Title: Assessing the impact of fire on spider abundance through a global comparative analysis

Running title: The impact of fire on spiders

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Abstract

Fire is an important ecological disturbance; however, in many regions fire regimes are changing due to anthropogenic factors. Understanding the responses of species and ecosystem to fire can help to develop predictive models and inform fire management decisions. Despite their massive diversity and abundance, relatively little is known about the impacts of fire on invertebrates. Spiders are a diverse and ubiquitous group, with variation in ecological, behavioural and life history traits, and can offer important insights into the impacts of fire on invertebrates and whether these depend on environmental factors, phylogenetic history, or species traits. We conducted phylogenetic comparative analyses of published data from studies investigating the impacts of fire on spiders. We investigated whether fire affects family level abundance and whether this effect depends on ecologically relevant traits or site-specific factors (vegetation, latitude, fire type, time since fire). We found that time since fire had a significant effect on the abundance of some spider families (Lycosidae, Linyphiidae, Agelenidae), and within forest vegetation types. There was no relationship between family level traits and response to fire, suggesting that a trait-based approach does not increase predictive power in this group at this taxonomic level. Overall, it is difficult to make broad generalisations about the impacts of fire on spider abundance due to variation in site- and fire-specific factors. We did, however, find evidence that short fire intervals may be a threat to some spider families, and in forest ecosystems, where abundance initially decreased after fire, which may have important implications for fire management strategies. Finally, we show that analyses of published data can be used to detect broad scale ecological patterns and provide an alternative to traditional meta-analytical approaches.

INTRODUCTION

Fire is an important ecological and evolutionary force that has shaped ecosystems worldwide (Bond & Keeley 2005; Pausas & Keeley 2009). While fire plays a role in maintaining species richness and ecological processes in fire-prone regions (reviewed in He et al. 2019), fire can also pose a significant threat to biodiversity and individual species in sensitive landscapes or under different regimes (Bond & Keeley 2005; Shlisky et al. 2009). One of the major consequences of global change has been the alteration of fire regimes; in many regions, wildfires are becoming more frequent and severe, as well as threatening sensitive ecosystems that have long been fire-free (Dowdy et al. 2019; Virgilio et al. 2019; Goss et al. 2020). Understanding the impacts of fire, and fire regimes, is therefore essential for effective conservation and natural resource management now and into the future (Driscoll et al. 2010).

Predictive models quantifying the impacts of fire on species and ecosystems can inform fire management strategies for biodiversity conservation. Such generalisation at broad scales is often difficult due to local variation in species assemblages and environmental factors. However, trait-based approaches, focusing on the properties of an organisms (its traits) rather than species and relating these traits to fire responses, may overcome this challenge (Keith 2012), and an understanding of which traits predict a species response to fire may be especially useful for the management of understudied taxa. Such predictive frameworks have been used to assess the impacts of fire regimes on plant communities (e.g. Menges 2007; Keith 2012; Enright et al. 2014; Clarke et al. 2015; Rodman et al. 2020), and to a lesser extent on animals (e.g. Moretti et al. 2009; Langlands et al. 2011; Driscoll et al. 2019). One constraint of this approach is that closely related species may share similar functional traits (though not always the case; Losos 2008), making it difficult to determine whether observed responses are due to traits or shared ancestry. However, analyses combining both trait and phylogenetic information can provide mechanistic insights into patterns of biodiversity across regions with different fire histories and help to identify species and ecosystems most at risk from changing fire regimes.

Despite their massive diversity and abundance, little is known about the impact of fire on invertebrates (New et al. 2010; Saunders et al. 2021). This is largely because, relative to vertebrate taxa, invertebrates have been poorly studied. It is estimated that around 80% of terrestrial arthropod species are yet to be described (Stork 2018), and fundamental information about their ecology, life history and geographic distribution remains largely

unknown (Cardoso et al. 2011a). Invertebrates play an important role in ecosystem function and changes to invertebrate assemblages can also have knock-on effects across the food web (Wurtsbaugh 1992; Benndorf et al. 2000). Therefore, understanding how invertebrates respond to fire is important at both the species and ecosystem level. Currently, this major knowledge gap makes it extremely difficult to make informed fire management decisions concerning invertebrates (Cardoso et al. 2011a; Saunders et al. 2021).

Spiders (order Araneae) are one of the most diverse and successful groups of animals (Agnarsson et al. 2013) and it is estimated that there are approximately 80,000 species worldwide (Raven & Yeates 2007; Agnarsson et al. 2013; World Spider Catalog 2021). They are found in almost all terrestrial ecosystems, on every continent except Antarctica, and are important invertebrate predators (Nyffeler 2017). Spiders exhibit diverse ecological, behavioural and life history traits (Pekár et al. 2021), including variation in microhabitat use, hunting strategies and dispersal ability. The number of studies measuring the response of spiders to fire is relatively high compared to other invertebrates, likely owing to their ubiquity and high capture rates in pitfall traps (the most commonly used survey method for invertebrates). Therefore, spiders are an ideal model system with the potential to be used as indicators of ecological disturbance (Churchill 1997), and can offer important insights into the impacts of fire on invertebrates and whether these depend on environmental factors, phylogenetic history or species traits.

