The fire ecology of spiders: investigating the effects of fire on spiders at the individual and community level.

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Thesis Abstract

Fire is a major disturbance event that can have profound effects on ecosystems and on the biota within. The increasing use of anthropogenic fire in Australia, as a means to control fuel loads and provide asset protection, coupled with predictions for larger and more frequent wildfires has meant that the need to understand, and make predictions about how these events affect ecosystems, and the biota within them, is high. This need is especially potent where burning is being conducted in areas of high conservation status or environmental concern, such as the *Eucalyptus cneorifolia* vegetation communities on Kangaroo Island, which are listed as Critically Endangered under the *Environment Protection and Biodiversity Conservation Act 1999*. The chapters of this thesis are dedicated to increasing the understanding of how fire affects spiders, both at an individual and community level, and is focussed on spiders occupying fragmented patches of threatened *E. cneorifolia* vegetation communities.

The first empirical chapter of this thesis used a controlled and replicated experimental design to show how burning small fragments of native vegetation affected the composition and diversity of spider communities within. We found burn temperature, burn treatment and vegetation structure to significantly affect the composition and diversity of spider communities. The second chapter expanded on these findings by analysing a functional response of spiders to fire, utilising two novel guild systems. In support of the findings from the analysis of a taxonomic response in Chapter One, we found burning to significantly affect the diversity and composition of functional guilds.

In order to accurately record and analyse patterns of spider community change following burning it is crucial to understand the implications of the method used to categorise the data and the effect it has on patterns of community response to environmental variables. We investigated this in the third empirical chapter. In order to do so we used multivariate techniques to analyse changes in the community composition and diversity of family, morphospecies and guild assemblages in response to environmental variables associated with burning. Ordinations revealed significant differences in the response of these three assemblages to burning.

The fourth chapter used a novel approach and experimental design to investigate the responses of individual spiders to exposure to smoke. We detected significant increases in the rate of movement following exposure to a smoke stimulus. These findings are novel and suggest a potential mechanism for emigration of spiders away from fire, however they require further testing.

This thesis covers diverse elements of spider fire ecology that link together, building on the findings of previous studies and adding new and novel insights. In it we cover aspects of spider community fire ecology with recommendations for management techniques, methodological suggestions for improving the use of spider data in ecological research and experimental analyses of behavioural responses by spiders to fire related stimuli.

Declaration

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Signed…………………………………………………………..

Date…………………16/12/2016…………………………..

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Contextual Statement

This thesis is divided up in to six chapters. Chapters One and Six form the Introduction to the thesis, comprising a review and discussion of the literature, and the Thesis Discussion. Chapters Two to Six present original research. These are in the format of scientific papers. For this reason, each chapter has a separate reference list, and the tables and figures are presented in the text.

CHAPTER ONE
Introduction to Thesis

Review of literature

Fire is a part of Australia's natural history. Humans have long been manipulating fire to manage the natural environment (Bowman, 1998); however, in recent years alterations to the natural fire regime have increased at a rate not seen before. Following recent large-scale wildfire events, the use of high frequency, prescribed burns as a method of fuel reduction and hazard prevention has increased, and models predict an increased potential for larger and more frequent natural fires as a result of changes in climate and drought (Gill & Allan, 2008; Liu et al., 2010). Unpublished data by the Department of the Environment and Natural Resources, Kangaroo Island (DEWNR) shows the number of hectares burnt through fuel reduction burns to have increased linearly with time, so that in 2007 13 Hectares of native vegetation were burnt on Kangaroo Island and this number had increased to 500 Hectares in 2014 (DEWNR unpublished data). Conversely, as fragmentation of the rural landscape has increased and remnant patches have become smaller and smaller, the chance that a patch alights has decreased and the ease of controlling fire in a small patch, coupled with the necessity to control fire near to human habitation, has increased. This has resulted in a dichotomy in rural Australia in which, in some areas fire frequency has significantly increased, whilst in others there has been a significant decrease. Both changes to the fire regime are likely to affect the biological communities existing within these fragments. The need for a better understanding of the interaction between fire and ecosystems is high, both from an ecological perspective in order to better understand how fire may affect the taxonomic and functional composition of a community, and also from an individual species perspective, in order to understand and make predictions about how individuals are likely to respond to exposure to fire and its components. This is especially true in areas of high conservation concern.

The effects of fire on an ecosystem and its biota are complex. Whelan (2002) identified three pathways by which fire may impact upon flora and fauna. Firstly are those factors associated with the immediate effects of fire. These effects may be direct, for example causing emigration away from fire, or mortality, as a result of exposure to smoke and/or radiant heat. Indirect effects may also occur and include fire-induced changes to the habitat or ecosystem that cause fatality or emigration, such as changes to, or the destruction of, suitable habitat, making it uninhabitable for organisms. The second pathway involves the impact of longer term influences of fire on ecosystems, once fire has passed. Examples include changes to food supply, or suitable habitat as a results of burning. The third pathway includes the effects of fire regime, such as the intensity of the fire and the frequency of fire, including long term fire suppression on ecosytems. A cessation in burning or a major reduction in fire frequency in a fire-adapted area, such as temperate Australia, can have deleterious effects on ecosystem diversity and function (Keith & Bradstock, 1994; Johnson, 1995; Leach & Givnish, 1996; Penman et al., 2009; Pyke et al., 2010).

In addition to the pathways described by Whelan (2002), it is likely that landscape attributes, such as long-term fragmentation and isolation have shaped the spider communities, the way they respond to disturbances such as fire, and the trajectory of post-fire recolonisation. Theory predicts that small patch size (as a result of fragmentation), and/or increasing degree of isolation and time since fragmentation leads to a general decline in diversity and abundance of populations (Harrison & Bruna, 1999). The equilibrium theory of island biogeography (MacArthur & Wilson, 1967) and metapopulation theory (Hanski & Simberloff, 1997; Hanski, 1998), assert that population size in a fragment is governed by an interaction between recolonisation ability (which is limited by the degree of isolation and the mobility of displaced biota) and the increased vulnerability of fragmented communities to stochastic extinction events, such as may be caused by burning. As the population size decreases, vulnerability to stochastic extinction events increases and as the size of most populations are proportional to the area they occupy, the chance of extinction of a given population is likely to be inversely proportional to fragment size (Preston, 1962). Thus theory would lead us to predict that invertebrate populations in small habitat patches, such as the spider communities in fragmented patches of *Eucalyptus cneorifolia,* will have small population sizes, low diversity, and be vulnerable to local extinction from disturbances such as burning. However, naturally common species that occur at a high abundance are less vulnerable to stochastic extinction events than those which naturally occur at lower numbers. They can therefore be regarded as being relatively more stable and more likely to survive a major disturbance event in a fragmented environment, and this has been supported by empirical studies (Davies et al., 2000; Steffan-Dewenter & Tscharntke, 2002; Cagnolo et al., 2009). Individual species traits, such as the increased dispersal ability of spiders able to balloon, can intensify or reduce the effects of fragmentation on a population (Davies et al., 2000; Cagnolo et al., 2009).

The Specialist-Disturbance hypothesis (Vazquez & Simberloff, 2002) predicts that resource specialists are more likely to be negatively affected by disturbance events than resource generalists. Resource specialists are confined to the resource they depend on; if this resource disappears they cannot move to another, whereas generalists can. With some exceptions spiders are generalist predators, being largely opportunistic in the invertebrate prey they consume. However, many are highly specialised in the microhabitat they occupy (Wise, 1993). The distribution and abundance of a species within an ecosystem is restricted by its niche requirements (Brown, 1984), and by definition a specialist species is one with restricted ecological niche requirements (Futuyma & Moreno, 1988; Devictor et al., 2010). This suggests that disturbance variables, such as fire intensity and the percentage of habitat burnt, will differentially affect specialists and generalists; a generalist is likely to show more flexibility in its ability to tolerate or recover from a disturbance. Studies have found generalists to benefit from disturbance, resulting in an increase in abundance (Robinson et al., 1992; Holt et al., 1999; Steffan-Dewenter & Tscharntke, 2000; Tscharntke et al., 2002; Krauss et al., 2003; Devictor et al., 2008; Cagnolo et al., 2009). It would be expected that microhabitat specialist spiders would be more negatively affected by fire in a fragmented ecosystem than niche generalists, and this has been supported by studies, for example Marshall et al. (2006) and Bonte et al. (2003). However, this may not be true where a specialist species has a biological trait that provides inherent protection from a disturbance, for example burrowing spiders living in tunnels are protected from lethal radiant heat (Carrel, 2008).

Fragmentation can favour exotic arthropods, which can increase in abundance in habitat fragments or along fragment edges (Suarez et al., 1998; Hobbs, 2001; Ness, 2004). The vulnerability of a patch to entry by exotic species increases with the relative amount (area) of edge (Saunders et al., 1991) and with the age of the fragment (Bolger et al., 2008). For example, the exotic pest cabbage white butterfly (*Pieris rapae*) is common on Kangaroo Island in disturbed areas where its brassicaceous food plants exist as roadside/pasture weeds or vegetable plantings, whereas only isolated individuals are observed amongst native vegetation (R. Glatz Pers. Comm.). Disturbance may also be associated with an increase in abundance of exotic invertebrates

(Szinetar & Samu, 2012; Hogg & Daane, 2013). Thus the age of the *Eucalyptus cneorifolia* fragments and their small size, in conjunction with burning, may make them vulnerable to colonisation by exotic invertebrates.

The post-fire recolonisation of a site by invertebrates occurs through in situ survival of species within a habitat patch, via emigration of individuals away from a site followed by later recolonisation, or by immigration by individuals from unburnt neighbouring habitat (Panzer, 2003; Brennan et al., 2011). For species occupying highly fragmented and isolated remnant patches of native vegetation survival in situ and early emigration from lethal heat, followed by later recolonization, become the primary mechanisms by which recolonization of a burnt area may occur. Burning would favour those individuals that are highly dispersive, that occupy a niche that favours survival (for example burrowing species) or that can escape early away from the fire and later recolonise, and this has been supported by some studies (Warren et al., 1987; Carrel, 2008). Where habitat is fragmented and geographically isolated from neighbouring populations, as is the case with the burn sites used in this study, immigration from unburnt neighbouring patches will likely occur in lower numbers, or be slower than it would for less isolated patches (Davies et al., 2000). This is especially true for ground-dwelling and flightless invertebrates, which generally have poor dispersal abilities and recolonise areas at a slower rate than more mobile invertebrates (Moir et al., 2005; Uys et al., 2009).

Background

The study sites

The following paragraphs provide a background to the *Eucalyptus cneorifolia* communities on Kangaroo Island and highlight the potential differences in this study compared to fire ecology studies in more ecologically intact landscapes.

As a result of large-scale land clearance for agriculture in the 1950s and 60s, native vegetation on the eastern end of Kangaroo Island (KI) now exists in a highly modified state. It is characterised by small, remnant fragments of native vegetation surrounded by a largely agricultural matrix. Approximately a quarter of these remnant patches are comprised of communities dominated by *Eucalyptus cneorifolia* (the Kangaroo Island narrow-leafed mallee). *Eucalyptus cneorifolia* is endemic to South Australia, with the main population being found on the eastern end of KI and some isolated pockets occurring on the southern tip of the Fleurieu Peninsula. *Eucalyptus cneorifolia* woodland was listed as Critically Endangered under the *Environment Protection and Biodiversity Conservation Act 1999* (the EPBC Act) in May 2014 (Department of the Environment, 2014). The *E. cneorifolia* patches on KI have been subject to various disturbances over the last 50 years, including increased fragmentation, altered fire regime, grazing (both by native fauna and stock), the permeation of pesticides/herbicides after use in the agricultural matrix, and drought and dryland salinity (Taylor, 2008). It is likely that these factors have all contributed in some part to deterioration in habitat quality and have impacted on the spider communities inhabiting the vegetation fragments; however, the Department of the Environment Water and Natural Resources (DEWNR) on KI has identified alterations to the natural fire regime as a key driver in the degradation of the patches (EPFT Working Group, 2008). Fragmentation of native vegetation can serve to insulate it from natural disturbance events, such as fire (Saunders et al., 1991). Additionally, small patch size and the proximity of patches to agricultural assets increases the need of landholders to control fire events in the patches and the ease of achieving this control (Gill & Williams, 1996). Not only is fire frequency altered, but so also are other aspects of the natural fire regime such as the type of fire, its intensity and the season in which it occurs, often causing impacts to ecosystem functions and biodiversity (Whelan, 2002; Bradstock et al., 2006; Bradstock, 2008). Records suggest that the *E. cneorifolia* patches involved in this study have not been burnt for over 30 years (Taylor, 2008).

The condition of the vegetation in these remnant *E. cneorifolia* patches varies but is typically depauperate and senescing. The *E. cneorifolia* vegetation communities in the fragments are characterised by a sparse to absent understorey, a ground cover of twig and leaf litter and a dense mallee canopy cover (Taylor, 2008). In many of the patches, the mallees are showing signs of stress-induced epicormic sprouting and some are dead or dying (pers. obs.).

The Eastern Plains Fire Trials

The Eastern Plains Fire Trials (EPFT), run by DEWNR on KI, was an experimental burn program to research the use of burning *per se*, and burns of different intensities, as a means to restore plant diversity to fragmented patches of senescent *E. cneorifolia* vegetation communities. Fire intensity was defined by the temperature reached at the soil surface during a burn, and by the degree of crowning and canopy scorch. High intensity burns were characterised by flame heights of above 2 metres, crowning into the canopy and a fast rate of spread (Keeley, 2009). Lower intensity burns were associated with smaller flame heights and fewer, or less widespread, incidents of crowning or canopy scorch. As part of the EPFT, fire intensity was manipulated using pre-burn vegetation treatments applied to individual experimental plots, which altered the amount of available fuel and so the temperature and the intensity of a burn.

Three different treatment types were investigated:

- Coppiced plot: Standing vegetation was coppiced prior to burning to increase the fuel load at ground level and produce a higher intensity burn.
- Standing plot: Vegetation was not manipulated (left standing) prior to burning, resulting in a lower and more patchy fuel load and creating a lower intensity burn.
- Control plot: A negative control plot where vegetation was not manipulated and fire was excluded.

This study was run in conjunction with the EPFT, utilising the burn sites.

Thesis overview

This thesis explores diverse elements of invertebrate fire ecology, discussing aspects of spider community fire ecology with recommendations regarding management techniques, methodological suggestions for improving the use of spider data in fire and general ecological research, and experimental analyses of behavioural responses by spiders to fire related stimuli. The research described in this thesis uses novel experimental methodology and community analytical techniques building on findings of previous studies, addressing knowledge gaps and producing novel insights.

The main body of this thesis is divided into an introductory chapter, four empirical chapters and a discussion chapter. Chapter Two, the first of the empirical chapters, focusses on spider community fire ecology and investigates how burning affects spider communities in fragmented patches of threatened remnant vegetation on KI, South Australia. A key aim of the chapter was to provide management advice for the optimum methods of conducting restoration burning of fragmented patches of remnant vegetation in order to conserve, or minimise the loss of, diversity of the spider community. This chapter describes the outcomes of a controlled, replicated study, using a high number of replicates, and includes pre-burn baseline invertebrate community data. Prior to burning, all sites were matched for area, historic land use and vegetation type. Few fire ecology studies have investigated fire temperature as a variable and been able to link invertebrate data to accurate temperatures recorded during each burn. This combination of attributes is unusual in fire ecology research where due to the costs and logistical problems of conducting large scale burns, studies are often based on smaller scale experimental burns with few replicates or on chronosequence studies comparing sites with different historical times since burning, where it is not possible to control for factors such as area or type of vegetation burnt; or they have been conducted on single wild-fire events.

Chapter Three researches the use of a novel functional guild system for classifying the spider community and measuring spider community responses to burning. We developed a system for categorising spiders into discrete guilds based upon measurable morphological traits. We used the fourth corner approach to assess and quantify relationships between species traits and environmental variables by combining data from environmental trait and species abundance matrices (Legendre et al., 1997; Dray & Legendre, 2008). The fourth corner approach is a relatively new technique, which has been used more widely in ecological studies of plant communities, for example by Lehsten et al. (2009) and Amatangelo et al. (2014), but recently has been used to test species trait relationships in invertebrate communities, such as in studies by Jonas & Joern (2007) and Langlands et al. (2011).

In Chapter Four we compare the efficacy of higher level taxonomic surrogacy, morphospecies and the novel guild system developed in chapter two, as categorisation systems for investigating and understanding the effect of fire on the spider fauna. A review of the spider fire ecology literature revealed a large number of different methods used in studies for categorising spiders into ecologically meaningful units, ranging from higher level taxonomic classifications to morphospecies and functional guilds. We found the apparent effect of fire upon the spider community to vary depending on the categorisation method employed. We also found that excluding immature specimens, as required for morphospecies or species level categorisation, affected the apparent community response to fire. The results of these findings are discussed along with methodological and analytical recommendations for future studies.

Chapter Five focusses on behavioural ecology. Emigration by spiders away from an area of fire activity has been recorded in a study by Brennan et al. (2011) and observed during prescribed burns and wildfires (Pers. Obs.); however, these amount to anecdotal evidence and such behavioural responses to fire-related cues has never been studied empirically. We investigated potential mechanisms driving spider emigration away from areas of fire activity, in relation to faunal adaptations to fire that may promote the survival of spiders in a fire prone landscape. To do this we used a novel methodological design, testing the responses of spiders to smoke stimuli in an experimental setting. This chapter thus investigated a novel area of behavioural fire ecology that added to the findings from the first three empirical chapters of this study and to field-based fire ecology research.

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CHAPTER TWO

The effect of experimental burning on the composition and diversity of spider communities in nationally threatened remnant vegetation communities

Abstract

Fire has been a major force shaping in the Australian biota. Changes in land use and fragmentation of native vegetation have led to alterations to natural fire regimes and to the way fire moves through the landscape. As apex predators, spiders are important components of the ecosystem, however it is not known how spider communities occupying small, isolated fragments of native vegetation will respond to burning. In a replicated and controlled study, we assessed the way the spider community responded to burning of small, remnant patches of nationally threatened native vegetation on Kangaroo Island, South Australia. In order to do this we used pitfall traps and sweep netting in pre-burn and successive post-burn surveys. Three burn treatments were investigated; a coppiced plot where vegetation was coppiced prior to burning, a standing plot where vegetation was un-manipulated prior to burning and a no-burn control plot. Spiders were identified to family and assigned to morphospecies. Ordinations revealed a significant effect of burn treatment, mean temperature of the burn, litter depth and vegetation structure on the composition of pitfall trapped and sweep net collected spider assemblages. The nature and direction of these effects and the environmental attributes driving them differed between the two communities. We found significant, non-linear changes in diversity and richness of spiders collected by sweep netting, but there were no significant changes in the diversity or richness of pitfall trapped spiders. Burning created a change in the dominance of some morphospecies, for example the dominant linyphiid of unburnt plots was scarce in burnt plots and was replaced by an exotic linyphiid, *Ostearius melanopygius,* which was associated with high burn temperatures and coppiced burn treatment. Our findings suggest the importance of an appropriate fire regime in fragmented, ecologically sensitive areas. Our findings indicate that if burning is to be conducted that lower intensity burns, which leave a spatially heterogeneous post-burn landscape and preserve some remnant coarse woody debris and organic material, may serve to better promote the conservation of native spider communities.

Introduction

Fire is an integral part of Australia's natural history and has been an important force in shaping Australia's biota. Post-settlement changes in land use and clearance of native vegetation have caused alterations to historic fire regimes and to the way fire moves through the landscape (Gill & Williams, 1996; Russell-Smith et al., 2003). On the eastern end of Kangaroo Island, changes in the natural fire regime have been marked by a suppression in the frequency of fires (Department of the Environment, Water and Natural Resources, 2014). A cessation in burning or a major reduction in fire frequency in a fire-adapted area, such as temperate Australia, can have deleterious effects on ecosystem diversity and function (Keith & Bradstock, 1994; Johnson, 1995; Leach & Givnish, 1996; Penman et al., 2009; Pyke et al., 2010, Teasdale et al., 2013). The adaptations that enable flora and fauna to survive a fire can make them vulnerable when fire is removed, for example exposure to fire and smoke-related compounds is required for germination of the seeds of obligate seeders. For example, some *Banksia* spp., need exposure to fire, or to the components of fire for mature fruits to open and/or for their seeds to germinate (Auld & Oconnell, 1991; Dixon et al., 1995; Denham & Auld, 2002; Nield et al., 2009). The use of prescribed burning as a restoration tool in fire supressed landscapes is gaining increasing attention in the literature (Baker, 1994; Penman et al., 2009; Pyke et al., 2010), although little research has been conducted analysing faunal responses to restoration burning of remnant vegetation fragments. The response of invertebrate communities is particularly poorly understood. In a meta-analysis of vertebrate responses to fire, Pastro et al. (2014) found divergent responses between vertebrates in the Northern Hemisphere and those in the Southern Hemisphere. There currently exists a Northern Hemisphere bias to invertebrate ecology studies and although an analysis comparing the responses of Northern and Southern Hemisphere invertebrates to fire has not been conducted, it cannot be assumed that they would be concordant. Thus recent studies of invertebrates in the Southern Hemisphere, for example by Langlands et al. (2012), Podgaiski et al. (2013) and this study, give valuable data on the responses of Southern Hemisphere invertebrates to fire.

Awareness of the importance of invertebrate data in ecological research is growing. Spiders provide important models for measuring and recording ecological change. They are abundant, diverse apex predators with a high species turnover (Kremen et al., 1993) and occupy a range of ecosystem niches. Most spiders are generalist predators that prey on a wide range of invertebrates from an array of different functional groups. Thus, changes to the spider community affect a wide range of ecosystem processes (Marc et al., 1999) and can cause alterations to lower level processes and ecosystem functionality (Lawrence & Wise, 2004; Miyashita & Niwa, 2006; Miyashita & Takada, 2007; Ruiz et al., 2009; Bucher et al., 2015). The many factors determining individual survivorship and the composition of communities in the post-fire environment are complex and interweaving. They consist of a mixture of fire-driven factors, habitat-driven factors and organism-driven factors.

Whelan (2002) identified three pathways by which fire may impact upon flora and fauna. Firstly, fire may have short-term effects on organisms. These effects may be direct, for example causing mortality as a result of exposure to smoke and / or radiant heat, or emigration away from fire. Indirect effects may also occur and include fire-induced changes to the habitat or ecosystem that cause fatality or emigration, such as changes to, or the destruction of, suitable habitat, making it uninhabitable for organisms

The second mechanism suggested by Whelan (2002) by which fire affects biota, focusses on the effects of the processes that happen after a fire has passed. An example is a population that survived a fire front, but then died as a result of starvation or predation pressures in the modified post-fire environment. The alteration to habitat following fire can be profound, especially where fires are of a high intensity (Wang & Kemball, 2005; Ruokolainen & Salo, 2009) and can affect both the short term (Whelan's first pathway), and the longer term (Whelan's second pathway) survival of organisms by, for example, reducing or eradicating food sources, removing cover and shade and removing habitat. These alterations are of a dynamic nature and change with post-fire succession and with the germination of seeds and re-sprouting of vegetation (Purdie & Slatyer, 1976). The extent of secondary effects of fire on organisms is therefore likely to be dynamic and follow a trajectory with time since burn. The nature of this trajectory may be predicted from variables such as the amount of shade and ground cover to provide shelter and to prevent desiccation of individuals and the amount of vegetation regrowth.

Whelan's (2002) third pathway links the influence that the fire history or fire regime of an area has on the survival of the organisms inhabiting it. Fire regime includes references to the historical regime of an area, for example the effect of the frequency of fire or long term suppression of burning, in addition to the nature of a contemporary fire itself, for example the intensity of the fire or the season of the burn. The effect of the interaction of the above variables with the influence of the fire regime, is complex and profound. Long term fire suppression, as has occurred in the *Eucalyptus cneorifolia* fragments on Kangaroo Island, can result in large-scale changes to vegetation structure and diversity and a reduction in the fecundity of the soil seed bank (Penman et al., 2009). The direct effect of long-term fire exclusion on fauna is not well known. Fire has been associated with an increase in diversity of saproxylic beetles (Moretti et al., 2010); however, studies have failed to find a link between extended time between burns and a decline in pyrophilic insects (for example Saint-Germain et al., 2008).

Typically the immediate effects of fire and heat result in a high level of mortality, and invertebrates generally show a decline in abundance immediately following a burn compared to unburnt areas (Dawes-Gromadzki, 2007; Sgardelis et al., 1995; Vasconcelos et al., 2009; Wikars & Schimmel, 2001).

Studies have recorded changes in the diversity, richness and composition of spider communities following fire (Moretti et al., 2002; Koponen, 2005). Fire-sensitive spiders, whose density is correlated to post-fire age of a burnt area, or to the habitat variables associated with post-fire age have been recorded, with some species only founds in unburnt ground and others only in areas that have been subjected to burning (Buddle et al. 2000, Moretti et al., 2002; Buddle et al., 2006; Gillette et al., 2008; Langlands et al., 2012; Teasdale et al., 2013). These species may be at risk of localised extinction if inappropriate fire management is applied. Due to the widespread use of pitfall trapping as a survey technique, the fire ecology of cursorial spiders is comparatively better known than that of arboreal spiders, such as those utilising vegetation, tree trunks, or the canopy. Changes in the structure of vegetation following fire influence the abundance and distribution of spiders (Ryndock et al., 2012), and particularly vegetation-dwelling, irregular web building and orb web spiders (Carrel, 2008; Podgaiski et al., 2013; Foster et al., 2015). Studies have shown the composition and relative dominance of cursorial spider guilds in burnt areas to be different to those of unburnt areas, typically open habitat ground runners dominate in burnt areas, whereas litter specialists represent the dominant group in unburnt areas (Buddle et al., 2000; Moretti et al., 2002; Koponen, 2005). Caution must be taken when making predictions about longer term survival, as a species' ability to survive a fire does not necessarily guarantee its survival in the post-fire environment. In a study of the response of Australian mygalomorphs to fire, Main (1995) recorded species that survived the initial fire event, but yet failed to survive in the post-fire environment. Adult spiders also may have a better ability to survive fire than juvenile spiders (Main, 2001), therefore following the immediate post-fire mortality a secondary wave of mortality may occur as the surviving adults perish and there are fewer juveniles to replace them. Links have been made between the presence (or absence) of specific morphological and behavioural traits of individuals and community or individual survival during a fire and in the post-fire environment. During a fire, some protection from lethal radiant heat may be offered to spiders inhabiting burrows (Carrel, 2008; Langlands et al., 2011). Traits such as increased sclerotisation of the cephalothorax, the presence of abdominal scutes or increased body size (Entling et al., 2010) may reduce the risk of desiccation in the exposed post-fire ecosystem. Langlands et al. (2011) found abdominal scutes to show a U shaped curve with response to time since burn, with scutes being found in recently and long unburnt sites.

Fire causes large scale changes to the physical and chemical characteristics of the post-fire ecosystem, for example fire causes changes to properties of the soil (Certini, 2005), to vegetation structure and density (Watson et al., 2009), to the amount of litter and fine woody ground cover (Wikars & Schimmel, 2001) and to the structure and quality of fallen timber (Croft et al., 2010). An important aspect of understanding how fire will affect an ecological community is to consider how the intensity and temperature of the fire may affect the post-burn ecosystem and the organisms within. The temperature and intensity of a fire has direct biological and land-management implications associated with changes to the composition and structure of the post-burn ecosystem, affecting the diversity and type of post-fire vegetation regrowth and the structure and amount of litter and woody debris (Smith et al., 2004; Wang & Kemball, 2005; Ooi et al., 2006; Tierney, 2006; Ruokolainen & Salo, 2009). Fire intensity is an important determinant of the immediate and longer-term survival of invertebrate populations. Ryndock et al. (2012) found a positive relationship between the abundance of open habitat specialist spiders and burn intensity following restoration burning of oak woodland in the USA. Trucchi et al. (2009) reported a significant effect of fire intensity on the composition and diversity of centipede communities, with high intensity burns resulting in a simplified centipede community structure compared to low intensity burns. A study by Rodrigo et al. (2008) found a similar effect of intensity on beetle composition, with a difference in dominant species between higher and lower intensity burn areas. Fire intensity may also affect the rate of post-fire population recovery, with studies finding populations from higher intensity burns taking longer to recover compared to those from low or medium intensity burns (Wikars & Schimmel, 2001; Bezkorovainaya et al., 2007). Leaf litter and fine woody debris are important determinants of spider community composition (Bultman and Uetz, 1982; Brennan et al., 2006; Ober & DeGroote, 2011), and these are typically lower in areas that have been burnt (Wikars & Schimmel, 2001). Uetz (1979) found spider abundance and diversity to be positively correlated with increasing litter depth. Coarse woody debris provides habitat and refuge for spiders and as such is important in influencing spider community composition (Varady-Szabo & Buddle, 2006; Hanula et al., 2009; Croft et al., 2010). The structural complexity of the standing vegetation community is also profoundly affected by fire. In the initial post-fire period the structural complexity of vegetation is low; however, following post-fire germination of seedlings and resprouting of vegetation that occurs in fire-adapted areas such as much of Australia, vegetation structural complexity can soon exceed that of the pre-burn state (Fisher et al., 2009). Spider communities are sensitive to manipulations in the structural complexity of the vegetation community (Langellotto & Denno, 2004; de Souza & Martins, 2005; Takada et al., 2008; Cobbold & MacMahon, 2012; Malumbres-Olarte et al., 2013). Following fire, the amount of canopy and/or vegetation cover is often significantly reduced. Canopy cover is an important attribute for soft-bodied invertebrates, such as spiders, which are vulnerable to desiccation (Oxbrough et al., 2005; Ziesche & Roth, 2008; Kwok & Eldridge, 2015)

Research has shown that habitats subjected to a higher level of disturbance, such as by more intense or hotter burns, may be more vulnerable to invasion by disturbance-tolerant exotic spiders and to the exclusion of disturbance-intolerant native species (Szinetar & Samu, 2012; Hogg & Daane, 2013). In their study investigating the burning of tussock grassland in New Zealand, Malumbres-Olarte et al. (2014) found an increase in the abundance of exotic spiders following burning, largely explained by an increase in exotic Linyphiidae.

The definition and measurement of fire intensity vary between studies, with definitions being based on the amount of canopy scorch (Trucchi et al., 2009; Rodrigo et al., 2008), or on the flame height and spread (Wikar & Schimmel, 2001). When discussing burn intensity I will follow the definition provided by Keeley (2009), pp123, as being ‘the energy outputs from fire’. To obtain a simplified quantitative measurement of burn intensity, mean burn temperature, as measured at ground level during a burn, will be used as a measure of intensity. During prescribed burning, burn temperature may be artificially increased via the manipulation of vegetation prior to burning. The coppicing of vegetation increases fuel load at ground level thereby resulting in a higher intensity burn, characterised by higher temperatures and more complete combustion of organic material (Keeley, 2009). Coppicing is often conducted where vegetation is sparse and a ‘natural’ burn would not carry sufficiently. In addition to creating a hotter burn, coppicing of vegetation *per se* has been shown to induce changes in the composition of spider communities (Matveinen-Huju & Koivula, 2008; Pinzon et al., 2011).

The structure of *Eucalyptus cneorifolia* communities in small isolated fragments is characterised by a depauperate understorey and midstorey vegetation and sparse to absent understorey, a twig and leaf litter ground cover and a dense mallee canopy cover (Taylor, 2008). This lack of low level vegetation has resulted in a reduced fuel load and a reduction in ladder fuels that carry fire up in to the canopy and increase fire intensity and fire spread (Raymond & Peterson, 2005). Burns of un-manipulated standing *E. cneorifolia* vegetation are therefore typically variable in intensity and temperature, with some areas burning at a higher intensity, whereas others remain untouched by flame (Pers. Obs.). This results in a higher level of spatial heterogeneity in the post-burn environment. The promotion of spatial heterogeneity and niche diversification by a lower intensity burn, along with the removal of competitive dominant species from the unburnt ecosystem, may serve to promote spider community diversity in areas subjected to a burn, if species are able to disperse amongst patches (Botkin & Sobel, 1975; Amarasekare & Nisbet, 2001; Bell et al., 2001; Cadotte & Fukami, 2005; Cadotte, 2006).

For restoration burns in areas of high conservation value, it is particularly important to gain an understanding of how burning affects spider populations and to assess how the risk of localised extinctions of fire-age specialist species is influenced by fire regime, particularly in areas with a history of long-term fire exclusion. In this study we examined the effect on spider family and morphospecies community composition, diversity and richness of experimental burning at different intensities of small senescent fragments of *E. cneorifolia* dominated mallee communities in eastern Kangaroo Island. The Eastern Plains Fire Trials, run by the Department for the Environment, Water and Natural Resources (DEWNR) on Kangaroo Island (Taylor, 2008) was an experimental burn program testing the use of prescribed burn treatments (coppicing followed by burning, and burning on its own) as tools to restore diversity to fragmented patches of senescent remnant vegetation. This study was run in conjunction with the Eastern Plains Fire Trials. A key aim of the study was to provide management advice regarding the optimum methods of conducting restoration burning of fragmented patches of remnant vegetation in order to conserve, or minimise the loss of, diversity in the spider community.

This study is based upon a large scale, controlled, and replicated fire experiment (Department of the Environment Water and Natural Resources, Kangaroo Island). Prior to burning, each site was matched for vegetation type and soil type, grazing history, landscape connectivity and area. Pre-burn baseline surveys of the composition of spider communities were conducted. Following burning, successive vegetation, litter, fine and coarse woody debris surveys were conducted. In addition, the accurate recording of temperature during the burn allowed us to test predictions on how fire temperature affects spider communities. Due to the sporadic nature of wildfires and the cost of larger scale planned burning, these aspects are often missing from fire ecology studies, which rely largely on data from one-off wildfires, small scale experimental burning, or on chronosequence studies.

We hypothesised that there would be a change in spider species composition and diversity following a burn and that this change would differ with burn treatment. In particular, we hypothesised that the spider community composition would become more distinct from unburnt communities with increasing burn temperatures. Thus, the high burn temperatures, high level of habitat disturbance and increased post-burn habitat spatial homogeneity following coppicing and burning would cause greater short term reductions in spider diversity compared to the lower intensity burns of the standing plots and the unburnt control plots. Similarly, we expected that in standing plots, the lower temperature burns would result in a combination of burnt and unburnt ground following the burn and that this habitat heterogeneity would result in a more diverse post-burn spider community in these plots than in the control or coppiced burn plots.

Following an initial post-burn decrease, we predicted that spider diversity in burnt plots would increase with time since burning and would eventually exceed that of the unburnt and senescent control plots, due to an increase in vegetation structural complexity following post-fire seedling germination and vegetation regrowth. We expected that spider diversity would increase with increasing structural complexity of living vegetation, due to the creation of new niches and to the regulatory effect of increased shade on ground level temperature and humidity.

Finally, we predicted that the high level of habitat disturbance following a fire would disadvantage some spiders and favour others, and specifically that there would be a greater proportion of disturbance-tolerant exotic spiders in the high intensity burn coppiced plots following burning.

The above can be summarised in to three questions and where appropriate, this chapter will be divided in to sections relating specifically to each of the three questions:

Question One:

Is there a change in the composition and diversity of cursorial and arboreal spiders following burning and does this vary with burn treatment burn temperature?

