley 2005), influencing how animals such as predators behave and are distributed in fire-prone landscapes (Hradsky *et al.* 2017; He, Lamont & Pausas 2019). In their native ranges, apex predators can have positive effects on ecosystems and biodiversity by limiting the activity or abundance of herbivores and smaller 'mesopredators', either through killing (Pasanen-Mortensen, Pyykönen & Elmhagen 2013) and/or by instilling fear (Swanson *et al.* 2014). In doing so, apex predators can diminish grazing pressure (Letnic & Ripple 2017), or reduce mesopredator abundance and activity (Pasanen-Mortensen, Pyykönen & Elmhagen 2013). Apex predator populations in many parts of the world are declining, due to anthropogenic threats including human persecution and habitat loss (Wolf & Ripple 2017). Understanding how fire affects predators (i.e. positively or negatively), and which species' traits mediate those responses, could help inform when and how fire management can aid the conservation and management of native predators and their ecological functions.

In contrast to native predators, invasive predators often exert negative impacts on native species, having contributed to more than 50% of bird, mammal and reptile extinctions worldwide (Doherty *et al.* 2016). Fire may favour some invasive predators by removing vegetation and reducing habitat complexity (McGregor *et al.* 2016; Hradsky *et al.* 2017), potentially exposing native prey species to an enhanced risk of predation by novel predators (Salo *et al.* 2007; Leahy *et al.* 2016). In this way, fire and invasive predators can interact to diminish populations of native species, potentially driving species towards extinction (Hradsky 2019). Understanding how fire affects invasive predators could help mitigate their impacts, for instance, by routinely coupling fire and invasive predator control, or implementing fire regimes that disadvantage invasive predators (Doherty *et al.* 2015).

Habitat composition and structure—and the processes that influence it—are important mediators of predator-prey and intra-guild predator interactions (Denno, Finke & Langellotto 2005; Janssen *et al.* 2007). By modifying habitats, fire can shape the activity and abundance of predators, but the specific way that predators respond to fire is likely to be determined by a combination of their behavioural and morphological traits, and the broader environmental context. While pursuit predators may be more efficient hunters in burnt areas where physical obstacles to pursuit are fewer (Torretta *et al.* 2017), ambush predators might be more successful in unburnt areas, as vegetative cover helps predators to avoid detection and launch short, explosive attacks on prey (Rosas-Rosas, Bender & Valdez 2010). Predators with large home ranges may be more resistant to the impacts of fire, as their broad-scale movements reduce their reliance on local habitats and allow them to exploit resources across both burnt and unburnt areas (Nimmo *et al.* 2019). The scale, patchiness, and severity of fires—and the ecosystem context in which they occur—may also influence how individual predators and their populations will respond. For instance, in Australia, low intensity fire might promote native predator occurrence (Bliege Bird *et al.* 2018), whereas severe fire can promote invasive predator occurrence (McGregor *et al.* 2016).

Despite the clear potential for important interactions between fire and predation, and their relevance to conservation science and management, there is currently no synthesis of these relationships. To address this knowledge gap, we systematically reviewed and synthesised the results of 160 empirical studies that examined predators' responses to fire. For the purposes of this study, a predator is defined as any predominantly carnivorous, terrestrial vertebrate that eats other vertebrates, and 'fire' refers to both wildfire and prescribed burns. Our principal objectives were to:

1. Synthesise the literature regarding predator responses to fire and analyse the importance of potential taxonomic, behavioural, and environmental factors in explaining variation in species' responses; and
2. Highlight the major knowledge gaps regarding the responses of predators to fire and how they might be addressed by future research and management experiments.

Methods

Systematic review

Our study had two stages: 1) a systematic review of the literature on predator responses to fire to identify broad publication trends, and 2) for a subset of studies in the systematic review, a meta-analysis examining the responses of predators to fire.

a) Search criteria

We defined a predator as any carnivorous terrestrial vertebrate that eats other vertebrates. This excluded amphibians and other predators that predominantly consume invertebrates from our search, and we acknowledge that future work should examine responses for this group, where information is available. We only considered studies that measured the effect of fire on predators using field-collected data. For inclusion in our systematic review, predators must have been responding to one of the following aspects of fire: burned vs. unburned areas, before vs. after fire, before-after-control-impact studies, fire severity, or variation in time-since-fire. Response variables included changes in predator abundance/activity indices, occupancy, or habitat/resource selection. We placed no restriction on publication date.

b) Literature search

We systematically searched the Web of Science database on 16th May 2019, using combinations of search terms relating to predators and fire (Supplementary Materials). To increase the specificity of the results, we also excluded some irrelevant terms (Supplementary Materials). We supplemented our literature search with further unstructured searches of published and grey literature (e.g. Google Scholar), including using the reference lists of returned studies. Our structured search returned 5,617 studies, and 17 extra studies were found using less-structured methods. After title and abstract screening, 330 studies were deemed appropriate for the systematic review. This was reduced to 160 studies after examining the full texts of each study (Figure S1.1). All studies used in the systematic review and meta-analysis are provided in the Data Sources section.

c) Data extraction

We categorised each study based on the type of fire studied (i.e. prescribed fire, wildfire or the historical fire regime), the experimental design, the maximum number of years since the 'burned' area was burnt and the response variable describing the species' response (Table S1.1). We initially considered recording other variables, such as fire intensity, extent and return interval, but these were insufficiently reported in the majority of studies to be useful for analysis. Within each study, we categorised each species based on its taxonomic class, hunting strategy, and whether it was invasive or native to the study location (Table S1.1). For mammals, we also categorised each species based on their body mass, diet breadth and trophic level using the Pantheria and Phylacine databases (Jones *et al.* 2009; Faurby *et al.* 2018).

Following the approach used by Foster, Barton and Lindenmayer (2014), we recorded the mechanism(s) (food, habitat cover, competition, mortality or other), if stated, to which each study attributed a species' response to fire. We also recorded whether these mechanisms were tested explicitly, or inferred by the authors from their knowledge of their study system.