Fire may impact spiders directly by increasing mortality, or indirectly by altering habitat structure and microclimate (Engstrom 2010; Underwood & Quinn 2010). A previous meta-analysis on the effects of land management (including fire) on spiders found that fire negatively affected spider abundance (Prieto-Benítez & Méndez 2011). However, the conclusions of this study were limited as the analysis was performed for the order Araneae as a whole and more informative impacts are expected at lower taxonomic levels (e.g. family, species). Additionally, the number of studies investigating the impact of fire on spiders has grown in the past ten years. Susceptibility to fire is likely to vary across taxonomic levels due to differences in the behavioural, life-history and morphological traits of the family or species, as well as their habitat (Engstrom 2010). For example, fire may have the greatest impact on taxa associated with leaf-litter, as this is the substrate most often burned during fires (York 1999; Hanula & Wade 2003; New et al. 2010), while burrowing species may be sheltered from the heat and flames (Carrel 2008). Additionally, the simplified habitat

structure following removal of leaf-litter may favour the more active hunting species (Niwa & Peck 2002), while burned habitats may be less favourable for web-building spiders if fire changes the vegetation structure and reduces the availability of web anchor sites (Robinson 1981; Uetz 1992). Overall, the response of animals to fire, and adaptations and traits underpinning this, is still poorly understood (Pausas & Parr 2018; Pausas 2019; Nimmo et al. 2021).

Here, we ask the question: can we utilise published data to detect global patterns of the impacts of fire on spiders? We use a phylogenetically informed framework to determine whether fire affects spider abundance at the family level. Since we can make some generalisations about the presence of behavioural and life-history traits within families (Cardoso et al. 2011b), we also investigate whether there is a relationship between response to fire and family level traits, which could contribute to the development of predictive frameworks for spiders and invertebrates more broadly. Additionally, ecosystems vary in their fire history and susceptibility, so we consider study level variation in location, vegetation type, fire type and time of sampling in our analyses. We show that there is huge variation in spider family responses to fire between studies, but that there are some broad scale patterns associated with time since fire which may have important implications for fire frequency management under a changing climate.

METHODS

Literature search

We conducted a systematic literature search in Web of Science on 12th September 2020. Titles, abstracts, and keywords were searched using the terms "(spider* OR araneae OR arachnid* OR arthropod*) AND (*fire* OR burn*)" from any date and in any language. We also performed further unstructured searches of published and grey literature (e.g. using Google Scholar, SCOPUS and Fire Research Institute) as well as citations within returned literature. Studies were included in our analysis if they: 1) used burned versus unburned, before versus after, or before, after, control, impact (BACI) study designs, 2) identified spiders to at least family level (but not studies that targeted a single species), 3) used pitfall trapping, and 4) measured abundance. Of the 1,105 studies found, 49 met the criteria for inclusion in the analysis and 33 of these provided usable abundance data with the manuscript (Supplementary Information Table S1). There were two cases where two studies had used the same underlying abundance data, so these were combined, resulting in 29 independent

datasets (see PRISMA 2020 diagram; Supplementary Information Figure S1). A list of the data sources is found in Appendix 1.

Data collection

For each study we recorded the major vegetation type (forest, grassland, shrubland or woodland), mean time since the last fire (in months, for the fire treatment), fire type (controlled, wildfire) and latitude, and collated raw family level abundance for both the fire (burned/after) and control (unburned/before) treatments. When a study contained multiple fire treatments, we used the data for the single and/or most recent fire. Given our aim was to analyse the effects of fire per family (and not per study), we did not extract the overall effect sizes per study, as would be done in a traditional meta-analytical framework. Abundance data were extracted from tables using Tabula (https://tabula.technology), or from figures using metaDigitise (Pick et al. 2019) in R (version 4.1.0; R Core Team 2021). Taxonomy was checked within each dataset and updated if necessary (i.e. we ensured the taxonomic classification of species and genera within families was current) (World Spider Catalog 2021).

Abundance was standardised across and within studies by dividing absolute family abundance by the number of plots, traps and sampling days (sampling effort), which allowed us to compare abundance between treatments and studies. We recognise that this is not a perfect calculation as it is based on our interpretation of the study design reported in the literature, but it was necessary because there were multiple instances where experimental designs were not uniform or directly comparable between treatments within studies. After calculating a standardised abundance per family per study and per treatment, we derived a measure of difference in abundance by subtracting the standardised abundance of the control treatment from that of the fire treatment, where a negative value indicated lower abundance in the fire treatment and a positive value indicated higher abundance in the fire treatment. This resulted in 563 data points. For some statistical models (1 and 3, see below) we further filtered the data to only include families with at least 5 data points (5 fire-control differences), resulting in 485 data points.

To determine whether ecologically relevant traits predict a family's response to fire, we compiled information on hunting strategies (whether species within the family use capture webs, sensing webs, active hunting and/or ambushing), habitat use (whether species within

the family are active within vegetation and/or burrow) and dispersal (whether species within the family use ballooning) based on the World Spider Trait database (Pekár et al. 2021) and published literature (Figure 1; Supplementary Information Table S2). All traits were binary (presence/absence). We investigated the relationships between these ecological traits using the R package corrplot (Wei & Simko 2021), and detected significant ($P < 0.05$) correlations between all hunting strategy traits and burrowing (Supplementary Information Figure S2). Consequently, we performed a logistic principal component analysis using the R package logisticPCA (Landgraf & Lee 2015) with the first two axes extracted explaining 88.1% of the total variation in ecological traits. The first axis (hunt_PC1) was associated with ambushing strategies (ambush, sensing web, burrow), while the second axis (hunt_PC2) separated capture web use from active hunting (Supplementary Information Figure S3). Hunt_PC1, hunt_PC2, vegetation and ballooning were used as predictors in Models 2 and 3 (see below).