Question Two:

Is changing vegetation structural complexity and litter depth in the post-burn environment a significant factor in determining composition and diversity of cursorial and arboreal spider community?

Question Three:

Do the conditions following a burn favour 'fire-specialist' spiders and does the number of exotic spiders change with burning and with burn treatment?

Methods

Study sites

The 13 study sites are located on eastern Kangaroo Island, South Australia (see Fig. One). The sites are small fragments of *Eucalyptus cneorifolia* dominated remnant vegetation, within an agricultural matrix, each fragment less than 5 ha in size. Due to a long history of fire exclusion the vegetation communities in these fragments are depauperate and senescing, and are characterised by a sparse to absent understorey, a twig and leaf litter ground cover and a dense mallee canopy cover (Department of the Environment, 2014). Seven of the sites were burnt in spring 2009 and six in spring 2010, with the allocation of each site to a burn year being random.

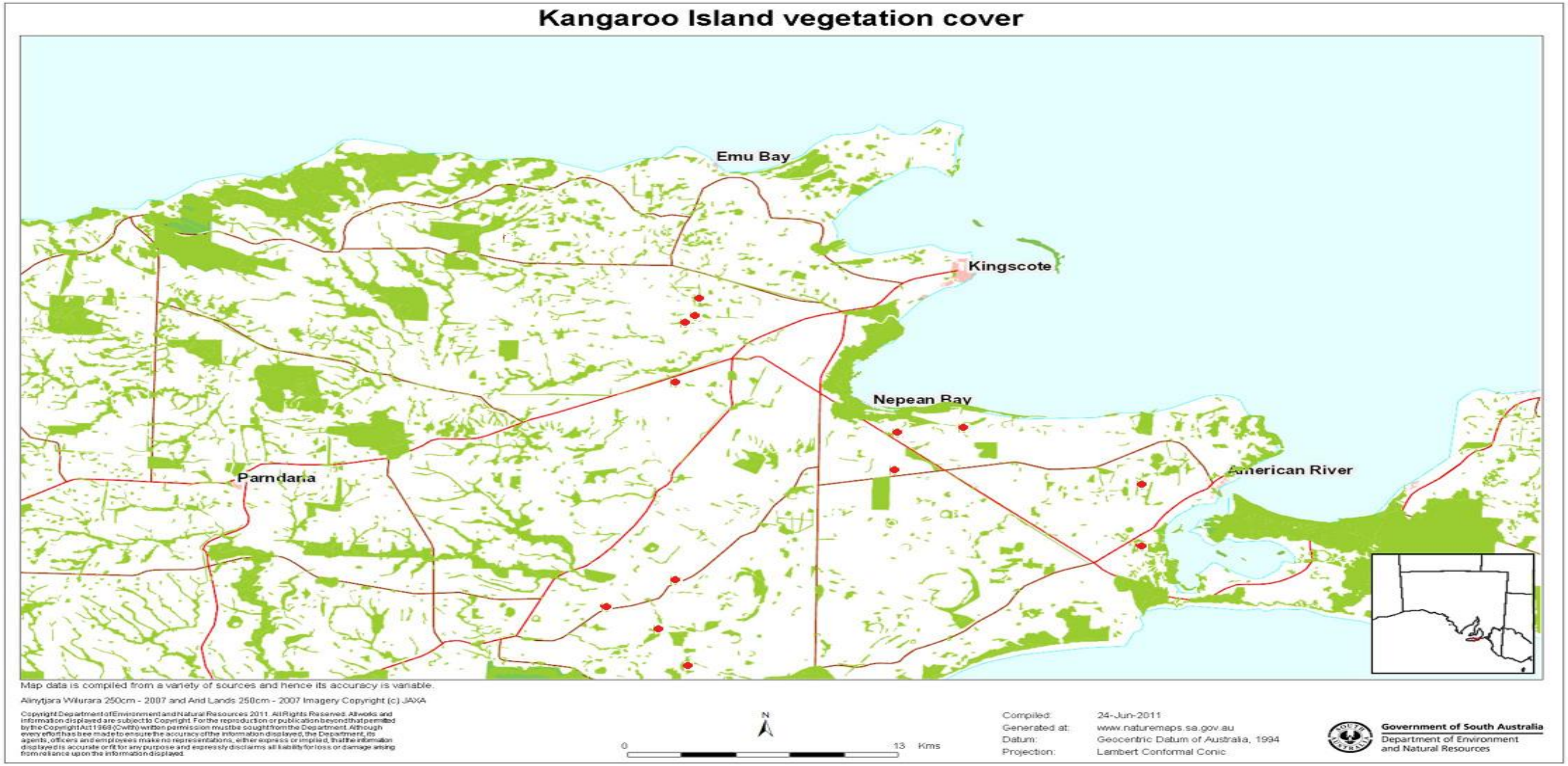


Figure One: Map of Eastern Kangaroo Island showing native vegetation cover, with the 13 study sites marked as red dots.

Experimental Plots

Three 10 x 10 m experimental plots were set up at each study site. Plots were positioned 30 m apart (see Figure Two), each one being subjected to a different treatment type. These treatments are being trialled by DEWNR, KI (Department of the Environment, Water and Natural Resources, Kangaroo Island) to research the optimal method for restoration burning of senescent fragments of native vegetation, and the treatments applied represent different management options for conducting a burn. Each site contained an unburnt control plot, a coppiced plot where trees were felled prior to burning to increase the fuel load and create a higher intensity burn, and a standing plot where vegetation was not manipulated prior to burning, creating a lower intensity, patchier burn. Apart from the control area (vegetation within 10 m of the control plot), all vegetation within the sites was burnt, the plots being located within this vegetation.

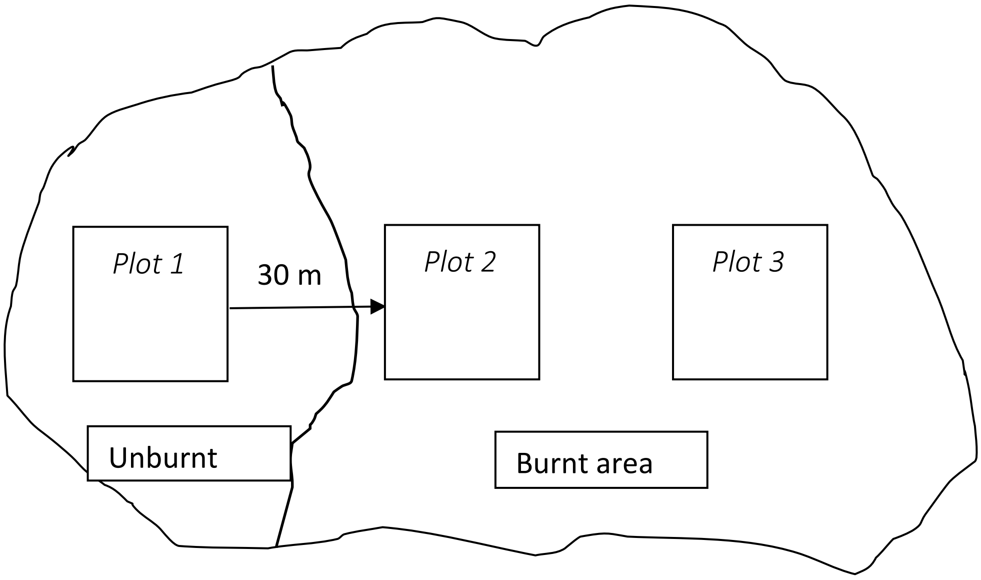


Figure Two: Schematic diagram of the layout of the experimental plots within the Eastern Plains Fire Trials study sites. The unburnt control plot was always located in plot 1, but the burn treatments, coppiced vegetation and standing vegetation, were randomly applied to plots 2 and 3.

The soil surface temperatures in the experimental plots were recorded using thermocouples positioned at the soil surface and left *in situ* during each burn. Four thermocouples were used per plot, with one located at the midpoint along each side of the plot.

Surveys

Pitfall traps only sample a section of the cursorial spider community and sweep nets only a section of the arboreal spider communities and there may be some cross over between the two. However, for the purposes of this chapter 'cursorial' will be used as a term to refer to those spider collected by pitfall trapping, 'arboreal' to describe those collected by sweep netting and beating.

Cursorial spider community

All surveys were conducted along a 40 m transect located around the perimeter of each plot. Pitfall traps were set up at four metre intervals along each transect, and ten traps were used per experimental plot. Pitfall traps comprised a plastic cup of 8 cm diameter and 10 cm depth, dug into the ground so the lip was flush with the surface. A preservative of 75 ml of 70 % ethanol with a couple of drops of detergent to break surface tension was put in each cup. Schmidt et al. (2006) found a mixture of ethylene glycol and water to be a better preservative and have a higher capture rate efficiency than an ethanol and water solution. However the toxicity of ethylene glycol presented a potential risk to stock and wildlife that may come in to contact with the pitfall traps, so it was decided to use a less toxic ethanol and water solution. A lid consisting of a 15 x 15 cm piece of plywood and held in place with three nails was placed 4 cm above each trap. This kept leaf litter and debris out of the traps and helped reduce evaporation of the preservative. Traps were left in place for seven days before they were removed and the contents transferred to fresh 70 % ethanol.

Arboreal Spider Community

Sweep netting and beating was conducted along two randomly chosen sides of each transect, resulting in 20 m of sweeping and 20 m of beating per plot. Fifteen sweeps and fifteen beats were made along each of the transect sides.

Vegetation structural complexity and litter depth surveys

A point intersect method was used to survey vegetation structure at 2 m intervals along the 40 m perimeter transect of each plot. At each point along the transect the number of times vegetation intersected a vertical pole at height classes of 0-25 cm, 26-50 cm, 51-100 cm, 101-150 cm and 150 cm plus was recorded, in addition to the broad vegetation type (graminoid herbs, non-graminoid herbs, shrubs, trees) and whether the vegetation was alive or dead. The type of ground cover and depth (if it was litter) and any intersecting fine or coarse woody debris or rocks were also recorded. Vegetation and microhabitat surveys were only conducted in survey years 2011 and 2012 (after burns in 2009 and 2010).

Spider identification and assignation of morphospecies

All spiders were identified to family level using Raven et al. (2002), and mature specimens were assigned to morphospecies. Immature specimens, where species level identification was not possible, were identified to family level.

Due to a high number of unidentified species and frequent sexual dimorphism in spiders it was not always possible to link males and females of the same species as belonging to a single morphospecies. Accordingly, we treated males and females as different morphospecies. This was unavoidable given the issues mentioned above, however it was decided that this was the best methodology for this project. For a detailed discussion of the issues surrounding the impediments to the use of spiders in ecological research please refer to the Introductions of Chapters Three and Four.

Timing of Surveys

Question One:

The pre-burn surveys from March 2009 were conducted by the author when employed by DEWNR (Department of the Environment, Water and Natural Resources) and prior to commencing the PhD. Only pitfall trapping was used as a survey technique in these pre-burn surveys. However, once the PhD was commenced sweep netting was included.

Half of the sites were burnt in 2009 and half in 2010 and resulted in an uneven number of pre-and post-burn surveys. To prevent confounding effects due to uneven pre- and post-burn surveys not all data were used in analyses. The following paragraphs describe which sites were used. Please refer to Table One for a summary of the sites and survey techniques used for each survey year.

Pitfall trap surveys-

- Pitfall trap surveys commenced in March 2009 and were repeated annually until March 2012.
- Sites burnt in 2009: Data from the 2009 (pre-burn), 2010 (6 months post-burn) and 2011 (18 months post-burn) survey years were included in analyses.
- Sites burnt in 2010: Data from the 2010 (pre-burn), 2011 (6 months post-burn) and 2012 (18 months post-burn) were included in analyses.

Sweep net surveys-

- Sweep net surveys commenced in March 2010 and were repeated annually until March 2012.
- In order to analyse a consecutive range of times-since-burn (pre-burn, 6 months post-burn, 18 months post-burn, 30 months post-burn) and to prevent the duplication of survey years, the following data were used in analyses of sweep net data:
    - Sites burnt in 2009: Data from the 2011 (18 months post-burn) and 2012 (30 months post-burn) were used in analyses.
    - Sites burnt in 2010: Data from the 2010 (pre-burn) and 2011 (6 months post-burn) were used in analyses.

Question Two:

- Surveys of vegetation structural complexity and litter depth were conducted in 2011 and 2012, therefore only the pitfall and sweep net data collected in these two survey years were used for analyses associated with litter depth or vegetation structural complexity.
- To prevent duplication in the 18 months post-burn surveys, data collected during the18 month post-burn surveys of the sites burnt in 20101 were omitted from analyses of vegetation structural complexity and litter depth. See Table One for a detailed list of the sites and survey years used for each data set.

Question Three:

Pre- and post-burn data from all survey years were used to address Question Three.

sites	Autumn 2009	Spring 2009	Autumn 2010	Spring 2010	Autumn 2011	Autumn 2012
AMD	pre-burn	burn	6 months post-burn		18 months post-burn	30 months post-burn
	P1		P1		P1S1 V2	P S1 V2
DA1	pre-burn	burn	6 months post-burn		18 months post-burn	30 months post-burn
	P1		P1 S		P1S1 V2	P S1 V2
RA2	pre-burn	burn	6 months post-burn		18 months post-burn	30 months post-burn
	P1		P1 S		P1S1 V2	P S1 V2
RLCL	pre-burn	burn	6 months post-burn		18 months post-burn	30 months post-burn
	P1		P1 S		P1S1 V2	P S1 V2
RS1	pre-burn	burn	6 months post-burn		18 months post-burn	30 months post-burn
	P1		P1 S		P1S1 V2	P S1 V2
TH5	pre-burn	burn	6 months post-burn		18 months post-burn	30 months post-burn
	P1		P1 S		P1S1 V2	P S1 V2
WR2	pre-burn	burn	6 months post-burn		18 months post-burn	30 months post-burn
	P1		P1 S		P1S1 V2	P S1 V2
DA2	pre-burn		pre-burn	burn	6 months post-burn	18 months post-burn
	P		P1S1		P1S1 V2	P1 S V
DA4	pre-burn		pre-burn	burn	6 months post-burn	18 months post-burn
	P		P1S1		P1S1 V2	P1 S V
PH2	pre-burn		pre-burn	burn	6 months post-burn	18 months post-burn
	P		P1S1		P1S1 V2	P1 S V
ROW	pre-burn		pre-burn	burn	6 months post-burn	18 months post-burn
	P		P1S1		P1S1 V2	P1 S V
SC2	pre-burn		pre-burn	burn	6 months post-burn	18 months post-burn
	P		P1S1		P1S1 V2	P1 S V
SC7	pre-burn		pre-burn	burn	6 months post-burn	18 months post-burn
	P		P1S1		PS1 V2	P1 S V

Table One: Timing of burning and surveys of the 13 burn sites. P denotes pitfall trap surveys, S sweep net surveys and a V denotes vegetation and litter surveys. A suffix of 1 indicates data used to answer Question One and a 2 data used to answer Question Two.

Statistical Analyses

Question One:

In order to examine the contribution of burn treatment, time since burn and burn temperature on spider community composition we conducted non-metric multidimensional scaling (NMDS) ordinations and non-parametric permutational MANOVA using the 'vegan' package in the R software language version 3.2.3, (R Core Team, 2015). For all analyses n=9999 permutations were used. For NMDS analyses plots that had zero specimens in a survey year were removed from analyses. This resulted in n=110 plots being available for ordinations of pitfall trap morphospecies data, n=115 plots for pitfall family data and n=70 plots for sweep net data ordinations. To minimise stress in NDMS ordinations, all data were transformed using a Wisconsin transformation, the ordinations were conducted in three dimensions and 100 random restarts were performed for each analysis to increase the chance of the algorithm finding a stable solution. Additionally to ensure the data converged in NMDS, rare morphospecies and families which numbered less than nine specimens across all survey years for cursorial pitfall trapped spiders, were removed from the dataset prior to NMDS analyses. Two survey years of sweep net data were used in these analyses. The sweep net data therefore contained a smaller total number of spider specimens than the pitfall trapped spider surveys, which included three years of surveys (see Table One). As a result rare morphospecies and families that numbered less than five specimens across all survey years for sweep net trapped spiders were removed from the dataset prior to NMDS analyses.

To examine differences in the diversity and richness of pitfall trap and sweep net spider communities following burning, mean species richness and Shannon's diversity were calculated and compared. The effects of post-burn environmental variables on diversity and richness were assessed using mixed linear models, using the 'lme4' package in R. In these models time since burn, mean burn temperature and burn treatment were fixed effects, sites were included as random factors. All specimens, including rare morphospecies or families were included in these analyses.

Question two:

In order to assess to the contribution of vegetation structural complexity and litter depth on spider community composition we conducted NMDS ordinations and non-parametric permutational MANOVA. In order to ensure the NMDS ordinations of pitfall trapped spider data converged, rare morphospecies, occurring at an abundance of less than 9 specimens across the two survey years were removed from the analyses.

To examine differences the influence of vegetation structural complexity and litter depth on pitfall trap and sweep net spider community diversity mean species richness and Shannon's diversity were calculated and assessed using the 'lme4' package in R.

Question three:

Kruskal-Wallis H tests were run to assess for differences in the abundance of spider morphospecies following burning.

Results

Datasets

Please refer to Table A1 of the Appendix for a list of families, their abbreviations used in the figures and the morphospecies.

Question one:

Pitfall trapping resulted in the collection of a total of 2723 spiders from 34 families and 148 morphospecies. Of the spiders collected, 40.0% (n= 1090 specimens) were sexually mature and were able to be used in morphospecies analysis; of these 73.0% were male and 27.0% were female. Once morphospecies represented by nine or fewer specimens across all survey years were removed, 805 specimens from 24 morphospecies were available for analyses, a significant drop from the original 2723. Once families occurring at less than nine individuals across all survey years were removed from the data set this left 2679 spiders from 22 families available for analyses. Inclusion of the pitfall trap data from the standing plot of site DA1 in survey year 2011 resulted in a skewed ordination of data from pitfall-trapped spider communities, which made it difficult to detect trends in the rest of the data (See Appendix, Figure A1). Accordingly, we also produced and analysed ordinations from which we had removed the data from this plot.

Sweep netting and beating resulted in the collection of 1075 spiders from 23 families. Of the spiders collected, 7.4% were sexually mature and of these 70.6% were male and 29.4% were female. Due to the small percentage of mature specimens collected by sweep netting, morphospecies level identification was usually not possible and therefore specimens were identified to family level. Once families numbering less than 5 specimens across all survey years were removed, 1054 specimens from 15 families were available for analysis.

Question two:

During the years the vegetation surveys were completed 567 mature spiders were collected, from 99 morphospecies. Once rare morphospecies numbering less than 9 across the survey years were removed this left 395 pitfall trapped spiders for pitfall trapping, from 15 morphospecies. Removal of these specimens resulted in three survey points in the data set where zero specimens were collected, these were removed from NMDS ordinations. These were; site DA1, coppiced plot, survey year 2011 and site SC7, coppiced plot, survey year 2011 and site RLCL, standing plot, survey year 2012. Similarly to Question 1, inclusion of the data from the pitfall trap survey of standing plot, site DA1, survey year 2011 resulted in a skewed ordination of data from pitfall-trapped spider communities, which made it difficult to detect trends in the rest of the data (See Appendix, Figure A2). Accordingly, we also produced and analysed ordinations from which we had removed the data from this plot. Sweep netting during the vegetation survey years produced 891 specimens from 23 families. Removing specimens numbering less than 5 across survey years left 870 specimens from 13 families. This resulted in 5 survey points were zero specimens were collected, which were consequently removed from the dataset. These were; site DA2, coppiced plot, survey year 2011, site ROW, coppiced plot, survey year 2011, site SC2, coppiced plot, survey year 2011 and site SC7, coppiced plot, survey year 2011.

Post-burn environmental variables

As expected, the mean temperature at the soil surface was higher in coppiced plots (range of 117.8 to 538 degrees Celsius) than in standing plots (range of 35.9 to 291.2 degrees Celsius). The temperature of the unburnt control plots during burns ranged between 20.7 to 48.5 degrees Celsius. (See Fig. Three).

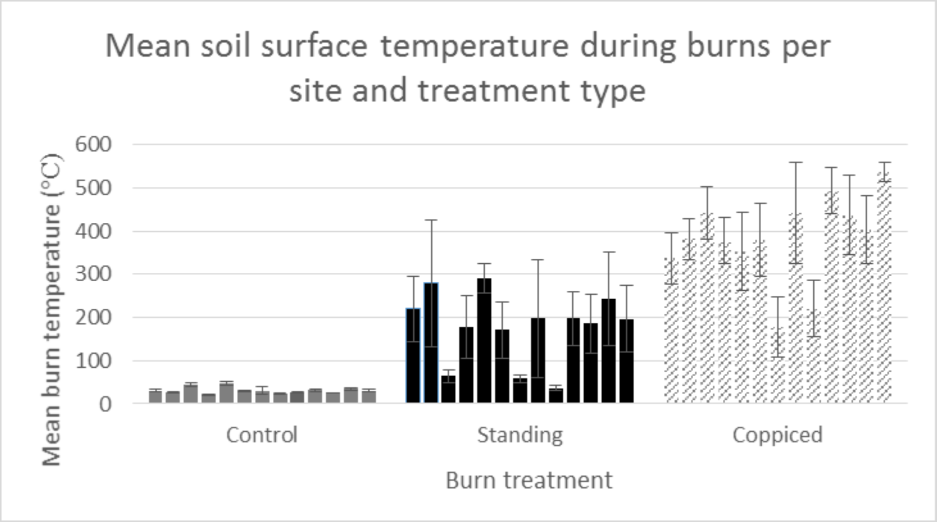


Figure Three: Mean soil surface temperature per site for the 24 hour period during which a burn was conducted. Error bars illustrate standard errors.

Question One: Burn treatment, burn temperature and time since burn on community composition and diversity

Cursorial spiders

Morphospecies assemblages

NMDS ordinations with environmental variables displayed using the 'Envfit' function, and multivariate permutational ANOVAs (produced using the 'Adonis' function) were used to test the effect of burn treatment, mean burn temperature and time since burn on the composition of the spider community. As expected the composition of the cursorial spider morphospecies assemblages changed significantly with burn treatment (ADONIS, df=2, 102, r^2= 0.061, p=0.0001), with time since burn (ADONIS, df=2, 102, r^2= 0.046, p=0.0001) and with the interaction between burn treatment and time since burn (ADONIS, df=4, 102, r^2= 0.065, p=0.0001). At six months post-burn coppiced plots were grouped on the right hand side of the ordination, pre-burn and control plots were situated to the left. Standing plots were located more centrally within the ordination and showed significant overlap with the communities of the unburnt control plots. At 18 months post-burn, the spider community of the standing plots shared characteristics of both the control and coppiced plots and there was an increased degree of overlap between coppiced and standing communities and between standing and control communities (See Fig. Four). The direction of the vector representing mean burn temperature was significantly correlated with the separation of points which represented the composition of assemblages (Envfit, r^2= 0.20, p=0.0001).

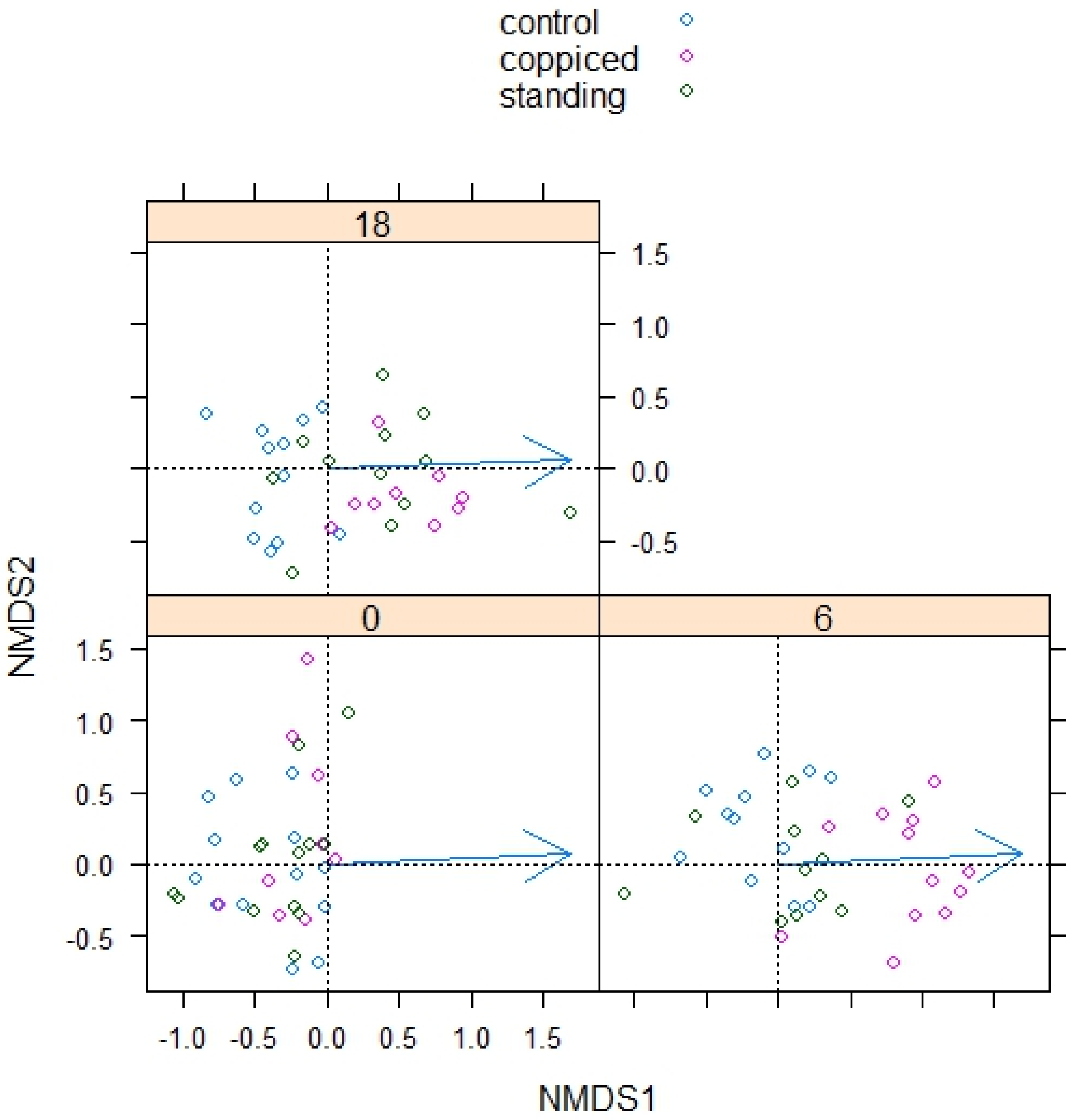


Figure Four: NMDS ordination plots of cursorial morphospecies, panelled by time since burn (months). Colours of data points indicate burn treatment. Arrows indicate the direction and strength of the correlation between mean burn temperature and the ordination. Stress= 0.137.

In order to further investigate the association between spider morphospecies distribution, burn treatment and mean burn temperature we plotted the NMDS ordination with morphospecies labelled as text. This revealed correlations between morphospecies and mean burn temperature, for example morphospecies Li8 of the Linyphiidae family was associated with higher mean burn temperatures. By contrast morphospecies G1 (Gnaphosidae) and morphospecies Z4 (Zodariidae) were associated with lower mean burn temperatures (see Fig. Five).

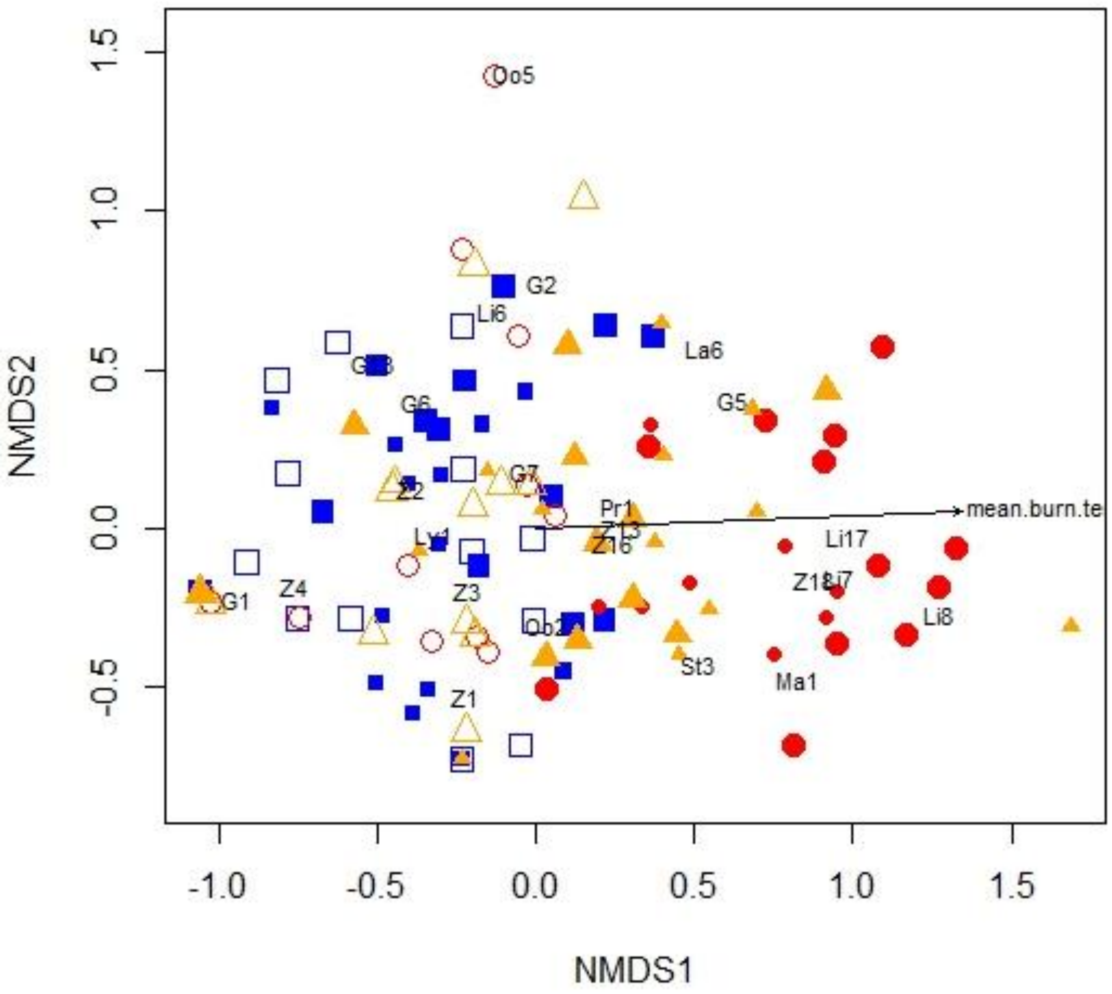


Figure Five: NMDS ordination for cursorial spider morphospecies community composition, showing the association of specific morphospecies with burn temperature and with burn treatment. The arrow indicates the direction and strength of the correlation between mean burn temperature and the ordination. Morphospecies are labelled as text. Blue squares represent control plots, red circles represent coppiced plots, and orange triangles represent standing plots. Hollow shapes represent pre-burn and solid shapes represent post-burn with the size of the shape representing time since burn, large - 6 months post-burn, small - 18 months post-burn. Stress = 0.137.

Family assemblages

NMDS ordinations with environmental variables displayed using the 'Envfit' function, and multivariate permutational ANOVAs (produced using the 'Adonis' function) revealed significant differences in the composition of cursorial spider family assemblages in response to burn treatment (ADONIS, df=2, 109, r^2=0.039, p=0.0007) and to time since burn (ADONIS, df=1, 109, r^2=0.065, p=0.0001), and a significant interaction between time since burn and burn treatment (ADONIS, df=2, 109, r^2=0.051, p=0.015). As for cursorial morphospecies assemblages, there was a greater degree of separation between treatment plots at 6 months post-burn compared to 18 months post-burn, with coppiced treatment plots grouped at the right hand side of the ordination, unburnt and control plots at the left and standing plots grouped centrally. At both 6 and 18 months post-burn standing plots shared characteristics of both the control and coppiced plots, and occupied the central part of the ordination. Mean burn temperature was found to significantly affect family community composition (Envfit, r^2= 0.14, p=0.0001). (See Fig. Six).

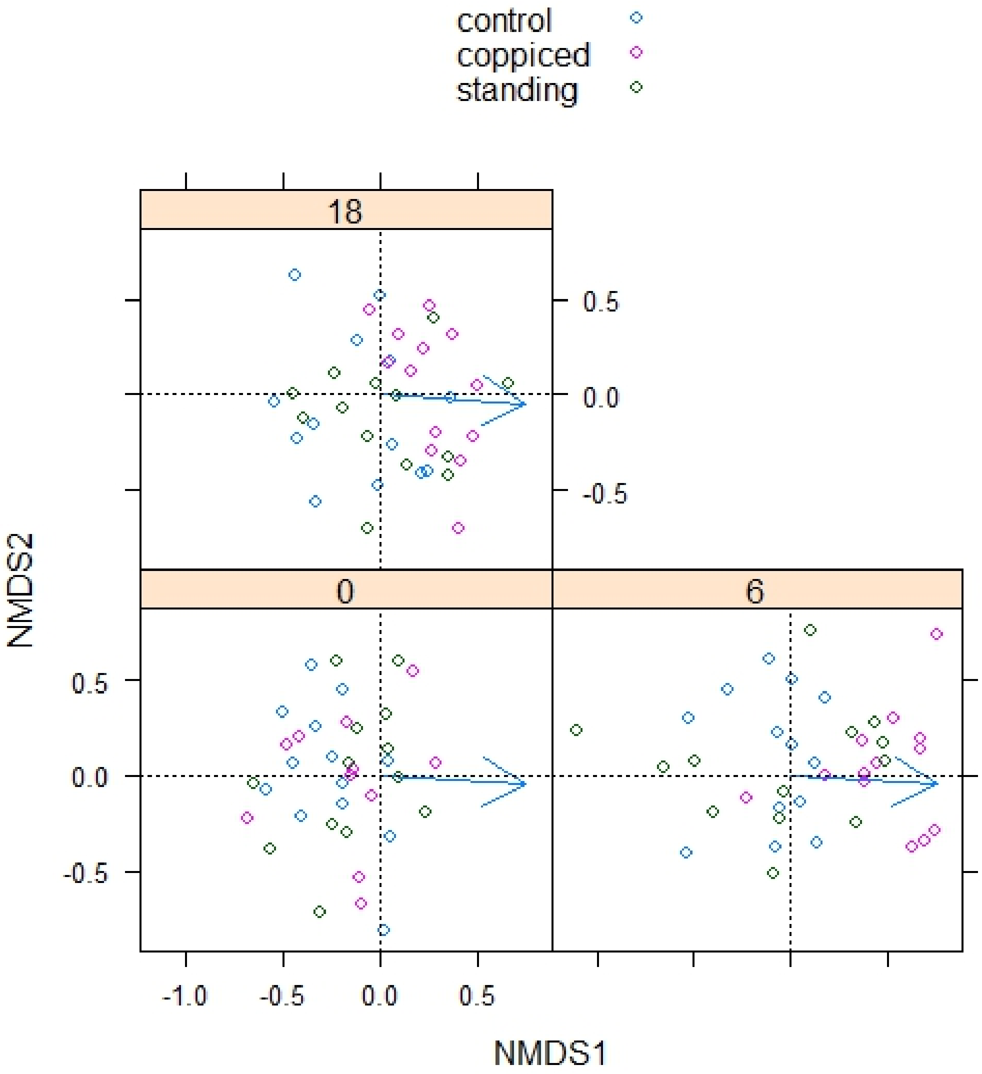


Figure Six: NMDS ordination plots of cursorial spider families, panelled by time since burn (months). Colours of data points indicate burn treatments. Arrows indicate the direction and strength of the correlation between mean burn temperature and the ordination. Stress= 0.230

In order to investigate the association between specific families, burn treatment and mean burn temperature we plotted the NMDS ordination with the family scores highlighted as text. These ordinations revealed that Gnaphosidae, Nemesiidae and Amaurobiidae were more strongly associated with pre-burn and control plots, and that the Lycosidae and Stiphidiidae were associated with burnt plots and the comb-footed spider family Theridiidae associated with hotter burns and specifically with the coppiced treatment plots (See Fig. Seven).