Meta-analysis

Our meta-analysis focused on a subset of the studies returned in the systematic review that met the meta-analysis inclusion criteria. In terms of study design, we focused on studies that measured changes in abundance indices, occupancy or resource selection with burnt vs. unburnt, before vs. after fire, and BACI study designs. For inclusion in our meta-analysis, studies must have provided sufficient information to derive means, standard deviations and sample sizes across fire treatments that were a maximum of 20 years post-fire, which left 36 studies and 96 effect sizes in total. Sample sizes were typically numbers of sites in each category, or total number of animals or location fixes used in data analysis. Where multiple years of data were provided for a given area (e.g. repeated sampling burned and unburned areas over multiple years), we averaged data across years to calculate pooled means and standard deviations. To convert before-after-control-impact values into control-impact values, we subtracted the means and standard deviations of the before measurements from the after measurements, as per Eales *et al.* (2018). Many otherwise appropriate studies from the systematic review were excluded from the meta-analysis because they did not provide adequate data to calculate effect sizes (e.g. only provided model coefficients and standard errors, not means and standard deviations).

For each study, we calculated the effect size Hedges' *g* (Gurevitch & Hedges 1999), which is an estimate of the standardised mean difference between a control (unburnt) and treatment (burnt), and its variance. This metric is also adjusted for variation in study effort and so is not biased by small sample sizes. A negative response by a species to fire is indicated by a value <0 (e.g. reduction in abundance following a fire, or lower occupancy in burnt areas), whereas values >0 are indicative of positive responses to fire. Variance for each effect size was calculated as per Koricheva, Gurevitch and Mengersen (2013), and was based on the effect sizes of each study, weighted by the sample sizes.

We used phylogenetic Bayesian Markov Chain Monte Carlo generalised linear mixed models to test the relative influence of different predictors on predator responses to fire, using MCMCglmm implemented in R v3.5.1 (Hadfield 2010). We fitted the models with Gaussian error distributions and a uniform prior distribution (V = 1, nu = 0.002). To obtain robust estimates of posterior means and credible intervals (i.e. an effective sample size ~1,000), we subsampled 1000 iterations from 400,000 iterations of each model, with a burn-in of 100,000 and a thinning interval of 300. To account for variation within and between effect sizes taken from the same study, we included Study ID as a random intercept in each model. To account for the non-independence of multiple effect sizes (within or between studies) from single species or closely related species, we used a phylogenetic meta-regression approach. Incorporating phylogeny into meta-analysis can have important outcomes for study results and so is now recommended where possible (Chamberlain *et al.* 2012). To inform the phylogenetic meta-regression models, we constructed a phylogenetic tree for the species in the meta-analysis dataset using the Integrated Taxonomic Information System and the R package taxize (Chamberlain & Szöcs 2013). In the models, each effect size was also weighted by the inverse of its variance to reduce the influence of studies with large variances.

For species with more than one effect size reported in the literature, we calculated the mean effect size and confidence intervals for each species using the metafor package in R by building a meta-analysis model with no fixed or random effects for each species (Viechtbauer 2010). For species with one effect size, we report the individual effect sizes extracted from the literature and the confidence intervals calculated from each model. We plotted these effect sizes against a phylogenetic tree. To illustrate the variation in effect sizes between studies on particular species, we created a forest plot of the individual and mean effect sizes for species for which at least three effect sizes had been reported in the literature.

We constructed phylogenetic meta-regression models for the full dataset of effect sizes (n = 96) using MCMCglmm to test the relative importance of Family, Class, Hunting Strategy, Max Burned Age, Biome and Continent for explaining effect sizes, as well as combinations of variables (Table S1.1). To use as null models, we also built two models with just Study ID as a random effect and no fixed effects, one with the phylogeny and another without. To identify the predictors correlated most strongly with effect size, and the most parsimonious model structures (e.g. accounting for phylogeny or not), we used an information theoretic model selection approach by comparing each candidate model's Deviance Information Criterion (DIC; Spiegelhalter *et al.* 2002). A candidate model was considered the most parsimonious if its DIC value was more than 2 units lower than the next best model or had a model weight > 0.9 (Spiegelhalter *et al.* 2002).

Because some traits were typically only available for mammal species (e.g. diet information, Table S1.1), we then repeated this procedure for a subset of the data containing only effect sizes of mammal responses to fire (n=48). In addition to the predictors above, we also constructed models to test for the relative importance of Mass, Diet, Trophic Level, IUCN status, Hunting Strategy and Diet Breadth in explaining effect size (Table S1.1). To test whether the effect of any predictors differed in studies involving recently burned areas, we ran models on a subset of the full dataset containing only effect sizes from studies with a Max Burned Age ≤1 year post-fire (n=33). For this subset of effect sizes, we used the same set of predictors as the full dataset models

Study heterogeneity, publication bias and sensitivity analysis

To test for the level of variation between study effect sizes included in the full meta-analysis and whether it was due to sampling error or true heterogeneity between studies, we conducted a Q heterogeneity test (I^2) using metafor in R. Higher I^2 values (i.e. closer to 1) indicate that a greater proportion of the variation between effect sizes is due to variation between studies and/or species, rather than chance (Higgins & Thompson 2002). We also report the outcomes of heterogeneity tests for random effects models for each species with at least three effect sizes.

To test for publication bias in each dataset (full dataset, mammal-only, recently burned), we used two different methods. First, we constructed a funnel plot of effect size and the inverse variance and visually inspected it for asymmetry. Second, we conducted a Kendall's rank correlation test using metafor on the full null model dataset to explicitly test whether the effect size variances and effect sizes are rank correlated, therefore indicating publication bias.

As predator responses to fire may be short lived, we tested the sensitivity of our results to this decision. To do this, we re-calculated the effect size for these studies using just the years or survey periods immediately before and after a fire event, and then replicated the meta-analysis protocol described earlier. Full methods and results are described in Supplementary Information 5.

Results

Systematic review

Our systematic review returned 160 studies of predator responses to fire for 188 species, with an increasing exponential trend over time (Figure 1a). Although the studies were conducted in 20 countries, the literature is geographically biased, with most studies occurring in either North America or Oceania (59% and 27%, respectively) and the least in Europe, Africa, Asia and South America (2.5-4% each; Figure 1a).

