TITLE: Assessing the impact of fire on spiders through a global comparative analysis

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RUNNING TITLE: The impact of fire on spiders

ABSTRACT

In many regions fire regimes are changing due to anthropogenic factors. Understanding the responses of species to fire can help to develop predictive models and inform fire management decisions. Spiders are a diverse and ubiquitous group 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 data from studies investigating the impacts of fire on ground-active spiders. We investigated whether fire affects spider abundance and whether ecologically relevant traits or site-specific factors influence species' responses to fire. Although difficult to make broad generalisations about the impacts of fire due to variation in site- and fire-specific factors, we find evidence that short fire intervals may be a threat to spiders, with abundance initially lower in the fire treatment. Additionally, mean abundance was higher in the fire treatment for forests but lower in both grasslands and woodlands. Orb weavers were also more likely to be absent after fire than ambush hunters, suggesting species traits may affect responses. Finally, we show that analyses of published data can be used to detect broad scale patterns and provide an alternative to traditional meta-analytical approaches.

KEYWORDS: Araneae, burn, invertebrate, phylogenetic signal, time since fire, trait-based approach

BACKGROUND

Fire is an important ecological and evolutionary force that has shaped ecosystems worldwide [1, 2]. While fire plays a role in maintaining species richness and ecological processes in fire-prone regions [reviewed in 3], fire can also pose a significant threat to biodiversity and individual species in sensitive landscapes or under different fire regimes [2, 4]. 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 [5-7]. Understanding the impacts of fire, and different fire regimes, is therefore essential for effective conservation and natural resource management now and into the future [8].

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 [9]. Additionally, an understanding of which traits predict a species response to fire may be 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. 9, 10, 11-13], and to a lesser extent on animals [e.g. 14, 15, 16]. One constraint of this approach is that closely related species may share similar functional traits (though not always the case; [17]), 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, we have a limited understanding of the impact of fire on invertebrates [18, 19]. 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 [20], and fundamental information about their ecology, life history and geographic distributions remains largely unknown [21]. Invertebrates play important roles in ecosystem function and changes to invertebrate assemblages can also have knock-on effects across the food web [22, 23]. Therefore, understanding how invertebrates respond to fire is important at both the species and

ecosystem level. Currently, this major knowledge gap makes it difficult to make informed fire management decisions concerning invertebrates [18, 21].

Spiders (order Araneae) are one of the most diverse and successful groups of animals [24] and it is estimated that there are approximately 80,000 species worldwide [24-26]. They are found in almost all terrestrial ecosystems, on every continent except Antarctica, and are important invertebrate predators [27]. Spiders exhibit diverse ecological, behavioural and life history traits [28], including variation in hunting strategies and body size. 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 common survey method for invertebrates). Therefore, spiders are a potential model system as indicators of ecological disturbance [29], 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 [30, 31]. A previous meta-analysis on the effects of land management (including fire) on spiders found that fire negatively affected spider abundance [32]. 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 [31]. For example, fire may have the greatest impact on taxa associated with leaf-litter, as this is the substrate most often burned during fires [19, 33, 34], while burrowing species may be sheltered from the heat and flames [35]. Additionally, the simplified habitat structure following fire may favour the more active hunting species [36], 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 [37, 38]. Overall, the response of animals to fire, and the adaptations and traits underpinning this, are still poorly understood [39-41].

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 ground-active spider abundance at the family or species level. We also investigate whether there is a relationship between response to fire and species 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 responses to fire between studies, but that there are some broad scale patterns associated with hunting strategy, vegetation type and time since fire which may have important implications for fire management decisions 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, 3) used pitfall trapping, and 4) recorded abundance or presence/absence. Requirement 3 was to allow us to standardise abundance measures and compare data between studies (i.e. adjust abundance according to sampling effort; more details below). Of the 1,105 studies returned by the literature search, 139 were relevant, 49 met the above criteria for inclusion in the analysis and 36 of these provided usable data with the manuscript (Table S1). There were four cases where two studies had used the same underlying data, so these were combined, resulting in 32 independent datasets (see PRISMA 2020 diagram; Figure S1). A list of the data sources used in the study is provided in the supplementary material (Table S1).

Data collection

For each study we recorded the major vegetation type (forest, grassland, shrubland, woodland), mean time since the last fire (in months, for the fire treatment), fire type (controlled, wildfire) and latitude, and collated raw family and species level abundance and species level presence/absence data 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/species (and not per study), we did not extract the overall effect sizes per study, as would be done in a traditional meta-analytical framework. Data were extracted from tables using Tabula (https://tabula.technology), or from figures using metaDigitise [42] in R [version 4.1.0; 43]. Taxonomy was checked for all datapoints and updated if necessary (i.e. we ensured the taxonomic classification of species, genera and families was current) [26].

Abundance (at the family and species level) was standardised across and within studies by dividing absolute 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/species 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. We also classified species into one of three categories: 1) present in control, absent in fire treatment ("disappeared"), 2) present in both control and fire treatment ("no change"), 3) absent in control, present in fire treatment ("colonised"). For the family level analysis, we removed families with fewer than five data points (five fire-control differences). The presence/absence dataset was larger than the abundance dataset because not all studies measured abundance or provided enough detail for us to standardise abundance. This resulted in 485 datapoints for the family level analysis and 2,328 for the species level analysis.

To determine whether ecologically relevant traits predict a species' response to fire, we compiled information on primary hunting strategies (whether the species uses orb, sheet or space webs, active hunting or ambushing) and female total body length (mm) using the World Spider Trait database [28] and taxonomic literature listed on the World Spider Catalog [26] (Figure 1; Table S2). Female body length was used as there were more data available for female than male spiders; however, given the huge diversity of spiders and the fact that many species are understudied, we were not able to obtain body length measurements for all the

species included in our study (female body length was missing for 21.7% of the dataset). Rather than perform list-wise deletion (removing datapoints with missing data), which can reduce statistical power and bias parameter estimates [44], we employed a data imputation procedure. The Amelia II R package [45] was first used to perform expectation-maximisation with bootstrapping for multiple imputation under an assumption of missing at random (MAR). All variables from Models 2 and 3 were included in the imputation step, and female body length was log transformed to meet the assumption of normality. We produced 10 imputed datasets (m = 10) and confirmed convergence of the chains visually. Each missing value was then replaced by the mean of its corresponding imputed values as per the Single Centre Imputation from Multiple Chained Equation (SICE) technique [46]. All analyses were performed with both the imputed and a reduced complete case dataset, which did not affect inferences about female body length (the imputed variable).