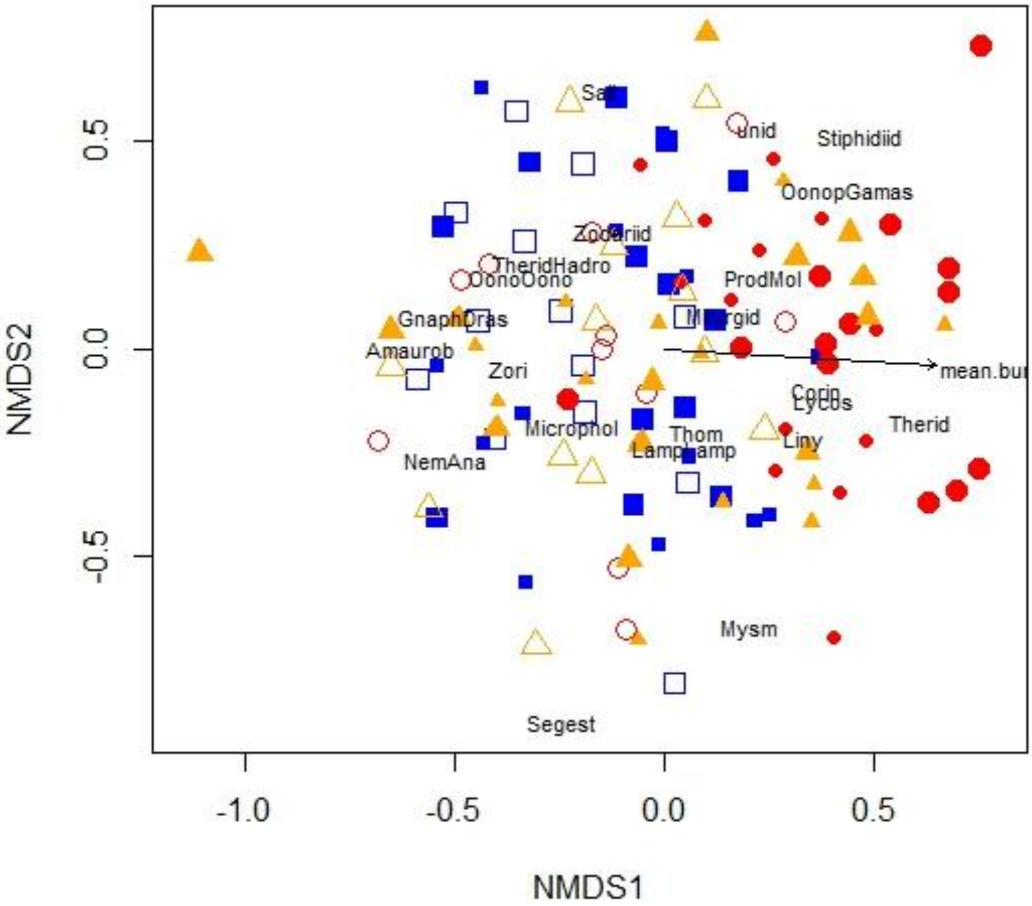


Figure Seven: NMDS ordination for cursorial spider family community composition, illustrating the association of specific families with burn temperature and with burn treatment. The arrow indicates the direction and strength of the correlation between mean burn temperature and the ordination. Families are labelled as text. Blue squares represent control plots, red circles represent coppiced plots, and orange triangles represent standing plots. Hollow shapes represent pre-burn and solid shapes represent post-burn with the size of the shape representing time since burn, large - 6 months post-burn, small - 18 months post-burn. Stress= 0.230.

Linear mixed models were constructed to predict the richness and diversity (Shannon’s index) of cursorial spider morphospecies and families as functions of burn treatment and mean burn temperature. We found a significant effect of the interaction between burn treatment and time since burn on cursorial morphospecies diversity (χ^2 (8) =16.753, p=0.0328); morphospecies diversity was significantly lower in standing plots at 6 months post-burn than in control plots (see Fig. Eight). Despite a significant interaction of time since burn and burn treatment, linear mixed models revealed no significant main effect of mean burn temperature on Shannon's diversity or richness for families or morphospecies of cursorial spiders, p>0.05.

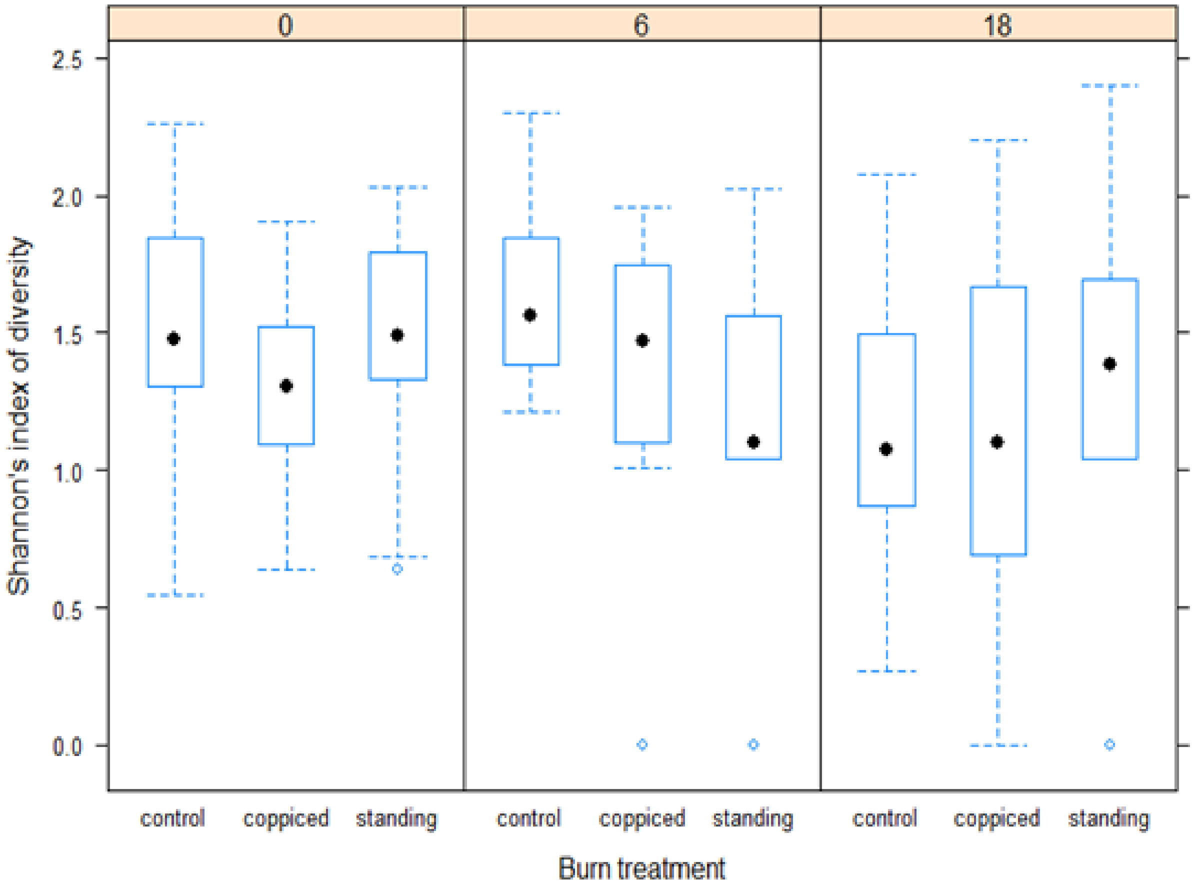


Figure Eight: Box plots showing the effect of burn treatment on Shannon's diversity of cursorial spider morphospecies with time since burn shown at the top of each boxplot. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

Arboreal spiders

NMDS ordinations with environmental variables displayed using the ‘Envfit’ function, and multivariate permutational ANOVAs (produced using the ‘Adonis’ function) were used to test the effects of burn treatment, mean burn temperature and time since burn on the community composition of arboreal spider families. The ordination plot showed distinct groupings of burnt and control plots, with plots that had been burnt, by both coppiced and standing treatments, grouped towards the lower right hand side of the ordination plot, and the unburnt controls to the left. (See Fig. Nine). Spiders in the families Lycoisdae, Salticidae and Theridiidae were most common in unburnt plots, whilst members of the Tetragnathidae, Araneidae, Thomisidae and Oxyopidae were more commonly found in burnt plots. Consistent with these patterns, we found significant effects of burn treatment (ADONIS, df=2, 58, r^2= 0.10, p=0.0001) and time since burn (ADONIS, df=3, 58, r^2= 0.12, p=0.0001) on arboreal spider family composition; however, no significant interaction effect was found between burn treatment and time since burn, $p>0.05$. Mean burn temperature was significantly correlated with the separation of points in the ordination of arboreal assemblages (Envfit, r^2= 0.20, p=0.00001).

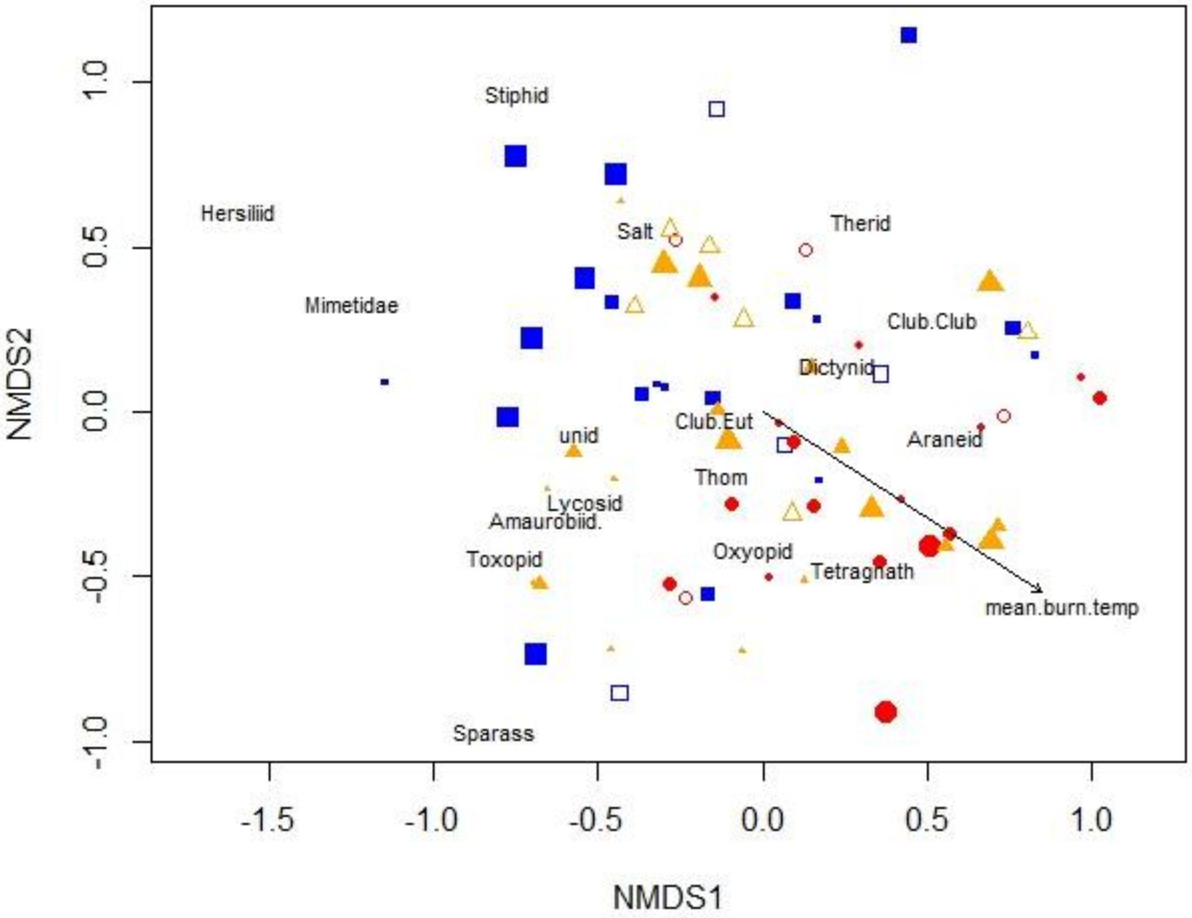
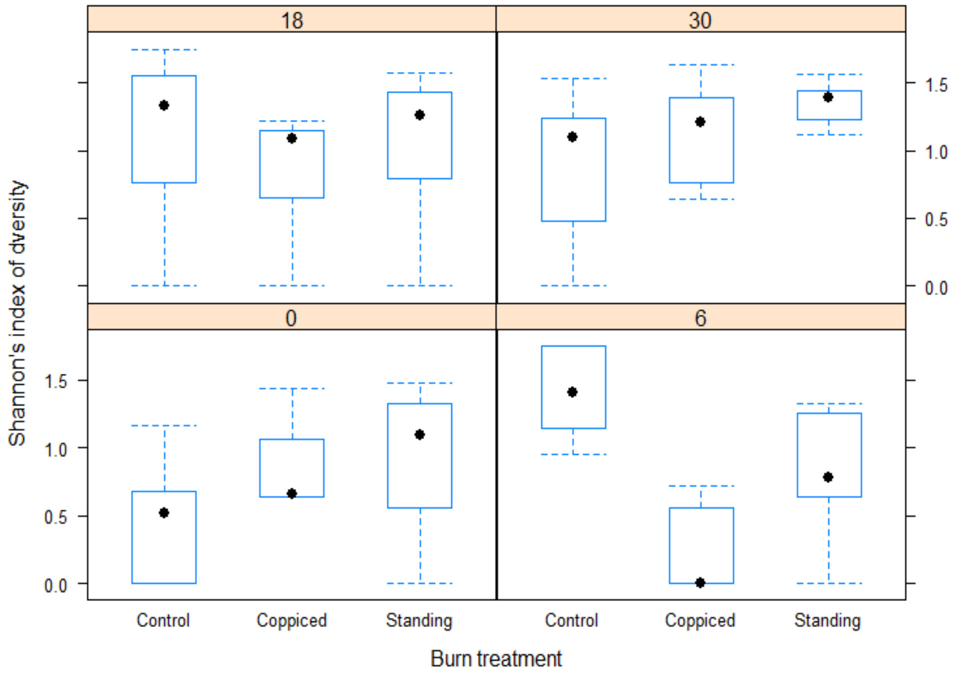


Figure Nine: NMDS ordination for arboreal spider family community composition, with Envfit to indicate the direction and strength of the correlation between mean burn temperature and the ordination, marked as an arrow. Families are labelled as text. Blue squares represent control plots, red circles represent coppiced plots, and orange triangles represent standing plots. Hollow shapes represent pre-burn and solid shapes represent post-burn with the size of the shape representing time since burn; large - 6 months post-burn, medium - 18 months post-burn, and small - 30 months post-burn. Stress= 0.189.

Linear mixed models were constructed to predict Shannon’s index of arboreal spider family diversity and family richness, as functions of burn treatment and time since burn. These revealed a significant effect of the interaction between burn treatment and time since burn on family diversity (χ^2 (11) = 42.10, p=0.000016). Six months after the burn, mean family diversity was significantly lower in coppiced and standing experimental plots than in control plots. At 18 months post-burn, mean family diversity remained significantly lower in coppiced plots than in control plots. However 30 months after the burn, the rank order of mean Shannon's diversity among the treatments was the same as before the burn (See Fig. Ten-a). Arboreal spider family richness followed a similar pattern, with a significant effect of the interaction between burn treatment and time since burn on family richness (χ^2 (11) =32.899, $p < 0.001$). Mean family richness was significantly lower at 6 months post-burn in both coppiced plots and in standing plots. However, as for the Shannon's index of family diversity, the rank order of mean family richness at 30 months post-burn had returned to pre-burn levels (See Fig. Ten-b).

a) Shannon's diversity for aerial spider families



b) Richness of aerial spider families

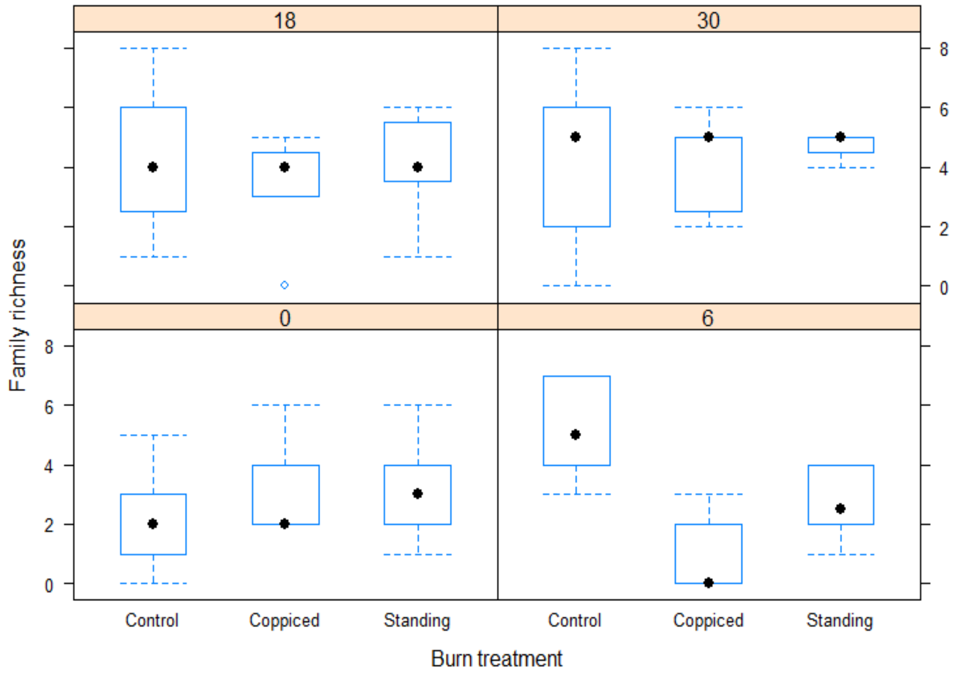
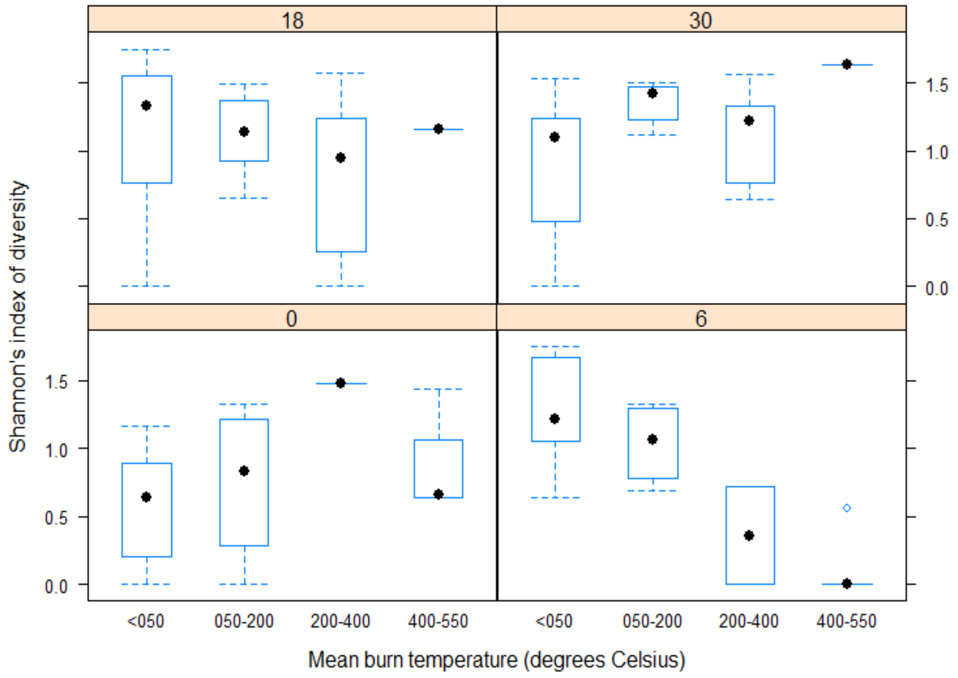


Figure Ten: Box plots showing the effect of burn treatment on a) Shannon's diversity and b) family richness of arboreal spider families with time since burn shown at the top of each box plot. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

A significant interaction between mean burn temperature and time-since-burn was found to affect both Shannon's index of arboreal family diversity (χ^2 (15) =44.612, $p < 0.001$) and family richness (χ^2 (15) =38.81, $p < 0.001$) of arboreal spiders. At six months post-burn mean burn temperature had a highly marked effect on both the diversity and richness of arboreal spider families, with both diversity and richness exhibiting a significant linear decrease with increasing burn temperature. By 18 months post-burn family diversity and richness had recovered to pre-burn levels and at 30 months post-burn diversity was highest in the plots that burnt at above 400 °C (See Fig. Eleven-a and Eleven-b).

a) Shannon's diversity for aerial spider families



b) Richness of aerial spider families

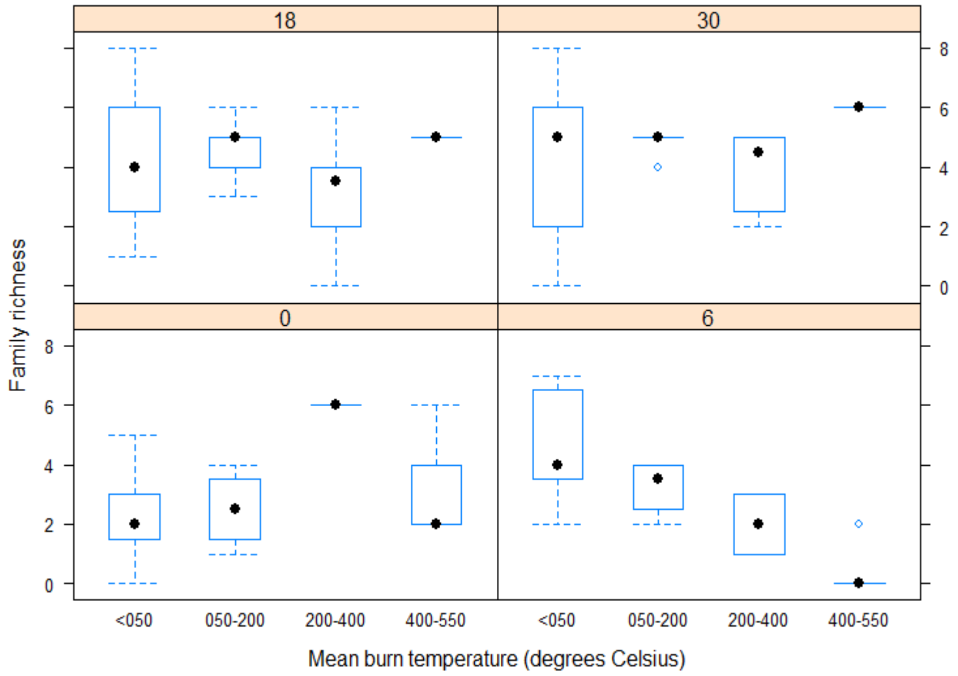


Figure Eleven: Box plots showing the effect of mean burn temperature on a) Shannon's diversity and b) richness of arboreal spider families, on the X axis, with time since burn shown at the top of each box plot. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

Question Two: Vegetation and litter depth on spider community composition and diversity

The following analyses are based upon pitfall trap collected and sweep net data from the 2011 and 2012 survey years, in which surveys measuring the structural complexity of vegetation and the depth of litter were conducted (Refer to the cells marked with a ‘2V’ in Table One).

Vegetation structural complexity and litter depth

In the immediate post-fire environment, the structural complexity of the vegetation and the depth of the litter layer was at its lowest. This is particularly true of the coppiced experimental plots, where standing vegetation was felled prior to burning, producing hotter burns, after which very little vegetation and litter remained. Following the lower intensity burns of the standing experimental plots post-burn vegetation structural complexity was typically higher than in coppiced burn plots; mallee trunks and complete trees were for the most part left standing and although fine fuels were reduced, coarse woody fuel remained. Burns of a lower temperature were generally less homogenous than those of a hotter temperature, resulting in a mosaic effect where some unburnt patches remained. Following burning there was an initial decrease in vegetation structural complexity, so at six months post-burn vegetation complexity was at its lowest in coppiced plots and highest in control plots. Vegetation complexity subsequently increased with time since burn, so that by 30 months post-burn, understorey vegetation (all vegetation under 100 cm in height) was more structurally complex in coppiced and standing plots than in control plots (See Fig. Twelve and Fig. Thirteen).

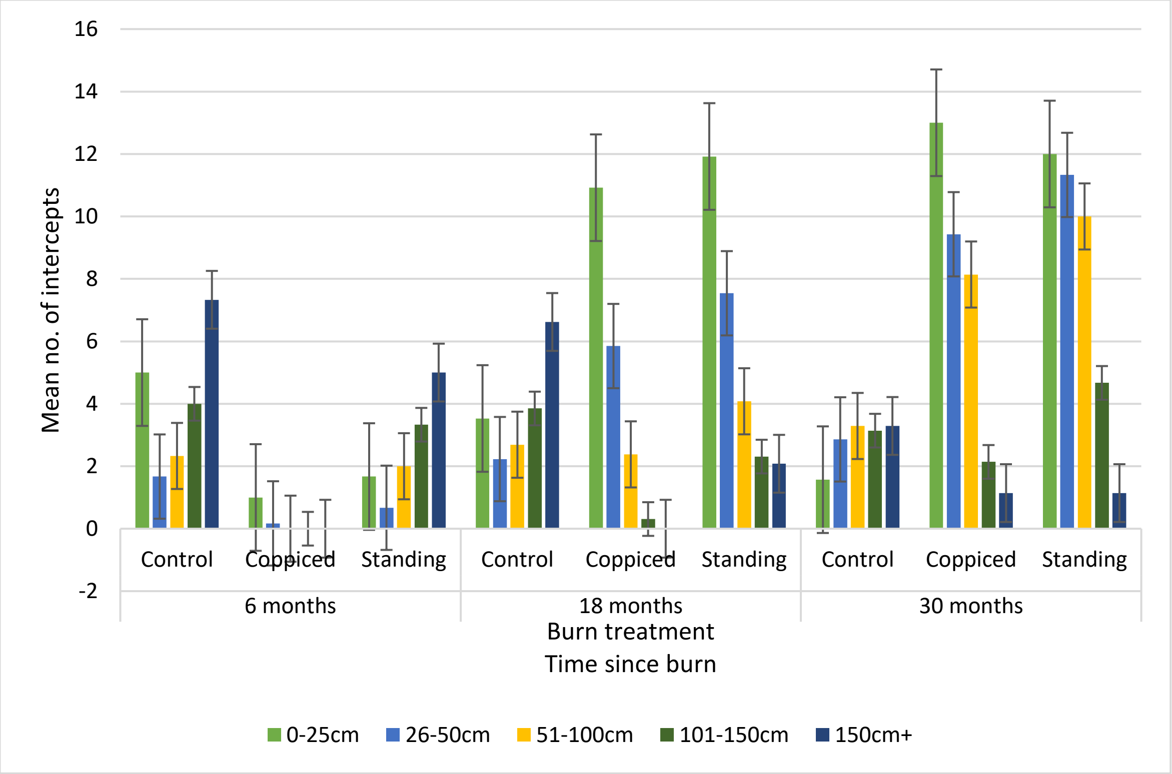


Figure Twelve: Living vegetation structural complexity, measured as the mean number of point intersects by living vegetation at height classes (0-25cm, 26-50cm, 51-100cm, 101-150cm and 150cm +) along a transect, with time since burn and burn treatment. Error bars are standard error.

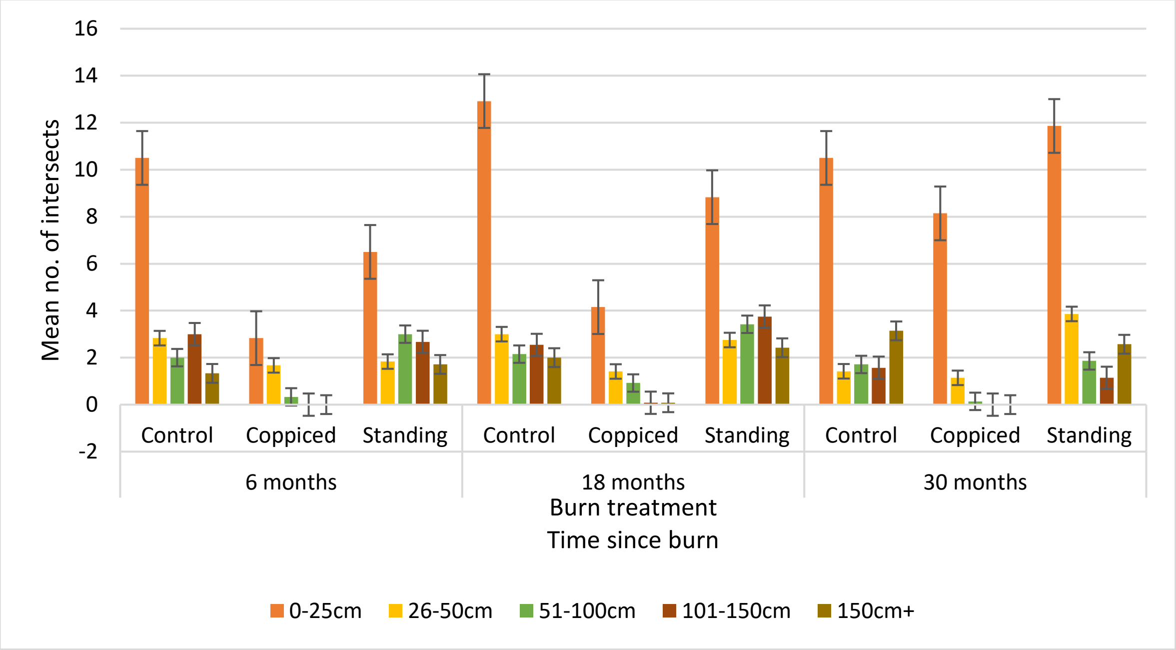


Figure Thirteen: Dead vegetation structural complexity, measured as the mean number of point intersects by dead vegetation at height classes (0-25cm, 26-50cm, 51-100cm, 101-150cm and 150cm +) along a transect, with time since burn and burn treatment. Error bars are standard error.

The depth of litter changed with time since burn and the impact of the burn treatments was correlated with mean burn temperature. Following fire, litter depth and within-plot variation in litter depth were reduced and showed a negative relationship with mean burn temperature. Both the depth of litter and its variation within plots were highest in control plots and lowest in coppiced plots (See Fig. Fourteen).

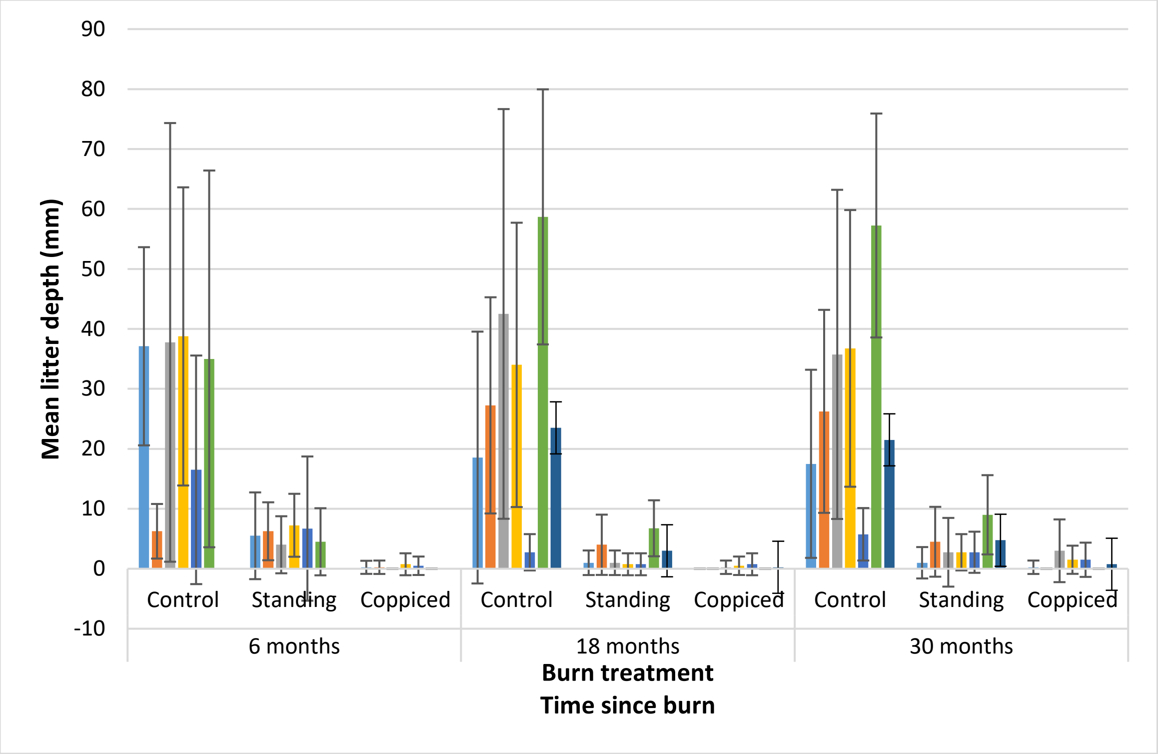


Figure Fourteen: Mean litter depth (mm) per plot with burn treatment and time since burn. Error bars are standard error.

Effect of vegetation structural complexity and litter depth on cursorial spiders

To test the effect of vegetation structural complexity and litter depth on the structure of cursorial spider assemblages we conducted ADONIS analyses and NMDS ordinations with Envfit on the pitfall trap data collected in the years the vegetation and litter depth surveys were conducted, marked with a ‘2V’ on Table One. Consistent with predictions we found mean litter depth (Envfit, $r^2=0.58$, $p=0.0001$), standard deviation in litter depth (Envfit, $r^2=0.52$, $p=0.0001$) and mean temperature of the burn (Envfit, $r^2=0.57$, $p=0.0001$) to significantly affect the composition of the cursorial spider morphospecies community. Morphospecies Li7, Li8, Z18 and Ma1 were associated with high burn temperatures and low litter depths, whereas morphospecies Li10, G1 and G13 were associated with high litter depths and low burn temperatures (See Fig. Fifteen).