Most studies focussed on canid and felid species (25% and 24% respectively, Figure 1b). In contrast, the seven avian families reported only accounted for 23% of studies combined, with Strigidae (true owls) and Accipitridae the most common (Figure 1b). The species most frequently studied was the feral domestic cat *Felis catus* (16 instances), followed by the red fox (*Vulpes vulpes*), spotted owl (*Strix occidentalis*), Canadian lynx (*Lynx canadensis*), wolf (*Canis lupus*) and coyote (*Canis latrans*) (15, 14, 9, 9 and 9 instances respectively). Sixty-one species (31%) had multiple studies of their responses to fire, whereas 135 (69%) species had only a single study.

Responses to wildfires (50% of instances) were more commonly studied compared with prescribed burns (27% of instances), and all fires were considered in 19% of instances (Figure 2). The average 'burnt' site had a median maximum burned age of 4 years post-fire (range 0–73 years), and 31% of instances measured short-term effects of fire (≤12 months post-fire). Studies most often focused on the responses of predators to single fire events, followed by responses to multiple fires (Figure 3a). The least common components of the fire regime studied were fire severity, frequency and return interval (Figure 3a). The most common experimental design was burnt-unburnt comparisons, followed by categorical representations of time since fire and before-after comparisons (Figure 3b). Twenty-nine instances measured responses along a fire succession (continuous or categorical). In terms of the fire characteristics quantified by each study, 48% of studies quantified the size of the fire in some way, 23% quantified the fire return interval, 17% quantified fire patchiness and 13% quantified fire severity.

The most common response variable used was an index of predator abundance or activity, followed by resource or habitat selection and the least common was survival (Figure 3c). The most common mechanisms that study authors suggested were driving predator responses to fire were changes in food opportunities (e.g. prey availability or hunting success), or changes in habitat cover (Figure 3d). More generally, 31% of studies recorded the presence of potential competing predators quantitatively or qualitatively. For the most part, authors appeared to infer their suggested mechanisms from their knowledge of the system and literature, rather than test them explicitly.

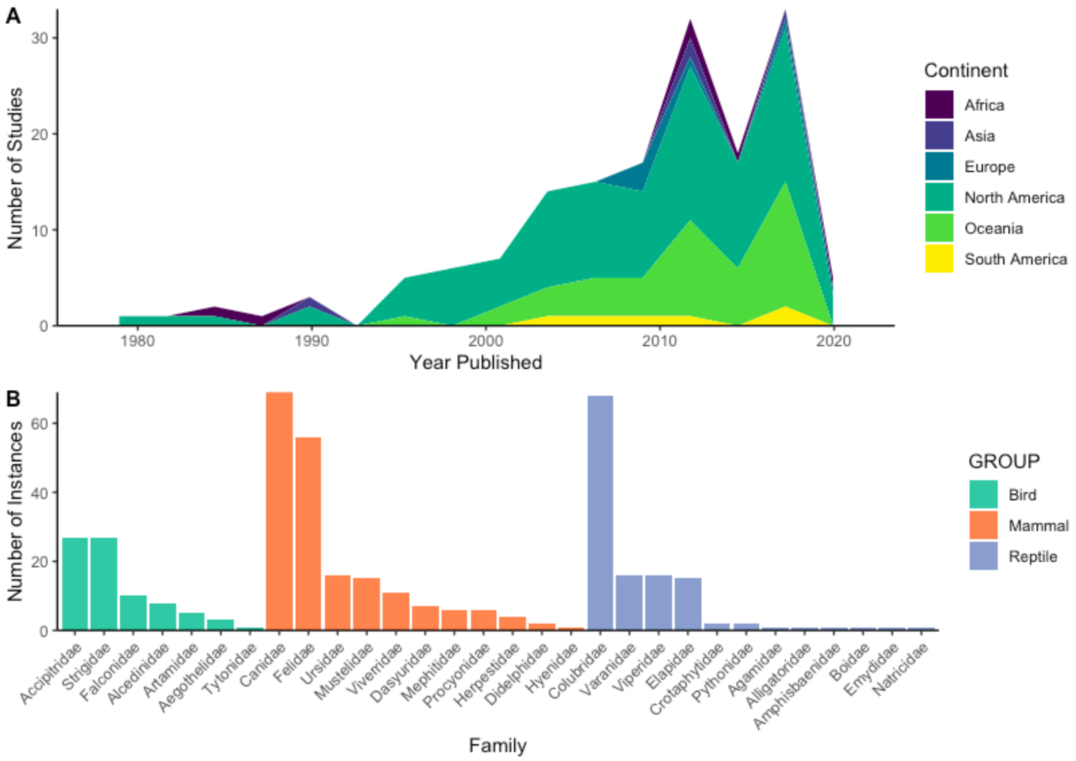
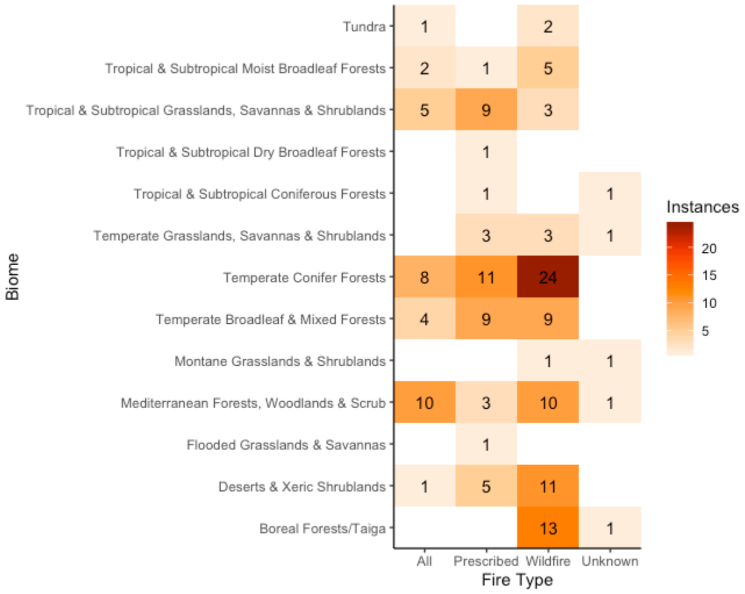


Figure 1: a) Number of studies in the systematic review dataset (total 160) published per continent, per year. Different coloured bands are cumulative within years such that a thicker band represents more studies published for that continent in a single year; b) Number of instances in the systematic review dataset a species from each taxonomic family occurs in a study.