Phylogeny and comparative analysis

Phylogenetically controlled mixed models were run using the R package MCMCglmm [47]. As a random factor, we used the phylogeny of Fernández et al. [48], which used data generated by the Spider Tree of Life project [49; 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 [50], 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 [51; Figure 1]. For each of the models described below, we visually assessed convergence and ensured effective sample sizes were above 900. Weak priors (inverse Wishart) were used for residuals (R) and random effects (G), with variance set to 1 and different degrees of belief parameters (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 [52, 53].

Using the family level dataset, we first tested whether family, time since fire (months), 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 (family = gaussian) 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 [54]. 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 effects of phylogenetic relationships, family and study ID. We also calculated the phylogenetic signal (lambda) and extracted the intercept for each family from random factor model A to identify differences across families in the effect of fire.

We next used the species level dataset to test whether species level traits or study level traits predicted the difference in abundance between the fire and control treatment (Model 2; family = gaussian; Table 1). For this model, we included primary hunting strategy (hunt), female body length (body length), vegetation type (vegetation), fire type, absolute latitude (latitude), and time since fire (months) as predictors. Phylogeny, species, and study ID were included as random factors, and datapoints were again weighted by sample effort (mev). Finally, we tested whether the same six variables predicted the presence/absence of species in the control and fire treatments (Model 3, family = threshold; Table 1). Given that the response variable was an ordinal factor for this model, we fixed the residual variance to 1 (Table S3). Models 2 and 3 were both run for 150 000 iterations, thinning every 100 iterations, with the first 15 000 iterations discarded as burnin.

RESULTS

Summary of literature used

We analysed data from 36 studies (32 datasets; Table S1), incorporating 66 families and 1319 species/morphospecies. The data spanned 16 countries across 6 continents, with North America having the most studies (13; Figure S2). The most common vegetation type was forest (14 studies), and most studies used a burned versus unburned study design (27 studies) and/or measured the effect of controlled burns (16 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 S3). Time since fire (months) 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 2). Conversely, the relationship was negative for the family Agelenidae, with decreasing abundance in the fire treatment over time, for at least 2 years (Figure 2). These relationships were significantly different to those observed in multiple other families (Figure S4, 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 (Figure S5; Table S5), and the posterior probability of the phylogenetic signal (lambda = 0.010, 95% CI = 7.96×10^{-9} – 0.041) 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 S3), 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 S3) and no change in abundance over time (e.g. Gnaphosidae, Hahniidae, Salticidae, Theridiidae, Thomisidae; Figure 3). Therefore, fire either did not affect the abundance of these families, or the effect of fire differed between studies and could be either positive or negative.

Species level (hunt, body length) and study level (vegetation, fire type, latitude, months) traits explained only a small proportion of the variance in the difference in abundance between fire and control treatments (Model 2; full model marginal $R^2 = 0.0000064$, conditional $R^2 = 0.000017$; Table 1). Vegetation type and time since fire were significant

predictors of the difference in abundance (Table S6). Forest differed from both grassland and woodland vegetation types, with the mean difference in abundance being positive (higher abundance in fire treatment) for forest, while negative (lower abundance in fire treatment) for all other vegetation types (Figure 3). The relationship between difference in abundance and time since fire 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 4).

There was a significant relationship between presence/absence category and hunting strategy (Model 1; marginal $R^2 = 0.012$, conditional $R^2 = 0.102$; Table 1). Orb web weavers differed from ambush hunters in that a greater proportion of orb web weavers "disappeared" and fewer "colonised" (Figure 5). This relationship was also observed between orb web weavers and active hunters but was marginally non-significant ($P = 0.059$; Table S7). Time since fire also had a significant effect on presence/absence (Table 1; Table S7). Species that "disappeared" were recorded sooner after fire than those that "colonised" (Figure 6). Additionally, there was a non-significant trend between vegetation types, with forest having more species that "disappeared" and "colonised" than grassland and woodland vegetation types (Figure S6).

DISCUSSION

We investigated the global impact of fire on ground-active spiders through a comparative analysis of published abundance and presence/absence 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. However, at the species level, we detected relationships between species presence and primary hunting strategy, and between abundance and vegetation type. We also found that time since fire had a significant effect on both abundance and presence, which highlights the importance of sampling across temporal scales. An understanding of this is needed to fully understand the impact of fire and increasing fire frequencies under climate change [5-7]. 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 [55, 56]. 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 [30, 57-60].

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 at both the family and species level. In particular, three spider families showed changes in abundance over time since fire: Lycosidae, Linyphiidae and Agelenidae. Lycosids (wolf spiders) are often reported to increase in abundance following fire [36, 59, 61]. 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 have previously been found to be effective colonisers of burned areas [62]. Conversely, spiders of the family Agelenidae (funnel weavers) decreased in abundance over time since fire. Two other families also showed a non-significant trend of a negative association with fire: Amaurobiidae (hacklemesh weavers) and Anyphaenidae (ghost spiders). Overall, analyses at the family level detected some relationships with time since fire, but this taxonomic level is too coarse to investigate the predictors of response to fire.

Of the nearly 50,000 spider species currently recognised [26], trait data are available for fewer than 8000 species (16%) [28]. Given this, we were only able to obtain species level trait data on primary hunting strategy and female total body length. Nonetheless, our results suggest that a trait-based approach could increase predictive power if applied at the species level. Although there was no relationship between species traits and abundance, we did detect a relationship with presence/absence categories. We found that orb web weavers differed from ambush hunters in that a greater proportion of orb web weavers “disappeared” and fewer “colonised” in the fire treatment. Orb web weavers rely on vegetation for web anchor points [63, 64], and vegetation structure is likely to be affected by fire [65]. The higher proportion of species that “disappeared” may reflect a lack of suitable vegetation for web sites, or decreased habitat complexity in burned habitats [37, 38]. Conversely, ambush

hunters are often also burrowers (e.g. mygalomorphs) or use retreat sites which may protect them during the fire event and/or be less altered in the post fire environment (soil and rock do not burn) [35]. We also found a similar pattern between orb web weavers and active hunters, although this was marginally non-significant. Active hunters may benefit from increased hunting success in the more open habitat after fire [36]. Previous studies, at the local scale, have detected associations between response to fire and species-level traits. For example, Malumbres-Olarte et al. [66] 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 [14]. We detected a broad-scale relationship with hunting strategy, but this is likely to interact with local site and fire specific factors.