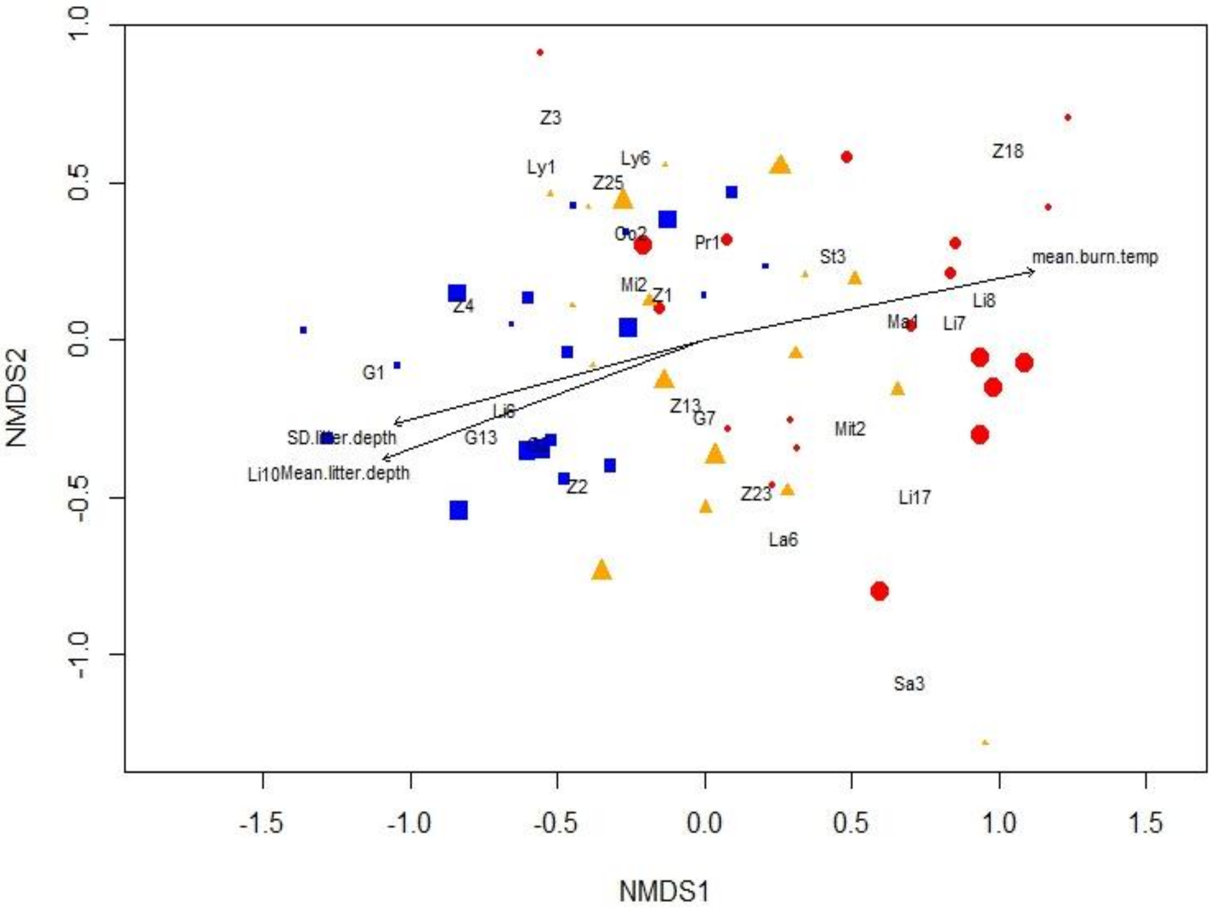


Figure Fifteen. NMDS ordination for cursorial spider morphospecies community composition, with Envfit to indicate the direction and strength of the correlation between mean and standard deviation (S.D.) of litter depth per plot, and mean burn temperature with the ordination. Morphospecies are marked as text. Squares represent control plots, circles represent coppiced plots, and triangles represent standing plots. The size of the shape represents time since burn, large - 6 months post-burn, medium - 18 months post-burn, and small - 30 months post-burn. Stress= 0.108.

Vector fitting of environmental variables on the NMDS ordination showed significant effects of the structural complexity of vegetation on pitfall trapped spider morphospecies, and a difference between the effects of living and dead vegetation on the spider community. Contrary to expectations the structural complexity of living vegetation had a lesser effect on the structure of the spider community than that of dead vegetation.

We found living vegetation to significantly affect the spider community, but only for vegetation at a height class of >150 cm (Envfit, $r^2=0.33$, $p=0.0001$). However the structural complexity of dead vegetation had a significant effect on the composition of the spider at height classes of 0-25 cm, (Envfit, $r^2= 0.16$, $p=0.0104$), 101-150 cm, (Envfit, $r^2=0.19$ $p=0.00388$) and at >150 cm (Envfit, $r^2=0.33$, $p=0.0001$). (See Fig. Sixteen).

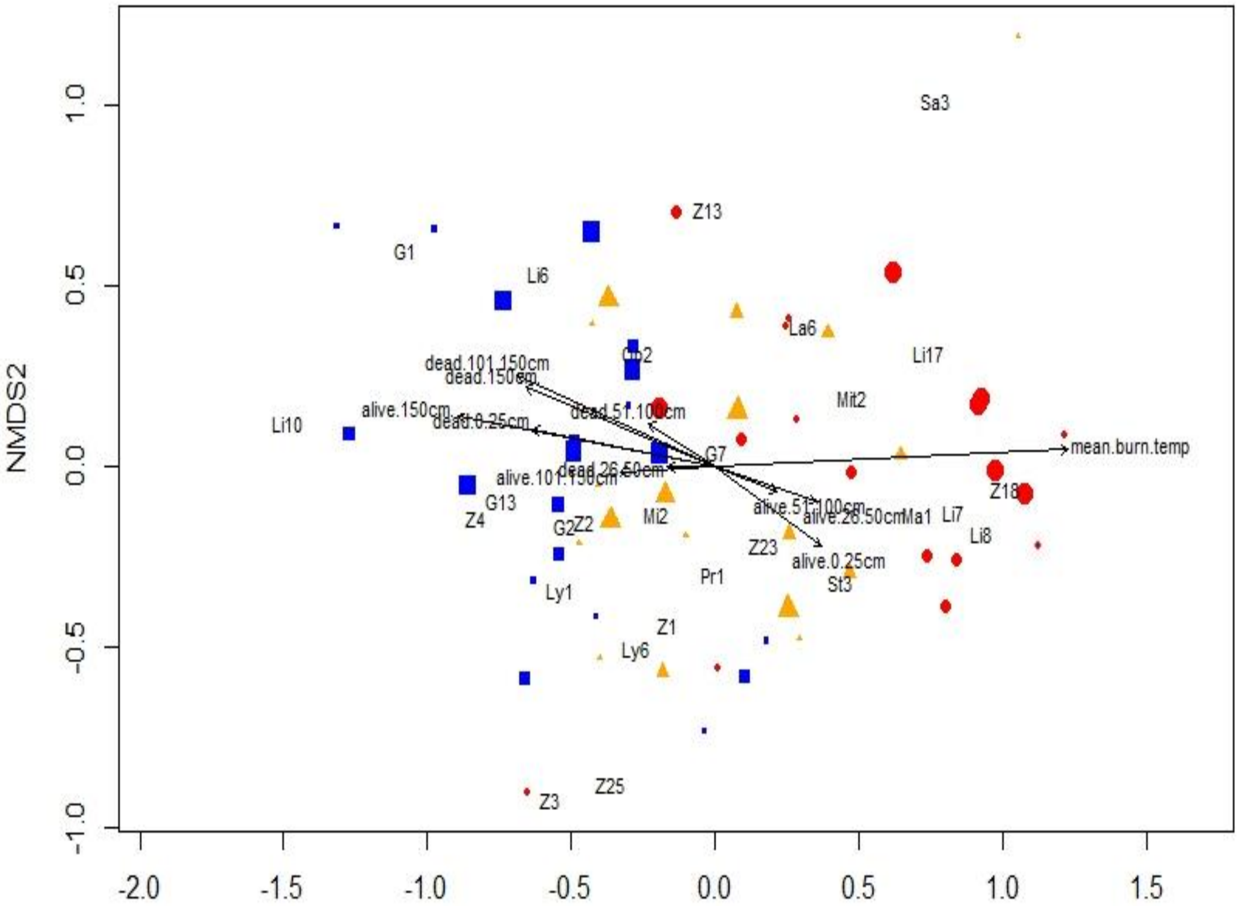


Figure Sixteen. NMDS ordination for cursorial spider morphospecies community composition, with Envfit to indicate the direction and strength of the correlation between the structural complexity of dead and living vegetation at different height classes, and the mean burn temperature and time since burn with the ordination. Morphospecies marked as text. Squares represent control plots, circles represent coppiced plots, and triangles represent standing plots. The size of the shape represents time since burn, large - 6 months post-burn, medium - 18 months post-burn, and small - 30 months post-burn. Stress = 0.108.

Linear mixed models were constructed to predict Shannon's index of cursorial spider morphospecies diversity and richness, as functions of vegetation structural complexity and litter depth. No significant effect of the structural complexity of living or dead vegetation, or the depth of litter, or variation in litter depth, was found on cursorial spider morphospecies diversity or richness, $p>0.05$.

Effects of vegetation structural complexity on arboreal spider communities

As could be expected, NMDS ordinations failed to find a significant effect of litter depth, or the variation in litter depth on the familial composition of the arboreal spider communities. However NMDS ordinations revealed a significant effect of the structural complexity of living vegetation at height classes 0-25 cm (Envfit, $r^2=0.14$, $p=0.00186$), 26-50 cm (Envfit, $r^2=0.16$, $p=0.0104$) and >150 cm (Envfit, $r^2=0.24$, $p=0.0015$) on the familial composition of arboreal spider communities. Interestingly, we found no significant effect of the structural complexity of dead vegetation, at any height class, $p>0.05$. (See Fig. Seventeen).

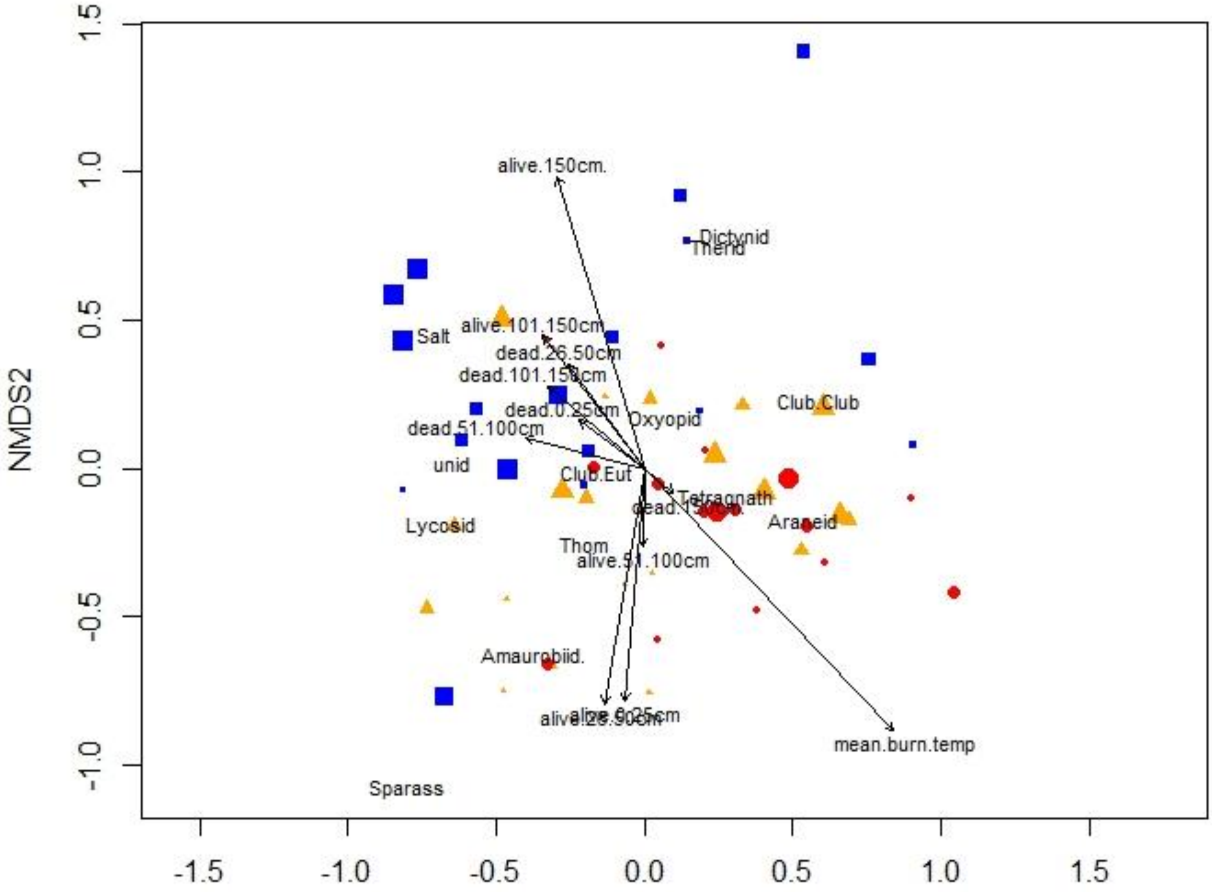


Figure Seventeen: NMDS ordination for arboreal family community composition, with Envfit to indicate the direction and strength of the correlation between the structural complexity of living vegetation at different height classes, and the mean burn temperature and time since burn with the ordination. Families marked as text. Squares represent control plots, circles represent coppiced plots, and triangle represent standing plots. The size of the shape represents time since burn, large - 6 months post-burn, medium - 18 months post-burn, and small - 30 months post-burn. Stress= 0.182.

Linear mixed models were constructed to predict Shannon’s index of family diversity and family richness of arboreal spiders, as functions of vegetation structural complexity. We found the structural complexity of living vegetation to significantly affect arboreal spider family diversity and richness at all height classes of vegetation, apart from for vegetation taller than 150 cm. Where a significant effect was present, both diversity and richness increased with increasing structural complexity of vegetation (See Table Two).

	Shannon's diversity		**Richness**	
Living vegetation (cm)	**χ^2 (df)**	**P value**	**χ^2 (df)**	**P value**
0-25	8.5118 (1)	* 0.0035	8.4197 (1)	* 0.0037
26-50	7.5139 (1)	* 0.0061	8.4095 (1)	* 0.0037
51-100	13.14 (1)	* 0.00029	12.491 (1)	* 0.00041
101-150	10.197 (1)	* 0.0014	9.75 (1)	* 0.0018
150+	2.3945 (1)	0.1218	2.69 (1)	0.10

Table Two: Values from linear mixed models for the effects of living vegetation structural complexity at different height classes on arboreal spider family Shannon's diversity and family richness. Significant results, where $p<0.05$, are marked by an asterisk.

In a similar pattern to the effects of dead vegetation complexity on family composition, the structural complexity of dead vegetation affected arboreal spider family richness and diversity differently to that of living vegetation. A significant effect on Shannon's index of family diversity was found only for dead vegetation in the 51-100 cm height category (χ^2 (1) =4.20, p=0.040), where an increase in structural complexity in this height category was associated with an increase in diversity of 0.062 (± 0.030 standard errors). Family richness followed a similar pattern, increasing by 0.3059 (±0.1268 standard errors) (χ^2 (1) =5.53, p=0.019).

Question Three: 'Fire specialist' species and burning

The families Zodariidae, Linyphiidae and Gnaphosidae were found at each site and contained morphospecies that displayed significant associations with conditions associated with burning or with the pre-burn or post-burn environment. As assessed by visual inspection of boxplots, the distributions of these 'fire-sensitive' morphospecies differed with burn treatment and time since burn. A Kruskal-Wallis H test was run to determine if these differences were significant. We found that the distributions of morphospecies Z1, Z18, G1 and Li7 and Li8 were statistically significantly different between treatment types and time since burn. Zodariidae morphospecies Z1 was significantly more abundant in pre-burn, control and standing plots than burnt plots ($\chi^2(8) = 27.490$, $p = 0.001$) whereas Z18 was significantly more abundant in coppiced burn plots pre-burn, control or standing plots ($\chi^2(8) = 26.812$, $p = 0.001$). Gnaphosidae G1 was significantly more abundant in pre-burn surveys and control plots than burnt plots ($\chi^2(8) = 29.832$, $p = 0.0001$) and Linyphiidae Li7 and Li8 (*Ostearius melanopygius*) in burnt plots (both coppiced and standing burn treatments) than unburnt plots ($\chi^2(8) = 44.752$, $p = 0.0001$). (See Fig. Eighteen).

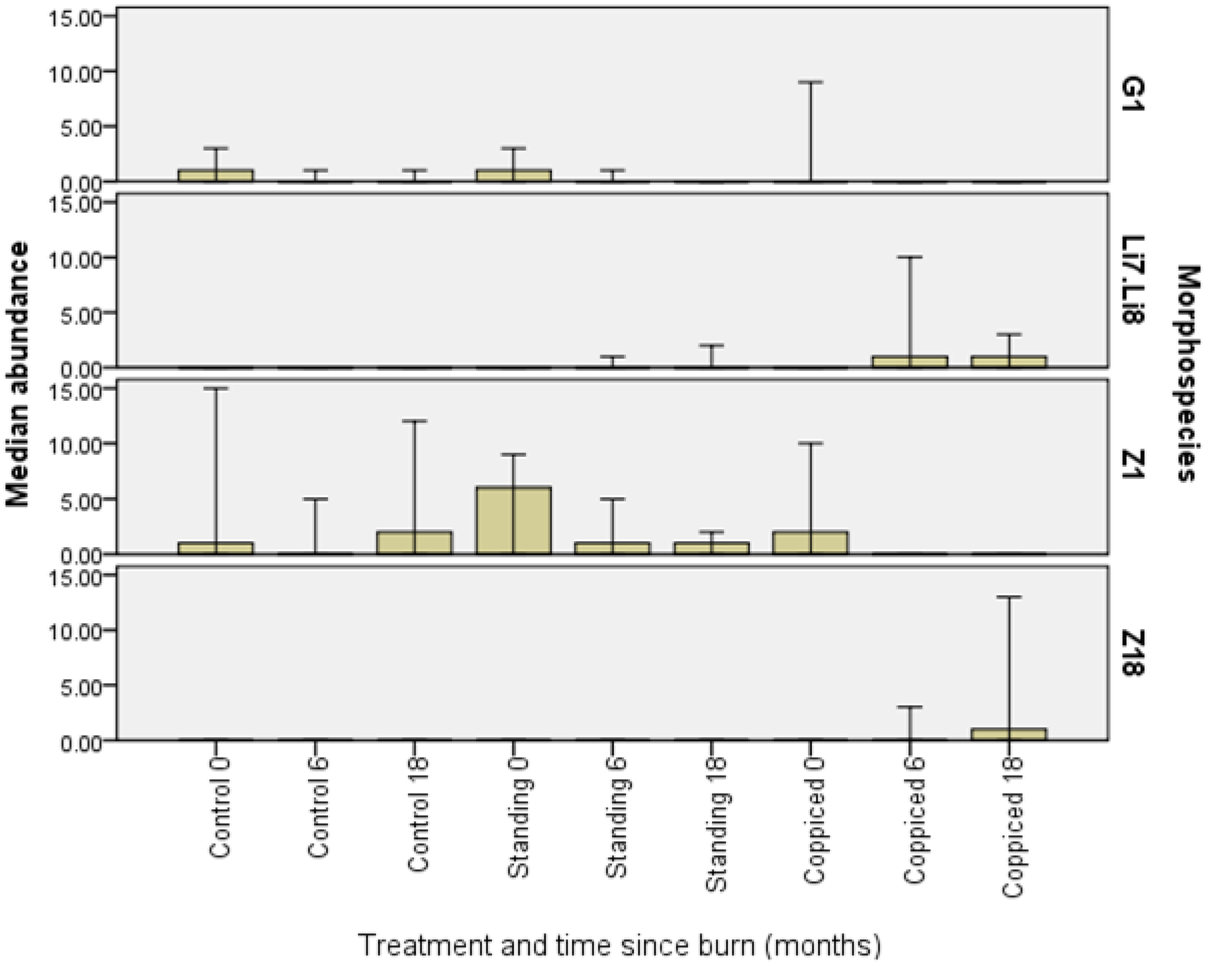


Figure Eighteen: Bar chart showing the median abundance per treatment plot of 'fire-sensitive’ morphospecies in control, coppiced and standing treatment plots, with time since burn. Error bars represent 95% confidence intervals.

Discussion

This study builds on the work of other fire ecology studies and offers significant novel findings. We showed that spider communities in small fragmented patches of native vegetation were clearly different following the application of different experimental burn treatments. Fire-related environmental variables and habitat attributes, such as the mean temperature at the surface of the soil during a burn, the depth and the variation in depth of litter and fine organic debris and the structural complexity of vegetation in the post-burn ecosystem, were significantly correlated with spider community changes. In support of our initial hypotheses, we found burn treatment, mean burn temperature and vegetation structure to be significantly affect the composition of both cursorial and arboreal spider assemblages; however, the environmental attributes involved and the nature and direction of their effects differed between the two communities. The experimental design of this project, the high level of replication and the use of control plots at all sites makes it novel in the area of invertebrate fire ecology. Additionally the measurements of changes in vegetation complexity, both living and dead, the presence of litter and coarse woody debris in addition to accurate measurements of the temperature of each fire, has allowed us to analyse the complex relationship between fire, burn temperature, vegetation structure and spider communities. These variables are dynamic and interrelated and therefore it is crucial to have some understanding of their impact in order to draw conclusions on how fire effects communities.

This chapter addressed three keys questions relating to the way that experimental burning affects spider communities in remote fragments of remnant vegetation. The findings of this study and how they relate to each of the questions will be discussed in the following paragraphs.

Question One: Is there a change in the composition and diversity of cursorial and arboreal spiders following burning and does this vary with burn treatment burn temperature?

Following burning, the cursorial spider communities in coppiced plots differed significantly from communities in control plots and, as hypothesised, there were similarities between communities in the control plots and the standing plots and between those in the coppiced plots and the standing plots. The spider communities of the different burn treatments were most dissimilar at six months post-burn and dissimilarities were still present at eighteen months post-burn; however, there was a greater degree of overlap between communities at eighteen months. These results support our hypotheses and likely reflect the structurally heterogeneous post-burn ecosystem of the standing plots, which contained areas of burnt vegetation and areas where vegetation remained unburnt. Thus the standing plots shared some niches with both the unburnt control plots and the higher intensity burn coppiced plots. These findings were true for spider communities at both the morphospecies and family levels. The community composition of arboreal spiders responded in a similar way to burning as the cursorial community, with distinct differences between the coppiced and control plots, and shared aspects between control plots and plots subjected to each burn treatment. These findings support the findings of other studies that intermediate levels of disturbance may serve to increase community diversity through the removal of dominant competitive organisms and the promotion of habitat spatial heterogeneity and niche diversification, if species are able to disperse among patches (Botkin & Sobel, 1975; Amarasekare & Nisbet, 2001; Bell et al., 2001; Cadotte & Fukami, 2005; Cadotte, 2006).

Contrary to expectations, we found Shannon's index of diversity for cursorial spider morphospecies to be significantly lower at six months post burn in standing plots than in control plots, but with no significant difference between coppiced and control plots. We had hypothesised that due to the high level of disturbance and the homogeneity of the post-burn ecosystem of the coppiced plots, spider diversity would be lower in these plots at six months post-burn than in the more structurally heterogeneous standing plots. We additionally found no significant effects of burn treatment or mean burn temperature on cursorial family or morphospecies diversity or richness. These findings do not support our hypotheses; however, they are consistent with results from other studies, which found no significant difference in pitfall trapped spider diversity and richness, in the short term after single fire events, whilst spider community composition was significantly affected (Moretti et al., 2002; Koponen, 2005; Langlands et al., 2006; Pompozzi et al., 2011; Podgaiski et al., 2013).

The observed effect of the coppicing treatment on the spider community is likely to be a cumulative effect of interacting covariates, including the effect of a high intensity burn, the effect of coppicing *per se* (Matveinen-Huju & Koivula, 2008; Pinzon et al., 2011) and the effects of a reduction in, or change to, environmental niches through a lack of remnant standing trees or coarse woody debris (Varady-Szabo & Buddle, 2006; Hanula et al., 2009; Croft et al., 2010). The observed changes in the spider community cannot be attributed to a singular cause, and are likely to be a cumulative effect of the above variables, and likely others.

Consistent with our hypotheses, both the community composition and Shannon's index of family diversity and richness of the arboreal spider community were significantly affected by burning. Family diversity showed a significant decrease in the initial period following burning in coppiced and standing plots, but subsequently increased with time since burn; at 30 months post-burn diversity was higher than in pre-burn surveys. Family richness followed a similar pattern. The mean temperature at which a plot burnt had a striking effect on Shannon's family diversity and family richness, which at six months post-burn decreased in an inverse linear relationship with burn temperature. Our results showed that by eighteen months following a burn family diversity and richness had recovered to pre-burn levels and by thirty months post-burn had exceeded them, with diversity being highest in plots which burnt at above 400 °C. The results support our hypotheses and likely reflect the depauperate nature of the senescent vegetation communities of the unburnt plots and the significant increase in vegetation diversity and structural complexity with seedling germination and mallee resprouting with time since burn. These findings of an initial post-burn decline in diversity and richness followed by an increase with time since burn were hypothesised in this study and have been recorded by other studies (Ryndock et al., 2012; Podgaiski et al., 2013).

By directly relating the effects of pre-burn vegetation treatment and burn temperature on the composition of spider communities this project provides novel insights to spider fire ecology. These novel findings are important, allowing predictions to be made upon the likely effect of pre-burn vegetation treatments, when conducting planned burns, on spider communities and therefore providing information to fire managers in the optimal way to conduct a prescribed burn with respect to conserving the spider community.

Question Two: Is changing vegetation structural complexity and litter depth in the post-burn environment a significant factor in determining composition and diversity of cursorial and arboreal spider community?

Mean litter depth and variation in litter depth significantly affected the composition of cursorial spider communities. The abundance of some morphospecies, particularly those belonging to the family Gnaphosidae, was highly correlated with increasing litter depth, and the abundance of others, for the example the abundance of morphospecies of the Salticidae family, were associated with an open habitat and decreased litter depth. These findings were consistent with hypotheses and support the findings of other studies, such as those by Uetz (1979), Bultman et al. (1982), Brennan et al. (2006), Castro& Wise (2009) that litter and fine woody debris are important determiners of spider community composition.

As hypothesised, the structural complexity of ground, mid and upper level vegetation had a significant effect on the structure of the cursorial spider community; however, contrary to expectations the structural complexity of dead vegetation had a greater effect on the cursorial spider community than did that of living vegetation. Dead vegetation is an important ecosystem attribute that enhances the structural architecture of the ecosystem, providing habitat for spiders and their prey. Studies have found that habitat structure *per se* is an important determinant of spider communities (Bowden & Buddle, 2010; Cobbold & MacMahon, 2012; Langellotto & Denno, 2004), and thus dead vegetation may play as much of a structural role as living vegetation. Our findings of the importance of ground level dead vegetation (also known as coarse and fine woody debris), are consistent with those of other studies (Castro& Wise, 2009; Hanula et al., 2009). We found only taller living vegetation, at above 150 cm, to significantly affect the composition of the cursorial spider community. Taller herbaceous vegetation and shrubs may provide shade for the cursorial spider community, reducing fluctuations in ground level temperature and relative humidity and decreasing the risk of desiccation for moisture dependent invertebrates.

Contrary to expectations we found no significant changes in cursorial spider morphospecies or family diversity or richness with changes in the structural complexity of vegetation. The reason for this is unclear; however, it is likely a range of factors are responsible. It may be simply because there was no effect of complexity or that the model of structural complexity used in this study did not encapsulate the structural variables important to the spider community. The time period may not have been long enough for community change to take place, or confounding variables or biases associated with the sampling method used for collecting the cursorial spider community may have masked any effect. Across all plots, the structural complexity of living vegetation at the height class of 0-25 cm was highest in the coppiced plot at thirty months following a burn, and increased linearly with time since burn and mean burn temperature. Thus the positive effects of increasing vegetation structural complexity on the diversity of the spider community in these plots, may be masked by the deleterious effects of hotter burn temperatures and the corresponding environmental changes associated with a high temperature burn, such as a reduction in litter depth and coarse and fine woody debris. It is known that pitfall trapping, as a survey method has a number of limitations. Pitfall trapping is a static collection method, which requires invertebrates to be moving past the trap to allow capture. This is associated with several sampling biases. Not only are pitfall traps biased towards the collection of active mobile invertebrates over more sedentary ones, but actual trapping success is also affected by factors which may influence the ease of movement of invertebrates through the habitat, such as the clearance of organic material and debris following coppicing and burning (Topping & Sunderland, 1992; Melbourne, 1999; Podgaiski et al., 2013). Thus the structurally homogeneous and barren habitat of the coppiced plots at six months post-burn may have served to increase the ease of movement of spiders through the habitat, meaning that the success rate of the traps in these plots was artificially high compared to that of the traps in the more structurally heterogeneous standing and control plots. These biases associated with pitfall trapping directly affect the probability that an individual is captured by a trap, and so have the potential to influence sampling results and potentially mask actual changes or produce spurious differences in community diversity or richness.

As hypothesised, the community composition of arboreal spiders was significantly affected by the structural complexity of living vegetation in the post-burn ecosystem; however, we found the structural complexity of dead vegetation to have no significant effect, this was the opposite finding to that for the cursorial spider community. Our findings of the importance of living vegetation structural complexity for the arboreal spider community are consistent with findings from previous studies (Oxbrough et al., 2005; Ryndock et al., 2012). The differences in the responses of the arboreal and cursorial spider communities to the structural complexity of living and dead vegetation suggest different mechanisms determining their composition. This finding highlights the importance of using a range of collection methods to sample both the cursorial (pitfall trapped) and arboreal (sweep net and beating collected) spider communities when monitoring for changes in the spider community following burning.

We found a significant positive correlation between the structural complexity of living vegetation and arboreal spider diversity and richness for vegetation at all height classes apart from upper storey vegetation, whereas dead vegetation only had a significant effect for the intermediate vegetation height classes. Increased vegetation structural complexity provides additional web anchor points for web spinning spiders and increases available niches for vegetation dwelling spiders and habitat for prey species, as well as providing shade to decrease the risk of dessication. The lack of significance for most height classes of dead vegetation suggests that habitat complexity *per se* may not be the primary driver for the significant correlation between living vegetation and arboreal spider diversity, but that other effects, such as shading or increased habitat for prey species or for predators and parasites of spiders (e.g. Pompilidae, Mantisipidae, Acroceridae), may be a more important driver. The findings from this study support those of previous studies that the structure of vegetation following fire influences the abundance, composition and distribution of the spider community (Carrel, 2008; Ryndock et al., 2012; Podgaiski et al., 2013), however they extend from these studies by separately analysing the effects of changes in the structure of dead and living vegetation and so enabling a correlation to be drawn assessing the relative importance of each on spider communities. These are novel findings and would be worthy of further research.

Question Three: Do the conditions following a burn favour 'fire-specialist' spiders and does the number of exotic spiders change with burning and with burn treatment?

The presence of a specialisation for unburnt or burnt ground by some spider species has been documented (Buddle et al., 2000; Moretti et al., 2002; Buddle et al., 2006; Langlands et al., 2012; Teasdale et al., 2013). This study found morphospecies from three families that showed significant preferences for conditions associated with burning or with the pre- or post-burn environment. A spider from the Gnaphosidae was highly associated with unburnt areas, and with increasing litter depth and increasing upperstorey vegetation cover, suggesting a closed habitat preference. We also found burning to induce a change in several numerically dominant Zodariidae morphospecies. The dominant zodariid in unburnt plots was associated with increased litter depth, and when found in burnt plots, was associated with plots that had burnt with a low mean burn temperatures. The dominant zodariid in burnt plots was associated with variables related to an open habitat type (i.e. decreased litter depth, reduced taller shrubs and canopy cover, and increased burn temperature). A switch in dominant morphospecies following burning was also recorded in the Linyphiidae family. NMDS ordinations suggested high litter depth and a variation in litter depth to be important variables for the dominant Linyphiidae morphospecies of unburnt plots. Following burning, a second linyphiid species*, Ostearius melanopygius*, became the numerically dominant member of Linyphiidae. We found *O. melanopygius* to be significantly associated with the coppiced burn treatment, with hotter burn temperatures and with decreasing litter depth. *Ostearius melanopygius* is an introduced species, first recorded in Australia in 1976 (Wunderlich, 1976). It now has a cosmopolitan distribution and is estimated to be spreading at a rate of 30 km per year (Ruzicka, 1995). It is a frequent aerial disperser and is often associated with human disturbance, being commonly found in gardens and rubbish dumps (Nellist, 2012). These findings support those from other studies that disturbance, such as is caused by coppicing and then burning a site, can exclude native or disturbance intolerant spiders and increase the risk of invasion by disturbance tolerant exotic species (Szinetar & Samu, 2012; Hogg & Daane, 2013). The results of this study are supported by the findings of Malumbres-Olarte et al. (2014), who found that exotic Linyphiidae explained an increase in exotic spiders following burning in New Zealand. These studies highlight the importance of appropriate fire regimes to maintain diversity, avoid localised extinctions of fire sensitive species and reduce the risk of invasion by exotic species, especially so in fragmented, nationally threatened plant communities, such as those of the *E. cneorifolia* study sites.

Conclusions

This study contributes valuable data on invertebrate fire ecology. It is a controlled and replicated study with pre and post-burn data, a rarity in invertebrate fire ecology research (Whelan et al., 2002). A key strength of this project, and one that makes it novel in spider fire ecology is the use of replicated experimental burns, where burn temperature was accurately measured and where each burn had a neighbouring unburnt control plot. This enabled a direct assessment of the effect of burn temperature and burn regime on spider communities.

The findings from this study suggest several avenues for further research. Results from multivariate analyses suggest individual species, for example Zodariidae Z18, which was associated with burns of a higher temperature, and Gnaphosidae G1, which was associated with unburnt ground, be main drivers of the observed changes in spider communities. Future research using univariate analyses to further assess the effect of fire on these species is recommended.

A key aim of this study was to provide recommendations to aid management decisions on optimal burn regimes for restoration burning of areas of fragmented senescent native vegetation, to conserve spider community diversity. The findings of this project indicate that whilst coppicing of vegetation, followed by a hot burn of above 400 °C, resulted in an increase in diversity of some spider guilds (namely arboreal spiders), it was also associated with a decrease in the abundance of other spider guilds and was associated with an increase in the abundance of an exotic, invasive spider. Therefore coppicing followed by burning would not be recommended as a management technique and the findings of this chapter suggest it may be detrimental to the overall conservation of the native spider community in small, fragmented patches of native vegetation. There exists a trade-off between the potentially beneficial effects to the ecosystem of a high temperature burn, in terms of increased vegetation growth and the increase in abundance of some spider species, and the negative effects of a hot burn via the removal of the litter layer, the reduction in abundance of some other spider species and the increase in an invasive, exotic spider. The findings of this chapter suggest that lower intensity, more variable burns that leave a spatially heterogeneous post-burn landscape with remnant coarse woody debris and organic material, may serve to better promote the conservation of native spider communities.