Biome	All	Prescribed	Wildfire	Unknown
Tundra	1		2	
Tropical & Subtropical Moist Broadleaf Forests	2	1	5	
Tropical & Subtropical Grasslands, Savannas & Shrublands	5	9	3	
Tropical & Subtropical Dry Broadleaf Forests		1		
Tropical & Subtropical Coniferous Forests		1		1
Temperate Grasslands, Savannas & Shrublands		3	3	1
Temperate Conifer Forests	8	11	24	
Temperate Broadleaf & Mixed Forests	4	9	9	
Montane Grasslands & Shrublands			1	1
Mediterranean Forests, Woodlands & Scrub	10	3	10	1
Flooded Grasslands & Savannas		1		
Deserts & Xeric Shrublands	1	5	11	
Boreal Forests/Taiga			13	1

Figure 2: Counts of the number of instances a fire type (prescribed fire, wildfire or all fires) was studied in each biome. Biomes are taken from Olson et al. (2001).

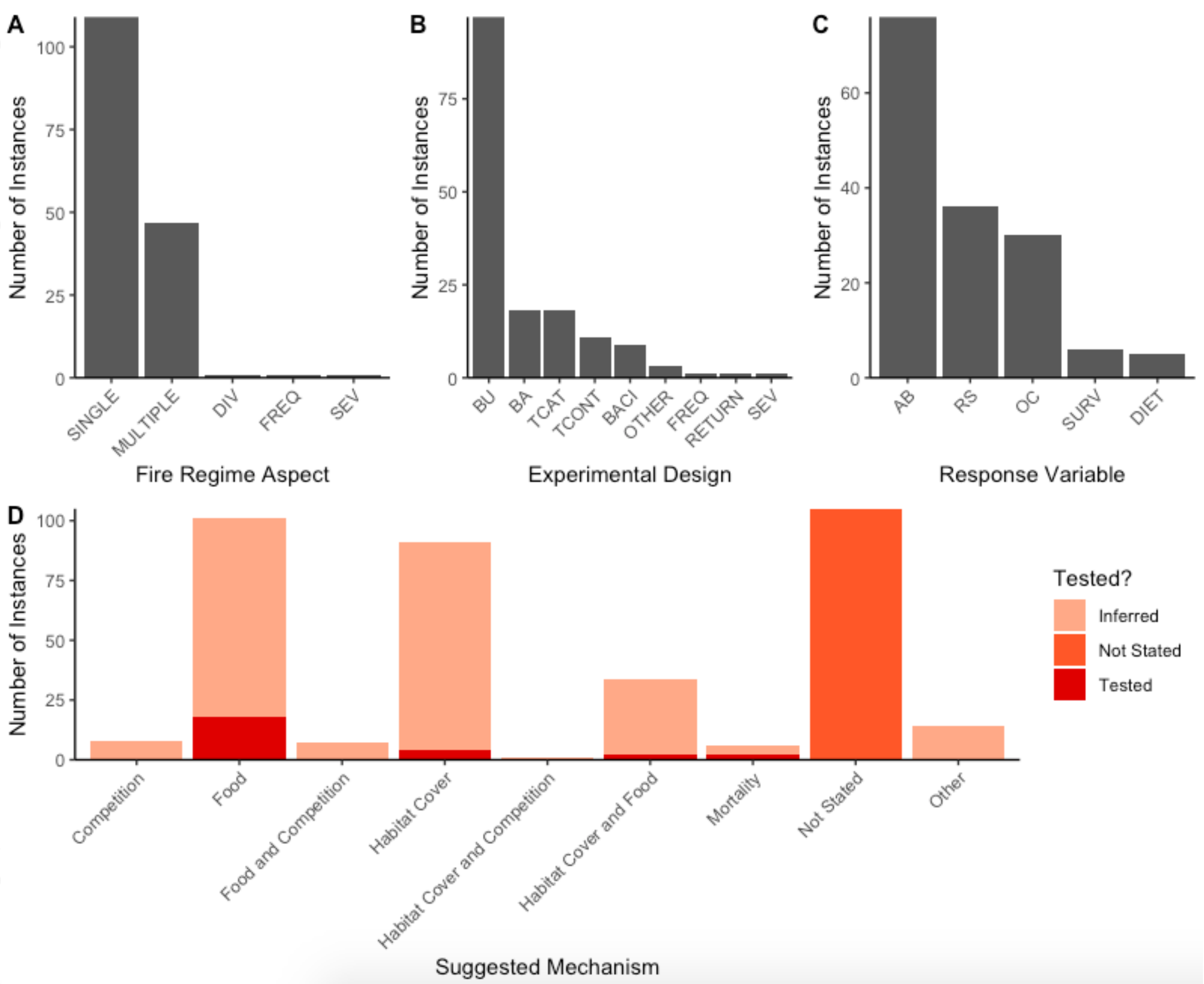


Figure 3: a) Number of instances where a study measured a predator's response to a particular fire regime variable, total = 163 instances (SINGLE = a single fire; MULTIPLE = multiple fires; DIV = fire diversity; FREQ = fire frequency; SEV = fire severity). b) Number of instances where a study measured a predator's responses to fire using a particular experimental design, total = 166 instances (BU = burnt vs. unburnt; BA = before-after comparison; TCAT = time-since-fire categories; BACI = before-after-control-impact design; TCONT = time-since-fire continuous; OTHER = other). c) Number of instances where a study measured a predator's response to fire using a particular response variable; total = 162 instances (AB = abundance or activity index, RS = resource or habitat selection; OC = occupancy; DIET = diet changes; SURV = changes in survival rate). d) Number of instances where study authors suggested different mechanisms to a predator's response to fire, split by whether the authors inferred their conclusion or explicitly tested it. The total number of instances are greater than the number of studies in the systematic review because some studies tested multiple response variables, fire variables and species.