Phylogeny and comparative analysis

Phylogenetically controlled mixed models were run using the R package MCMCglmm (Hadfield 2010). As a random factor, we used the phylogeny of Fernández et al. (2018), which used data generated by the Spider Tree of Life project (Wheeler et al. 2017; 3 mitochondrial and 3 nuclear markers) with transcriptomic data as a backbone constraint. This was the most complete (at the family level) phylogeny available. We pruned all non-focal families using the R package phytools (Revell 2012), and missing taxa were added to the tree next to sister families using the minimum branch length (1.349), in particular the infraorder mygalomorphae was updated based on a more recent phylogeny incorporating all recognised mygalomorph families (Opatova et al. 2019; Figure 1). For each of the models described below, we visually assessed convergence and ensured effective sample sizes were above 900. With the exception of Model 1, all models were run for 150 000 iterations, thinning every 100 iterations, and the first 15 000 iterations were discarded as burnin. Weak priors (inverse Wishart) were used for residuals (R) and random effects (G), with variance set to 1 and different degrees of belief parameters (Supplementary Information Table S3), and for fixed effects we used default Gaussian priors (B). Prior choice did not affect results. We extracted a statistic that quantifies the percentage of variance explained by just the fixed factors, and by both the fixed and random factors (equivalent to marginal and conditional R^2 respectively), in each of our models (Nakagawa & Schielzeth 2013; Nakagawa et al. 2017).

We first tested whether family, time since fire (in months, for the fire treatment), or their interaction predicted the difference in abundance between the fire and control treatment (Model 1; Table 1). We included phylogeny and the study ID as random factors to control for phylogenetic relatedness between families and multiple data points per study. Data points were weighted by the sample effort for the study (sample effort = (plots*traps*days of fire treatment + plots*traps*days of control treatment)/2) using the mev argument. We ran the model for 500 000 iterations, thinning every 100 interactions, and discarded the first 50 000 iterations as burnin. To further investigate the relationship between family and difference in abundance we ran an intercept only model (difference in abundance ~ 1) with 3 different random factor structures, and compared them based on Akaike's information Criterion (AIC) using the R package MuMIn (Bartoń 2020). The random factors used were A) phylogeny, family and study ID, B) phylogeny and study ID, and C) study ID. This intercept-only model allowed us to explicitly quantify the separate effect of phylogenetic relationships, family and study ID. We also calculated the phylogenetic signal (lambda) and extracted the intercept for each family from model 1 to identify differences across families in the effect of fire.

We next tested whether family or study level traits predicted the difference in abundance between the fire and control treatment (Model 2; Table 1). For this model, we included the interaction between all variables and time since fire (months), and phylogeny, family and study ID as random factors, and again weighted data points by sample effort. Given the high number of predictors in this model, to determine the best fitting model for the response variable, we employed an all-subset model selection approach (dredge, MuMIn) based on corrected AIC (AIC_C). Although models with $\Delta AIC_C < 2$ are generally considered to be as good as the top model, we considered models with $\Delta AIC_C < 7$ to increase the probability of retaining the best model (Symonds & Moussalli 2011). The cumulative AIC_C weight for models with $\Delta AIC_C < 7$ was 0.77, equating to 77% confidence that the best model was included in this subset (compared to 0.30 for models with $\Delta AIC_C < 2$). From this subset of models we measured the relative importance of each variable (RIV) by summing the normalised AIC_C weights across all models in which that variable appeared (Symonds & Moussalli 2011).

Lastly, we extracted the slopes of the interaction term for each family from Model 1 (i.e. change in difference in abundance over time since fire) and tested whether these relationships were predicted by family level traits (Model 3, Table 1). Specifically, this model tested

whether the increase or decrease in abundance through time after fire could be explained by family traits. We included phylogeny as a random factor.

RESULTS

Summary of literature used

We analysed abundance data from 33 studies (29 datasets; Supplementary Information Table S1), incorporating 67 spider families. The data spanned 15 countries across 6 continents, with North America having the most studies (13; Supplementary Information Figure S4). The family Thomisidae had the most datapoints (51), followed by Lycosidae (47) and Gnaphosidae (45), and the most common vegetation type was forest (16 studies). Most studies used a burned versus unburned study design (28 studies) and/or measured the effect of controlled burns (17 studies). Only a few studies provided details about fire intensity, severity, frequency, or the fire history of study sites (e.g. the age of the long-unburned site) and we were therefore unable to include this valuable information in our analysis.

Comparative analysis

Most families showed both positive and negative differences in abundance between treatments (Figure 2). Time since fire (in months, for the fire treatment) had a significant effect on the difference in abundance between fire and control treatment for the families Lycosidae, Linyphiidae and Agelenidae (Model 1; marginal $R^2 = 0.159$, conditional $R^2 = 0.505$; Table 1). The relationship was positive for the families Lycosidae and Linyphiidae, with abundance initially lower in the fire treatment for both families. However, from around two years after fire onwards abundance was higher in the fire treatment for Lycosidae, and around equal in both treatments for Linyphiidae (Figure 3). Conversely, the relationship was negative for the family Agelenidae, with decreasing abundance in the fire treatment over time, for at least 2 years (Figure 3). These relationships were significantly different to those observed in multiple other families (Supplementary Information Table S4).