Fires cause large-scale change to ecosystems, organisms’ responses to these changes is likely to be affected by a range of interacting variables and their impact is likely to be dynamic and to change over the post-fire period. In this study we measured a range of environmental parameters to attempt to explain changes in spider community following burning. This approach highlights the importance of the analysis of a range of environmental parameters in order to provide a better understanding of the changes an ecosystem undergoes following burning, of the organism’s response to burning and in order to better advise fire management.

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CHAPTER THREE

A novel morphological trait-based system for categorising the spider community into guilds and measuring community response to burning.

Abstract

A guild-based approach to analysing spider communities offers researchers opportunities to assess the impacts of environmental variables on ecosystem functionality. Currently there is no standard method with which to categorise spiders in to guilds, and due to a high number of unidentified species, and a scarcity of knowledge in the biology of many identified species, there has been difficulty developing a meaningful basis on which to classify and separate guilds. Thus, guild systems are often very general, or are based heavily on inferences about traits or behaviour drawn from family level categorisations and are therefore somewhat subjective or arbitrary. Where this is the case there is increased risk that the conclusions drawn may be an artificial construct of the categorisation process. We developed a quantifiable system with which to categorise spider communities in to functional guild based upon a series of measurable morphological traits. We tested this system using pitfall trap spider data collected following experimental burning of remnant patches of native vegetation. We found the composition of guilds to change significantly with mean burn temperature and burn treatment. Guild diversity was significantly affected by the interaction of mean burn temperature, and burn treatment with time since burn. Fourth corner analyses revealed an effect of environmental variables on morphological traits. We found the presence of false tufts to decrease and eye size to increase with increasing burn temperature, both suggesting the presence of active hunters to increase following hotter burns. The guild system has advantages over standard guild systems for categorising spiders, it is quantifiable and replicable and negates the need for inferences drawn from higher level taxonomic classifications, however it requires further testing in a range of ecosystems to establish its use as an alternative to morphospecies.

Introduction

Recent large-scale fire events, an increasing awareness by the general public of fire's role in shaping the Australian landscape, and the increasing use of prescribed fire as a management tool for asset protection and fuel reduction have meant that studies into fire ecology are increasingly becoming acknowledged as an important component of ecological research.

The inclusion of invertebrate community data in fire ecology research is essential for a full understanding of the impact of fire on an ecosystem and on ecosystem processes, given that they make up the vast bulk of terrestrial animal biodiversity and are similarly dominant in a functional sense. The majority of invertebrate fire ecology studies have been conducted in the Northern Hemisphere, and there is a need for more information on how fire affects invertebrates in Southern Hemisphere ecological systems. Recent work, based in the Southern Hemisphere (Langlands et al., 2012; Podgaiski et al., 2013; Malumbres-Olarte 2013, and this study) are addressing this imbalance.

Spiders play important and complex roles in many ecosystems. They are ubiquitous apex predators, which are found in virtually all terrestrial habitats and have colonised fresh water and littoral environments (Wise, 1993). Spiders show a high degree of functional diversity and display a large range of predation strategies and prey capture techniques. The spider community can be broadly divided into those that use webs to catch prey, and those that do not, and within these two groups there is a considerable amount of diversity. Web types vary widely and include the stereotypical orb web made by spiders in families such as the Araneidae, horizontal sheet webs made by members of the Linyphiidae, tangle webs made by members of the Theridiidae and highly specialised webs, which characterise the prey capture technique of ogre-faced spiders in the genus *Deinopis.* A *Deinopis* spider builds a cribellate net that it holds in its two front legs and casts over passing invertebrate prey (Wise, 1993; Foelix, 2011). The diversity of hunting techniques used by different groups of non web-building spiders is also high and includes active hunters (for example Lycosidae), camouflaged ambushers such as members of the Thomisidae, and highly specialised hunters, such as *Habronestes bradleyi* of the 'ant spider' family Zodariidae. *Habronestes bradleyi* is a specialist hunter of the meat ant, *Iridomyrmex purpureus*, and locates its prey by detecting the alarm pheromone released by injured ants (Allan et al., 1996). Zodariid spiders mimic ants both morphologically and behaviourally and show a sophisticated suite of behaviours to deceive their ant prey and gain entry into their nest. Spiders will carry a dead ant to an approaching ant and use a tactile cue by tapping the approaching ant's antennae with their front legs, they then hold the dead ant up for the approaching ant to inspect, so employing an olfactory cue (Pekar & Kral, 2002; Cardenas et al., 2012).

With the exception of such specialist groups as the Zodariidae, most spiders are generalist and largely opportunistic predators, preying on a wide range of invertebrates from an array of different invertebrate functional groups; however, the prey captured is restricted by the microhabitat the spider occupies. For example, aerial orb webs typically ensnare flying invertebrates, whereas the tangle webs of the Theridiidae are typically closer to the ground and capture ground dwelling invertebrates, such as ants. Similarly, camouflaged ambush hunters, such as members of the Thomisidae, ambush invertebrates that frequent flowers, such as pollinators, whereas most of the Zoridae are ground-running spiders that actively hunt and capture any terrestrial invertebrates (Framenau, 2014). Change to the composition of the spider community therefore has the potential to impact a range of invertebrate functional groups and affect ecosystem functionality (Marc et al., 1999). Indeed studies have demonstrated changes in the spider community to filter down through the food web and affect a range of lower level ecosystem processes, such as nutrient turnover, seedling recruitment and invertebrate herbivory (Lawrence & Wise, 2004; Miyashita & Niwa, 2006; Miyashita & Takada, 2007; Ruiz et al., 2009; Bucher et al., 2015).

Whilst most spiders are generalist predators, many are habitat specialists occupying distinct microhabitats that are defined by climatic variables such as temperature and humidity, or by biological variables such as vegetation type, litter depth or food supply (Foelix, 2011). This makes them particularly sensitive to changes in microhabitat availability and studies have shown changes to the spider community following manipulations to litter depth and the amount of fine woody debris (Bultman and Uetz, 1982; Brennan et al., 2006; Ober & DeGroote, 2011) and to the structural complexity of vegetation communities (Langellotto & Denno, 2004; de Souza & Martins, 2005; Takada et al., 2008; Cobbold & MacMahon, 2012; Malumbres-Olarte et al., 2013). The roles spiders play in the ecosystem and their sensitivity to ecological change make it particularly important to gain an understanding of how disturbances affect spider populations and to assess how the risk of localised extinctions of habitat specialist species is influenced by land management. This is especially true in areas of high conservation importance, such as the nationally threatened *Eucalyptus cneorifolia* vegetation communities on Kangaroo Island, in which this study was conducted, and when the purpose of the land management is ecosystem restoration.

The use of functional guilds and functional traits in ecological analyses is well established in the study of plant communities and is a growing trend in animal ecology. A guild- or trait-based approach provides additional ecological information to a purely taxonomic approach, allowing an understanding of how disturbances affect the roles organisms play within an ecosystem and of which individual traits are promoted or filtered out by disturbance, thereby giving a potentially more meaningful interpretation of community ecology (McGill et al., 2006). As discussed, spiders show a high level of functional diversity, both in prey capture techniques and in the microhabitats they occupy, making them potentially good candidates for analysis via a functional guild approach. However, the criteria used for categorising spiders into functional guilds are currently somewhat subjective, with little standardisation between studies. Most guild classification systems follow a resource-centred approach, as proposed by Root (1967), and are based upon the foraging technique with which the spider captures prey and on the niche it occupies within an ecosystem (Uetz et al., 1999). A review of the literature found a large range of guild categorisation methods, ranging from classifying the community into two guilds, active hunters and web spinners (Cobbold & MacMahon, 2012), to up to five or more guilds, for example Rodrigues & Mendonca (20012) who categorised spiders as orb weavers, space web-sheet builders, hunters, hunting runners and ambush/stalkers. Where guild assignations are somewhat subjective or arbitrary, there is a risk that the outcomes and conclusions drawn may be an artificial construct of the categorisation process. Additionally, due to such variation in guild categorisation among papers, it is often difficult to meaningfully compare the findings of these studies. Cardoso et al. (2011) attempted to address these issues and devised a method, based upon hierarchical clustering, for defining spider guilds globally, based upon inferences about function related to family level taxonomic identification. They categorised spiders into eight guilds; ‘sensing, sheet, space, and orb web weavers; specialists; and ambush, ground, and other hunters’. This was an interesting approach, which provided a globally comparable, standardised system for categorising spiders in to guilds, so addressing the key issues of a lack of standardisation and inter-study comparability. However, an inevitability of such a global system is the crude clustering of spiders in to guilds and a reliance on inferences based upon higher taxonomic surrogates to ascribe function.

Although, for the reasons outlined above, it is not easy to directly compare the findings of different studies, some general trends appear to be repeated. Typically, open habitat ground runners dominate in burnt areas, whereas litter specialists represent the dominant group in unburnt areas (Buddle et al., 2000; Moretti et al., 2002; Koponen, 2005; Podgaiski et al., 2013).

The use of a trait-based approach is a variation on the guild-based approach and offers some potential as a way to bypass the ambiguity of guild-based classifications. Using a trait-based approach guilds are defined on the basis of individual morphological or behavioural traits and their occurrence is linked back to environmental variables. This provides a quantitative and objective method by which traits can be directly linked to environmental parameters and niches (McGill et al., 2006).

Spiders have well-defined morphological traits that relate to specific functions. Examples include claw tufts that enable spiders to walk on smooth, vertical surfaces and that are found in guilds of spiders inhabiting vegetation (Rovner, 1978; Wolff & Gorb, 2015), and accessory hairs that are found on the tarsi of web building spiders and are associated with web spinning (Foelix, 1970).

Malumbres-Olarte et al. (2014) investigated changes in the composition of traits in a spider community following fire in native grassland communities in New Zealand. They found body size to be positively linked with colonisation and establishment success of spiders in the post-fire environment. This finding was matched in studies by Langlands et al. (2011) in Australia and by Carrel, (2008) who found a positive relationship between size and survival of lycosid spiders following burning in Florida. Spiders with behavioural traits, such as living within a burrow or under rocks and logs, may experience a greater level of protection from the lethal effects of radiant heat than spiders that live on the soil surface or in vegetation. In a replicated pre- and post-burn study in Florida, the differential survival of two lycosid spiders was found to be dependent on the depth of their burrows, such that the species that lived in deeper burrows received more protection from lethally high temperatures and had a higher survival rate than those living in shallower burrows (Carrel, 2008). Langlands et al. (2011) also found the abundance of burrowers and burrow ambushers in Australia to be greater in recently burnt sites. However, in their study looking at assemblage patterns of spider traits following fire in Brazil, Podgaiski et al. (2013) found no significant link between body size and survivorship following fire, although chelicera size was found to be greater in the immediate post-burn assemblages. For individuals that survive a fire *in situ*, unburnt refuge areas, shelter beneath coarse woody debris or rocks and shelter within burrows or in the soil offer a survivorship advantage with regard to radiant heat (Panzer, 2003; Carrel, 2008; Brennan et al., 2011; Gongalsky et al., 2012).

The survival rate of spiders following a fire event has also been linked to their maturity, with adult spiders surviving a fire whereas juveniles may not (Main, 2001). Thus, changes to the population may not be detectable in an initial survey but may become apparent over time, as mature spiders expire and there are fewer juveniles in the population to replace them. Complex changes in morphology, behaviour, habitat preference and prey choice often occur when spiders reach sexual maturity. For example, many male wandering spiders become nomadic, cease eating, increase their mobility and roam in search of mates (Framenau, 2005; Foelix, 2011). These behavioural differences are often associated with morphological differences between the two sexes, for example male wandering spiders often are smaller bodied and longer legged than females, whilst orb weaving males often have a significantly smaller body size than mature females (Grossi & Canals, 2015). Studies have similarly shown habitat preferences and niche specialisation to vary between juvenile and mature individuals of the same species. Upon reaching sexual maturity, female and male lycosids occupy distinct microhabitats from each other and also from juvenile spiders and spiderlings (Kronk & Riechert, 1979; Wise, 1993; Framenau, 2005; Aisenberg et al., 2007). Kronk & Riechert (1979) showed how juveniles of the lycosid *Lycosa santrita* are associated with a wooded habitat and grass cover; however, once reaching maturity females move out to bare, rocky ground, whilst mature males move towards areas of high leaf litter cover. Sanders et al. (2015) showed that the trophic niche size of *Philodromus sp*. spiders increased with age, such that younger spiders were specialist feeders restricted to a small diversity of prey, whereas older spiders were more generalist feeders. Although differences in gender and maturity are not necessarily reflected in the ecology of every spider species, they do influence a high proportion of species across a range of different families and potentially functional guilds, although this research has not been conducted yet.

In this study we employ the definition of a trait as proposed by Violle et al. (2007) - that functional traits are measurable units that influence fitness and growth, reproduction and survival in different environments. Where species identification is not possible, in order to define a trait, most studies use a combination of data gained from morphological analysis and inferences about behavioural traits drawn from higher-level taxonomic groupings (Post & Riechert, 1977; Langlands et al., 2011; Podgaiski et al., 2013). If the life history and ecology of a group is poorly known or complex and diverse, inferences based on higher-level taxonomic identifications (e.g. family) are by their nature crude, and are associated with a degree of error. Members of the family Gnaphosidae, or the ground spiders, which are abundant spiders in *E. cneorifolia* vegetation communities on Kangaroo Island, provide an example of this. As their common name suggests, gnaphosids are generally ground-running spiders and are nocturnal vagrant hunters. They typically have a standard prograde orientated leg arrangement (legs facing forwards and backwards) and two claws. However, gnaphosids of the genus *Hemicloea*, which are also present in the *E. cneorifolia* vegetation communities, have a flattened body, and laterigrade legs (legs are orientated sideways, ‘crab-like’) and live beneath the bark of eucalypt trees (Framenau, 2014). Gnaphosidae is a large and poorly studied family, its taxonomy and biology are not well characterised and species identification is, in many cases, impossible. In a system that makes assumptions based upon family-level traits, members of the genus *Hemicloea* would be placed within the same guild as the rest of the Gnaphosidae, even if their morphology, life history, and typical prey, and hence their ‘ecosystem function,’ may well be very distinct. The poorly-resolved taxonomy and poorly known biology of the group means that the potential for error in grouping all the ‘ground spiders’ (Gnaphosidae) in a single functional guild is high.

Further potential for misinterpretation may occur where a family includes abundant, exotic species that do not conform to the life history of the native representatives of the same family in a given region. An example is the exotic spider *Ostearius melanopygius* (Linyphiidae), which was the dominant linyphiid in the burnt *E. cneorifolia* sites on Kangaroo Island. It was absent from pre-burn and control sites, where a different species of Linyphiidae was dominant (refer to Chapter Two).

Ostearius melanopygius is endemic to England, but now has a world-wide distribution. It is frequently associated with human disturbance and is commonly found in gardens and rubbish dumps (Nellist, 2012). In Chapter Two we found *O. melanopygius* to be associated with a greater degree of habitat disturbance, bare ground produced by hotter burns and decreased litter depth. Conversely, the dominant native linyphiid in the control plots was correlated with increased litter depth and was only recorded from unburnt plots or those that had burnt at a lower temperature. The grouping together of these two disparate species into the same functional guild would make very little ecological sense and would confound analyses. Whilst they are both members of the same family, they have very different habitat requirements and ecologies and are also morphologically distinct, with *O. melanopygius* being larger, and so it cannot be assumed that their prey base is congruent.

Trait-based approaches, where individual traits rather than guilds are analysed to determine community patterns, are subject to the same set of limitations, if species identification is not possible and therefore inferences based upon higher taxonomic classifications used to define behavioural and/or morphological traits. To date, the main methods used in the literature to overcome these limitations have been to restrict the types of specimens that can be used in analyses. For example, in their study investigating the use of a trait-based approach for predicting the post-fire response of spiders in Australia, Langlands et al. (2011) used in their analyses only mature male spiders that could be identified to species, and all behavioural traits were inferred from family/sub-family level information.

Here I propose the use of an objective and quantitative, novel morphological trait-based approach to categorise spiders into guilds and to analyse spider community responses to fire. In the guild system (hereafter referred to as the RGS) I categorise spiders into guilds based upon groupings of morphological traits measurable on individuals, thereby eliminating the need for inferences based on higher-level taxonomic categories. Morphological traits were selected that were linked to a known life history function - for example the presence of a claw tuft, which is associated with increased hold on smooth surfaces and therefore with spiders inhabiting vegetation (Rovner, 1978). Each of the traits were present and measurable on immature and mature spiders. The traits selected resulted in the recognition of a high number of 'guilds', roughly equating to the number of morphospecies recorded in the study ecosystem, thus preserving some of the fine community detail that are masked by cruder groupings. Despite resulting in a roughly equivalent number of groupings as morphospecies assignations, the basis of the RGS on morphological traits results in novel groupings to those created by morphospecies. By grouping specimens by morphological trait the RGS crosses taxonomic boundaries, combining similar spiders from different families and separating dissimilar spiders from within the same families. In addition to this it allows the assessment of immature spiders, something that is not possible for morphospecies.

The RGS was developed to encompass several key values; that it be quantifiable and replicable, that it should avoid the need for inferences about behavioural or morphological traits drawn from the use of family level relationships; that it should allow analysis of the entire spider community, including mature, immature and male and female specimens and that it should maintain a high level of community detail, by maximising the number of guilds. A final, but important criteria is that it should be able to be conducted by non-expert taxonomists and should take roughly equivalent time, or shorter than morphospecies assignations.

To relate the traits defining groups to environmental variables, we used a recent statistical technique called a ‘fourth corner’ analysis. The fourth corner approach is a statistical method to quantify relationships between species traits and environmental variables by combining data from environmental trait and species abundance matrices (Legendre et al., 1997; Dray & Legendre, 2008). The fourth corner approach has been used more widely in ecological studies of plant communities (Lehsten et al., 2009; Amatangelo et al., 2014), but recently has also been used to test environment and species trait relationships in invertebrate communities (Jonas & Joern, 2007; Langlands et al., 2011).

The fourth corner approach is a promising technique, is subject to the same limitations as guild-based techniques in overcoming the taxonomic impediment and poor ecological knowledge of species. The RGS developed in this chapter will be used in conjunction with the fourth corner technique, so reducing the need for inferences and thus increasing the accuracy and usefulness of the fourth corner technique.

We hypothesise that traits of ground-running guilds, namely increased evenness of leg length and larger body sizes, will be favoured in the post-burn environment. As post-burn vegetation regrowth and seedling germination increase over time in the post-burn environment, we hypothesise that there will be an associated increase in guilds characterised by morphological traits associated with dwelling in vegetation, for example claw tufts and scopulae.

Methods

Experimental sites

This study utilised six burn sites, a subset of the data from 13 burn sites used in Chapter Two, to analyse the functional response of the spider community to fire and to make suggestions regarding novel approaches to categorising the spider community into guilds. The six sites selected for analysis were; AMD, DA1, RA2, RLCL, RS1, WR2. These sites were chosen on the basis that they were all burnt in spring 2009, thus removing year of burn as a variable (some of the sites from Chapter Two were burnt in 2009 and some in 2010). One site that was burnt in 2009, site Th5 was selected at random to be excluded from these analyses due to time constraints.

All of the data analysed in this chapter were derived from pitfall trapping and the surveys were conducted in March at six months, 18 months and 30 months following burning. As in Chapter Two, there were three treatment plots at each site; a coppiced plot where vegetation was felled prior to burning, a standing plot where vegetation was not manipulated prior to burning and a no burn control plot. This resulted in a total of 54 experimental plots used in analyses. They are all located on eastern Kangaroo Island, South Australia and are small fragments of *E. cneorifolia* dominated remnant vegetation, each less than 5 ha in size. (Fig. One). More detail on the experimental design and treatments are presented in Chapter Two.

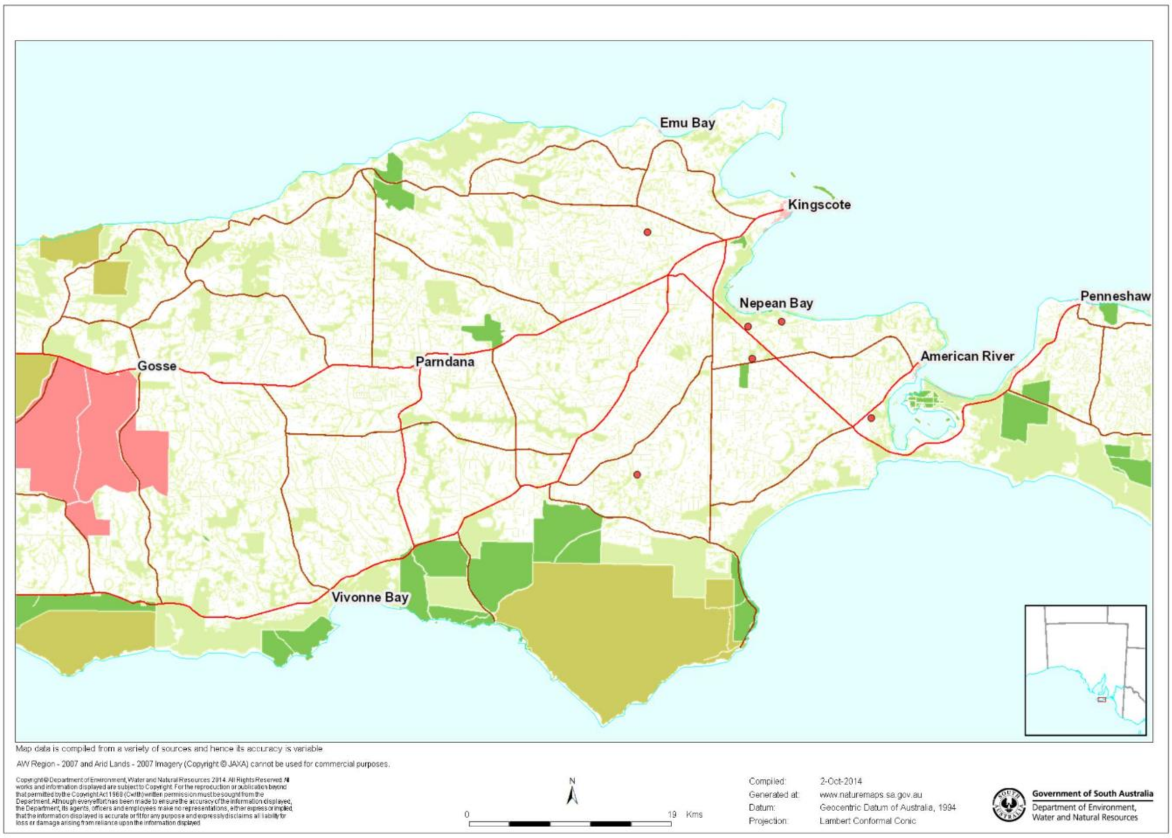

Figure One: Map of Eastern Kangaroo Island showing native vegetation cover, with the six study sites marked with red dots.

Functional guild classification

This study proposes a novel morphological trait classification procedure, termed the Refined Guild System (RGS), with which to describe and classify spider communities. All traits used in the RGS are functional, morphological and measurable on individual specimens and this provides some key advantages over other current guild classification systems used for spiders. By selecting measurable traits, the need for inferences about behaviours drawn from higher level taxonomic classification was removed, thus eliminating a key source of error and also the need to make the higher level classification from which the inferences were drawn. Additionally, all of the traits are distinguishable on mature and immature specimens, meaning that the entire sample may be analysed, not just a subset as is the case when species or morphospecies classifications are employed. This morphological guild approach is accessible to non-skilled technicians and is approximately equivalent in terms of the time and equipment needed to classify individuals to morphospecies. Each of the traits selected is readily measurable using a standard dissecting microscope and graticule.

We selected measurable morphological traits that were associated with a known function (refer to Table One). For the purposes of this study we have classed sexual maturity as a trait. As discussed in the introduction, sexual maturity, causes measurable differences in body morphology, mobility and feeding of some spiders and this has been shown (Main, 2011) to cause a differential effect on survival following fire. As a result mature specimens and immature specimens, which may share the remaining sets of morphological traits, will be categorised in to different guilds. Traits were divided into three broad, and interrelated, groups based on their functionality:

- Traits relating to microhabitat preference. For example the presence of a claw tuft and scopulae, are traits that indicate a decreased likelihood to be a web builder and an increased likelihood of inhabiting vegetation e (Rovner, 1978; Foelix, 2011).
- Traits relating to hunting technique. Traits such as increased eye width to carapace width ratio and a low variance in leg length indicate an increased likelihood of being an active, free running hunter (Foelix, 2011). Traits such as the presence of accessory hairs or the presence of a serrated comb on tarsi four indicate an increased likelihood of web-building (Foelix, 1970; Huber & Fleckenstein, 2008).
- Traits relating to survivorship in the post-burn environment. For example increased sclerotisation (Langlands et al., 2011) and increased body size that reduces the risk of desiccation (Entling et al., 2010), both correlate with increased fire survival.

Trait scoring

Each spider was measured for the functional traits listed in Table One, using a standard dissecting microscope and a graticule. The graticule was not calibrated, however the measurements were taken in order to determine the relative differences between the sizes of morphological structures within each individual spider (for example the ratio of eye width to the carapace width, or the variability in leg lengths of a spider) and not to directly compare the direct measurements *per se* between spiders. The measurements were therefore not absolute, but relative. This level of accuracy was sufficient for the purposes of measuring the traits as it was the intra-spider relative values of morphological traits that was imortant. All measurements were taken whilst the microscope was at full zoom.

Most of the traits are binary in nature (present or absent), however variance in leg length, eye group and carapace length required measurements on a continuous scale. Table One summarises the values used to define each trait type. Equal leg lengths in spiders is often associated with increased running speed and with a terrestrial, mobile existence, whereas spiders with highly variable leg lengths are typically slower moving, web inhabiting spiders (Foelix, 2011). Thus I used variance in leg length as an indication of running speed and habitat type. I measured variance as the length of the shortest leg (in standardised units) divided by the length of the longest leg.

The size of a spider’s eyes may be related to prey capture technique, typically with active hunters having larger eyes than web builders (Foelix, 2011). I measured eye group as the width of the largest of either the anterior or posterior eye row, divided by the width of the carapace, measured across the point at which the largest eye row was located.

The length of the carapace was used as a measure of spider size. Spiders are soft bodied and the abdomens shrink when preserved in ethanol, meaning total spider length of preserved specimen is an unreliable measure of living spider size. The carapace, however, is sclerotized, more stable in size after preservation, and is therefore a better surrogate of the size of living spiders. Carapace length was measured as the longest point between the anterior and posterior central apices of the carapace, when viewed from above.

Once traits had been measured and assessed, spiders were allocated a ‘guild identifier’ code, grouping together all spiders with matching sets of traits. The guild identifier consisted of a letter followed by a number. The letter denoted the life history of the spider, as determined by the trait scores. The earlier in the alphabet, the more likely the spider was to have a nomadic, ground running life history, whereas the later in the alphabet the code letter occurs, the more likely the spider was to be a web spinner. The numeric section of the code denoted the size of the spider, higher numbers denoting larger sizes. This guild identifier code was then used in trait analyses as a surrogate for a taxonomic classification. Guilds of mature spiders had a suffix m attached to their code, (see Table One).

In order to examine the effect of the level of community detail on the fourth corner analyses and compare it to the results of the RGS, we developed a second guild system termed the morphological guild system (MGS). The MGS lessened the complexity of the RGS by reducing the number of guilds and increasing their breadth. This was manipulated via changes to the groupings of the carapace length trait. In the MGS, carapace length was separated in to four broad, discrete categories in to which spiders with the same morphological traits were divided. This resulted in fewer guilds with a larger span. For the RGS, carapace length was treated as a continuous variable and rounded up to the nearest five units (Table One). All spiders that shared traits were placed in the same guild based on these measurements. This resulted in a large number of narrow group-width guilds.

Once spiders were classified as different guilds a group category was added, where all spiders which had the same morphological traits were grouped, irrespective of their size.

Trait	**Scores**	**Function**	**Citation**
Scutes/ sclerotisation	Nominal. *Scute* no, yes	Survivorship. Lowers risk of desiccation.	Whyte & Anderson (2016);(Langlands et al. (2011)
Sexual maturity	Nominal. *Sex.mat*. mat, juv	Survivorship, feeding specialisation, niche preferences.	Main (2001); Framenau (2005); Sanders et al. (2015)
Scopulae	Ordinal. *Scop* no=2, Yes= 1	Microhabitat. Non-web building / hunting spiders. Increases hold on smooth surfaces. Prey capture.	Rovner (1978), Foelix (2011), Lapinski et al. (2015)
Claw tuft	Nominal. *Tuft*. none=3, false tuft=2, true tuft= 1	Microhabitat. Non-web building/ hunting spiders. Increases hold on vegetation.	Rovner (1978); Wolff& Gorb (2015)
Cribellate	Ordinal. *Crib* no=1, yes=2	Hunting technique. Web building. Cribellate silk webs.	Foelix (2011)
Variance in leg length	Ordinal. *Leg*. 0.71-0.90 (low var.) = 1 0.61-0.70 (medium var.)= 2 <0.60 (high var.) = 3	Hunting technique. Equal leg length associated with faster running.	Foelix (2011)
Third claw	Ordinal. *Third.claw*. no=1, Yes=2.	Hunting technique. Used in web spinning.	Foelix (1970)
Serrated comb on tarsi four	Ordinal. *Comb* no=1, yes=2	Hunting technique. Tangle web and sticky silk to wrap prey.	Huber& Fleckenstein (2008)
Carapace length	Ordinal *cara.length*. RGS: Round to nearest 5 units. MGS: 0-15, 16-35, 36-45, 46 +	Survivorship. Decreased desiccation risk with increased body size.	Entling et al. (2010); Foelix (2011)
Eye group. Ratio of width of anterior median eye group: width of carapace.	Ordinal. *Eye*. <0.5 small eyes=2 >0.5 large eyes=1	Hunting technique. Active hunting spiders: large, well developed eyes.	Foelix (2011)
Accessory hairs	Ordinal. *Acc.hairs*. yes=2, no=1	Hunting technique. Serrated hairs used to assist grasping the thread in web spinning.	Foelix (1970); Foelix (2011)

Table One: Morphological and developmental traits, with scores assigned for categorising spiders in to guilds, and the function of the trait.

Statistical analysis

All analyses were conducted in R software language version 3.2.3, (R Core Team, 2015). In order to compare the responses of spider guild assemblages (those that share the same guild identifier code) to burning we conducted non-metric multidimensional scaling (NMDS) ordinations and non-parametric permutational MANOVA using the ‘vegan’ package in the R in order to examine the contribution of burn treatment, time since burn and mean burn temperature. The Bray-Curtis dissimilarity matrix was used with n=9999 permutations.

So as to analyse changes in diversity and richness of guild following burning we calculated Shannon’s Index of diversity and mean richness of the guild assemblages. Following the same methods as in Chapters Two and Four, we used linear mixed models to assess the effects of post-burn variables, using the ‘lme4’ package in R and we compared the results graphically. Time since burn, mean burn temperature and burn treatment were fixed effects, sites were included as random factors. We included all specimens, including rare morphospecies or families in these analyses.

The fourth corner method was used to analyse and quantify the relationships between spider morphological traits and the environmental variables of the sites (Legendre et al., 1997; Dray & Legendre, 2008). This involved the use of three matrices; matrix **L** ($n \times p$) was a matrix of the abundance of p guilds at n localities, matrix **R** ($n \times m$) contained data about m environmental variables and habitat characteristics at each of the n localities, and matrix **Q** ($q \times p$) listed the q functional traits for each of the p guilds. As the guild classifications were created from trait data, we assumed a relationship between matrix L and matrix Q (i.e. the guilds have fixed trait values) and therefore selected permutational model two for analyses (Legendre & Legendre 2012). We conducted fourth corner analyses using the combined permutational model six, as recommended by ter Braak et al. (2012) and Dray and Legendre (2008). In order to control the Type One error rate the data were adjusted using the false discovery rate “fdr” adjustment for multiple comparisons (Benjamini & Hochberg, 1995). Dray (2013) recommended a high number of repetitions (n=49999) be used to maintain enough power in corrected tests for fourth corner permutational method six. However, with this number of permutations the computers available for this study did not have enough memory to compute the calculations. Therefore a lower number of repetitions were used (n=999). To enable a direct comparison of trait presence to be used, rather than abundance of traits, the data was converted to presence-absence. This removed variations in the data caused by differences in the abundances of traits and therefore allowed a more direct analysis of the role of each trait.

For plotting purposes, the relationships between environmental variable and traits were measured using stat D2 (Legendre et al., 1997). This measures the association between the environmental variable and each trait category separately and gives a correlation coefficient to indicate the strength of the association.

The RGS produced a relatively high number of guilds (n=88), and was a complex dataset. In order to further assess the trait- environment relationship we performed the above calculations on a reduced guild dataset, the MGS, which had a lower number of guilds (n=51).

Refer to the Appendix, Tables A2, A3 and A4 for the Q, R and L matrices. This includes a list of spider guild codes and their corresponding traits.

Data manipulations

To minimise stress in NDMS ordinations, all data were transformed using a Wisconsin transformation, the ordinations were conducted in three dimensions and 100 random restarts were performed for each analysis to increase the chance of the algorithm finding a stable solution.

To reduce the risk of obtaining a false positive we removed from analyses any guilds that occurred singly over all survey years. The guilds were assigned an alphanumeric code; a letter (from A-Y), followed by a number (see Trait Scoring for more detail on guild codes).

Results

Spider guilds

Once guilds that occurred on only one occasion over all survey years were removed from analysis this left 1092 specimens from 88RGS guilds and 1052 specimens from 52 MGS guilds.

Fire effects on spider guild composition

NMDS ordinations Envfit and Adonis revealed the composition of the guild community to be significantly affected by burn treatment, (Adonis, $r^2=0.070$, $p=0.0005$), and mean burn temperature (Envfit, $r^2= 0.223$, $p=0.0011$). The community composition of coppiced plots and control plots was most distinct at six months post-burn, however with increasing time since burn this difference reduced, so that by 30 months post-burn coppiced and control communities occupied similar areas on the ordination. At six months post-burn guilds from control plots tended to be grouped towards the bottom left of the ordination, with those from coppiced plots towards the top left. Whilst coppiced and control plots were clearly defined in the ordination, as expected, there was some cross-over in the ordination between communities from coppiced and standing plots (See Fig. Two).