Summary of effect sizes across species

By calculating mean effect sizes for each species that had >1 effect size (67 species), we found that some species (e.g. *Canis lupus* and *Vulpes vulpes*) had positive mean effect sizes, whereas other species (e.g. *Coluber constrictor*) had negative mean effect sizes (Figure 4). Most mean and individual effect sizes had variances that overlapped zero, suggesting fire had no effect on these species or it was highly variable and uncertain, in the studies included in the meta-analysis.

There were varying levels of heterogeneity between studies for species with at least three effect sizes (Figure 5). *Coluber constrictor* had low heterogeneity, with a negative mean effect size. In contrast, *Vulpes vulpes* had a positive effect size, but relatively high heterogeneity (I^2=82%; Figure 5) across its four studies. The mean effect sizes and variance of each species overlapped zero, but only *Canis latrans* and *Strix occidentalis* had relatively high heterogeneity (I^2=78% & 91.6% respectively).

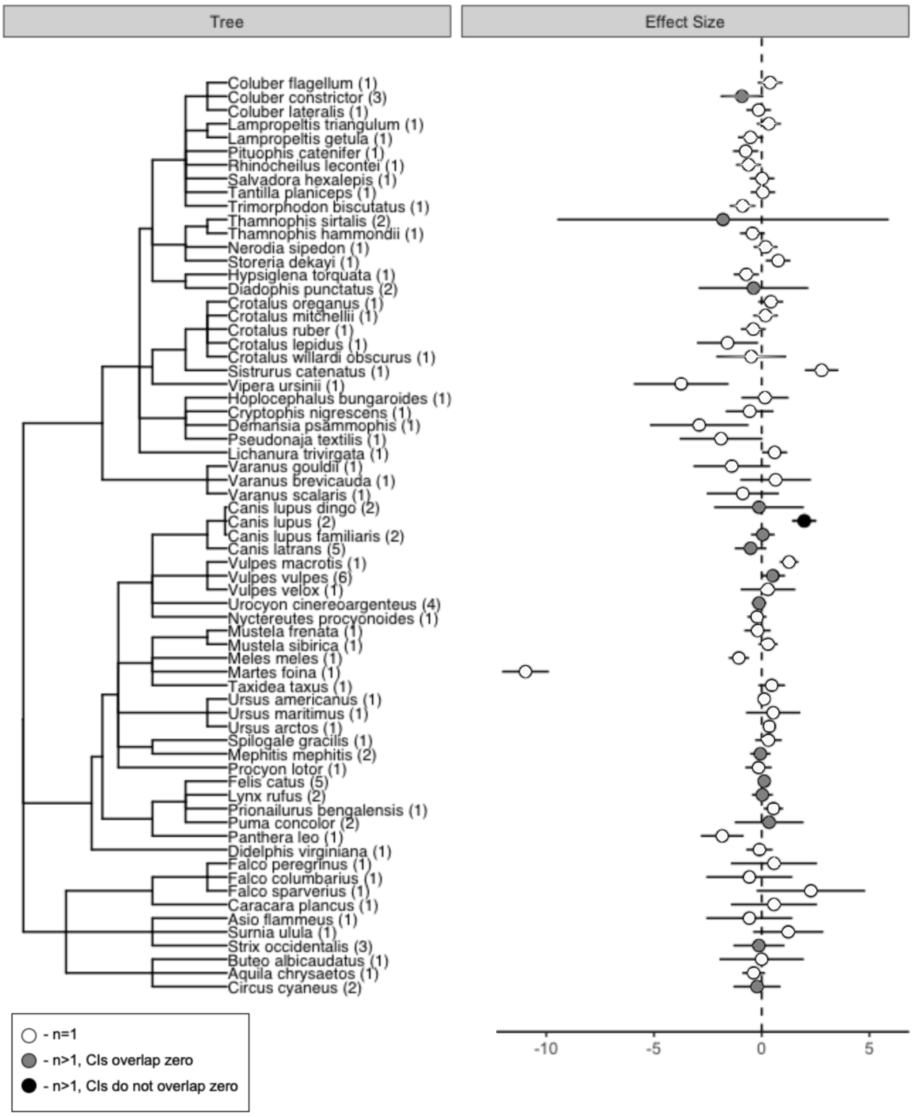


Figure 4: Phylogenetic tree, modelled mean effect sizes (Hedges *g*, x-axis) and 95% confidence intervals of the meta-analytical generalised linear mixed model with Species as a fixed effect. Solid dots indicate species with more than one effect size and confidence intervals that don't overlap zero. Grey dots indicate species with more than one effect size and confidence intervals that overlap zero. Hollow dots indicate species with a single effect size. Sample sizes (number of effect sizes) for each species are shown in brackets.