Phylogenetic relatedness between families was not a strong predictor of the difference in abundance between fire and control treatments, as confirmed by examination of the random effect of family (Supplementary Information Figure S5; Table S5), and the posterior probability of the phylogenetic signal (l = 0.007, 95% CI = 1.08×10^{-10}–0.028) in the intercept only model. Abundance tended to be lower in the fire treatment for the families Agelenidae, Amaurobiidae and Anyphaenidae (in > 80% of studies including these families there was

lower abundance in the fire treatment and mean differences in abundance < 0; Figure 2) although these families had a low number of datapoints, so we interpret this with caution (9, 6 and 10 datapoints respectively). Conversely, multiple families with a high number of datapoints (≥30) showed mean differences of close to zero (Figure 2) and no change in abundance over time (e.g. Gnaphosidae, Hahniidae, Salticidae, Theridiidae, Thomisidae; Figure 3). Therefore, fire either does not affect the abundance of these families, or the effect of fire differs between studies and can be either positive or negative.

Family level and study level traits (family: hunt_PC1, hunt_PC2, vegetation, ballooning; study: latitude, time since fire, fire type, vegetation type) explained only a small proportion of the variance in the difference in abundance between fire and control treatments (Model 2; full model marginal R^2 = 0.00018, conditional R^2 = 0.00024; Table 1). Time since fire, vegetation type, and their interaction were the most important predictors in the top-model set (models with $\Delta AIC_C < 7$; Supplementary Information Table S6). These three predictors appeared in all 47 top models (RIV = 1.00), while other predictors in the top-model set had much lower relative importance (RIV 0.02–0.42; Supplementary Information Table S6). Time since fire was a significant predictor of difference in abundance within the forest vegetation type (Supplementary Information Table S7). The relationship was such that abundance was initially lower in the fire treatment, but higher in the fire treatment from around two years after fire onwards (Figure 2). The change in difference in abundance over time within the forest vegetation type was also significantly different from grassland and woodland vegetation types (Figure 4; Supplementary Information Table S7). Results were qualitatively the same when we used an alternative flat prior (Longdon et al. 2011) for this model (Supplementary Information Table S3, Table S7).

No family level traits predicted the slope of the relationship between time since fire and difference in abundance within each family (Model 3; Supplementary Information Table S8; marginal R^2 = 0.121, conditional R^2 = 0.192).

DISCUSSION

We investigated the global impact of fire on spider abundance through a comparative analysis of published data. Our results show that the effect of fire on spider families is independent of phylogenetic relatedness, and closely related families do not tend to show similar responses. In fact, we found that the effect of fire is highly variable among studies, and there is no

consistency in responses within families. It is therefore difficult to make broad generalisations about the impacts of fire on spiders at the family level. We did, however, find that time since fire had a significant effect on the abundance of some spider families, and within forest vegetation types, which highlights the importance of sampling across temporal scales. This is needed to fully understand the impact of fire and increasing fire frequencies under climate change (Dowdy et al. 2019; Virgilio et al. 2019; Goss et al. 2020). In particular, ecosystems may experience greater impacts when fire intervals are short, due to reduced time for re-establishment and for ecological succession to progress (Kral et al. 2017; Whitman et al. 2019). We found that any negative impacts of fire on spider abundance were restricted to the first few years after fire, demonstrating at a broader scale what previous studies have shown within invertebrate communities (e.g. Brennan et al. 2006; Underwood & Quinn 2010; Pryke & Samways 2012; Radford & Andersen 2012; Podgaiski et al. 2013).

Most spider families in our study showed both positive and negative responses to fire. This is likely due to variation in other site-specific factors that influence abundance, such as species interactions, habitat structure, climate and seasonality, as well as fire history variables that we were unable to include in our models (because they were not known/not reported), and other ecological disturbances (e.g. logging). Time since fire did have a significant effect on abundance, but only in three spider families: Lycosidae, Linyphiidae and Agelenidae. Lycosids (wolf spiders) are active hunting spiders and are often reported to increase in abundance following fire (Niwa & Peck 2002; Brennan et al. 2006; Haddad et al. 2015). Our results showed a global pattern of higher abundance of lycosids in the fire treatment, but only from around two years after fire onwards, suggesting that fire may have direct impacts (mortality) but that burned habitats are beneficial to, or highly colonised by lycosids. Similarly, the abundance of linyphiids (dwarf spiders) was initially lower in the fire treatment but increased over time after fire. Linyphiids are very small, sheet web weaving spiders and have been found to be effective colonisers of burned areas (Malumbres-Olarte et al. 2014). Conversely, spiders of the family Agelenidae decreased in abundance over time since fire. Agelenids (funnel weavers) build sheet webs in the open on grass and shrubs and the negative relationship observed may reflect a lack of suitable vegetation for web sites in burned habitats. Two other families showed a non-significant trend of a negative association with fire: Amaurobiidae (hacklemesh weavers) and Anyphaenidae (ghost spiders). Amaurobiids are sheet web weavers while anyphaenids are active hunters; however, along with agelenids,

all three families build silken retreats in vegetation. Therefore, response to fire may be associated with finer details of vegetation structure that we were not able to test here.