Species level responses to fire also differed between vegetation types, with mean abundance higher in the fire treatment for forests, but lower in the fire treatment for grassland, shrubland and woodland habitats. Although not significant, there was also a trend of a higher proportion of species that “disappeared” or “colonised” in the fire treatment for forest compared to grassland and woodland vegetation types, suggesting there may be a higher turnover of species in forests following fire. We did not analyse other diversity or community composition indices in this study, but this would likely give a more complete picture of the effects of fire than abundance alone. For example, de Brito et al. [67] found that arachnid abundance was lower, but diversity was higher in burned areas of Brazilian savannah. Similarly, Langlands et al. [68] found no difference in spider abundance across post-fire years, but significant changes in species composition in Australian spinifex habitat. Moretti et al. [69] 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. Changes in abundance and/or species assemblages are predicted to be driven by changes to vegetation structure and habitat openness as the result of fire rather than fire *per se* [70, 71]. Therefore, the impacts of fire may 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 [72]. These

differences in fire behaviour are likely to influence the extent of vegetation modification and have direct and indirect impacts on invertebrate taxa. The response of individual species to fire is also likely to be associated with finer details of vegetation structure that we were not able to test here.

It is important to note that our analyses reflect 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 [73]. It was necessary to restrict our analysis to data obtained from pitfall trapping as it allowed us to standardise abundance within and between studies. However, studies that employ multiple sampling techniques designed to capture the full spider assemblage 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 [74, 75]. 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 [39, 76]. 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 easily included in analyses such as this one.

CONCULSIONS

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, but that a trait-based approach may increase predictive power when employed at the species level. Currently, our ability to predict the responses of individual species and communities 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 spiders, with abundance initially decreasing after fire, and "disappearing" species detected sooner after fire than "colonising" species. This is important for considering the impact of changing fire regimes and designing fire 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 an 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.*

REFERENCES

1. Pausas, J.G. & Keeley, J.E. 2009 A burning story: The role of fire in the history of life. *BioScience* **59**, 593–601. (doi:10.1525/bio.2009.59.7.10).

2. Bond, W.J. & Keeley, J.E. 2005 Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**, 387–394. (doi:10.1016/j.tree.2005.04.025).

3. He, T., Lamont, B.B. & Pausas, J.G. 2019 Fire as a key driver of Earth's biodiversity. *Biol. Rev.* **94**, 1983–2010. (doi:10.1111/brv.12544).

4. Shlisky, A., Alencar, A., Manta, M. & Curran, L.M. 2009 Overview: Global fire regime conditions, threats, and opportunities for fire management in the tropics. In *Tropical Fire Ecology* (Springer, Berlin, Heidelberg, Springer Praxis Books.

5. Virgilio, G.D., Evans, J.P., Blake, S.A.P. & Armstrong, M. 2019 Climate Change Increases the Potential for Extreme Wildfires. *Geophysical Research Letters* **46**. (doi:10.1029/2019GL083699).

6. Goss, M., Swain, D.L., Abatzoglou, J.T., Sarhadi, A., Kolden, C., Williams, A.P. & Diffenbaugh, N.S. 2020 Climate change is increasing the risk of extreme autumn wildfire conditions across California. *Environmental Research Letters* **15**, 094016 (doi:10.1088/1748-9326/ab83a7).

7. Dowdy, A.J., Ye, H., Pepler, A., Thatcher, M., Osbrough, S.L., Evans, J.P., Di Virgilio, G. & McCarthy, N. 2019 Future changes in extreme weather and pyroconvection risk factors for Australian wildfires. *Scientific Reports* **9**, 1–12. (doi:10.1038/s41598-019-46362-x).

8. Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., et al. 2010 Fire management for biodiversity conservation: Key research questions and our capacity to answer them. *Biol. Conserv.* **143**, 1928–1939. (doi:10.1016/j.biocon.2010.05.026).

9. Keith, D.A. 2012 Functional traits: their roles in understanding and predicting biotic responses to fire regimes from individuals to landscapes. In *Flammable Australia: Fire*

Regimes, Biodiversity and Ecosystems in a Changing World (eds. R.A. Bradstock, G.A. M. & R.J. Williams). Clayton, CSIRO Publishing.

10. Menges, E.S. 2007 Integrating demography and fire management: an example from Florida scrub. *Aust. J. Bot.* **55**, 261–272. (doi:10.1071/BT06020).

11. Enright, N.J., Fontaine, J.B., Lamont, B.B., Miller, B.P. & Westcott, V.C. 2014 Resistance and resilience to changing climate and fire regime depend on plant functional traits. *J. Ecol.* **102**, 1572–1581. (doi:10.1111/1365-2745.12306).

12. Clarke, P.J., Lawes, M.J., Murphy, B.P., Russell-Smith, J., Nano, C.E.M., Bradstock, R., Enright, N.J., Fontaine, J.B., Gosper, C.R., Radford, I., et al. 2015 A synthesis of postfire recovery traits of woody plants inAustralian ecosystems. *Sci. Total Environ.* **534**, 31–42. (doi:10.1016/j.scitotenv.2015.04.002).

13. Rodman, K.C., Veblen, T.T., Andrus, R.A., Enright, N.J., Fontaine, J.B., Gonzalez, A.D., Redmond, M.D. & Wion, A.P. 2020 A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. *J. Ecol.* **109**, 313–326. (doi:10.1111/1365-2745.13480).

14. Langlands, P.R., Brennan, K.E.C., Framenau, V.W. & Main, B.Y. 2011 Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* **80**, 558–568. (doi:10.1111/j.1365-2656.2010.01795.x).

15. Moretti, M., de Bello, F., Roberts, S.P.M. & Potts, S.G. 2009 Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology* **78**, 98–108. (doi:10.1111/j.1365-2656.2008.01462.x).