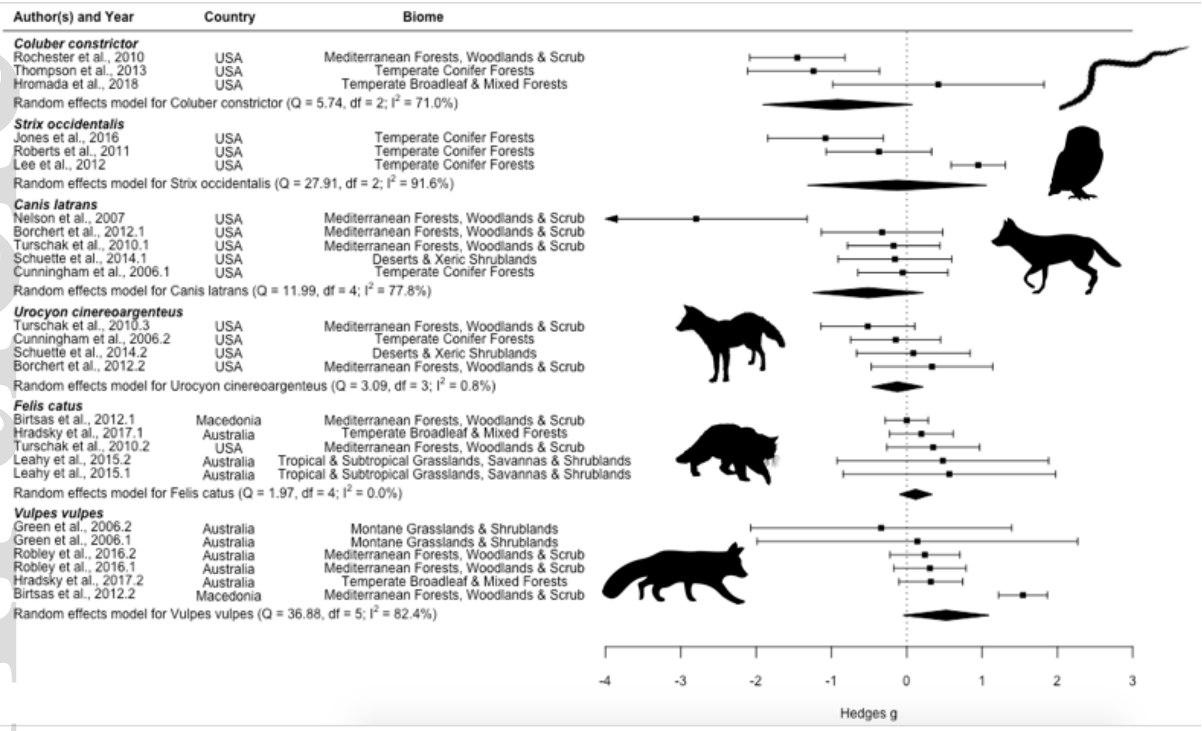


Figure 5: Forest plot of effect sizes (Hedges' *g* and 95% confidence intervals) for the species that had at least 3 effect sizes. Each row shows the study from which each effect size was obtained, duplicates are where a given study reported two effect sizes for the same species. The outputs of a random effects model, created in metafor, for each species are also reported along with Q and I^2 values that represent the level of heterogeneity in each model, with the black polygon representing the mean effect size and variance for each species.

Meta-analysis

The full phylogenetic meta-regression model was based on 96 effect sizes from 67 species. The best model had Family as a fixed effect (w = 0.71), however all mean effect sizes had confidence intervals that overlapped zero (Figure S3.1, Table S2.1). The next best model (ΔDIC = 1.79; w = 0.29) had Family and Fire Age as fixed effects, but all mean effect sizes had confidence intervals that overlapped zero and hence provided little additional insight.

Our mammal-only dataset of predator responses to fire had 48 effect sizes from 25 different species. The model with an interaction between Biome and Fire Type as a fixed effect fit the data best (w = 0.99), but all mean effect sizes had confidence intervals that overlapped zero (Figure S3.2, Table S2.2). The next best model (ΔDIC = 10.34; w = 0.01) had an interaction between Biome and Fire Age as a fixed effect. The dataset of effect sizes measuring responses to recent fires (≤1 years post-fire) had 33 effect sizes from 25 species. Of the candidate model set, the Family model fit the data the best (w =

1.00), but all modelled mean effect sizes had confidence intervals that overlapped zero (Figure S3.3, Table S2.3).

Study heterogeneity, publication bias and sensitivity analysis

The random effects only model for the full dataset had an I^2 value of 98.87% ($p < 0.001$), suggesting a high level of estimated heterogeneity in the dataset. More specifically, the heterogeneity in the full dataset was estimated to be 19.7% due to variation between studies and 79.14% due to variation between species (i.e. the two random effects in the random effects only model).

We detected some evidence of publication bias in the full dataset. By inspecting funnel plots, we identified that this was mostly driven by an outlier effect size which suggested a strong negative effect of fire on *Martes foina* (Birtsas, Sokos & Exadactylos 2012). A rank correlation test of the data suggested that there was significant asymmetry in the funnel plot (Kendall's tau = -0.153, p = 0.03). However, when removing this outlier from the dataset, the test was not statistically significant (Kendall's tau = -0.134, p = 0.055), suggesting that there is not a strong signal of publication bias in our dataset. However, the magnitude of the difference between the two rank correlation tests was minimal, so our results should be interpreted with this in mind. Publication bias test outputs are in the Supplementary Material (S4). Finally, our sensitivity analysis suggests that our results and conclusions were not sensitive to our decision to pool pre- and post-fire means across sampling periods when calculating effect sizes (Supplementary Information 5).

Discussion

Our systematic review and meta-analysis reveal that fire is an important factor influencing predators for some species and ecosystems, but not others. Contrary to our expectations, we found no consistent relationships between effect sizes and any of the variables tested in our phylogenetic meta-analysis. Fourteen of 67 species had significant responses to fire (e.g. *Canis lupus*), but thirteen of these were species with single effect sizes (e.g. *Panthera leo*, *Martes foina*). This suggests that many predators may be resistant to the impacts of fire. We found variable responses to fire for individual predator species, such as spotted owl, red foxes and feral cats, indicating that any species' response to fire can vary between locations, habitat types or with species assemblages. As such, the response of a predator to fire in one region may not be able to be extrapolated and assumed to be the same in other regions, which makes generalisation of study results focused only on a single region challenging. The number of studies of predator responses to fire is increasing rapidly, but an in-depth understanding of these effects is severely hampered by a lack of replication of studies for most species, and inadequate or inconsistent reporting of critical components of study systems and the properties of fire. Our study suggests strong taxonomic and geographic biases (e.g. the vast majority of studies to date are from North America and Australia) in research on predator responses to fire, limiting inferences for managing biodiversity in many regions, such as African savannas and South American forests. However, the geographic trends found may simply reflect locations where fire is a major disturbance (i.e. temperate and arid ecosystems).