Time since fire also had a significant effect on spider abundance in forests, with abundance initially lower in the fire treatment but increasing over time, while there was no effect of fire in grassland, shrubland or woodland habitats. A meta-analysis of the impact of fire on ants found that ant diversity and abundance decreased in forest biomes, but not deserts, grasslands or savannahs (Vasconcelos et al. 2017). This is hypothesised to be due to changes in vegetation structure and habitat openness as the result of fire rather than fire *per se* (Vasconcelos et al. 2017; Andersen 2019). Therefore, the impacts of fire are expected to be greater for assemblages from more complex habitats (i.e. forests) where habitat modification is more pronounced. Additionally, fire behaviour differs between vegetation types, with grasslands and woodlands showing higher spread rates and intensities, more fine fuel biomass consumption, and increased release of heat when compared to forest ecosystems (Gomes et al. 2020). These differences in fire behaviour are likely to influence the extent of vegetation modification and have direct and indirect impacts on invertebrate taxa.

We found no relationship between response to fire and family level traits, suggesting that a trait-based approach does not increase predictive power at this taxonomic level. The traits that we selected for this study can be somewhat generalised to the family level in spiders; however, within families there will be variation between species in these and other unmeasured traits (e.g. body size, longevity, diet). Previous studies, at the local scale, have detected associations between response to fire and species-level traits. For example, Malumbres-Olarte et al. (2013) found that ambushing, stalking and sheet web building spiders were associated with unburned sites in New Zealand grasslands. Another study in an Australian desert ecosystem found that recently burned sites had a higher abundance of individuals with large body size, limited dispersal ability, burrowing habit and ambush hunting strategies, but that patterns were not consistent across post-fire ages (Langlands et al. 2011). Additionally, species-level data would allow for detection of changes in species composition and diversity, as well as abundance. For example, de Brito et al. (2011) found that arachnid abundance was lower, but diversity was higher in burned areas of Brazilian savannah. Similarly, Langlands et al. (2012) found no difference in spider abundance across post-fire years, but significant changes in species composition, in Australian spinifex habitat. Moretti et al. (2002) found that spider community composition (but not overall abundance)

varied between areas of Swiss chestnut forest experiencing different fire regimes. In all cases there were species unique to certain post-fire ages. Here we analysed data at the family level as this was the taxonomic resolution provided by most studies and gave us the largest dataset to work with. One of the major challenges of working with invertebrate taxa is the high proportion of unknown and undescribed species. It is estimated that fewer than half of all spider species have been formally described (Agnarsson et al. 2013), meaning it is often not possible to identify specimens to species level during surveys. Additionally, of the nearly 50,000 species currently recognised (World Spider Catalog 2021), trait data are available for fewer than 8000 species (16%) (Pekár et al. 2021), and phylogenetic data is available for fewer again. Therefore, although it would be more informative to investigate species-level responses to fire (Brennan et al. 2006), this is often not possible given current knowledge gaps.

It is important to note that our analysis reflects the available data, and studies testing the response of spiders to fire are limited. Additionally, the data are biased towards ground-dwelling taxa (which are captured most frequently in pitfall traps) but arboreal species contribute to species richness in many ecosystems and may be more influenced by changes to vegetation structure as the result of fire (Frizzo et al. 2012). Therefore, studies that employ multiple sampling techniques designed to capture the full community assemblage, and that identify specimens to species/morphospecies level, are likely to detect more informative patterns in spider responses to fire, and life history traits underpinning responses. We also recognise that replicated studies are challenging to achieve when working with large-scale disturbances such as fire. Studies utilising future management burns (e.g. before-after-control-impact studies) may provide the most robust design (Green 1974; Stewart-Oaten & Bence 2001). These studies should sample at multiple time points post-fire and consider each of those time points separately (i.e. not combine temporal sampling into one “after fire” group). Additionally, we were not able to include fire regime characteristics in our analysis, which are likely to be key factors affecting how animals respond to fire (Keeley et al. 2011; Pausas 2019). Where possible, studies should report detailed information about fire severity, intensity, frequency, season, size and time since last fire, for both the treatment and control sites. Finally, we encourage authors to publish datasets along with their manuscripts so that their studies can be included in analyses such as this one.

In conclusion, more research is needed to understand the impacts of fire on spiders and invertebrates more broadly, and this will be most informative for management decisions when conducted at the local scale due to site-specific factors. We show that caution is needed when making broad-scale assumptions about spider family responses to fire, as fire can affect closely related taxa differently. Currently, our ability to predict individual species and community responses to fire is somewhat limited by a lack of knowledge, which highlights the importance of further taxonomic research and fundamental studies of the biology and ecology of invertebrate species. Although difficult to make global generalisations, we did find evidence that short fire intervals may be a threat to some spider families, and in forest ecosystems, where abundance initially decreased after fire. This is important for considering the impact of changing fire regimes and designing management strategies. Finally, although not without limitations (noted above), we show that analyses of published raw data can be used to detect broad scale ecological patterns and provide a novel alternative to traditional meta-analytical approaches, which is not limited by the questions asked in the original studies.

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COMPETING INTERESTS

The authors declare that they have no competing interests.