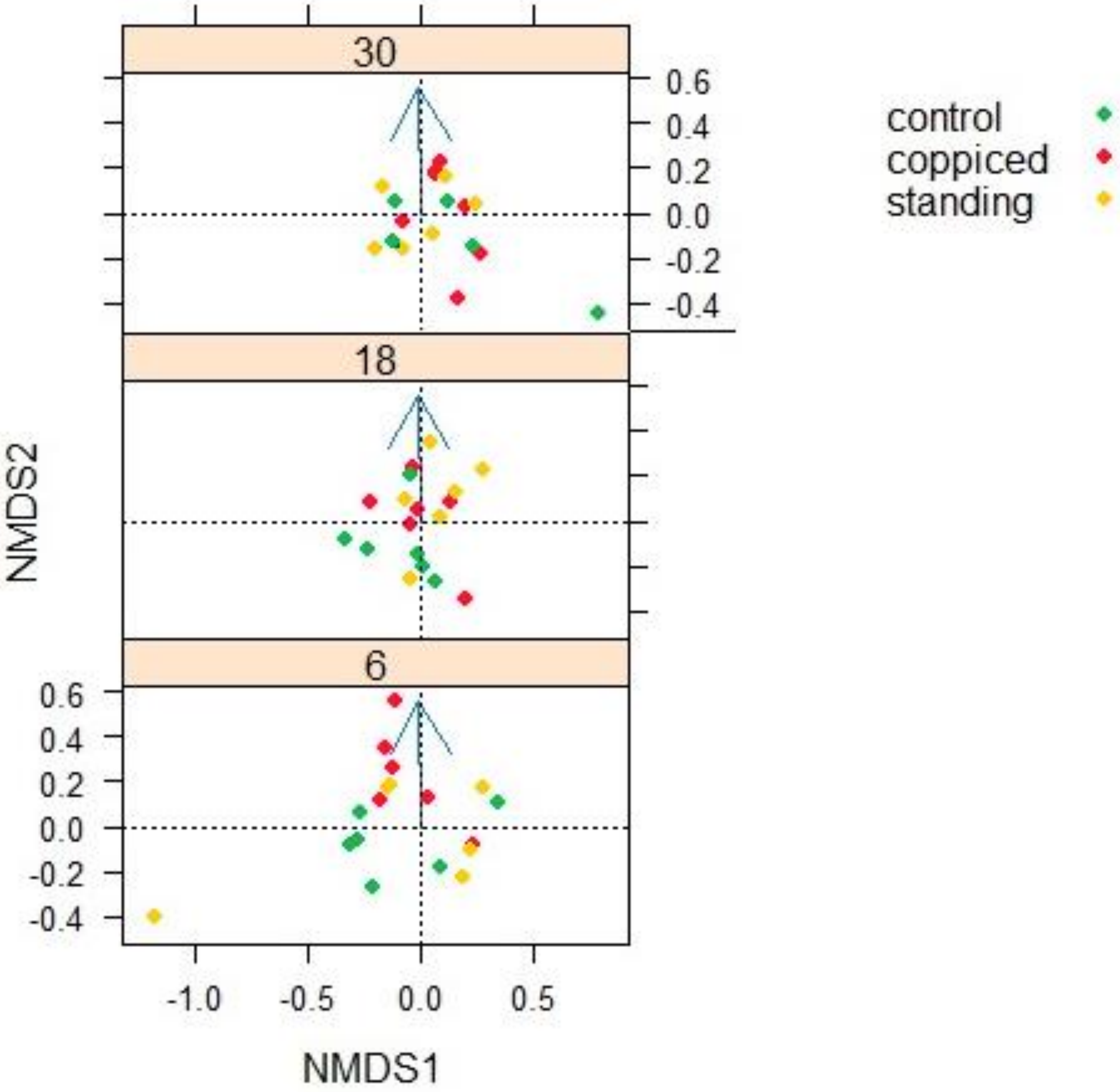

Figure Two: NMDS ordination plot for pitfall-trapped RGS spider guild assemblages, panelled by time since burn (months). Mean burn temperature is denoted by an arrow and vegetation treatment (coppiced vegetation, standing vegetation and unburnt control) by points. Stress= 0.193

In order to illustrate the association of specific guilds with time since burn and burn-treatment a second ordination plot was produced in which guilds were labelled as text. Guild J10 is a guild of small spiders with scutes, which was placed by trait analysis for the RGS into non-web building groups. This guild was associated with coppiced plots and increasing burn temperature, whereas guilds B30 and B25, guilds of medium sized spiders, with false tufts and scopulae, and F80m a guild of very large mature spiders with a ground running tendency, were more highly associated with lower burn temperatures and control plots, (see Fig. Three).

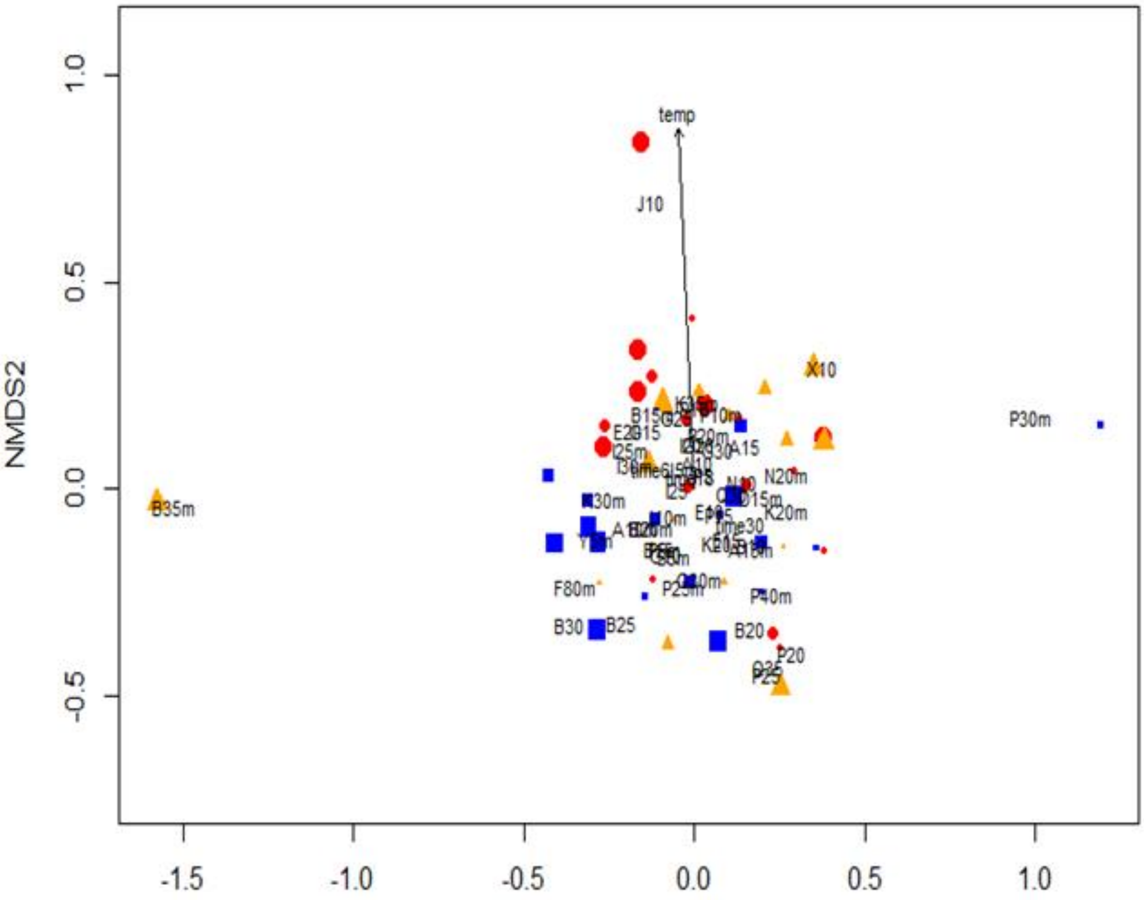

Figure Three: NMDS ordination plot for pitfall-trapped spider guild assemblages, showing the effects of mean burn temperature, time since burn and pre-burn vegetation treatment (coppiced vegetation, vegetation un-manipulated and unburnt control) on community composition. Guilds are marked as text. Blue squares represent control plots, red circles represent coppiced plots, orange triangles represent standing plots. The size of the shape represents time since burn, large - 6 months post-burn, medium - 18 months post-burn, small - 30 months post-burn. Stress= 0.193

Diversity and richness

Linear mixed models were constructed to predict Shannon's Index of guild diversity and richness, as functions of burn treatment, mean burn temperature and time since burn. Burn treatment and time since burn individually did not significantly affect guild diversity; however, the interaction between treatment and time since burn had a significant effect ($\chi^2_{(2)}$ =6.55, p=0.0379). There was no significant effect of treatment, time since burn, or their interaction on guild richness, p>0.05.

Individually mean burn temperature and time since burn did not significantly affect guild diversity; however, the interaction between time since burn and temperature did have a significant effect ($\chi^2_{(1)}$ =6.93, p=0.008). Guild diversity increased with time since burn for plots with a mean soil surface temperature of 200-400 °C, (see Fig. Four). Mean burn temperature, time since burn, and the interaction between the two had no significant effect on the richness of spider guilds, p>0.05.

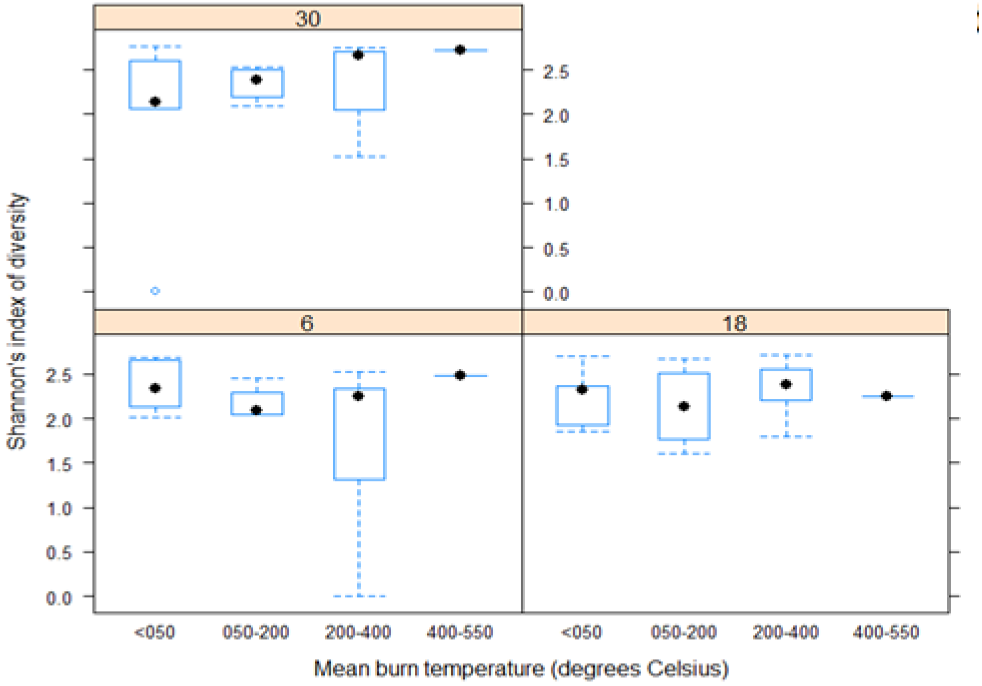

Figure Four: Boxplot illustrating changes in Shannon's diversity with time since burn and mean burn temperature. Time since burn, in months, is indicated at the top of each panel. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

How does trait distribution affect species' responses to environmental variables?

The fourth corner technique was used to assess relationships between environmental variables and spider morphological traits. Due to insufficient computer memory the number of permutations were limited to n=999. The data sets were transformed to presence-absence.

RGS classification

We found no significant effect of environmental variables on traits when using presence-absence data, when the data were adjusted for multiple comparisons using “fdr”, or when no adjustment was employed.

MGS classification

Significant correlations between traits and environmental variables for MGS presence-absence data were identified only when there were no adjustments made for multiple comparisons. False tufts were negatively correlated with mean burn temperature (r=-0.102, p=0.019), and eye size was significantly and positively correlated with time since burn (r=-0.0877, p= 0.034), (see Fig. Five).

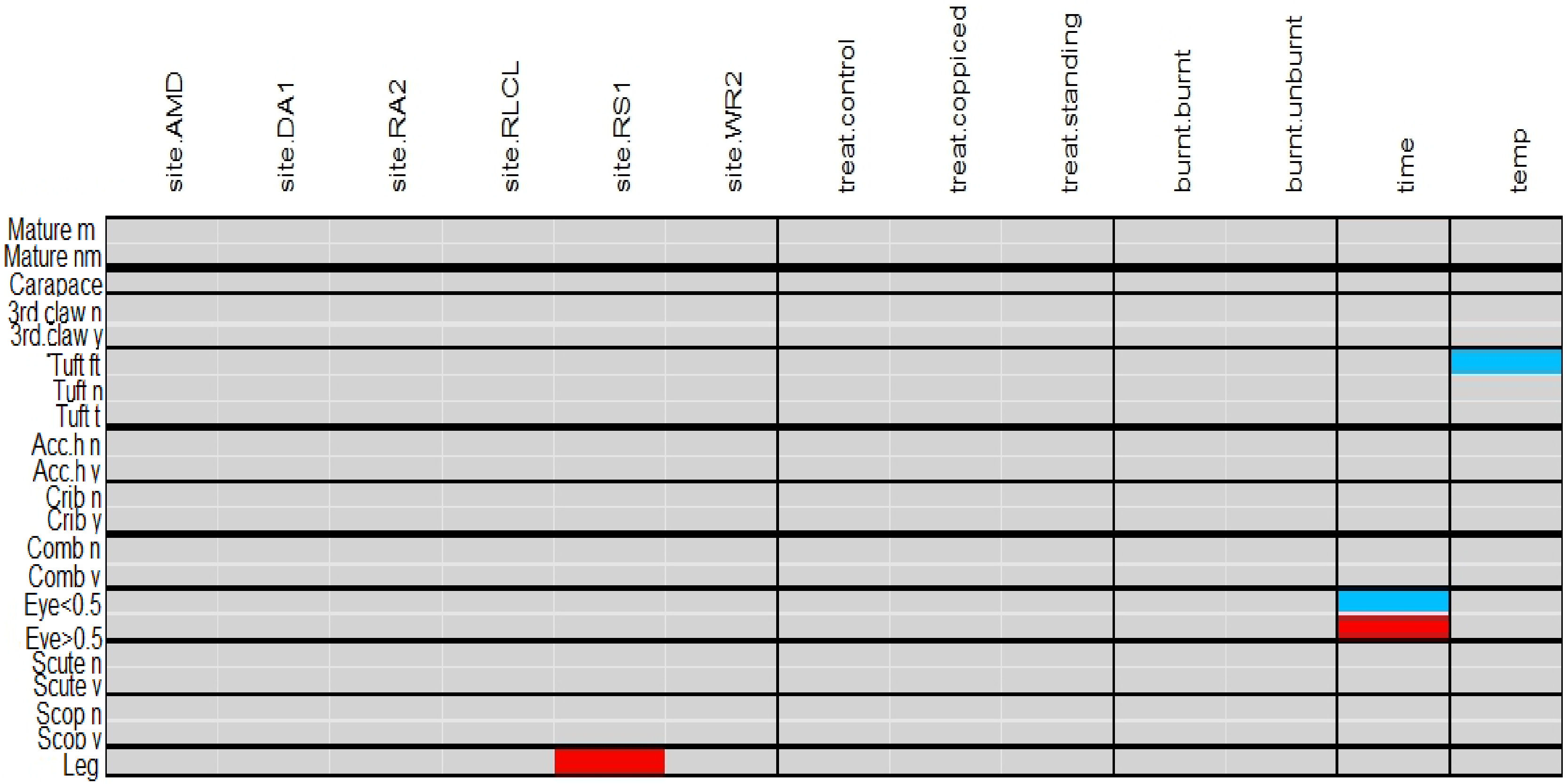

Figure Five: Fourth corner analyses on presence-absence data, using stat =D2, showing relationships between environmental variables and morphological traits of pitfall trap collected spiders, for MGS guilds. Morphological and developmental traits are presented on the Y-axis and environmental variables along the X-axis. For clarity we have only presented the sections of the plot relating to morphological traits. Red shading indicates a significant positive relationship, blue shading a significant negative relationship. Permutational model six was used, with n=999 permutations and no adjustment for multiple comparisons

Discussion

This study investigated the use of a novel, morphological and developmental (in the case of maturity being included as a trait) based functional guild system for measuring and recording ecological change in spider communities exposure to fire. The RGS was developed with key values in mind; that it be quantifiable and replicable, that it should avoid the need for inferences about behavioural or morphological traits drawn from the use of higher level taxonomic data; that it should allow analysis of the entire spider community, male and female and mature and immature specimens, that it should maintain a high level of community detail and that it should not require more time or taxonomic expertise than morphospecies assignations. We found the RGS to meet these key values. The traits selected were measurable and replicable across different species and different spider communities. Spiders were grouped in to guilds based upon these traits, so avoiding the need to make assumptions based upon family level data to assign traits. An important component of the RGS was that it could be applied to mature and immature specimens, male and female. The RGS categorised spiders in to a high number of guilds. This number was greater than the number of morphospecies for the same data due to the fact that 40% of specimens were immature, and therefore could not be included as morphospecies, therefore the dataset for the RGS.

RGS guilds showed changes in community composition, diversity and richness following burning. We recorded significant changes in the composition of the RGS communities in response to mean burn temperature and to burn treatment. The effect of burn treatment was most strongly marked at six months post-burn and this effect reduced with increasing time since burn. This is contrasted with the findings of morphospecies analysis of Chapter Two, where the effect of burn treatment on morphospecies composition was still marked at 18 months post-burn. This may be because morphospecies analysis gives a greater level of resolution, or that the factors acting upon guild communities and morphospecies communities differ. A guild can contain more than one family, and families may be split between guilds, if their functional traits determine it. The changes we recorded following burning might be driven by variables in the initial post-burn ecosystem that favour particular traits, or functional guilds, which are not present with increasing time since burn. We found increased eye size, which determines an active hunting life history, to be correlated with increasing mean burn temperatures. Several spider families have members with large eyes and the

Lycosidae are one of these. Lycosids are active hunters, with large eyes. Mature female lycosids of some species are associated with bare, rocky ground (Framenau, 2005; Aisenberg et al., 2007). As shown in Chapter Two the coppiced plots, where burn temperatures were highest, had a very low level of organic material at six months post-burn, however by 18 months post-burn there was a large amount of vegetation regrowth in these plots. Thus the selection pressures, which might favour these lycoids at six months post-burn would not be present at 18 months post-burn.

Guild J10, a guild of small spiders with abdominal scutes, which were placed by trait analysis into a non-web builders were associated with coppiced plots and increasing burn temperatures. Abdominal scutes serve to reduce the risk of desiccation and in families such as the Oonopidae the scutes contract when humidity is low, so preserving moisture and expand when humidity is high (Whyte & Anderson, 2016). Following coppicing of vegetation and a hot burn there was very little litter or organic material remaining, therefore scutes offer a survival advantage by reducing the risk of desiccation, where shade from the sun was minimal. This finding was not detected during fourth corner analyses, however due to the low number of permutations, the analyses may have had insufficient power. Equally it might be a combination of traits, not just scutes *per* se, that determine the distribution of the guild. Guild diversity was significantly affected by the interactions of burn treatment and mean burn temperature with time since burn and mean burn temperature with time since burn. Diversity was lowest at six months following burning in coppiced plots. Guild diversity increased with time since burn for plots with a mean soil surface burn temperature of 200-400 °C.

We found no significant correlation between environmental variables and morphological guilds when using the RGS system. Subsequently we trialled the reduced guild system, the MGS (morphological guild system). Similarly to the findings for the MGS we found no significant correlations between environmental variables and guilds when adjustments were made for multiple comparisons. However, once this adjustment was removed we found significant correlations between some environmental variables and morphological traits. False tufts decreased with increasing burn temperature. False tufts were often found on vagrant ground runners, such as the Gnaphosidae and some Zoridae and this finding supports those of Chapter Two that gnaphosids and zorids were associated with control plots or standing plots that burnt at lower temperatures. We also found eye size to increase with time since burn, suggesting an increase in active hunters, such as the Lycosidae and the Salticidae.

Individual trait analysis using the fourth corner method of the guild data was problematic. Although the RGS dataset was roughly equivalent in size, in terms of number of categories (i.e. guilds / morphospecies), to that of a community categorised to morphospecies, the dataset was too large and complex to be able to be analysed using a large number of permutations using the computers available for this study. When data were adjusted to control for multiple comparisons we found no significant correlation between environmental variables and traits for either the RGS or MGS classifications. This may be because no correlation existed, or it may be a result of insufficient power, due to the small number of permutations. For example Legendre et al (1997) found that following correction for multiple comparisons they could not detect significant findings using n=999 permutations, but significant findings were detected at n=9999. In their study on trait based analyses, Langlands et al., (2011) did not adjust for multiple comparisons, they did however use n=9999 permutations. It is recommended that this data be further tested on computers capable of processing a large amount of information. The validity of the results of the fourth corner analyses is limited by the probability of an increased Type One error rate due to the removal of the adjustment for multiple comparisons and by a lack of power, due to the restriction in the number permutations able to be processed.

Whilst the RGS offers an important method by which to overcome the impediments to the classification of spider communities, it is associated with some drawbacks, which require further research to overcome. The RGS categorised the community based on a restricted number of traits, where in reality a massive range of traits, both physical and behavioural, are likely to influence the ecology of an individual spider. However, the system was designed as a method to summarise the composition of the spider community, and not to analyse an exhaustive list of traits. The traits that we included were selected on the basis that they conferred a function relating directly to either a web-building or active hunting lifestyle, or that they conferred a survival advantage in the post-burn environment, for example the presence of abdominal scutes reducing the risk of desiccation in the exposed post-burn ecosystem (Langlands et al., 2011).

A potential limitation of this system is the grouping of traits with the assumption that they confer the same function. In most cases a trait can be reasonably assumed to reliably infer a function, for example the presence of accessory hairs, which are associated with web building and which are found on web building spiders (Foelix, 1970, Foelix 2011). However, there are cases where traits are not linked unambiguously to particular functions, or have a general role in many functions. The presence of a third claw is an example of such an occurrence. A third claw is an adaptation to a web-building life and is found on all web-building spiders, it is used during web building to grasp hold of the thread (Foelix 1970, Foelix, 2011). Most hunting spiders have lost the third claw and possess claw tufts or scopulae to allow adhesion to smooth surfaces; however, the Lycosidae (wolf spiders), which are vagrant hunters, have retained the third claw and lack scopulae or tufts. The third claw of the Lycosidae is thought to be a reflection of a web-building ancestry (Jocque, 2005). For the purposes of the RGS, whilst the Lycosidae scored positively for the third claw, so separating them from other hunting spiders, and linking them with web builders, they also scored positively for large eyes, a trait linked to actively hunting spiders (and a trait shared with the Salticidae). Thus, for Lycosidae, the RGS would categorise them as active hunting spiders, despite the third claw, so the guild system remains valid. However, it is possible that there may be other less obvious situations, where spiders that occupy disparate functional niches are grouped together based on similar morphology. As long as this is not a frequent or widespread occurrence, it should not invalidate the application of this method.

The use of the RGS for categorising the spider community requires further testing, using a range of spider communities, ecological systems and different environmental variables and better understanding on how traits should be split. However, the RGS produced an analysis comparable with a taxonomy-based classification and in some cases might have identified further detail. Additionally it takes no longer to classify spiders to guild than it does to morphospecies and it can be conducted by biologists who are not trained taxonomists. The system allows researchers to investigate the responses of guilds *per se* to environmental change, as well the interaction between individual traits and environmental variables. This combination, as a method of analysing the response of the spider community to environmental change, provides a valuable alternative to other common methods by which to analyse spider communities.

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CHAPTER FOUR

How to define a spider community? Comparing the use and limitations of common methods for categorising spider communities in ecological studies.

Abstract

Spiders are important component of ecosystems, however limitations exist to their use in ecological studies. A high number of unidentified species and a paucity in knowledge of the biology of many species has driven the necessity for the use of alternatives to species identification. We used multivariate analyses to compare common method used to categorise spider communities; family, morphospecies and guilds, and to determine whether their use affected patterns in the composition and diversity of spider communities following burning. Data was collected during post-burn surveys of experimental burn sites of fragmented patches of native vegetation. We tested two guild systems, the first had a high level of community detail, with a large number of narrow guilds and a second where community detail was reduced and spiders were categorised into fewer, broad guilds. We further tested whether the exclusion of immature specimens, as required for morphospecies or species categorisations, affected the outcome of analyses. We found morphospecies and the guild system that maintained community detail to be most sensitive to environmental variables, whereas broad guild and family communities were less sensitive. In summary, the exclusion of immature specimens did affect the outcome of analyses. This is an important and interesting finding, which highlights the need for researchers to take in to account the effect the method of categorising spider communities, and the type of spiders included, has on the outcome of analyses. Each of the methods currently available to researchers by which to categorise the spider community is associated with limitations that may affect the interpretation of the results. Further testing is required on the guild system developed in this paper, using a range of spider communities from different habitat types.

Introduction

Ecology is defined as the study of the relations and interactions between flora, fauna and abiotic factors (Dunn, 1986). In order to study these interactions and to model ecological change an ecologist needs to accurately measure communities at the individual, community or landscape level and be able to relate the composition of these communities back to environmental variables and abiotic parameters. In complex and dynamic real-life systems the conclusions drawn from such research are simplified interpretations formed by the analysis of an ecological sample, which acts as a temporal and spatial snapshot of a dynamic ecological community. Whether selected as an indicator to model wider ranging ecological change or out of interest in the particular organism itself, the value of the ecological sample to summarise a population is governed by its ability to be sampled in a manner that is replicable and unbiased and which gives an accurate representation of the population as a whole.

Spiders have many qualities that make them good candidates for measuring ecological change. They are abundant, ubiquitous apex predators that are sensitive to a range of ecological disturbances; such as grazing (Gibson et al., 1992; Bell et al., 2001; Churchill & Ludwig, 2004), logging (Pinzon et al., 2011), fragmentation (Bonte et al., 2003; Marshall et al., 2006), and fire (Langlands et al., 2006; Podgaiski et al., 2013); are sensitive to changes in vegetation structure (McNett & Rypstra, 2000; Jimenez-Valverde & Lobo, 2007) and vary across vegetation type (Hore & Uniyal, 2008; Schaffers et al., 2008)**.** Despite having many qualities that makes them excellent candidates for ecological research, there remain barriers to the effective use and meaningful interpretation of spider community data (New, 1999; Cardoso et al., 2011; Foord et al., 2013).

Species level identification of spiders is plagued by a series of constraints and limitations, particularly in understudied taxa that have a high number of unidentified species. The so-called taxonomic impediment is a problem that faces many invertebrate ecology studies (Cardoso et al., 2011; Fattorini et al., 2012). Difficulties accessing literature, a shortage of people with sufficient taxonomic expertise, and the relatively long time needed to identify species often means that species identification is not feasible. This is particularly the case with Australian spiders where estimations suggest that 75% are unidentified (Raven et al. 2002) and most families of spiders in

Australia are likely to contain many unidentified species (Raven, 1988). Of the identified species, approximately 75% are unrecognisable to most workers due to limited access to scarce literature (Raven, 1988). Additionally, whilst species identification gives the highest level of taxonomic detail, where the biology of the organisms is poorly known it will provide little additional information, compared to a morphospecies approach, other than a name. A further constraint, and one that is particularly applicable to spiders, is the necessity of specimens to be sexually mature for species identification to take place. Thus, even in a known system where every species is identifiable, only a proportion of the population, the mature spiders, will be available to be used in ecological analyses that require identification. This has obvious drawbacks. The sample base from which analyses can be made is restricted and the potential value of the sample as an accurate representation of the population as a whole is reduced. This is particularly true in populations where mature specimens have different ecological requirements to juveniles. Upon reaching sexual maturity spiders often undergo complex changes in morphology, behaviour, habitat preference and prey choice, which leads to divergence in the behavioural and ecological characteristics of the spider. As discussed in the Introduction to Chapter Three of this thesis, Female spiders typically remain sedentary, whereas male spiders may cease eating and become nomadic, showing a marked increase in mobility as they roam in search of mates (Framenau, 2005; Foelix, 2011). During the penultimate moult, morphological differences between male and female spiders become apparent. Male wandering spiders are often smaller-bodied, with longer legs, whereas male web building spiders are often significantly smaller than mature females (Grossi & Canals, 2015). Habitat preference and prey choice of each sex and of adults and juveniles may differ (Kronk & Riechert, 1979; Framenau, 2005; Aisenberg et al., 2007; Sanders et al., 2015), and these differences have been linked to differences in post-fire survival (Main, 2001).

Bias in the population sample may be amplified when using activity-based trapping methods, such as pitfall trapping, where the probability of capture of active, mobile individuals, such as nomadic males, is greater than that of more sedentary individuals, such as females (Topping & Sunderland, 1992). This may create problems in interpretation of sample data because drivers of habitat preference, such as prey availability or adequate web-building locations, may be of lesser importance to nomadic males. Thus, any measures that over-catch mature males can lead to a significant underestimate of the response of the spider community as a whole to habitat change.

Any over-representation of one particular group, with its own unique habitat and ecological requirements, effectively reduces the value of the sample for measuring the actual effects of ecological change or disturbance on the spider community as a whole.

Various methods are used in the literature to overcome the taxonomic impediment, each with associated benefits and downsides. Higher level taxonomic classifications, such as to order (Andersen & Muller, 2000; Collett, 2003; Vasconcelos et al., 2009; Jacobs et al., 2015) or to family (Brennan et al., 2006; Underwood & Quinn, 2010), are widely used as discrete taxonomic units for analysis when measuring the response of the spider community to burning. Higher level surrogates avoid many of the impediments associated with species level identification. They are relatively rapid, require less specialised taxonomic expertise and do not rely on mature specimens (New, 1999). However, higher level surrogates effectively simplify ecological data and may fail to reflect changes in the spider community following disturbance that are evident at a finer level of taxonomic resolution (Podgaiski et al., 2013; Timms et al., 2013). This is especially true for large, diverse families that have a broad intra-family niche span and show a range of sensitivities or tolerances to disturbance, and for families that contain invasive or abundant, disturbance-tolerant exotic species. In reality it makes little ecological sense to group all spiders from such large families into one single ecological unit or community, and higher taxa have been found to be poor indicators of species level changes in non-spider invertebrates (Rosser & Eggleton, 2012; Heino, 2014). A perhaps more reliable approach is the use of selected families, whose ecology is better known, as indicators for the rest of the spider community. Studies suggest a two family indicator group may be a good surrogate for species richness; Foord et al. (2013) found Salticidae and Thomisidae to be good estimators of total community species richness in the Savanna biome in South Africa and Cardoso et al. (2004) found Gnaphosidae and Theridiidae to be good indicators in Portugal. However, as illustrated by the selection of four different families as indicators in the examples above, the likelihood of the same families being good indicators of spider species richness across a broad range of geographic locations, ecosystems and habitat types is perhaps small. Generic classification of spiders has been identified as the most reliable higher taxon surrogate for species when analysing richness (Cardoso et al., 2004; Kallimanis et al., 2012; Foord et al., 2013); however, generic identification is associated with many of the same taxonomic impediments as species level identification, requiring time and taxonomic expertise (Foord et al., 2013).

The use of morphospecies has been considered to be a reliable surrogate for alpha diversity (species richness) and beta diversity (species turnover) of the spider community (Oliver & Beattie, 1996). Morphospecies preserve the fine community detail offered by species level analysis, whilst allowing rapid assessment of specimens by non-taxonomists. However, whilst being potentially valuable tools to ecologists, morphospecies are associated with some limitations. Morphospecies can only be assigned to mature spiders, which as discussed above limits the sample size and potentially could lead to erroneous assessment of community dynamics. When categorisation is conducted by non- experts, studies have found high rates of error from grouping, where more than one species is erroneously assigned to one morphospecies, and from splitting, where a species is erroneously split in to more than one morphospecies (Derraik et al., 2002). This error rate is difficult to predict, and therefore to control and test for, as it depends not only on the taxonomic group being sorted, but also on the sample itself and the person doing the sorting (Krell, 2004). In addition, as morphospecies are not formally described and the sorting criteria are often not identified, it is difficult to have controls in place to check the validity of assignations (Krell, 2004). Due to a paucity of knowledge about many spider communities, the high level of unidentified species and frequent sexual dimorphism, it is often not possible to assign males and females of the same species to a single morphospecies. A review of the literature found two primary methods by which this constraint was dealt with; firstly, by restricting the sample base to only one sex (Langlands et al. 2011) and secondly, by treating males and females as separate morphospecies (as used by Katayama et al., 2015 and in Chapter Two of this thesis). Both methods have limitations. The first method restricts the sample to one sex, which as discussed above limits the ability of the findings to apply only to a sub-section of the community. The second method may artificially inflate estimates of morphospecies diversity, richness and abundance.

The use of functional guilds based upon morphological and behavioural traits is an alternative approach that is gaining standing in the literature. The criteria for selecting traits and guilds with which to categorise the spider community varies between studies; however, most guild classification systems use information relating to the niche a spider occupies within an ecosystem and the foraging technique by which the spider captures prey (Uetz et al. 1999). Most studies use a combination of morphological data combined with inferred behavioural traits; these inferences are usually made using data from higher level taxonomic identifications (Post & Riechert, 1977; Langlands et al., 2011; Podgaiski et al., 2013). Such inferences are generalisations and are inherently crude. This is especially the case where life history and ecological data is not well understood or where the families on which the inferences are based are large and ecologically diverse. Guild systems that rely on information derived from taxonomic detail to assign trait characteristics face similar constraints to their application as the purely taxonomic approaches, namely a paucity of taxonomic information, a large number of unidentified species and an inability to reliably match mature females, males and juveniles of the same species. There is currently no ideal solution to this problem. One method to overcome it, is to restrict analyses to only one sex. This was used by Langlands et al. (2011) in their study trialling the use of traits to predict the post-fire response of spiders in Australia. This, therefore restricted the ability of the findings of the study to be applied to the entire spider community.

The guild system developed in Chapter Three was designed to address many of these impediments to the use of spiders in ecological research. I developed a rapid classification system for spiders that allows the inclusion of mature and juvenile specimens, and that is based upon measurable morphological traits, thus avoiding assumptions based on higher level taxonomic data.

Impediments to the use of spiders in ecological research are applicable to many, if not all, ecological studies involving spiders and present researchers with a quandary; use species/ morphospecies level identification and only utilise a (sometimes small) proportion of the spider community, or use higher level taxonomic classification or guilds based on inferences taken from family level data, which allow analysis of the entire population, but with the loss of biological, ecological and taxonomic detail. However, the ecological importance of spiders, and their apparent sensitivity to ecological disturbances drive the necessity for an alternative approach. The wide variety of methods used in the literature to overcome these taxonomic limitations is large and this in itself has created a lack of standardisation of techniques and makes comparing the results of different studies difficult (Cardoso et al., 2011).

This chapter investigates the current limitations associated with the use of spider data in ecological surveys and provides recommendations for improving the efficacy of spider samples to more accurately represent populations. We investigate whether such limitations influence the interpretation of ecological data and the conclusions drawn from it. In investigating these questions this paper aims to increases the usefulness and accuracy of the interpretations of spider data in ecological studies and to suggest alternative methods with which to more accurately classify the spider community. The novel morphological guild system (RGS) developed in Chapter Three was based upon measurable morphological traits and was designed to be quantitative and replicable and to preserve the taxonomic detail of morphospecies / species level categorisations, whilst allowing analysis of the entire sample. Whilst the RGS could be used for NMDS ordinations and diversity analyses, it was too complex for fourth corner analyses. We therefore trialled a second guild system, the MGS, where the spider community was categorised in to a smaller number of broader guilds, so reducing the complexity of the community. We found that fourth corner analyses were better performed on the MGS.

In this chapter we tested how categorising the spider community into families, morphospecies (and so excluding immature specimens), or by using the RGS or MGS classifications developed in Chapter Three, affected the interpretation of how the spider community responds to fire. We investigated whether the increased level of community detail of the RGS, created by the use of a larger number of more refined guilds, gives a more sensitive reading of changes in the spider community compared to the MGS. A second aim of this paper was to assess whether the removal of mature specimens, as is required for morphospecies and species categorisation of the spider community, affected the conclusions drawn from analyses of community responses to burning.