16. Driscoll, D.A., Smith, A.L., Blight, S. & Sellar, I. 2019 Interactions among body size, trophic level, and dispersal traits predict beetle detectability and occurrence responses to fire. *Ecol. Entomol.* **45**, 300–310. (doi:10.1111/een.12798).

17. Losos, J.B. 2008 Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11**, 995–1003. (doi:10.1111/j.1461-0248.2008.01229.x).

18. Saunders, M.E., Barton, P.S., Bickerstaff, J.R.M., Frost, L., Latty, T., Lessard, B.D., Lowe, E.C., Rodriguez, J., White, T.E. & Umbers, K.D.L. 2021 Limited understanding of bushfire impacts on Australian invertebrates. *Insect. Conserv. Divers.* **14**, 285–293. (doi:10.1111/icad.12493).

19. New, T.R., Yen, A.L., Sands, D.P.A., Greenslade, P., Neville, P.J., York, A. & Collett, N.G. 2010 Planned fires and invertebrate conservation in south east Australia. *J. Insect Conserv.* **14**, 567–574. (doi:10.1007/s10841-010-9284-4).

20. Stork, N.E. 2018 How many species of insects and other terrestrial arthropods are there on Earth? *Annual Review of Entomology* **63**, 31–45. (doi:10.1146/annurev-ento-020117-043348).

21. Cardoso, P., Erwin, T.L., Borges, P.A.V. & New, T.R. 2011 The seven impediments in invertebrate conservation and how to overcome them. *Biol. Conserv.* **144**, 2647–2655. (doi:10.1016/j.biocon.2011.07.024).

22. Wurtsbaugh, W.A. 1992 Food-web modification by an invertebrate predator in the Great Salt Lake (USA) *Oecologia* **89**, 168–175. (doi:10.1007/BF00317215.).

23. Benndorf, J., Wissel, B., Sell, A.F., Hornig, U., Ritter, P. & Böing, W. 2000 Food web manipulation by extreme enhancement of piscivory: an invertebrate predator compensates for the effects of planktivorous fish on a plankton community. *Limnologica* **30**, 235–245. (doi:10.1016/S0075-9511(00)80053-5).

24. Agnarsson, I., Coddington, J.A. & Kuntner, M. 2013 Systematics: progress in the study of spider diversity and evolution. In *Spider research in the 21st century: trends & perspectives* (ed. D. Penney). Manchester, UK, Siri Scientific Press.

25. Raven, P.H. & Yeates, D.K. 2007 Australian biodiversity: threats for the present, opportunities for the future. *Australian Journal of Entomology* **46**, 177–187. (doi:10.1111/j.1440-6055.2007.00601.x).

26. World Spider Catalog. 2021 World Spider Catalog ver. 22.0. (Natural History Museum Bern.

27. Nyffeler, M. 2017 An estimated 400 – 800 million tons of prey are annually killed by the global spider community. *The Science of Nature* **104**, 30. (doi:10.1007/s00114-017-1440-1).

28. Pekár, S., Wolff, J., Černecká, Ľ., Birkhofer, K., Mammola, S., Lowe, E.C., Fukushima, C.S., Herberstein, M.E., Kučera, A., Buzatto, B., et al. 2021 The World Spider Trait database: a centralised global open repository for curated data on spider traits. Database 2021: baab064. (Masaryk University, Brno.

29. Churchill, T.B. 1997 Spiders as ecological indicators: an overview for Australia. *Mem. Mus. Vic.* **56**, 331–337. (doi:10.24199/j.mmv.1997.56.21).

30. Underwood, E.C. & Quinn, J.F. 2010 Response of ants and spiders to prescribed fire in oak woodlands of California. *J. Insect Conserv.* **14**, 359–366. (doi:10.1007/s10841-010-9265-7).

31. Engstrom, R.T. 2010 First-order fire effects on animals: review and recommendations. *Fire Ecology* **6**, 115–130. (doi:10.4996/fireecology.0601115).

32. Prieto-Benítez, S. & Méndez, M. 2011 Effects of land management on the abundance and richness of spiders (Araneae): A meta-analysis. *Biol. Conserv.* **144**, 683–691. (doi:10.1016/j.biocon.2010.11.024).

33. York, A. 1999 Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. *J. Insect Conserv.* **3**, 191–199. (doi:10.1023/A:1009643627781).

34. Hanula, J.L. & Wade, D.D. 2003 Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. *For. Ecol. Manage.* **175**, 163–184. (doi:10.1016/S0378-1127(02)00130-5).

35. Carrel, J.E. 2008 Differential survival of Geolycosa xera archboldi and G. hubbelli (Araneae, Lycosidae) after fire in Florida scrub. *J. Arachnol.* **36**, 595–599. (doi:10.1636/T08-14.1).

36. Niwa, C.G. & Peck, R.W. 2002 Influence of prescribed fire on carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in Southwestern Oregon. *Environ. Entomol.* **31**, 785–796. (doi:10.1603/0046-225X-31.5.785).

37. Robinson, J.V. 1981 The effect of architectural variation in habitat on a spider community: an experimental field study. *Ecology* **62**, 73–80. (doi:10.2307/1936670).

38. Uetz, G.W. 1992 Foraging strategies of spiders. *Trends in Ecology and Evolution* **7**, 155–159. (doi:10.1016/0169-5347(92)90209-T).

39. Pausas, J.G. 2019 Generalized fire response strategies in plants and animals. *Oikos* **128**, 147–153. (doi:10.1111/oik.05907).

40. Pausas, J.G. & Parr, C.L. 2018 Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology* **32**, 113–125. (doi:10.1007/s10682-018-9927-6).

41. Nimmo, D.G., Carthey, A.J.R., Jolly, C.J. & Blumstein, D.T. 2021 Welcome to the Pyrocene : animal survival in the age of megafire. *Global Change Biology*. (doi:10.1111/gcb.15834).

42. Pick, J.L., Nakagawa, S. & Noble, D.W.A. 2019 Reproducible, flexible and high-throughput data extraction from primary literature: The metaDigitise R package. *Methods in Ecology and Evolution* **10**, 426–431. (doi:10.1111/2041-210X.13118).

43. R Core Team. 2021 R: A language and environment for statistical computing. (Vienna, Austria, R Foundation for Statistical Computing.

44. Nakagawa, S. 2015 Missing Data: Mechanisms, Methods and Messages. In *Ecological Statistics: Contemporary Theory and Application* (eds. G.A. Fox, S. Negrete-Yankelevich & S.V. J.), pp. 81–105. Oxford, Oxford University Press.