DATA ACCESSIBILITY

The datasets and code used during the current study are available from the Dryad Digital Repository: doi XXXXXX**.** *Data will be archived upon acceptance of the manuscript.*

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TABLES AND FIGURES

Table 1. Summary of the three models tested in this study and their main findings.

Model	Response variable	Predictor variable/s	Random variable/s	R^2	Results	Summary
1	Difference in abundance (fire - control)	Family × Months	Phylogeny Study ID	$R^2m = 0.159$ $R^2c = 0.505$	Figure 3 Figure S6 Table S4	Change in difference in abundance over time for families Lycosidae, Linyphiidae, Agelenidae
2	Difference in abundance (fire - control)	Hunt_PC1 × Months Hunt_PC2 × Months Vegetation × Months Ballooning × Months Fire type × Months Vegetation type × Months Latitude × Months	Phylogeny Study ID Family	$R^2m = 0.00018$ $R^2c = 0.00024$	Figure 4 Table S6 Table S7	Vegetation type, months and their interaction are the most important predictors Change in difference in abundance over time for Forest vegetation type, which differs from Grassland and Woodland vegetation types
3	Slope (change in difference in abundance over time)	Hunt_PC1 Hunt_PC2 Vegetation Ballooning	Phylogeny	$R^2m = 0.121$ $R^2c = 0.192$	Table S8	No relationship

Figure 1. Reduced version of the spider phylogeny used in this study listing the use of capture web (cWeb), sensing web (sWeb), active (Act.), and ambush (Amb.) foraging strategies, burrowing (Burr.), vegetation (Veg.) and ballooning (Ball.). Images of unburned (top) and burned (bottom) woodland vegetation show how recent fire alters habitat structure. Species from some key families are shown: *Jotus* sp. (Salticidae; image credit: J. Schubert), *Tasmanicosa* sp. (Lycosidae; image credit: J. Schubert), *Eratigena duellica* (Agelenidae; image credit: T. Killick), *Neriene montana* on a sheet web (Linyphiidae; image credit: T. Killick) and *Idiommata* sp. in a burrow (Barychelidae; image credit: J. Schubert).

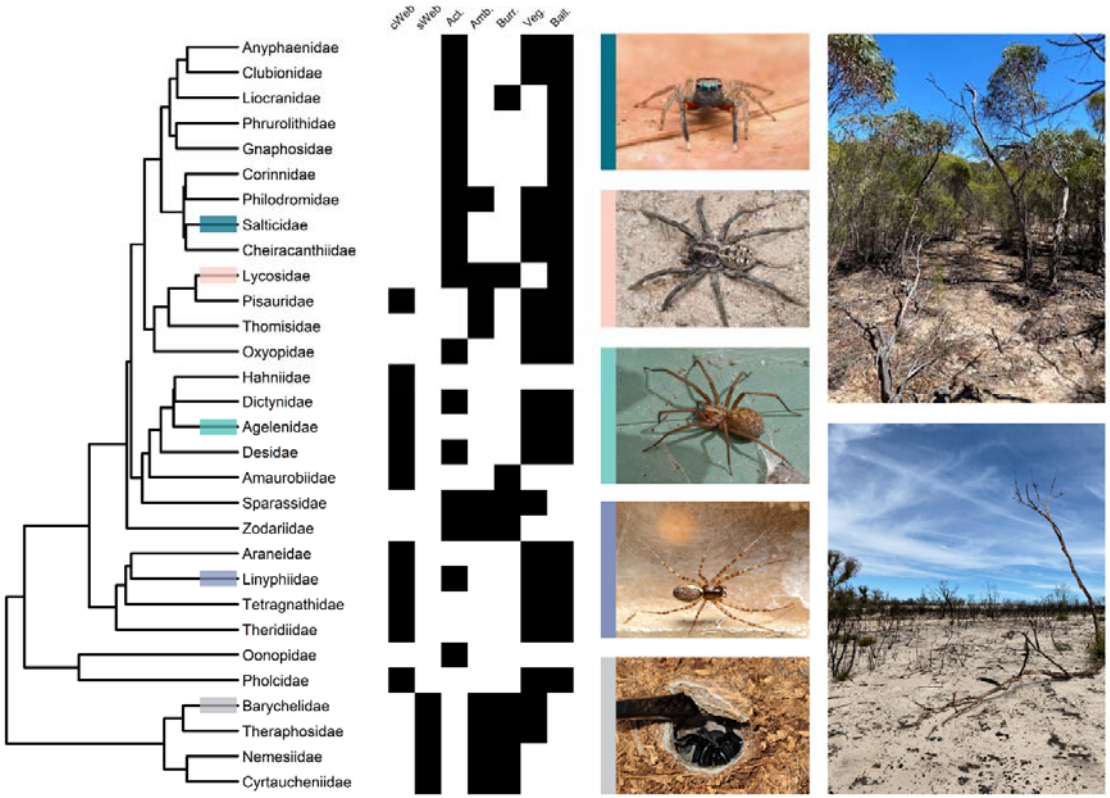


Figure 2. Difference in abundance between fire and control treatments for each family, for each study. Blue = higher abundance in fire treatment, red = lower abundance in fire treatment, small black dot = mean difference in abundance for that family. Only data for families with 5 or more datapoints are presented. Four outlying datapoints were removed for visualisation.