Over 90% of species had mean effect sizes with confidence intervals overlapping zero, potentially because a) fire has a limited effect on these species (at least in the context of the study, and recognising that 69% species were only represented by a single study), and b) some studies have insufficient power to detect responses. However, the confidence intervals of *Vulpes vulpes* and *Coluber constrictor* overlapped zero only slightly. Variable responses of individual species to fire also likely contributed to overall (i.e. mean) effects being uncertain. Summarising the effects of fire (e.g. across sampling periods) to calculate effect sizes also likely contributed to the unexpectedly large proportion of confidence intervals that overlapped zero. For example, Leahy *et al.* (2016) found an initial increase in dingo detections two weeks after a high severity fire, but because we calculated pooled mean abundances in burnt and unburnt areas across the whole sampling period, the short-term response was not clearly captured in the effect size calculation. The lack of predator responses to fire was unexpected given the broad potential effects of fire on ecosystems (Bond & Keeley 2005; He, Lamont & Pausas 2019). Many predators, especially mammals and birds, use a wide variety of habitats due to their large home ranges and generalist diets (Santos *et al.* 2014). For example, species such as pumas and spotted-tailed quolls (*Dasyurus maculatus*) are able to change their diets through prey switching after fires (Dawson *et al.* 2007; Monroy-Vilchis *et al.* 2009). Therefore, the ability of many predators to adapt to changing environmental conditions may enhance their resistance to fire (sensu Nimmo *et al.* 2015), explaining why so many predators do not display a clear response to fire.

Species responses to fire are often difficult to detect, meaning fire studies can have high type II error rates (Smith, Michael Bull & Driscoll 2013). This may be especially the case for predators due to their often wide-ranging movements and relatively low densities. Detecting changes in the abundance or habitat use of predators often requires large-scale and intensive surveys to ensure that survey sites are independent and predators are detected in sufficient numbers to allow analysis (Thorn *et al.* 2011).

This is further complicated by the fact that fire studies are often opportunistic, taking advantage of a single large fire, leading to pseudo-replication (i.e., multiple surveys sites but within the footprint of an individual fire event). The most common experimental designs in our review were those that used multiple survey sites but only measured responses to a single fire (i.e. the treatment was not replicated), which was likely driven by the difficulties associated with obtaining replicates of fires at meaningful (large, landscape-scale) spatial scales and over relevant time periods (e.g. controlling for seasonal and/or annual effects associated with rainfall variation).

Individual predator species exhibited fire responses that varied across studies. The responses of species to fire are a function of the vegetation succession, environmental variables (e.g. climate, other disturbances), inter-specific interactions and species demography (Smith 2018). The variable effect sizes observed here may be driven by the types of fire being studied, and the broader environmental contexts of the studies (Nimmo *et al.* 2014). An example of this is the differing responses of red foxes to fire. In montane grasslands, Green and Sanecki (2006) found red foxes had a neutral response to fire. Similarly in semi-arid woodland vegetation, red foxes exhibited no response to a 100 year chronosequence of fire at both the site and landscape scales (Payne *et al.* 2014). However, in Mediterranean forests, foxes exhibited a positive response immediately following fire (Birtsas, Sokos & Exadactylos 2012). For red fox the included studies measured responses to fire in both their native (Birtsas, Sokos & Exadactylos 2012) and invasive ranges (Payne *et al.* 2014). Species can behave differently in their native and invasive ranges, so this may also have contributed to the variation in responses observed. Further, while the timing of survey (i.e. long-term regimes compared with weeks post-fire) may have contributed to the differences observed, the environmental and landscape context in which fire events occur could also have an important bearing on how predators respond to fire.

The composition of local predator guilds may also have a strong effect on intra-guild interactions and hence how predators respond to fire. Our systematic review revealed 16 instances where interactions with competing predators were used to explain observed predator responses to fire. Given that predation rates and predation and risk are often stronger in simplified habitat (McGregor *et al.* 2015; Norbury & van Overmeire 2018), a predator's response to fire might also be affected by the presence or absence of larger, more dominant competing predators. Changes to apex predator habitat selection and behaviour following a fire event may impact mesopredators (Nelson *et al.* 2007; Geary *et al.* 2018). For instance, Schuette *et al.* (2014) suggested that the preferences of bobcats and coyotes for unburnt habitat may be driving the selection by smaller grey foxes for burnt habitat.

Although many predators do not show a clear and consistent response to fire, there are of course situations in which fire shapes the spatial distribution of predators (McGregor *et al.* 2016), their diet (Dawson *et al.* 2007), hunting success (Eby *et al.* 2013), competitive interactions (Nelson *et al.* 2007) and population dynamics (Cunningham & Ballard 2004). Many of these drivers are rooted in the hunting strategy used by a predator species. For example, red foxes and feral cats in Australia can use burnt landscapes to their advantage immediately post-fire, as the open vegetation of recently burnt areas leaves particular prey species more vulnerable to predation (Leahy *et al.* 2016; Hradsky *et al.* 2017). Food was the most frequently hypothesised reason for predator responses to fire in our systematic review, with similar responses across different taxonomic classes. Both birds (e.g. Swainson's hawk, *Buteo swainsoni*; Hovick *et al.* 2017) and mammals (e.g. grey wolves, *Canis lupus*; Arjo & Pletscher 2004) can take advantage of the post-fire landscape for hunting as it is easier to locate and pursue prey. Black kites (*Mivus migrans*) in Australia actively spread fire to facilitate hunting by carrying burning leaves and wood to unburnt areas (Bonta *et al.* 2017). By contrast, fire might negatively impact some ambush predators. For instance, lions (*Panthera leo)* prefer habitat with thick vegetation cover to facilitate hunting and so select unburnt habitat preferentially (Eby *et al.* 2013).

Habitat cover was the second most commonly reported mechanism driving predator responses to fire. Some species depend on dense habitat cover for denning and protection, and given fire reduces vegetation cover, some predators were found to have negative relationships with burned areas (although in almost all significant cases these relationships were inferred from a single study). Eastern racers (*Coluber constrictor*) rely on vegetation cover to avoid predation, therefore they avoid burnt habitat (Rochester *et al.* 2010), and this likely explains the significant negative responses to fire by this species across two studies. By contrast, the reduction in habitat cover caused by fire can favour predators such as snakes (e.g. massasauga rattlesnake, *Sistrurus catenatus*; Steen *et al.* 2015) as burnt habitat has better thermoregulatory properties. Predator species that rely on vegetation cover for denning, avoiding competitors or to ambush prey, and those that are less-able to move long distances to new habitat, are likely to avoid burnt areas.