45. Honaker, J., King, G. & Blackwell, M. 2011 Amelia II: A Program for Missing Data. *Journal of Statistical Software* **45**, 1–47. (doi:10.18637/jss.v045.i07).

46. Khan, S.I. & Hoque, A.S.M.L. 2020 SICE: an improved missing data imputation technique. *Journal of Big Data* **7**, 37. (doi:10.1186/s40537-020-00313-w).

47. Hadfield, J.D. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1–22. (doi:10.18637/jss.v033.i02).

48. Fernández, R., Kallal, R.J., Dimitrov, D., Ballesteros, J.A., Arnedo, M.A., Giribet, G. & Hormiga, G. 2018 Phylogenomics, Diversification Dynamics, and Comparative Transcriptomics across the Spider Tree of Life. *Current Biology* **28**, 1489–1497. (doi:10.1016/j.cub.2018.03.064).

49. Wheeler, W.C., Coddington, J.A., Crowley, L.M., Dimitrov, D., Goloboff, P.A., Griswold, C.E., Hormiga, G., Prendini, L., Ramírez, M.J., Sierwald, P., et al. 2017 The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* **33**, 574–616. (doi:10.1111/cla.12182).

50. Revell, L.J. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x).

51. Opatova, V., Hedin, M., Montes de Oca, L., Král, J. & Bond, J.E. 2019 Phylogenetic systematics and evolution of the spider infraorder Mygalomorphae using genomic scale data. *Systematic Biology* **69**, 671–707. (doi:10.1093/sysbio/syz064).

52. Nakagawa, S. & Schielzeth, H. 2013 A general and simple method for obtaining R2 from generalized linear mixed effects models. *Methods in Ecology and Evolution* **4**, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x).

53. Nakagawa, S., Johnson, P.C.D. & Schielzeth, H. 2017 The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface* **14**, 20170213. (doi:10.1098/rsif.2017.0213).

54. Bartoń, K. 2020 Mu-MIn: Multi-model inference. (

55. Whitman, E., Parisien, M.-A., Thompson, D.K. & Flannigan, M.D. 2019 Short-interval wildfire and drought overwhelm boreal forest resilience. *Scientific Reports* **9**, 18796. (doi:10.1038/s41598-019-55036-7).

56. Kral, K.C., Limb, R.F., Harmon, J.P. & Hovick, T.J. 2017 Arthropods and Fire: Previous Research Shaping Future Conservation. *Rangel. Ecol. Manag.* **70**, 589–598. (doi:10.1016/j.rama.2017.03.006).

57. Pryke, J.S. & Samways, M.J. 2012 Importance of using many taxa and having adequate controls for monitoring impacts of fire for arthropod conservation. *J. Insect Conserv.* **16**, 177–185. (doi:10.1007/s10841-011-9404-9).

58. Radford, I.J. & Andersen, A.N. 2012 Effects of fire on grass-layer savanna macroinvertebrates as key food resources for insectivorous vertebrates in northern Australia. *Austral Ecol.* **37**, 733–742. (doi:10.1111/j.1442-9993.2012.02413.x).

59. Brennan, K.E.C., Ashby, L., Majer, J.D., Moir, M.L. & Koch, J.M. 2006 Simplifying assessment of forest management practices for invertebrates: How effective are higher taxon and habitat surrogates for spiders following prescribed burning? *For. Ecol. Manage.* **231**, 138–154. (doi:10.1016/j.foreco.2006.05.035).

60. Podgaiski, L.R., Joner, F., Lavorel, S., Moretti, M., Ibanez, S., Mendonça, M.d.S. & Pillar, V.D. 2013 Spider Trait Assembly Patterns and Resilience under Fire-Induced Vegetation Change in South Brazilian Grasslands. *PLoS One* **8**, e60207. (doi:10.1371/journal.pone.0060207).

61. Haddad, C.R., Foord, S.H., Fourie, R. & Dippenaar-Schoeman, A.S. 2015 Effects of a fast-burning spring fire on the ground-dwelling spider assemblages (Arachnida: Araneae) in a Central South African Grassland Habitat. *Afr. Zool.* **50**, 281–292. (doi:10.1080/15627020.2015.1088400).

62. Malumbres-Olarte, J., Barratt, B.I.P., Vink, C.J., Paterson, A.M., Cruickshank, R.H., Ferguson, C.M. & Barton, D.M. 2014 Big and aerial invaders: dominance of exotic spiders in burned New Zealand tussock grasslands. *Biol. Invasions* **16**, 2311–2322. (doi:10.1007/s10530-014-0666-5).

63. Cunha, E.R., Thomaz, S.M., Mormul, R.P., Cafofo, E.G. & Bonaldo, A.B. 2012 Macrophyte structural complexity influences spider assemblages attributes in wetlands. *Wetlands* **32**, 369–377. (doi:10.1007/s13157-012-0272-1).

64. Mcnett, B.J. & Rypstra, A.L. 2008 Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. *Ecol. Entomol.* **25**, 423–432. (doi:10.1046/j.1365-2311.2000.00279.x).

65. Foster, C.N., Barton, P.S., Robinson, N.M., MacGregor, C.I. & Lindenmayer, D.B. 2017 Effects of a large wildfire on vegetation structure in a variable fire mosaic. *Ecological Applications* **27**, 2369–2381. (doi:10.1002/eap.1614).

66. Malumbres-Olarte, J., Barratt, B.I.P., Vink, C.J., Paterson, A.M., Cruickshank, R.H., Ferguson, C.M. & Barton, D.M. 2013 Habitat specificity, Dispersal and burning season: Recovery indicators in New Zealand native grassland communities. *Biol. Conserv.* **160**, 140–149. (doi:10.1016/j.biocon.2013.01.004).

67. De Brito Freire-Jr, G. & Motta, P.C. 2011 Effects of experimental fire regimes on the abundance and diversity of cursorial arachnids of Brazilian savannah (cerrado biome). *J. Arachnol.* **39**, 263–272. (doi:10.1636/CP10-85.).

68. Langlands, P.R., Brennan, K.E.C. & Ward, B. 2012 Is the reassembly of an arid spider assemblage following fire deterministic? *Austral Ecol.* **37**, 429–439. (doi:10.1111/j.1442-9993.2011.02299.x).