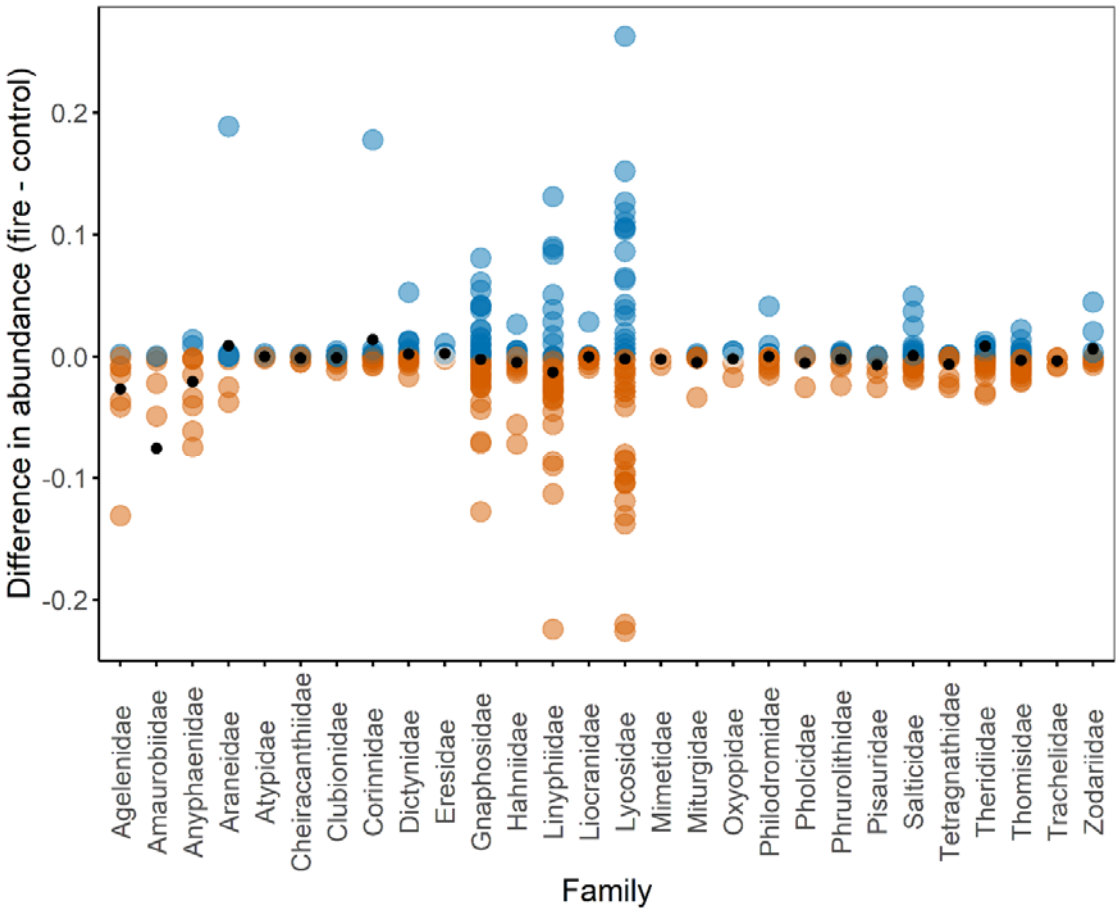


Figure 3. Relationship between time since fire (months) and difference in abundance between fire and control treatment within each family (Model 1). There was a significant effect of months for the families Agelenidae, Linyphiidae and Lycosidae (colours correspond to images in Figure 1), and the relationship differed between multiple families (see Supplementary Information Table S4). Three outlying datapoints removed for visualisation. Grey shading = 95% confidence bounds