We hypothesised that the practical limitations associated with family and morphospecies approaches, namely the loss of ecological detail when using family level surrogates and the restriction to only mature specimens for morphospecies, would affect the interpretation of spider community data. Due to their broad nature, we predicted that analyses of family categorisations would be less sensitive to patterns of community change, when compared to morphospecies and guild categorisations. In contrast, we hypothesised that the greater ecological sensitivity of the RGS and its basis on measurable morphological traits, would allow it to detect a greater number of changes in the post-burn spider community. We also predicted that the level of community detail embodied in the RGS would allow a greater number of changes in the spider community to be detected compared to the MGS. We hypothesised that due to the morphological, ecological and behavioural differences shown between mature and immature spiders, there would be differences in the measurable responses of the spider community when all specimens are included in analyses compared to when only mature or immature individuals are included.

Methods

This study utilises data from Chapter Two on pitfall-trapped spiders from 6 of the 13 burn sites. These were the same sites and specimens used for analyses in Chapter Three. All sites are located on eastern Kangaroo Island, South Australia and are small fragments of *Eucalyptus cneorifolia* dominated remnant vegetation, each site being less than 5 ha in size. The six sites used in this chapter were AMD, DA1, RA2, RLCL, RS1, WR2. These sites were selected on the basis that they were all burnt in spring 2009, thus removing year of burn as a variable (some of the sites from Chapter Two were burnt in 2009 and some in 2010). One site that was burnt in 2009, site TH5, was selected at random to be excluded from these analyses due to time constraints.

As for Chapter Three, this chapter uses data from surveys conducted at 6 months, 18 months and 30 months post-burn. Within each of the six sites, there were three treatment plots; a coppiced plot where vegetation was coppiced prior to burning, a standing plot where vegetation was un-manipulated prior to burning and a no-burn control plot. This resulted in a total of 54 plot samples used in analyses. In Chapter Two, in order to prevent confounding effects due to uneven numbers of pre and post-burn surveys, the 30 months post-burn surveys were excluded from analyses.

In the first section of this chapter we compare the outcomes of the analyses of the spider community categorised using the MGS and RGS (developed in Chapter Three), with the results from morphospecies and family level categorisations of the same dataset. By doing this we will investigate the efficacy of common methods of categorising the spider community for interpreting ecological changes. In addition, we compare the results of the fine level of community detail of the RGS with the less detailed MGS. Where comparison of plots involve figures from Chapter Three, the relevant figures will be duplicated in this chapter for ease of comparison. An acknowledgement will be made where this is the case.

The third section of this chapter compares the results of community analyses when all specimens are included in analyses to those when only mature specimens are included.

Spider identification and trait classification

All spiders were identified to family using Raven et al. (2002). Mature specimens were assigned to morphospecies. As morphospecies assignations could only be conducted on mature specimens, only 44% of the specimens collected were able to be categorised into morphospecies. Due to frequent sexual dimorphism and a paucity of taxonomic knowledge of the spider communities on Kangaroo Island, it is currently not possible to identify the majority of male and female spiders of the same species as belonging to the same species, therefore in this study male and female spiders were classified as separate morphospecies. Refer to Appendix, Table A1 for a list of families, morphospecies and the abbreviations and codes used for each.

This study assessed and compared the responses of morphospecies, family, MGS and RGS guild assemblages to burn treatment (coppiced vegetation followed by burning, vegetation left standing followed by burning, and unburnt control) and mean burn temperature.

Statistical analyses

In order to compare the responses of spider morphospecies, family, MGS and RGS assemblages to burning we conducted NMDS ordinations followed by vector fitting of environmental variables using Envfit and permutational MANOVAs using Adonis and in R, version 3.2.3 (R Core Team, 2015) to quantify the effects of burn treatment, time since burn and mean burn temperature. Procrustean superimposition analyses were conducted to graphically assess the similarity of the results of the ordinations of the spider communities, followed by the ‘Protest’ test in R, a permutational approach to determine whether the similarities of the ordinations were statistically significant.

To further analyse how diversity and richness of family, guild and morphospecies changed after burning, we constructed linear mixed models to assess changes in Shannon’s Index of diversity for each of the categorisation methods. The results were compared graphically to assess similarities, or differences in responses between each of the categorisation methods. Time since burn, mean burn temperature and burn treatment were fixed effects, sites were included as random factors. All specimens, including rare morphospecies or families were included in the analyses.

Comparisons of morphospecies, family MGS and RGS assemblages using Protest require matrices to have equal row numbers. Zero rows, where zero specimens were collected for an entire plot, occurred in the morphospecies dataset and for a subset of the RGS dataset where only mature specimens were included in analyses. Thus to equalize row numbers across the matrices of the different assemblages, a ‘pseudo-species’ column was added to the original morphospecies abundance dataset and to the RGS dataset when only mature specimens were used in analyses. This effectively added a value of one for all sites (Clarke et al., 2006), and so allowed all sites to be directly compared and used in the procrustean superimposition. This pseudo-species column was not used for the linear mixed model analyses of Shannon’s index of diversity or richness.

To test the hypothesis that the exclusion of non-mature specimens, as required by species and morphospecies analyses, results in inaccuracies in interpretations of ecological data we used RGS community data and conducted procrustean superimposition analysis, followed by the Protest test of significance, as well as linear mixed models to compare changes in diversity and richness.

Results

Environmental variables

As expected, there was a direct relationship between mean temperature at the soil surface during a burn and burn treatment. The soil surface temperature during burning was higher in coppiced plots than standing plots, and lowest in control plots (See Chap. One - Results - Fig. Three).

Datasets

A total of 1136 spider specimens were used in these analyses, comprising 32 families, 98 morphospecies, 66 MGS guilds and 99 RGS guilds. Singleton morphospecies, families or MGS and RGS guilds (those that were only represented by a single individual over the entire survey period) were removed from analyses. This left 1123 specimens from 25 families available for family analysis, 1096 specimens from 51 MGS guilds, and 1112 specimens from 88 RGS guilds to analyse. Of the 1136 specimens collected, 44% were sexually mature and therefore only this number was available for analyses of morphospecies; once rare morphospecies had been removed this left 454 specimens from 44 morphospecies available for analysis.

Prior to the removal of rare morphospecies and prior to the addition of the pseudo-morphospecies column, the morphospecies data matrix had one row where zero specimens were collected from a plot in a particular survey year. Each row in the dataset corresponds to a specific survey, collected from a treatment plot, at a site, in a particular survey year (for example site: AMD, treatment plot: coppiced, survey year: 2012). Once rare morphospecies were removed, the data set contained three empty rows, effectively resulting in a total of 51 out of a potential 54 plots being available for analysis. There were no empty rows in the family or guild data matrices.

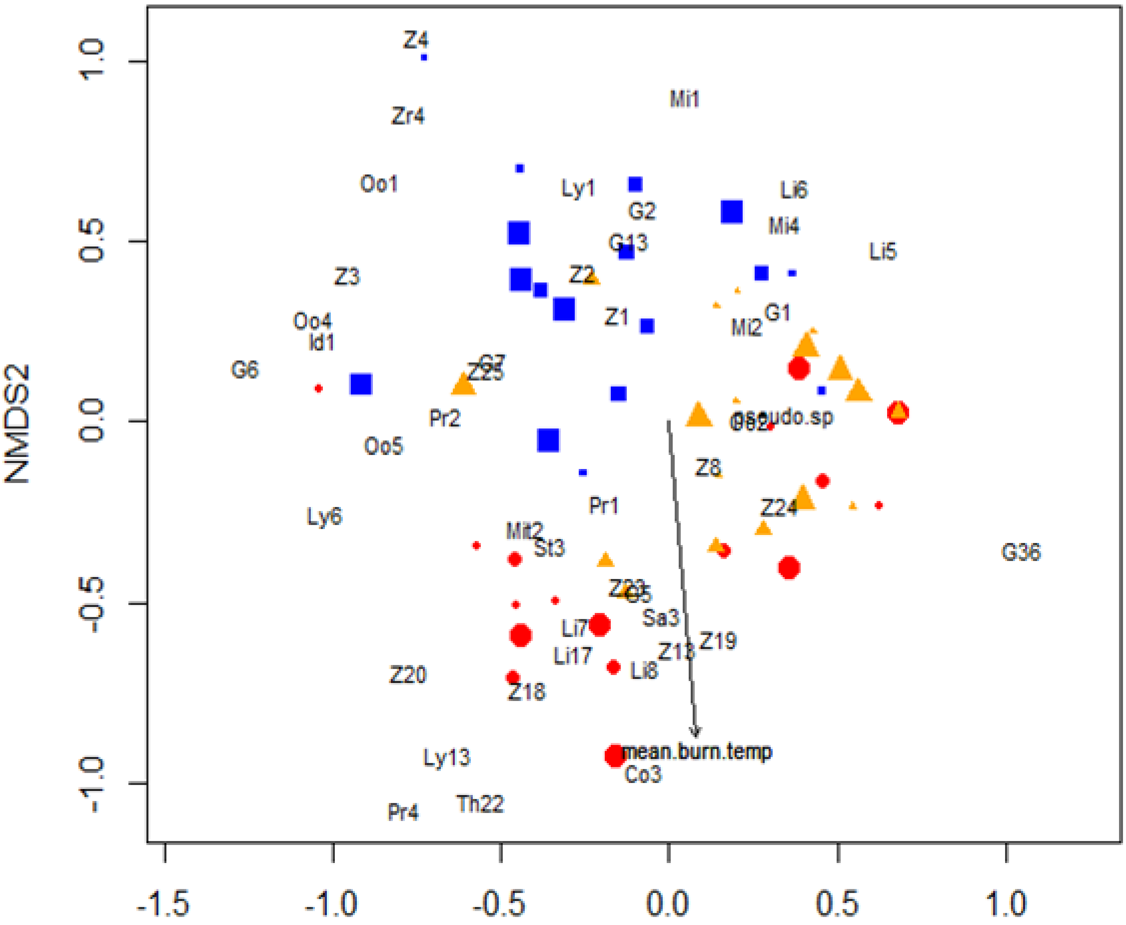
Patterns of response of morphospecies, family, RGS and MGS guild assemblages

To investigate whether there were common patterns of response between morphospecies, guild and family community assemblages to mean burn temperature and burn treatment, we first tested for an effect of burnt treatment and mean burn temperature on the diversity and composition of each assemblage and then directly compared the congruence of the composition of each assemblage. We conducted NMDS ordinations to assess the effect of burn treatment and mean burn temperature on the composition of the four assemblages. We found significant changes to the composition of the morphospecies community with mean burn temperature (Envfit, r^2=0.468, p=0.0001) and with burn treatment (ADONIS, r^2= 0.101, p=0.0001). (See Fig. One). Control plots were clearly grouped in the top left of the ordination, coppiced plots towards the lower half of the ordination and standing plots occupied the middle of the ordination.

RGS guild community composition was also significantly affected by mean burn temperature (Envfit, r^2= 0.177, p=0.0055) and burn treatment, (Adonis, r^2=0.0680, p=0.0005). The separation of the treatments was not as distinct as for the morphospecies communities, although coppiced plots occupied the upper right of the ordination and control plots the lower right, (see Fig. Two).

Our analyses revealed a significant effect of mean burn temperature on MGS guild community composition (Envfit, r^2=0.1194, p=0.0383), but we found no significant effects of burn treatment or time since burn, $p>0.05$. (See Fig. Three).

NMDS revealed a significant effect of mean burn temperature on family community composition, (Envfit, r^2=0.1178, p=0.034), however neither burn treatment nor time since burn had a significant effect, $p>0.05$. Stress = 0.193. No visible patterns in burn treatment could be detected on inspection of the ordination plot. (See Fig. Four).



Figure

Figure One: NMDS ordination plots for morphospecies assemblages of pitfall trapped spiders, showing the effects of mean burn temperature and pre-burn vegetation treatment on morphospecies community composition. Morphospecies are indicated in text- see Appendix, Table A1 for a list of abbreviations used for morphospecies. Blue squares represent control plots, red circles represent coppiced plots, and orange triangles represent standing plots. The size of the symbols is inversely proportional to time since burn: large - 6 months post-burn, medium - 18 months post-burn, small - 30 months post-burn. Stress = 0.182

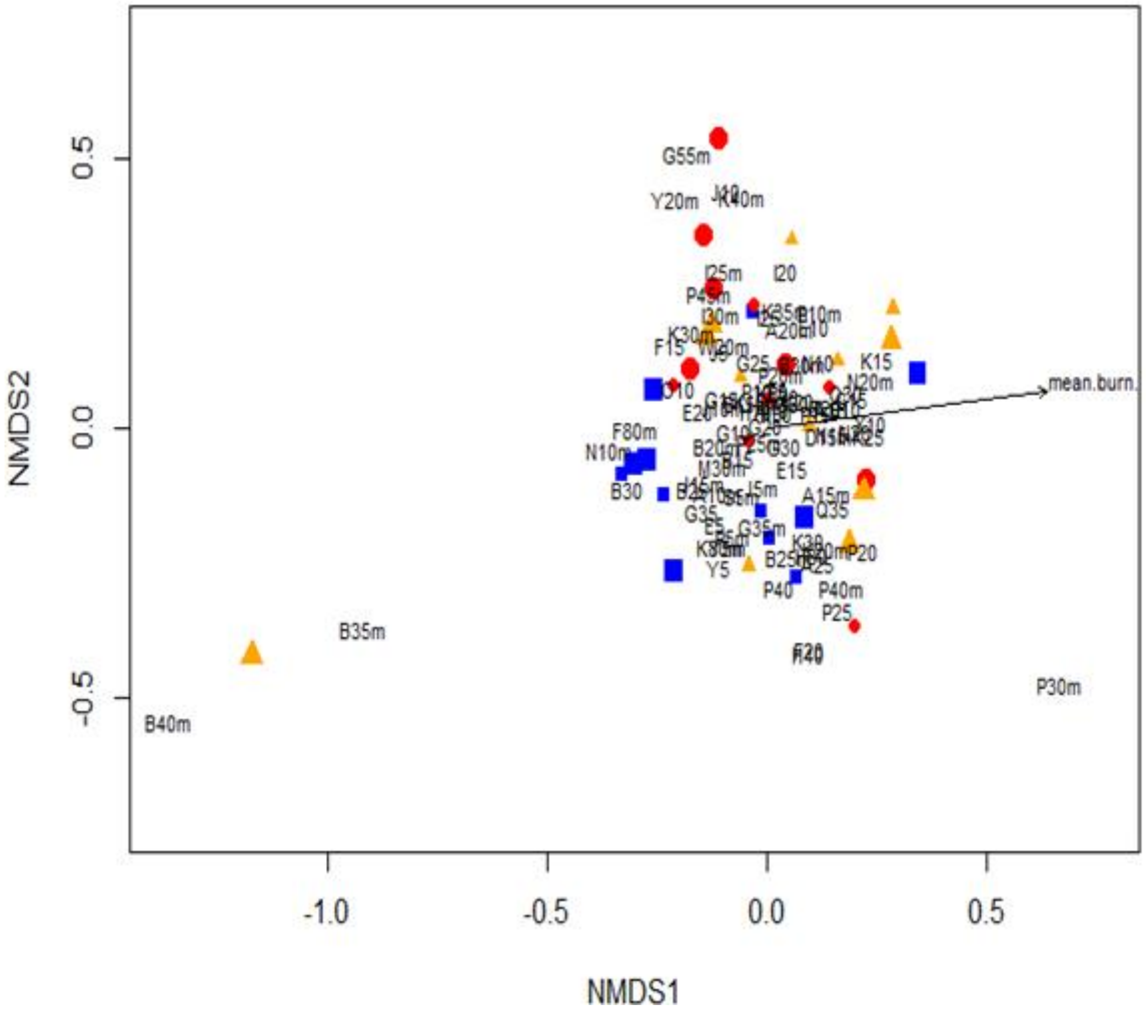


Figure Two: NMDS ordination plot for RGS guild assemblages of pitfall trapped spiders RGS, showing the effects of mean burn temperature, time since burn and pre-burn vegetation treatment on community composition. Guilds are indicated in text. See Appendix, Table A2 for list of guild abbreviations used, and their corresponding traits. Blue squares represent control plots, red circles represent coppiced plots, and orange triangles represent standing plots. The size of the symbols is inversely proportionate to time since burn, large -6 months post-burn, medium -18 months post-burn, small -30 months post-burn. Stress = 0.195. This figure is repeated from Chapter Three.

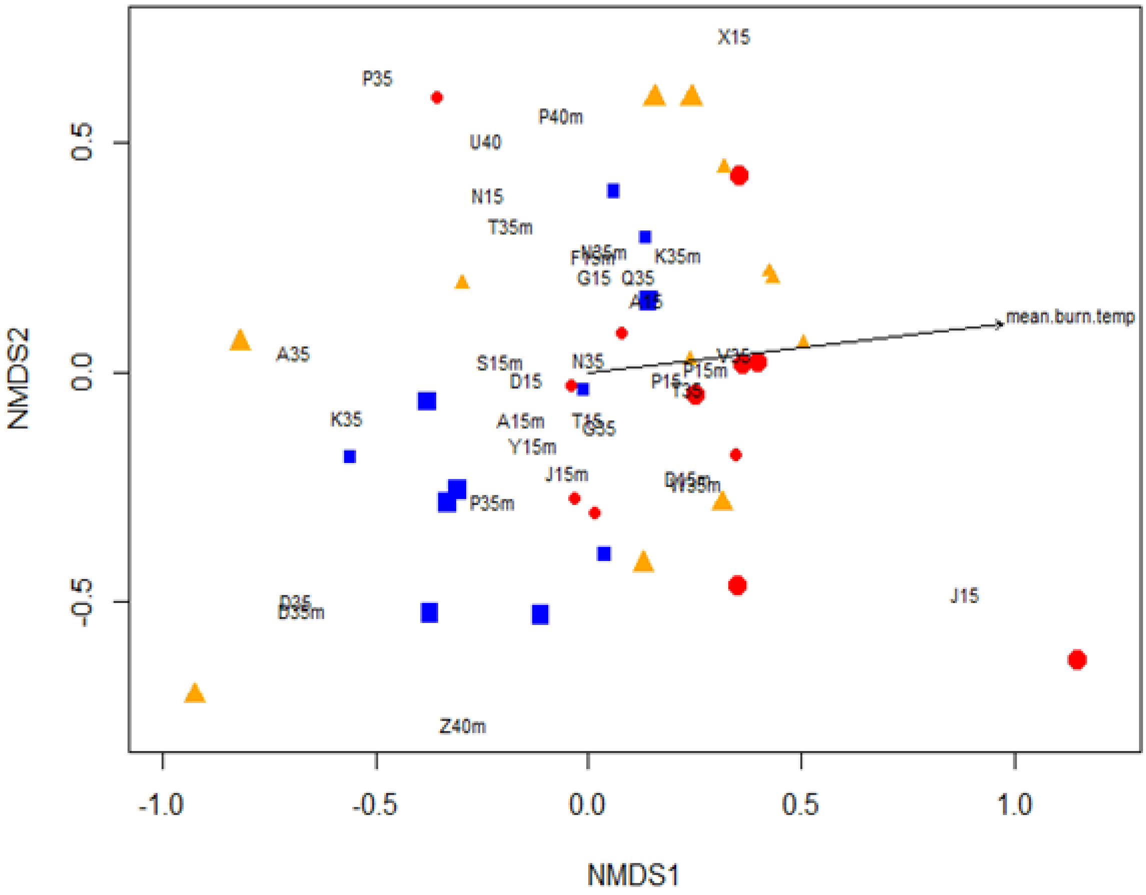


Figure Three: NMDS ordination plot for MGS guild assemblages of pitfall trapped spiders, showing the effects of mean burn temperature, time since burn and pre-burn vegetation treatment on community composition. Guilds are indicated in text. See Appendix, Table A2 for a list of guild abbreviations used and their corresponding traits. Blue squares represent control plots, red circles represent coppiced plots, and orange triangles represent standing plots. The size of the symbols is inversely proportionate to time since burn, large -6 months post-burn, medium -18 months post-burn, small -30 months post-burn. Stress =0.204.

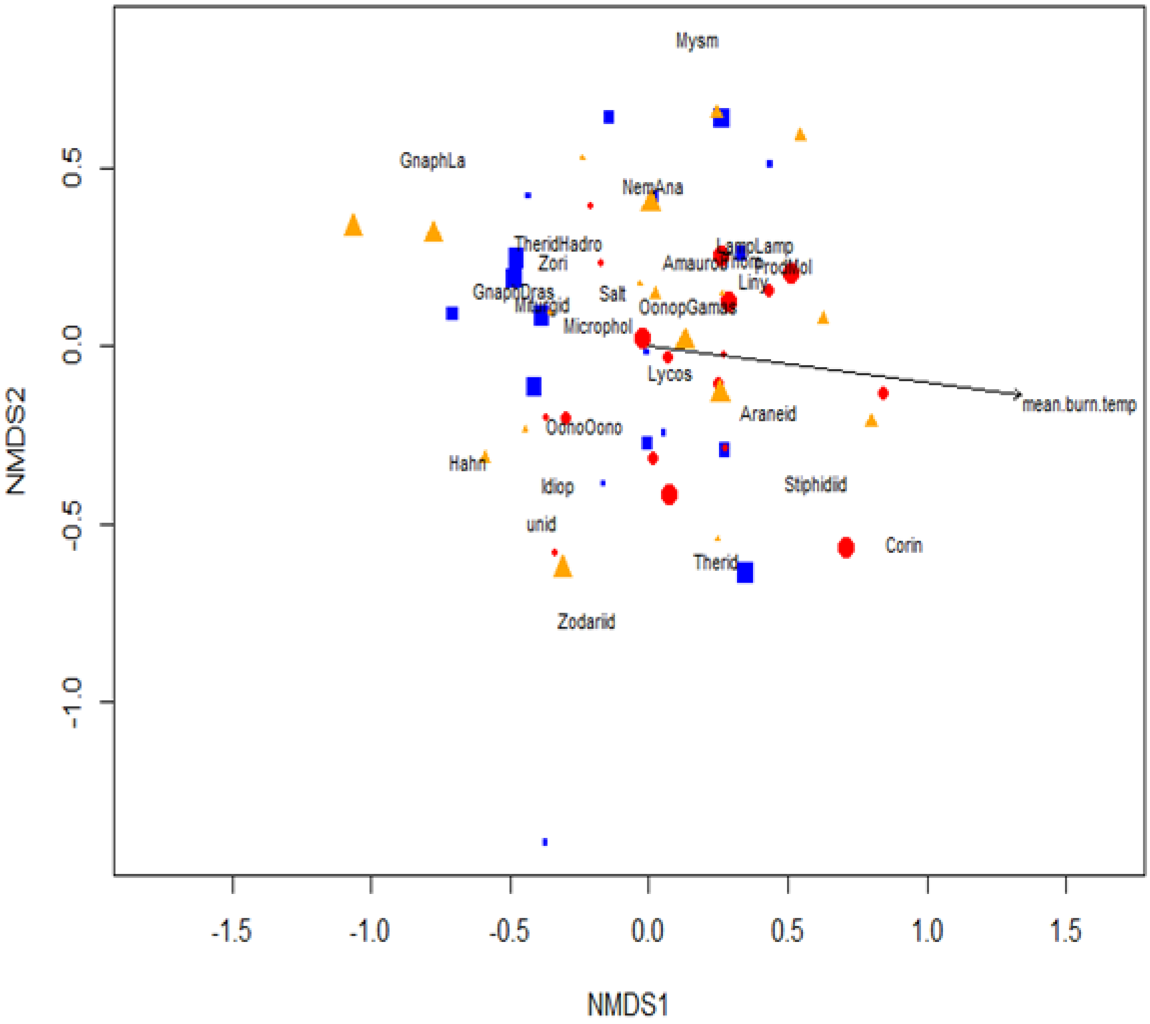


Figure Four: NMDS ordination plot for family assemblages of pitfall trapped spiders, showing the effects of mean burn temperature, time since burn and pre-burn vegetation treatment on community composition. Families are indicated in text. See Appendix, Table A1 for abbreviations of family names. Blue squares represent control plots, red circles represent coppiced plots, and orange triangles represent standing plots. The size of the symbols is proportionate to time since burn, large -6 months post-burn, medium -18 months post-burn, small -30 months post-burn.

We measured concordance between the NMDS ordinations of the distributions of pitfall-trapped morphospecies, families and guilds using the routine Protest in the ‘vegan’ package of R . This analysis found significant concordance between the NMDS ordinations of the RGS guild and morphospecies matrices (Protest, SS=0.845, r=0.393, p=0.0001) and between RGS guild and family ordination matrices (Protest, SS=0.798, r=0.450, p=0.0001). However the NMDS ordinations of the morphospecies and family matrices were not concordant. We found the ordinations of the RGS and MGS guild communities to be significantly concordant (Protest, SS=0.7, r=0.5478, p=0.0001), those of the MGS and family communities to be significantly concordant (Protest, SS=0.5885, r=0.6415, p=0.0001) and significant concordance between the ordinations of the MGS guild and morphospecies communities (Protest, SS=0.7025, r=0.5454, p=0.0001).

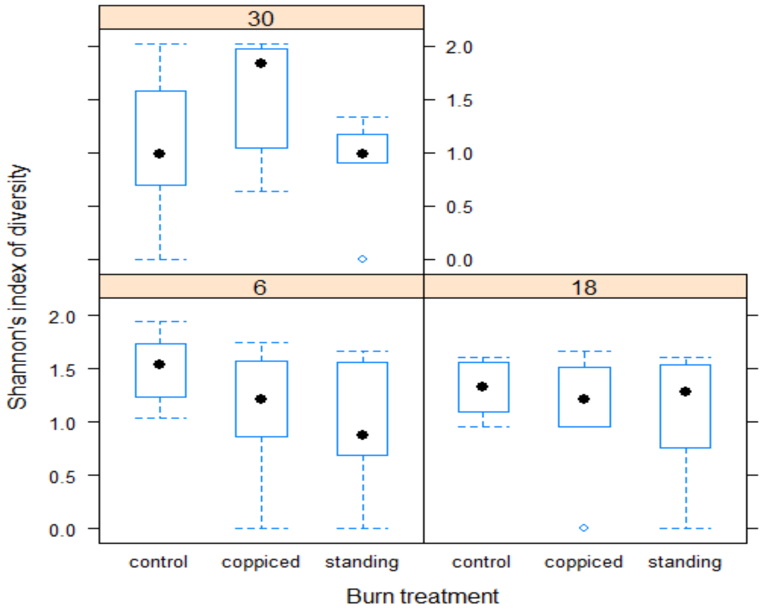
Linear mixed models were constructed to predict Shannon's index of morphospecies, guild and family diversity, and richness, as functions of burn treatment, mean burn temperature and time since burn. This revealed a significant effect of burn treatment and time since burn on Shannon's index of diversity for morphospecies (χ^2 (5) =12.06, p=0.0340), and a significant interaction between time since burn and burn treatment (χ^2 (2) =6.935, p=0.0312). Morphospecies diversity was significantly lower for coppiced plots and standing plots than for control plots. The location of the significant interaction was in the coppiced plots, morphospecies diversity increasing with time since burn (see Fig. Five-a). Morphospecies richness followed a similar pattern as for diversity, with a significant effect of burn treatment and time since burn on morphospecies richness (χ^2 (5) =12.51, p=0.0284).

There was no significant effect of burn treatment, time since burn, or their interaction on the diversity or richness of spider families, p>0.05.

Burn treatment and time since burn did not significantly affect RGS guild diversity, p>0.05, however the interaction between treatment and time since burn did have a significant effect (χ^2 (2) =6.547, p=0.0379). The pattern of response of RGS guild diversity was similar to that of morphospecies, the significant interaction occurred in coppiced plots, with diversity increasing with time since burn. There was no significant effect of treatment, time since burn, or their interaction on RGS guild richness, P>0.05. (See Fig. Five- b).

We found no significant effect of treatment or time since burn on MGS guild diversity, or richness, p>0.05.

a) Shannon's diversity of spider morphospecies



b) Shannon's diversity of RGS spider guilds

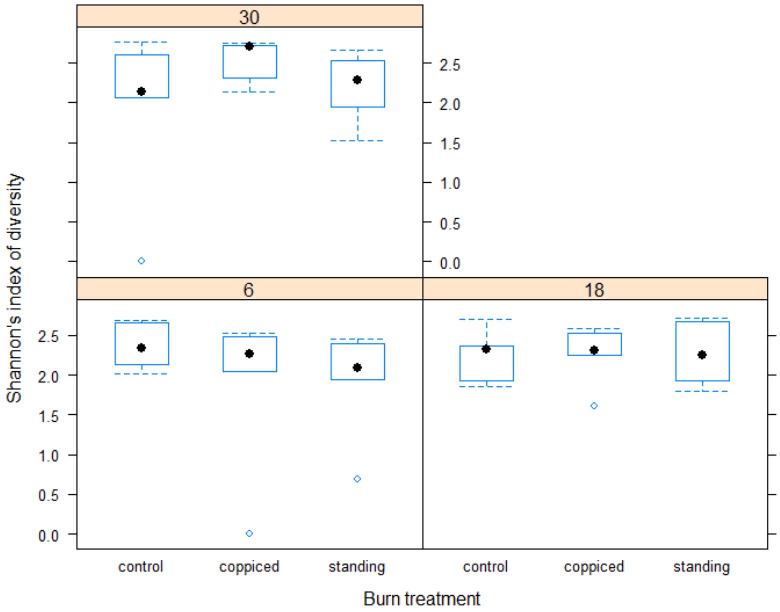
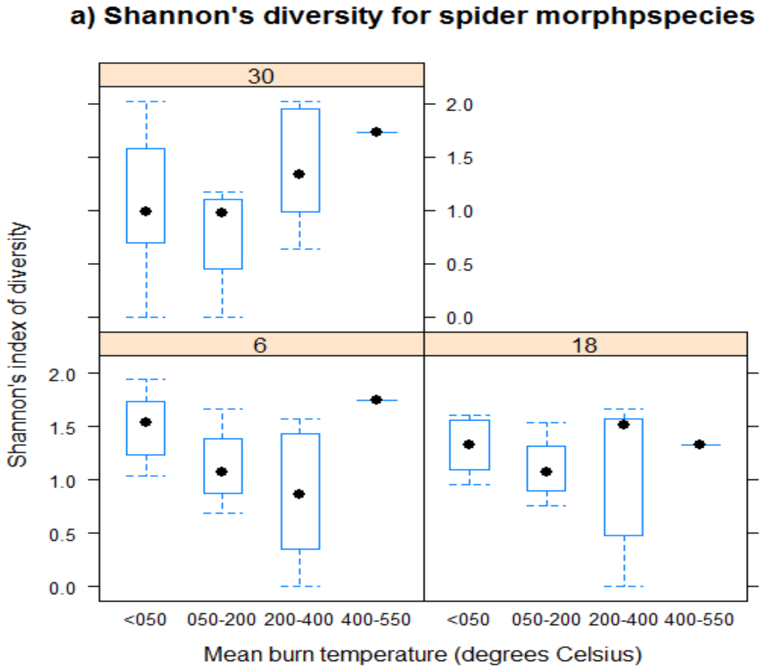


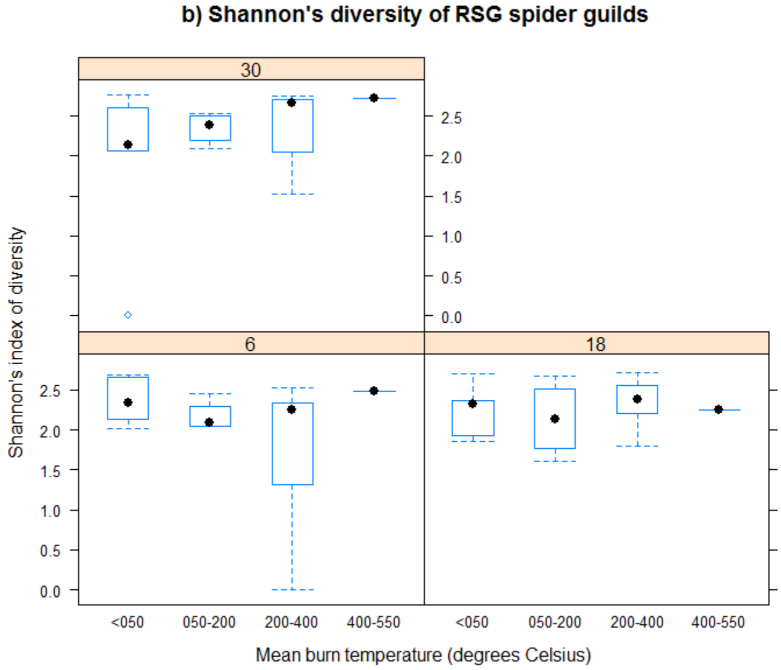
Figure Five: Boxplots illustrating changes in Shannon’s diversity for a) morphospecies and b) RGS guild with time since burn and burn treatment. Time since burn in months is indicated at the top of each panel. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

When analysed individually, the mean burn temperature and the time since burning failed to have a significant effect on morphospecies diversity, $p>0.05$. However we did record a significant effect of the interaction between mean burn temperature and time since burn on Shannon's index of diversity for spider morphospecies (χ^2 (1) = 7.362, $p=0.00666$). Morphospecies diversity showed a significant increase with time since burn in plots which burnt at between 200 and 400 °C. (See Fig. Six-a). Morphospecies richness followed a similar pattern, with a significant interaction between mean burn temperature and time since burn (χ^2 (1) = 5.658, $p=0.0174$).

RGS guild diversity followed a similar pattern to morphospecies diversity in response to mean burn temperature. (See Fig. Six-a and Six-b). Individually mean burn temperature and time since burn did not significantly affect guild diversity, $p>0.05$, however the interaction between time since burn and temperature was significant (χ^2 (2) =7.12, $p=0.0285$). RGS guild diversity increased with time since burn for plots with a mean soil surface temperature of 200-400 °C. Mean burn temperature, time since burn, and the interaction between the two had no significant effect on the richness of spider guilds.

MGS guild diversity was significantly affected by the interaction between mean burn temperature and time since burn, (χ^2 (2) =6.6847, $p=0.035$) and followed a similar pattern as for RGS guild diversity and morphospecies. (See Fig. Six-c). Refer to Table One for a summary of the results from these analyses.


a) Shannon's diversity for spider morphpspecies


b) Shannon's diversity of RSG spider guilds

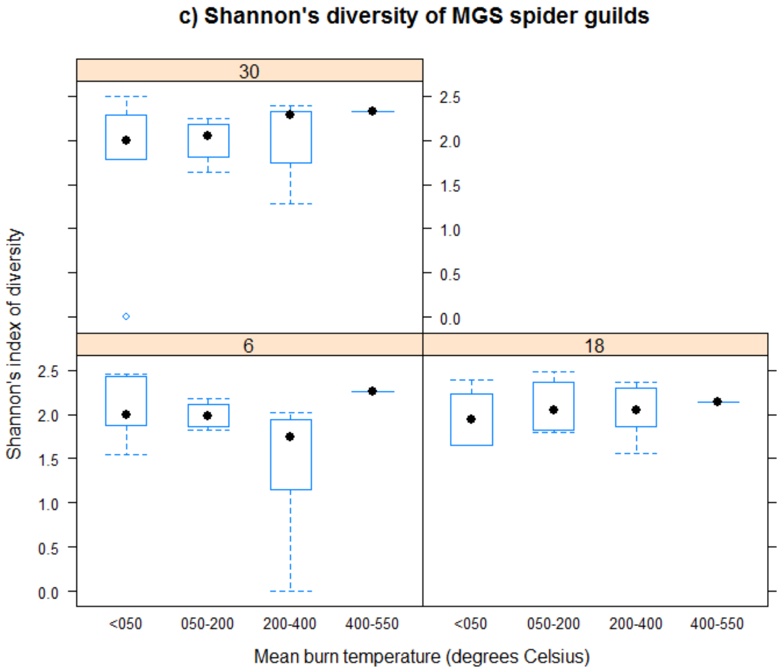


Figure Six: Boxplots illustrating changes in Shannon's diversity for a) morphospecies, b) RGS guild and c) MGS guilds with time since burn and mean burn temperature. Time since burn in months is indicated at the top of each panel. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values.