69. Moretti, M., Conedera, M., Duelli, P. & Edwards, P.J. 2002 The effects of wildfire on ground-active spiders in deciduous forests on the Swiss southern slope of the Alps. *J. Appl. Ecol.* **39**, 321–336. (doi:10.1016/S0378-1127(03)00314-1).

70. Vasconcelos, H.L., Maravalhas, J.B. & Cornelissen, T. 2017 Effects of fire disturbance on ant abundance and diversity: a global meta-analysis. *Biodivers. Conserv.* **26**, 177–188. (doi:10.1007/s10531-016-1234-3).

71. Andersen, A.N. 2019 Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. *Journal of Animal Ecology* **88**, 350–362. (doi:10.1111/1365-2656.12907).

72. Gomes, L., Miranda, H.S., Silvério, D.V. & Bustamante, M.M.C. 2020 Effects and behaviour of experimental fires in grasslands, savannas, and forests of the Brazilian Cerrado. *For. Ecol. Manage.* **458**, 117804. (doi:10.1016/j.foreco.2019.117804).

73. Frizzo, T.L.M., Campos, R.L. & Vasconcelos, H.L. 2012 Contrasting effects of fire on arboreal and ground-dwelling ant communities of a neotropical savanna. *Biotropica* **44**, 254–261. (doi:10.1111/j.1744-7429.2011.00797.x).

74. Green, R.H. 1974 *Sampling design and statistical methods for environmental biologist*. Chichester, UK, Wiley Interscience.

75. Stewart-Oaten, A. & Bence, J.R. 2001 Temporal and spatial variation in environmental impact assessment. *Ecological Monographs* **71**, 305–339. (doi:10.2307/2657220).

76. Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. 2011 Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**, 406–4011. (doi:10.1016/j.tplan ts.2011.04.002).

Figure 1. Reduced version of the spider phylogeny used in this study listing the use of active (Act.), ambush (Amb.), orb, sheet and space web hunting strategies by species within families. 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). Images of unburned (top) and burned (bottom) woodland vegetation show how recent fire can alter habitat structure.

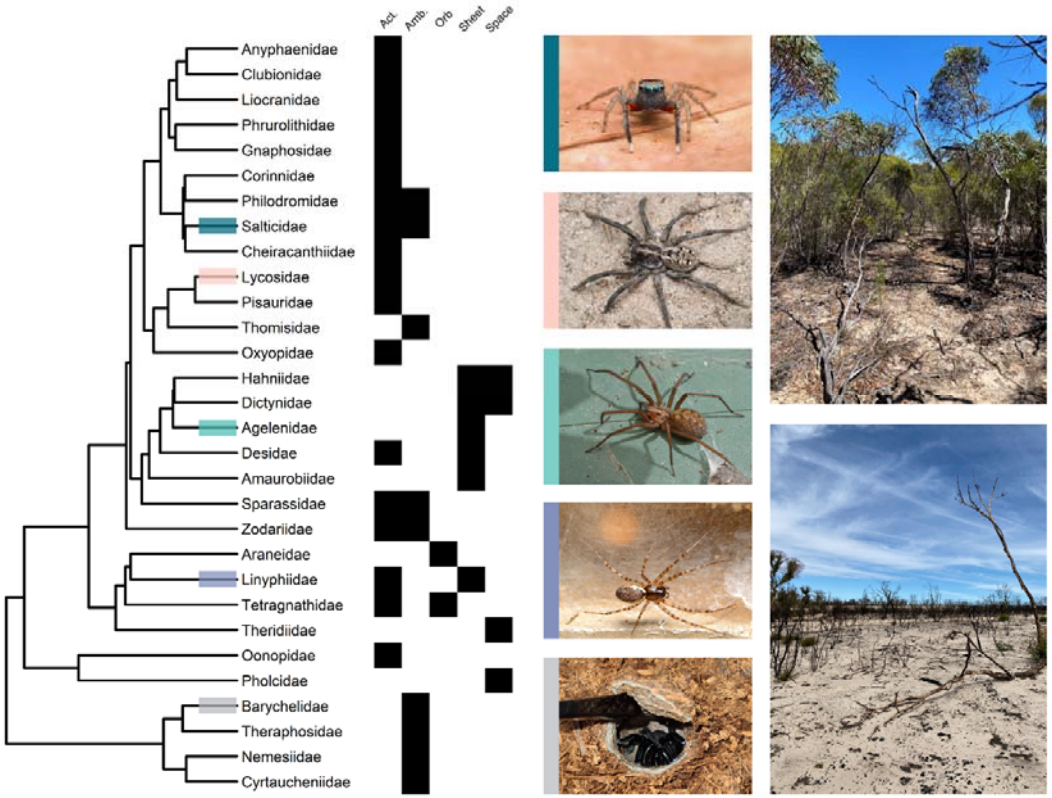

Figure 2. Relationship between time since fire (months) and difference in abundance between fire and control treatment within each family (Model 1). There was a significant effect of months for the families Agelenidae, Linyphiidae and Lycosidae (colours correspond to images in Figure 1), and the relationship differed between multiple families (see Table S4). Three outlying datapoints were removed for visualisation. Grey shading = 95% confidence bounds (N = 485).