Currently, most of our understanding about the relationships between predators and fire comes from the temperate and arid environments of Australia and North America, and hence the generality of our findings require testing in other systems. This includes the extensive savannah, woodland and forest ecosystems of Africa, Asia and South America that comprise diverse assemblages of small to large predators, and where fire is common. Fires are also becoming more common in environments once regarded as less flammable (e.g. arctic circle, equatorial rainforests), and may continue to do so with ongoing climatic change (Mariani *et al.* 2018). For such environments, there is little information regarding how climate change, predators and fire might interact to restructure ecosystems. Similarly, there are large taxonomic gaps in the literature examining predator-fire relationships—canids and felids feature disproportionately (although this may partly reflect the search terms we used). An important focus for future research should be elucidating relationships across different taxonomic and ecological contexts, as well as the underlying mechanisms of those responses.

There is some evidence of publication bias in our dataset as a result of an outlier effect size (i.e. Birtsas, Sokos & Exadactylos 2012). This may be partially a result of using effect sizes from only 23% of studies returned in the systematic review due to the types of data available for extraction (e.g. studies not providing means, standard deviations and sample sizes) and that the effects of fire in some studies were confounded with other disturbances (e.g. logging). The asymmetry in the funnel plot was not significant when the single outlier was removed (despite the removal of the outlier causing only a small change in the correlation coefficient), we conclude that the effect of publication bias in our meta-analytical models is probably minimal. Improved reporting of results of predator-fire interactions may help overcome risks of publication bias in future syntheses and provide a more comprehensive dataset for meta-analysis. We urge researchers and journals to continue to publish 'negative' results of predator-fire studies, even when they do not conform with conventional wisdom.

Enhanced research design and reporting on predators and fire

Measuring responses to disturbances in an informative and repeatable way is difficult and requires consistent approaches to allow for comparability between studies (Foster *et al.* 2016). Fire size, severity, patchiness, season, and edge configuration can all influence how fauna, including predators, respond to fire spatially and temporally (Parkins, York & Di Stefano 2018; Nimmo *et al.* 2019). For example, how a predator responds to a small fire might be very different to its response to a large fire, because changes in resource availability may differ. Time since the last fire is another important variable, as the response of a predator may be limited to a very short window (potentially days, weeks or months) immediately post-fire that is not detected by certain study designs (e.g. measuring a response to a >1 year old burn). We outline key variables that should be considered in future predator-fire studies in Table 1.

Table 1: A minimum set of variables that should be collected during studies examining the response of predators to fire, in order to make inferences about the major drivers of an observed response.

Category	Variable	Description
Fire	Size	The size (in hectares, or similar) of the last fire(s) that occurred in the study area.
	Severity	The severity (e.g. high, medium or low) of the last fire(s) that occurred in the study area
	Time since last burnt	The length of time since the last fire occurred in the study area
	Fire 'season'	The season in which the fire occurred (e.g. summer, autumn, winter or spring.)
	Patchiness	The spatial configuration of the fire mosaic in an area (e.g. is the fire history uniform or is there a mosaic of burnt and unburnt patches). Comparable with measures of fire diversity.
	Frequency	The mean frequency of fires in the study area
	Return interval	The mean return interval of fires in the study area
Predator	Focal predator(s)	A measure of changes in abundance, occupancy or density of the focal predator in response to some variation in the fire regime.
	Competing predators	A measure of changes in abundance, occupancy or density of competing predator in response to some variation in the fire regime.
	Prey species	A measure of changes in abundance, occupancy or density of prey species in response to some variation in the fire regime.
Environmental Context	Habitat type	The broad habitat type(s) that the fire has occurred in and the focal predator species may be using.
	Habitat structure	A measure of the habitat structure of the study area and how it varies spatially, but also how it changes before and after fire.
	Topography	The topography of the study area, including variation across the study area (e.g. altitude, ruggedness)
	Weather	Trends in weather patterns (temperature, precipitation) before and after the fire being studied, and during the survey.
	Climate	The prevailing climate of the study area (i.e. long-term precipitation, temperature).

Fire management experiments, with adequate controls, are a sound method for understanding how fire influences predator-predator and predator-prey relationships (see McGregor *et al.* 2014; Cherry, Warren & Conner 2016; Hradsky *et al.* 2017). Taking advantage of future burns and experimental predator manipulation (e.g. fencing, lethal control) is a major opportunity for disentangling the relationship between fire and predators further. Globally distributed experiments could improve this further by providing standardised experimental design and reporting protocols (Borer *et al.* 2014). Multiple approaches to measuring predator responses to fire, such as measuring predator abundance, movement and diet in tandem, are likely to be most insightful (McGregor *et al.* 2016; Hradsky *et al.* 2017).

Conclusions

As wildfires are predicted to become more frequent and more intense under climate change (Jolly *et al.* 2015), understanding how fire intensity and frequency shapes predator distribution, behaviour and interactions with prey is critical for biodiversity conservation and fire management. Our results suggest that approaches to predator-fire research can become more unified to facilitate enhanced comparisons across species and ecosystems, particularly through the use of consistent, replicated management experiments. In addition, given the divergent responses between species reported in our study and the potential undesirable consequences of some predators taking advantage of fire, our meta-analysis highlights that prescribing a one-size-fits-all approach to managing predators and fire risks unexpected and potentially negative biodiversity outcomes.

Acknowledgements

WLG was supported by Department of Environment, Land, Water and Planning and Parks Victoria. T.S.D. was supported by an Alfred Deakin Post-Doctoral Research Fellowship. D.G.N. was supported by an Australian Research Council Discovery Early Career Researcher Award. A.I.T.T. was supported by an Australian Research Council Discovery Early Career Researcher Award. We acknowledge and thank the researchers that collected the data and conducted the research that this meta-analysis was based on. We thank the reviewers and editors for comments and suggestions that greatly improved the manuscript.

Author contributions

All authors conceived the ideas and methodology for the paper. WLG reviewed the literature, collected data and performed the data analysis. WLG led the writing of the manuscript with contributions from all authors. The authors declare no conflict of interest.

Data availability statement

Data are available through the Dryad digital repository: https://doi.org/10.5061/dryad.rr4xgxd56 (Geary *et al.* 2019).

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