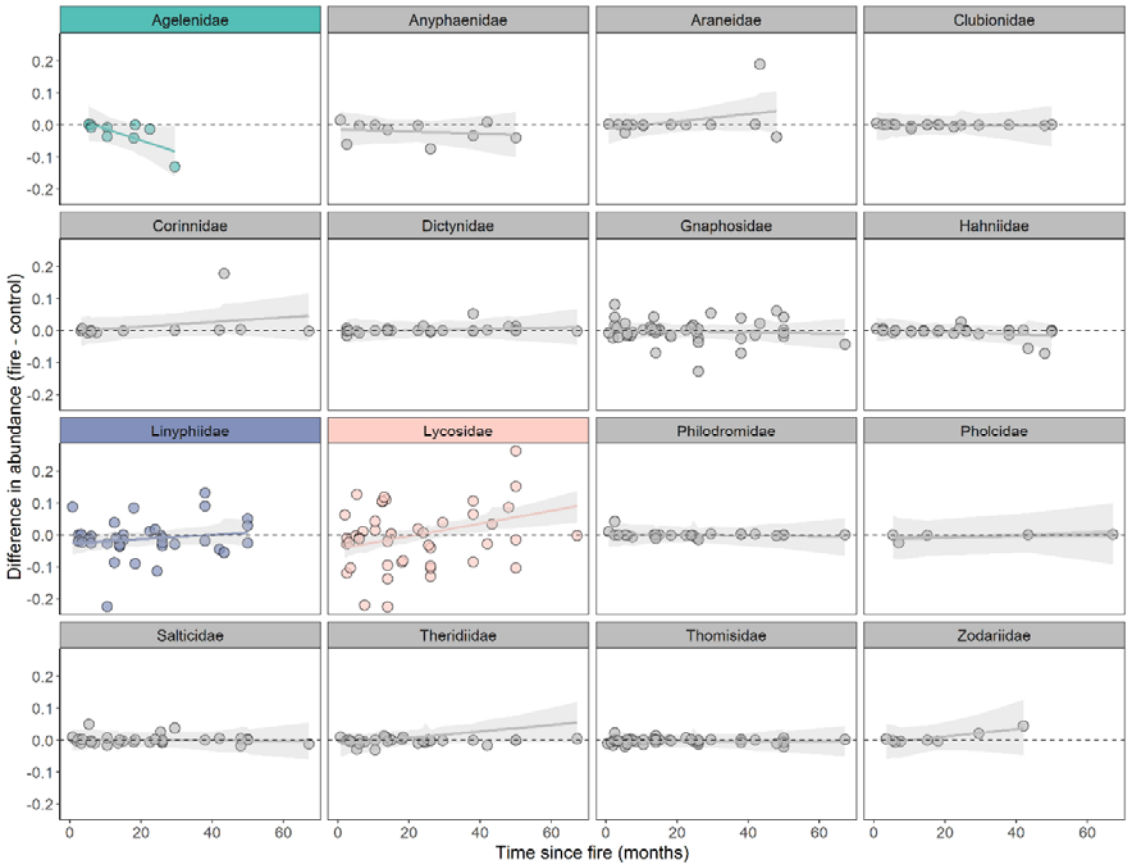
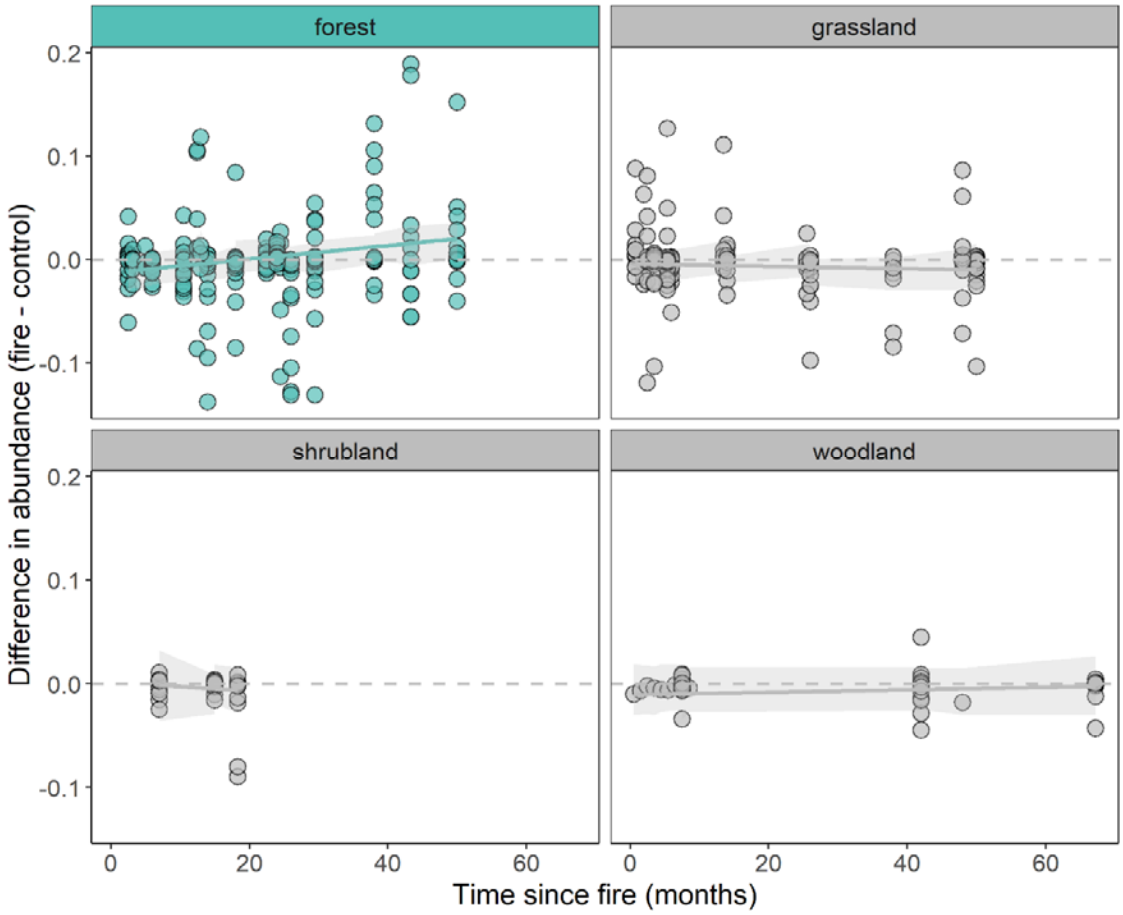


Figure 4. Relationship between time since fire (months) and difference in abundance between the fire and control treatment in each of the four major vegetation types (Model 2). The relationship was significant in the forest vegetation type, and this differed significantly from grassland and woodland. Eight outlying datapoints were removed for visualisation. Grey shading = 95% confidence bounds.



APPENDIX 1 – Data sources

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