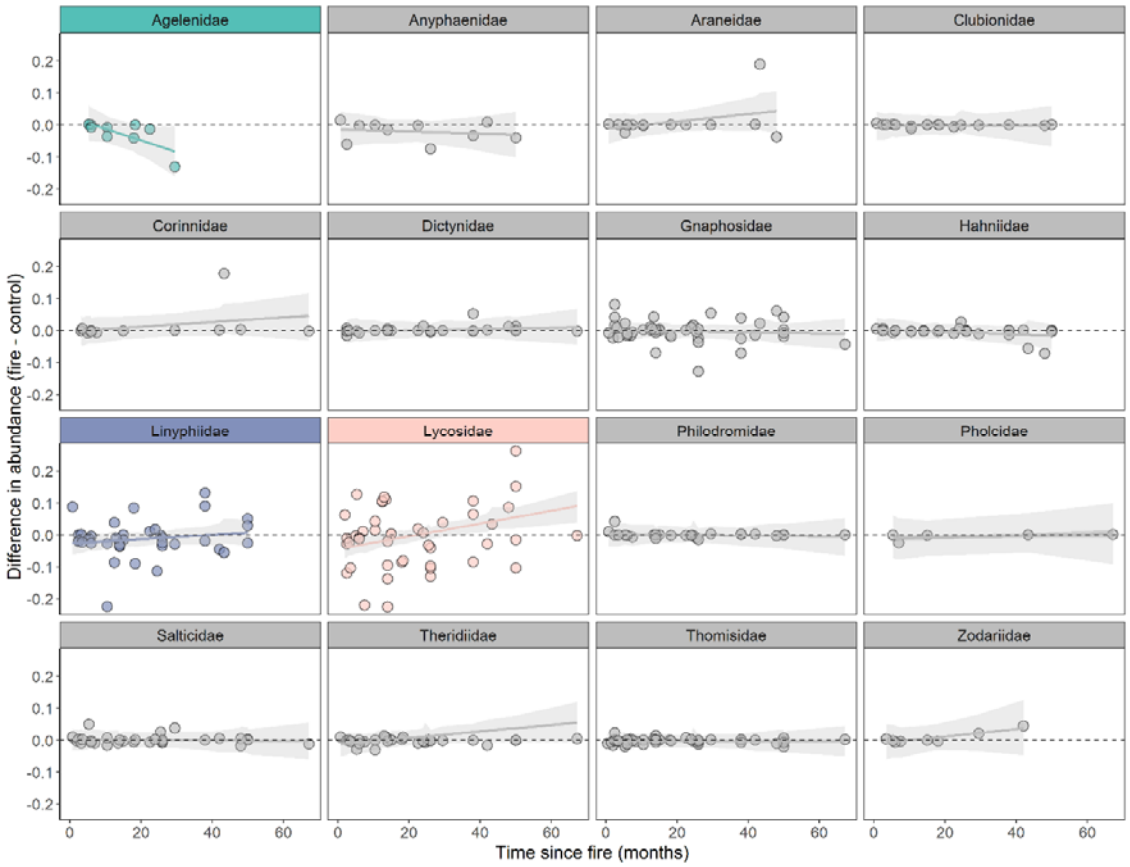

Figure 3. Difference in abundance between fire and control treatments for each vegetation type, for each species in each study. Blue = higher abundance in fire treatment, red = lower abundance in fire treatment, white = no difference, small black dot = mean difference in abundance for that vegetation type. Plot has been zoomed in to abundance differences between -0.02 and 0.02 for visualisation (N = 2009).

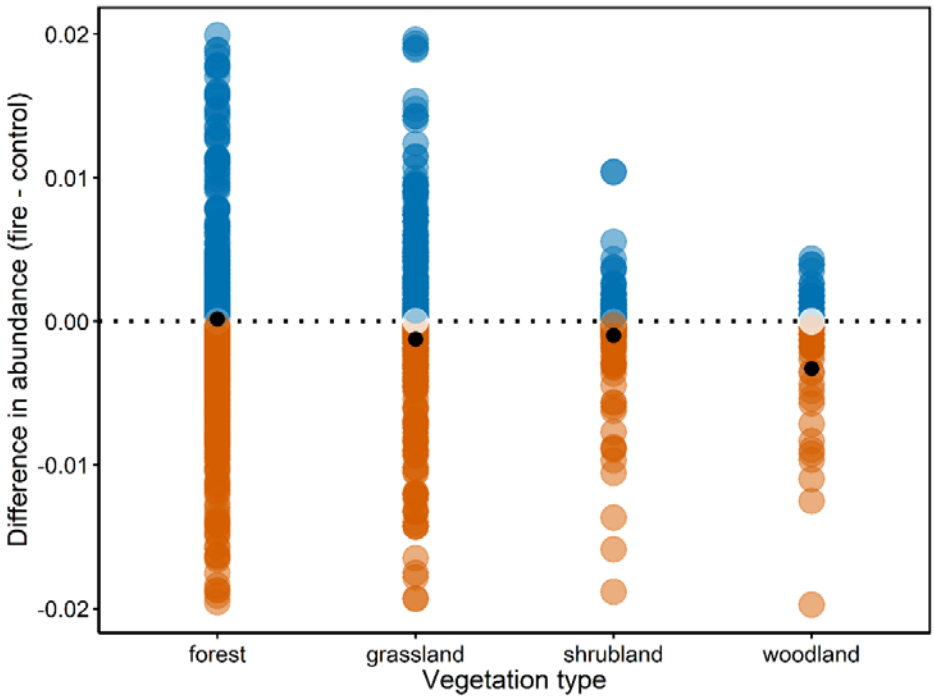

Figure 4. Relationship between difference in abundance between fire and control treatments and time since fire, for each species in each study. Blue = higher abundance in fire treatment, red = lower abundance in fire treatment, white = no difference. Plot has been zoomed in to differences between -0.02 and 0.02 for visualisation. Grey dashed lines = 95% confidence bounds (N = 2009).

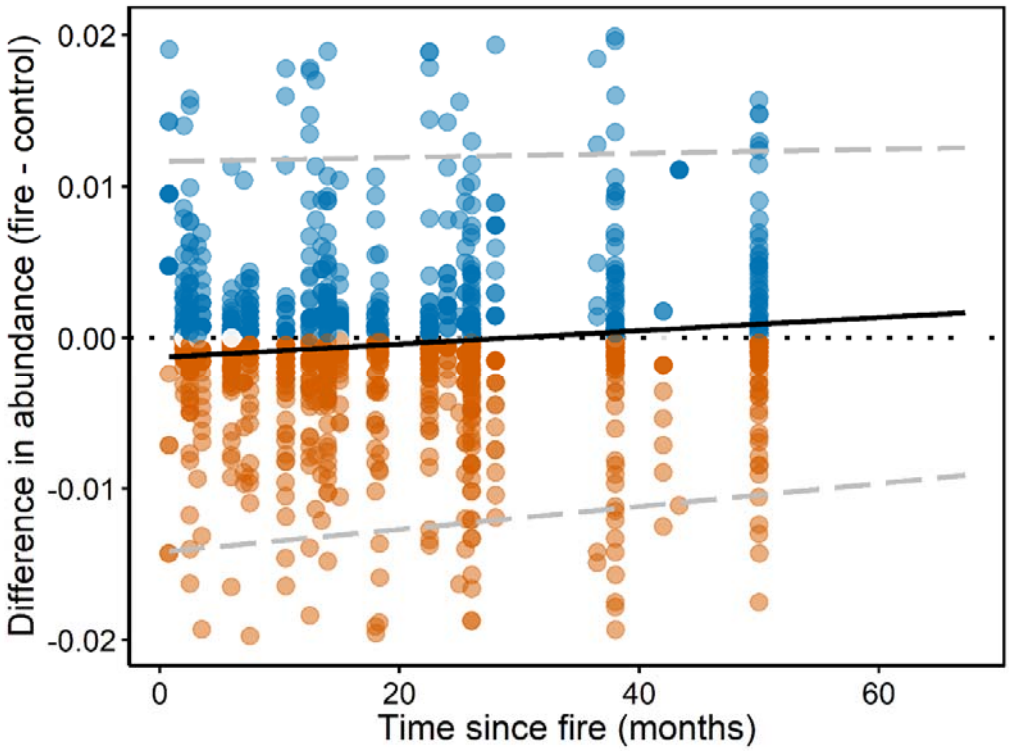

Figure 5. Proportion of datapoints for each hunting strategy that fell into the three presence/absence categories: present in control-absent in fire treatment ("disappeared"), present in both control and fire treatment ("no change"), absent in control-present in fire treatment ("colonised"). The total number of datapoints are shown within bars. There was a significant difference between orb web weaving and ambushing spiders (N = 2328).

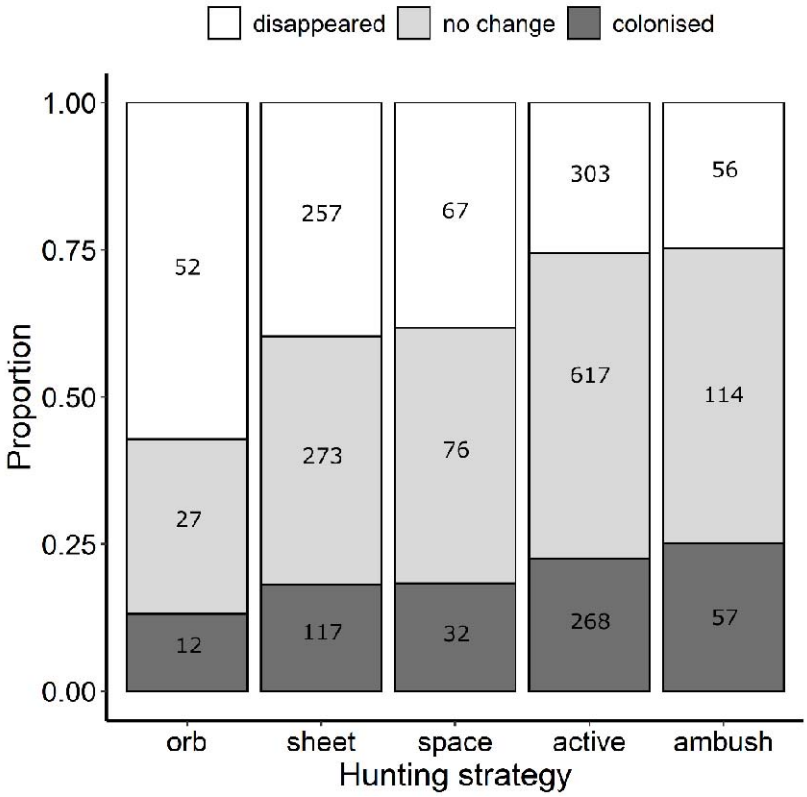

Figure 6. Relationship between time since last fire and the three presence/absence categories: present in control-absent in fire treatment ("disappeared"), present in both control and fire treatment ("no change"), absent in control-present in fire treatment ("colonised"; N = 2328).

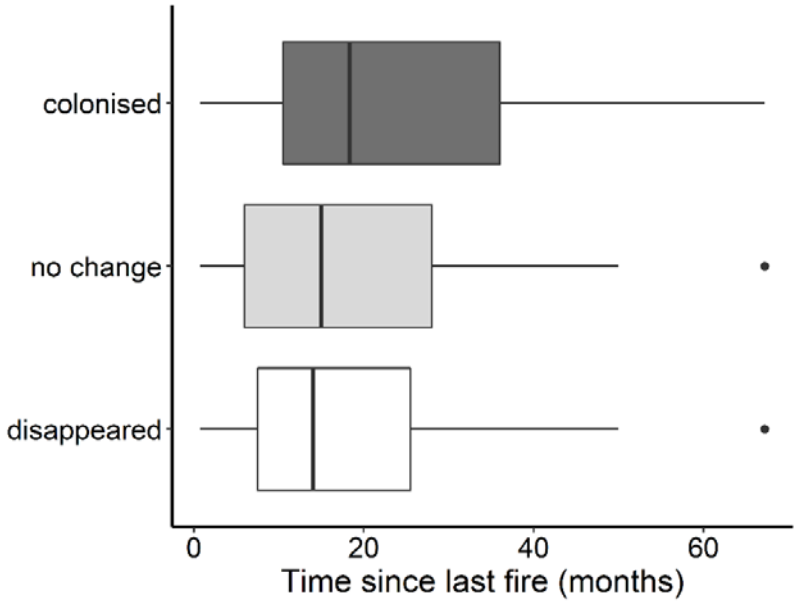

Table 1. Summary of the three models tested in this study and their main findings.

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 2 Figure S4 Table S4	Change in difference in abundance over time for families Lycosidae, Linyphiidae, Agelenidae.
2	Difference in abundance (fire - control)	Hunt Body length Vegetation Fire type Latitude Months	Phylogeny Study ID Species	$R^2m = 0.000006$ $R^2c = 0.000017$	Figure 3 Figure 4 Table S6	Forest vegetation type differs to both grassland and woodland. Change in difference in abundance over time since fire.
3	Difference in presence/absence (3 categories: disappeared, no change, colonised)	Hunt Body length Vegetation Fire type Latitude Months	Phylogeny Study ID Species	$R^2m = 0.012$ $R^2c = 0.102$	Figure 5 Figure 6 Table S7	Orb web weavers differ to ambush hunters. Relationship with time since fire.