	Burn treatment			**Burn treatment x time since burn**	
	Composition	**Diversity**	**Richness**	**Diversity**	**Richness**
Msp	p=0.0001 *	P=0.0340*	p=0.0284*	P=0.0312*	p>0.05
RGS guild	P=0.0005 *	p>0.05	p>0.05	P=0.0379 *	p>0.05
MGS guild	p>0.05	p>0.05	p>0.05	p>0.05	p>0.05
Family	P>0.05	p>0.05	p>0.05	p>0.05	p>0.05

	Mean burn temp			**Mean burn temp x time since burn**	
	Composition	**Diversity**	**Richness**	**Diversity**	**Richness**
Msp	p=0.0001*	p>0.05	P>0.05	P=0.00666*	P=0.0174*
RGS guild	p=0.0055 *	p>0.05	p>0.05	P=0.00847*	p>0.05
MGS guild	p=0.0383*	p>0.05	p>0.05	p=0.0141*	p>0.05
Family	p=0.0411*	p>0.05	p>0.05	P>0.05	p>0.05

Table One: A basic summary of the outcomes of analyses for morphospecies, guild and family methods of categorising spider data in response to burn treatment, mean burn temperature and their interaction with time since burn. Significant effects are marked with a *.

Exclusion of immature specimens

In order to test if the exclusion of immature specimens from the dataset, as is required for morphospecies/ species level classifications of spiders, affects the measurable community response to fire we ran a series of analyses on the RGS guild data, with and without immature specimens included.

Zero rows were present in the immature-only and mature-only databases and therefore in order for NMDS ordinations and Procrustean superimposition to be conducted we added a pseudospecies column to each data set (see above). To maintain comparability a pseudospecies column was added to all three data sets, mature-only, immature-only and mature and immature combined. The pseudospecies column was removed for the diversity calculations.

We constructed linear mixed models to predict Shannon's index of guild diversity and richness, as functions of burn treatment, mean burn temperature and time since burn, when mature specimens were included, or excluded in analyses.

We found a significant effect of the interaction between burn treatment and time since burn on guild diversity when all specimens were included in analyses, (χ^2 (2) =6.547, p=0.0379). Diversity was lowest at six months post-burn in coppiced plots. However, when only mature specimens were included in analysis there was no significant effect of treatment on diversity, p>0.05. We found no significant effect of treatment on the richness of guilds when only mature specimens were analysed or when all specimens were analysed, p>0.05.

The interaction of mean burn temperature with time since burn, significantly affected guilds when mature and immature specimens were included (χ^2 (1) =6.931, p=0.00847), when only mature specimens were included, (χ^2 (1) =4.937, p=0.0263), and when only immature specimens were included in analyses (χ^2 (1) =3.945, p=0.047).

We ran NMDS ordinations with Envfit and Adonis to determine the effects of mean burn temperature and burn treatment on the composition of the spider community when only immature specimens, only mature specimens and both were used in analyses. We found a significant effect of burn treatment (Adonis, r^2=0.0684, p=0.0008) on the composition of the spider community when all specimens were used in analysis, however no significant effect of mean burn temperature, p>0.05. When only immature specimens were used in analyses there was no effect of burn treatment or mean burn temperature on community composition, p>0.05. When only mature specimens were used in the analyses, we found a significant effect of burn treatment (Adonis, r^2=0.0875, p=0.0011) and mean burn temperature (Envfit, r^2=0.300, p=0.0001) on community composition. Stress=0.196 (see Table Two).

	Burn treatment x time since burn		Mean burn temperature x time since burn	
	Community composition	**Diversity**	**Community composition**	**Diversity**
Mature only	p=0.0011*	p>0.05	p=0.0001*	p=0.0263*
Immature only	p>0.05	p>0.05	p>0.05	p=0.047*
All specimens	p=0.0008*	p=0.0379*	p>0.05	p=0.00847*

Table Two: A summary of the results of analyses comparing spider communities where all specimens were included, where only immature specimens were included and where only mature specimens were included. Significant results were marked by an *.

The Procrustean superimposition method revealed significant concordance between NMDS ordinations of guild data containing all specimens and mature-only (Protest, SS=0.5383, r=0.6795, p=0.0001), between guild communities containing all specimens and immature-only (Protest, SS=0.4846, r=0.7179, p=0.0001), and between mature-only and immature-only (Protest, SS=0.907, r=0.305, p=0.016).

Discussion

Spider communities have many features that make them good candidates for understanding and interpreting patterns of ecological change following disturbance because spiders are ubiquitous apex predators that show sensitivity to a range of ecological disturbances, with a range of specialised prey capture techniques. However, like all groups they are subject to collecting bias and currently there are several limitations to the effective use and interpretation of spider data in ecological surveys. Here I discuss the limitations associated with the use of spider data in ecological studies and investigate whether current methods to counter these limitations (namely taxonomic surrogacy and morphospecies classification and the novel MGS and RGS developed in Chapter Three) influence the interpretation of ecological data and the conclusions drawn from it. We recorded significant differences in the outcomes of analyses of spider community data when it was categorised using the two most common classification methods (morphospecies and family classifications) and also by the RGS and MGS approaches. In addition we found the exclusion of immature specimens, as is required for species and morphospecies categorisations, to significantly alter the outcome of analyses compared to when all specimens were included.

Consistent with our stated hypotheses, we found that the categorisation method did affect the results of community analyses. Of the spider community categorisation methods analysed, family level data showed the least sensitivity in response to the ecological variables measured, and failed to detect changes in the community, which were evident at a finer level of community resolution. Family level surrogacy is a generalised approach to categorising the spider community and as we have shown may fail to detect community changes that are evident at a finer taxonomic resolution. A lack of sensitivity of family data to ecological change, and in particular to burning, is supported by other studies, (Kallimanis et al., 2012; Podgaiski et al., 2013; Timms et al., 2013). Significant changes to the composition of family communities were evident in response to mean burn temperature, but not to burn treatment and neither burn treatment nor mean burn temperature significantly affected family diversity or richness. In addition Procrustean superimposition analyses found the composition of the family community to be significantly different to that of the morphospecies community. Analysis of the results from MGS community data showed that whilst it showed a greater level of sensitivity to community change than family classification, it failed to detect all the patterns of change that morphospecies and RGS data exhibited. Therefore, the categorisation of the spider community into fewer and broader guilds resulted in a less sensitive system for detecting community change following burning. In contrast, the composition of both RGS and morphospecies communities were significantly affected by burn treatment and mean burn temperature, and their diversity and richness showed similar trajectories in their patterns of response with mean burn temperature and burn treatment over increasing time since burning.

The above findings make ecological sense and are a key advantage of identification to morphospecies / species. The effect of sufficiently fine-scale taxonomic resolution on the analysis of ecological data may be illustrated with data from Chapter Two, using the families Zodariidae and Linyphyiidae. In both these families we recorded a change in the dominant morphospecies following burning, with one morphospecies numerically dominant in plots that had not been burnt (pre-burn and control), and another morphospecies numerically dominant in plots that had been burnt. These changes occurred at the species level, and in both families there was a size difference between the dominant species in burnt and unburnt areas. In the Zodariidae the carapace length of the dominant species was smaller in burnt areas, whereas in the Linyphiidae carapace length was larger in burnt areas. These changes would not be detected if analysing at family level, or at a level that would not be sensitive enough to detect the differences in size (i.e. the MGS). Whilst disturbance may cause gross changes to the spider communities at the family level, in real life situations a greater degree of change usually occurs at the species level and often these species level changes would be missed if only analysing higher level taxonomic data, or a crude guild system.

When conducted accurately morphospecies and species are quantitatively the same, with an equivalent level of community detail, although neither can include immature specimens. By categorising the community into a high number of individual guilds (n=88 where mature male and female specimens with the same traits were classed as different guilds), I designed the RGS with the aim of better preserving the community detail of morphospecies / species level categorisations, whilst allowing the analysis of the entire spider community. The findings of this study provide preliminary support of this aim. We recorded significant changes in the composition of both RGS and morphospecies communities in response to mean burn temperature and to burn treatment. The diversity of both communities was significant affected by temperature and treatment, and showed similar patterns of response to these variables. Whilst these results show that the RGS can detect patters of community change in response to burning, it is important to acknowledge that it is still a simplification of the spider community, and not all change will be detected.

The RGS has multiple benefits over morphospecies or species level categorisations; namely it allows analysis of the entire community (male and female, mature and immature) it can be conducted by any technician with a minimal amount of training and takes an equivalent amount of time to conduct as morphospecies assignations. Furthermore, the grouping of spiders based on the presence, or absence of a series of defined morphological traits means that from a practical perspective the RGS is objective, replicable, may be checked for errors and avoids the use of inferences based on higher level taxonomic information.

Does exclusion of immature specimens from analysis affect the conclusions drawn from ecological data?

This section sought to determine whether the exclusion of immature spiders from analyses results in a change in the measurable response of the community to burning. We found significant differences in the way the diversity and the composition of the assemblages responded to mean burn temperature and burn treatment, depending on whether immature, mature or combined specimens were analysed. These findings indicate that the exclusive use of mature specimens in analyses can influence the interpretation of the spider community's response to ecological change. As discussed in the introduction to this chapter, mature spiders often show distinct behavioural, ecological and morphological characteristics to immature spiders of the same species (Grossi & Canals, 2015; Kronk & Riechert, 1979 and Sanders et al., 2015). Our findings indicate that there are differences in the responses of mature and immature spiders to burning. This finding supports those of Main (2001) who found a differential effect of fire on the survival of juvenile and mature spiders, with some species of juvenile spiders perishing following a fire, whereas adults survived.

The findings of this study highlight the importance of researchers having a full understanding of the effect that sampling, and categorisation of the spider community may have on the interpretation of ecological data. Even if time and resources are available, species identification is not possible for many spider communities world-wide. To date there has been little consensus, or testing of the most appropriate method by which to categories the spider community. In many cases this has resulted in researchers choosing methods ad hoc, resulting in analyses being based upon broad higher taxonomic groupings, or being restricted to a sub-set of the community, sometimes with little acknowledgement in the analyses and interpretation of the data that this is the case and of the impacts this may have on the conclusions drawn. As illustrated in this chapter both these methods can lead to a misinterpretation of the dynamics of the spider community following ecological change. The necessity for a standardized, replicable system with which to categorise and compare the spider community is great.

A cost-benefit trade off exists between the increased time and expertise required to classify the spider community to a finer level of detail and the increased sensitivity or accuracy of the system in detecting community change. Overall, morphospecies assignations were the quickest method to categorise the spider community. However, this was because of the high number of immature specimens, and hence the reduced sample size. Where categorisation time was measured as the time taken to categorise one spider, then if used by a non-experienced technician, the RGS and MGS were the fastest categorisation technique. This was because each spider could be categorised without the need to refer to external resources or keys to aid identification. For a technician experienced with spider identification, family level categorisation was the fastest method. The findings of this study lead us to suggest recommendations for researchers interested in spider community ecology. At a minimum, much greater acknowledgement must be made and consideration taken of the potential effects of excluding immature specimens and of the method of community categorisation on the interpretation of spider community data. Further research is required to refine and test the use of the RGS as a method to categorise and define spider communities, until such research is conducted each current method is associated with limitations.

The novel RGS developed in this chapter offers an objective, replicable alternative to the currently available spider categorisation techniques. It allows analysis of the entire spider community and maintains a strong level of community detail however further testing is required to assess its suitability for use in a range of spider communities in different geographical locations. Where conservation or land management decisions are to be made based on the results of surveys, the loss in scientific integrity as a result of under-recording, or missing changes in the focus community is high. Surrogates for species data are valuable tools, which when used and interpreted appropriately are of great benefit to ecological studies.

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CHAPTER FIVE

Smoking spiders: Investigating the response of spiders to exposure to smoke.

Abstract

Adaptations to surviving in a fire prone environment have been recorded in plants and some invertebrates. The bulk of research on invertebrates has focussed on pyrophily, where individuals are attracted to fire or its components. Pyrophobic behaviour of spiders, where individuals move away from fire, has been recorded but its mechanism has not yet been researched. Using a set of repeated, controlled experiments we investigated the effect of the application of a cold smoke stimulus on spider behaviour, specifically on the rate of movement. Three treatments were used - smoke from burning paper, smoke from burning *Eucalyptus* leaves, and air. We found exposure to smoke to significantly increase the rate of movement of spiders, compared to the control treatment of air. We also found a differential in the response depending on the smoke source, with the movement rate significantly greater on exposure to *Eucalyptus* smoke than on exposure to paper smoke. These findings require further research, but suggest a possible adaptation of spiders to fire.

Introduction

Fire, from both anthropogenic and natural sources, has long been a part of Australia's ecological history and a major force in shaping the responses of its biota (Bowman, 1998; Bowman, 2012). The responses of organisms to a fire event or to a fire regime, and their ability to survive and/or recolonise a burnt area is dependent on many factors, including the individual characteristics of the organisms, the structure and connectivity of the surrounding landscape and the physical aspects of the fire, such as the fire intensity and rate of spread (Whelan et al., 2002; Gongalsky et al., 2012). Understanding how individuals respond to fire and the mechanisms behind that response is crucial in order to gain a full picture of how fire affects the ecosystem and to allow predictions to be made about the way that future fire events may affect communities.

Specific adaptations to enable population recovery in the post-fire environment are well recorded for the Australian flora. Fire-adapted plants are often divided into two broad categories based on the strategies employed in response to fire: resprouters where the plant resprouts following a fire, usually via surviving underground epicormic structures, and seeders, where the individual plant is destroyed but re-establishment takes place through the germination of seeds (Bell, 2001; Burrows et al., 2010). Fire- and smoke-related compounds promote the germination of seeds of some fire-tolerant and fire-intolerant species, and obligate fire-related seeders (for example some *Banksia* spp.), require exposure to fire or to fire-related compounds for mature fruits to open and/or for the seeds to germinate (Auld & O'Connell, 1991; Dixon et al., 1995; Denham & Auld, 2002; Nield et al., 2009). Although the exact mechanisms vary, the main active component of smoke that triggers germination is butenolide, a compound produced by combustion of cellulose (Flematti et al., 2004). For triggering germination the source of butenolide, other than being from plant-based cellulose, is not important.

Faunal adaptations to surviving in a fire prone environment are less well understood; however, some behaviours, such as pyrophily in insects, have been well documented (see below). There is currently no evidence that spiders are specifically adapted to fire (Main, 2001).

Pyrophilous behaviour in invertebrates is known to occur in Coleoptera, Heteroptera, Diptera and Lepidoptera (Wikars, 1992). Pyrophilous invertebrates are favoured either directly by burnt wood or by the conditions associated with a recent fire. For example, invertebrates are attracted to fire because they feed on ascomycete fungi which are favoured by burning (Wikars, 2002; McMullan-Fisher et al., 2011). Also, larvae of the Australian buprestid *Merimna atrata* (Coleoptera, Buprestidae) develop in freshly burned wood (Schmitz et al., 2000). The exact mechanisms by which invertebrates detect fire vary. *Merimna atrata*, and beetles of the genus *Melanophila*, have thoracic pit infra-red organs by which the beetles can orientate towards heat sources (Evans, 1964,1966). In addition they also have olfactory receptors in their antennae, which can detect substances found in smoke from burning wood (Schutz et al., 1999). Antennal smoke-detecting receptors are also found in Cerambycidae (Alvarez et al., 2015). The dipteran families Empididae (or ‘smoke-flies’) and Platyplezidae also show an ability to detect, and an attraction to, smoke (Snoddy & Tippins, 1968; Milberg et al., 2015).

Spiders have a strong olfactory sense (Foelix, 2011; Jackson & Cross, 2011), use chemoreception for a range of behaviours and are sensitive to a variety of chemicals. Spiders are able to detect kairomones and pheromones of other spiders and other invertebrates via contact chemoreception of silk draglines and olfaction of airborne chemicals, by which they find and capture prey and locate mates (Clark et al., 2000; Jackson et al., 2002; Hostettler & Nentwig, 2006; Cerveira & Jackson, 2013). Spiders can detect some odours, for example they are sensitive to tobacco smoke (Keller, 1961; Dumpert, 1978), and are able to detect odours released by flowers, which are used to aid selection of a foraging site (Heiling et al., 2004; Dodson et al., 2013) and for locating a mate (Stellwag & Dodson, 2010).

The organs generally considered to be responsible for chemoreception in spiders are chemosensitive hair sensilla, which are located on the distal segments of the extremities, and the tarsal organs, which contain sensilla and are located on the tarsus of the legs and on the pedipalps (Foelix & Chuwang, 1973; Anton & Tichy, 1994). The sensilla are likely to be contact chemoreceptors and the tarsal organs have been suggested as a likely site for spider olfaction; however, this is still debated (Blumenthal, 1935; Dumpert, 1978; Foelix, 2011). The primary role of the tarsal organ is likely to act as a hygroreceptor to detect changes in temperature and humidity (Ehn & Tichy, 1994). The combined role of chemoreception of smoke and sensitivity to changes in temperature and humidity would hypothetically allow spiders to be sensitive to the environmental changes that occur during a fire.

The responses of organisms to a fire and their ability to recolonise a burnt area are dependent on many factors, including the individual characteristics of the organisms, the structure and connectivity of the surrounding landscape and physical aspects of the fire, such as fire intensity and rate of spread (Whelan et al., 2002; Gongalsky et al., 2012). In contrast to pyrophilly, pyrophobic behaviour, where individuals emigrate from a fire, has been less well recorded. Few studies have specifically examined the emigration of invertebrates whilst a fire is occurring; however, anecdotal reports have recorded mobile invertebrates, such as grasshoppers, escaping fire through flight (Warren et al., 1987; Swengel, 2001). During prescribed burns, ranging from five to several hundred hectares in size, of native bush on Kangaroo Island, SA, it was common to see large numbers of invertebrates, predominantly spiders, emigrating from areas of fire activity to unburnt ground. Observed emigration was terrestrial, and occurred during high and lower intensity burns and in the presence of smoke (pers. obs.). Beetles of the family Chrysomelidae were observed flying away from a fire site at a small-scale burn on Kangaroo Island (R. Glatz, pers. comms.). Brennan et al. (2011) experimentally investigated the role of fire refugia and invertebrate emigration away from fire activity. Spiders were observed emigrating away from fire; however, the authors concluded that the practise was rare as only eight individuals were observed. The burn in the study was small in scale, consisting of a single burning grass tree (*Xanthorrhoea*: Xanthorrhoeaceae); therefore, the intensity of the fire and smoke and the strength of potential stimuli, may have been weaker than in larger-scale burn situations.

Survival and recolonization of the post-burn ecosystem by invertebrates is governed by three main mechanisms: *in situ* survival, recolonisation of a burnt area by populations from neighbouring unburnt refugia, and the emigration of individuals from a fire, followed by their later recolonisation (Whelan et al., 2002; Panzer, 2003; Brennan et al., 2011). As a survival mechanism, pyrophobic behaviour may promote the survival of individuals inhabiting fire-prone areas by triggering dispersal from areas of fire activity or by promoting *in situ* survival by causing a spider to retreat down a burrow (Carrel, 2008). Similarly, soil organisms may retreat to greater depths (Gongalsky & Persson, 2013) and so avoid lethal radiant heat.

The survival rate of individuals emigrating from a fire is influenced by the effectiveness of their dispersal method. The primary methods of dispersal used by spiders are terrestrial dispersal along a substrate and aerial dispersal via ballooning. Terrestrial dispersal is generally a short distance dispersal method and the distance travelled depends upon the movement ability of the spider. Arboreal spiders, such as the Araneidae, generally do not disperse terrestrially; however, wandering spiders, such as the Ctennidae, can move on average 20 m per night (Marc et al., 1999), and when subjected to a stimulus, for example starvation, have been recorded moving 100-200 m in one night (Schmitt et al., 1990). Ballooning enables spiders to travel much further distances, these distances vary from a few hundred metres to several hundreds, or even thousands, of kilometres (Marc et al., 1999; Bell et al., 2005). The exact ballooning method varies between spiders of the infraorders Araneomorphae, in which it is more prevalent, and the Mygalomorphae and between species within these groups; however, the basic principle is that a thread of silk is produced from the spinnerets, which is exposed to air currents. The silk line creates drag, which generates an upward lift, and this along with behavioural responses and meteorological conditions allows the spider to become airborne and travel with the air currents (Bell et al., 2005). Araneomorph spiders show a characteristic suite of behaviours as a prelude to becoming airborne, i.e. the spider stands on ‘tip-toe’, a behaviour known as tiptoeing (Bell et al., 2005), faces towards the wind and lifts its abdomen in to the air whilst releasing a silk thread (Foelix, 2011). Ballooning occurs largely in juveniles; however, adults from some families, for example the Araneidae and Linyphiidae, show a propensity to balloon (Dean & Sterling, 1985; Bell et al., 2005), and it is more common in smaller spiders (Larrivee & Buddle, 2011). Microclimate factors, such as temperature, humidity and air movement, have been identified, amongst other factors, as likely triggers for ballooning behaviour (Weyman, 1993; Weyman et al., 2002). In addition to microclimatic factors, studies have found an increase in the rate of ballooning in spiders that come from areas with a high levels of habitat disturbance, for example in areas with agricultural disturbance (Entling et al., 2011; Blandenier et al., 2013) and in naturally disturbed areas, such as those subjected to flooding (Lambeets et al., 2008; Lambeets et al., 2008). The tendency to balloon is higher in habitat generalist spiders than in habitat specialists (Bonte et al., 2003), suggesting that ballooning may be a risk dissipation strategy, evolved to assist survival in a heterogeneous environment (Kisdi, 2002).

A primary aim of this study is to observe and describe the behaviour of spiders when exposed to a smoke stimulus, using a controlled and replicated experimental design. By doing so I aim to provide suggestions for a possible mechanism behind the emigration of spiders away from areas of fire activity.

I hypothesise that spiders will show sensitivity to exposure to smoke and that this will be in the form of increased movement in the presence of a smoke stimulus. If this sensitivity is a mechanism behind pyrophobic behaviour, then we would expect movement to be orientated away from the source of smoke. From a functional viewpoint, horizontal movement away from fire activity would infer a greater survival advantage to vertical movement that would increase the likelihood of spiders moving up vegetation and so perishing in the fire. I hypothesise that the rate of horizontal movement would increase in the presence of smoke at a greater rate than that of vertical movement. The primary long distance dispersal technique of spiders is ballooning; and as such, there would conceivably be a survival advantage to spiders able to balloon over those that could only disperse terrestrially when emigrating away from areas of fire activity. The spiders in this study were collected form a fire-prone environment and I hypothesise that a proportion of the spiders tested will show ballooning behaviour on exposure to smoke.

The guild concept for spiders is increasingly being used as an alternative to taxonomic classification for categorising and understanding the spider community. Although the exact criteria vary between studies, spiders are usually grouped into guilds based upon the foraging technique with which the spider captures prey (Uetz et al., 1999). For the purpose of this study, I followed the system used by Uetz (1977) and categorised spiders into two broad guilds, web builders and free runners. Free running spiders characteristically have a higher level of terrestrial mobility and are faster moving than web building spiders, which are more sedentary, typically slower moving and less capable of running over open ground (Foelix, 2011). We hypothesise that free running spiders will show a higher rate of movement following exposure to smoke than web building spiders, and that due to their lesser ability to run over open ground, web-building spiders would show a greater tendency to balloon.

Methods

Specimen collection

Spiders were collected using hand searching, sweep netting and beating from areas of native vegetation on the eastern end of Kangaroo Island, South Australia. Spiders were held for a maximum of 12 hours prior to experimentation in plastic vials and kept at room temperature.

Equipment and experimental design

In order to test the response of spiders to smoke we developed a novel experimental chamber. See Fig. One. The left and right chambers were identical, each contained substrate on the base and a stick positioned vertically to allow web building and climbing. The chambers were connected via an open connecting tube. For the duration of the experiment spiders were able to move freely between the chambers, through the connecting tube. A 10 mm x 10 mm grid was marked on to the walls of each experimental chamber, with which to quantitatively measure spider movement. A bee smoker was used to introduce room temperature smoke to the experimental chambers at a controlled pace. The bee smoker was connected to the top of the smoking chamber by tubing, 500 mm long by 10 mm diameter. We tested three treatment types; smoke produced by burning paper, smoke produced by burning *Eucalyptus* leaves and air (the control treatment). The same volume of either paper or eucalypt leaves, depending on the treatment, was used in the bee smoker for each trial.

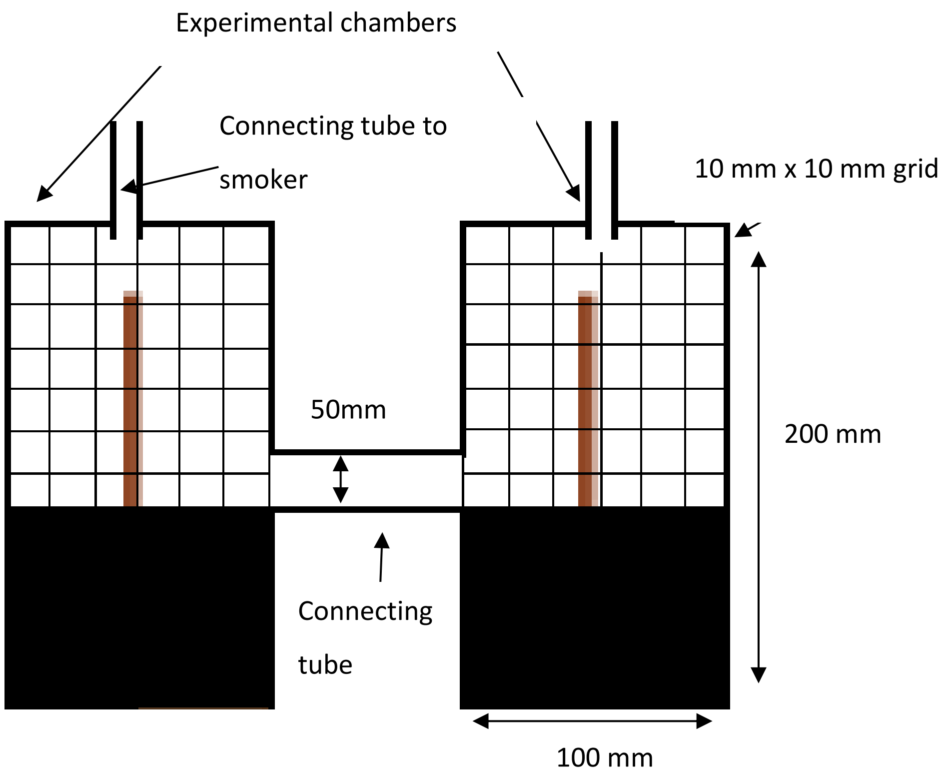

Figure One: Schematic of the experimental set up for the smoking chamber

Methodology

Each spider was introduced into a randomly chosen smoking chamber and left for a minimum of 30 minutes to settle before experimentation began. If the spider settled in the connecting tube, the experiment was aborted, the spider repositioned to an experimental chamber and the 30 minutes settling period began again. Once the spider settled, the smoker was connected to the tube attached to the opposite experimental chamber to the one which the spider settled in. The bee smoker was lightly filled with either paper or eucalypt leaves, which were then lit using a burning wick. Once the substrate was well alight with active flames, the lid of the smoker was shut and the bellows of the smoker compressed 10 times to propel smoke down the tube and into the smoking chamber. This was followed by a 20 second gap and then a further 10 more smoke compressions. For the control treatment the smoker was empty, however apart from this the same methodology was followed as for the smoking trials; the bellows compressed 10 times to propel air down the tube and in to the experimental chamber, followed by a 20 second gap and a further 10 compressions.

To record the movement of a spider, the number of vertical and horizontal squares the spider passed over was counted. Counting began one minute prior to the introduction of smoke and continued for one minute after. A camera recorded the spider's horizontal and vertical movement during the entire experimentation period, for one minute before a treatment was added and for one minute after.

This experiment involved a repeated measure design because the same spiders were tested for each of the three treatments (paper smoke, *Eucalyptus* smoke and air) in a randomised order, with a 20 minute gap between the end of one trial and the start of the settling period of the next.

Eighty spiders were tested, of these 11 underwent one treatment trial because they escaped after the initial trial. The remaining 69 spiders were each subjected to the paper smoke treatment, the Eucalypt smoke treatment and a no-smoke control, in a randomised order. This resulted in a total of 218 experimental trials. See the Appendix, Table A5 for a summary of the families tested and the guild they were assigned to.

Results

Consistent with our hypotheses the movement rate of spiders increased significantly on exposure to a smoke stimulus. The net movement rate (measured as the total movement in the minute following a treatment being introduced minus the total movement in the minute prior to the treatment being introduced) was highest following the application of *Eucalyptus* smoke (median rate = 12 cm per minute, range= -10 to 81 cm per minute) as compared to paper smoke (median rate = 5 cm per minute, range= -5 to 79 cm per minute) and air (median rate = 0 cm per minute, range= -6 to 4 cm per minute). The data were non-normally distributed and contained missing values, therefore to test the statistical significance of these differences we conducted Skillings-Mack tests (Skillings and Mack, 1981), to assess the effect of smoke type on the net movement rate of the spiders. The Skillings-Mack is a non-parametric Friedman-type statistic, which can be used on data with missing values. It is equivalent to the Friedman test where there is no missing data. (Chatfield & Mander, 2009). We found a significant difference in the total net rate of movement when the spiders were exposed to smoke as compared to the control ($t = 61.1$, $p < 0.001$). *Post hoc* analyses were conducted with Wilcoxon signed-rank tests with a Holm-Bonferroni correction, to determine the location of the differences. The total net rate of movement was significantly higher following the application of paper smoke than following the application of air, ($Z = -6.15$, $p < 0.001$); following the application of *Eucalyptus* smoke than following the application of air, ($Z = -6.45$, $p < 0.001$) and following the application of *Eucalyptus* smoke than following the application of paper smoke ($Z = -2.12$, $p=0.034$). See Fig. Two.

Figure Two: The median net total movement by spiders following the application of air (the control), paper smoke and *Eucalyptus* smoke. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

In order to test for within treatment differences between the rate of horizontal and vertical movement by spiders following exposure to smoke we conducted Wilcoxon signed-rank tests. Following treatment with air most spiders remained motionless and the median total net rate of horizontal and vertical movement was 0 cm per minute. However where spiders did move there was a significantly higher rate of horizontal (median rate = 0 cm per minute, range= -2cm, to 7 cm per minute) than vertical movement (median rate = 0 cm per minute, range= -6cm, to 0 cm per minute), Z=-2.38, p=0.018 (see Fig. Three).

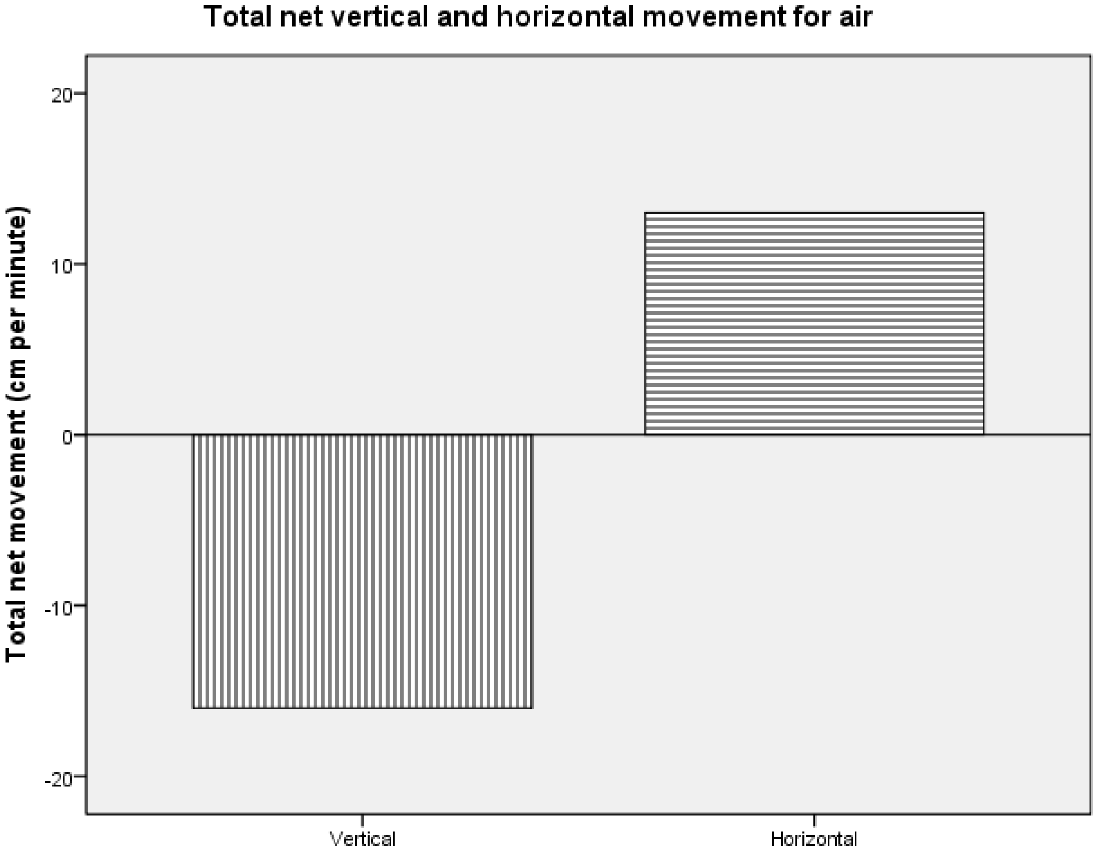

Figure Three: The total net vertical and horizontal movement (in cm) by spiders following treatment with air. Total net movement is defined as the total movement by all spiders in the minute following a treatment being added minus the total movement in the minute prior to the treatment being added. Due to the median movement rate for both horizontal and vertical movement being zero cm per minute, a graph showing median movement rates would be meaningless. Thus we have presented a bar chart of the total net movement rate, instead of the medium net movement rate. This figure therefore does not have confidence intervals.

Following treatment with *Eucalyptus* smoke, the rate of horizontal movement (median rate = 7.5 cm per minute, range= -4cm, to 56 cm per minute) was significantly higher than vertical movement (median rate = 3.5 cm per minute, range= -18cm, to 44 cm per minute), Z=-1.97, p=0.048 (see Fig. Four).

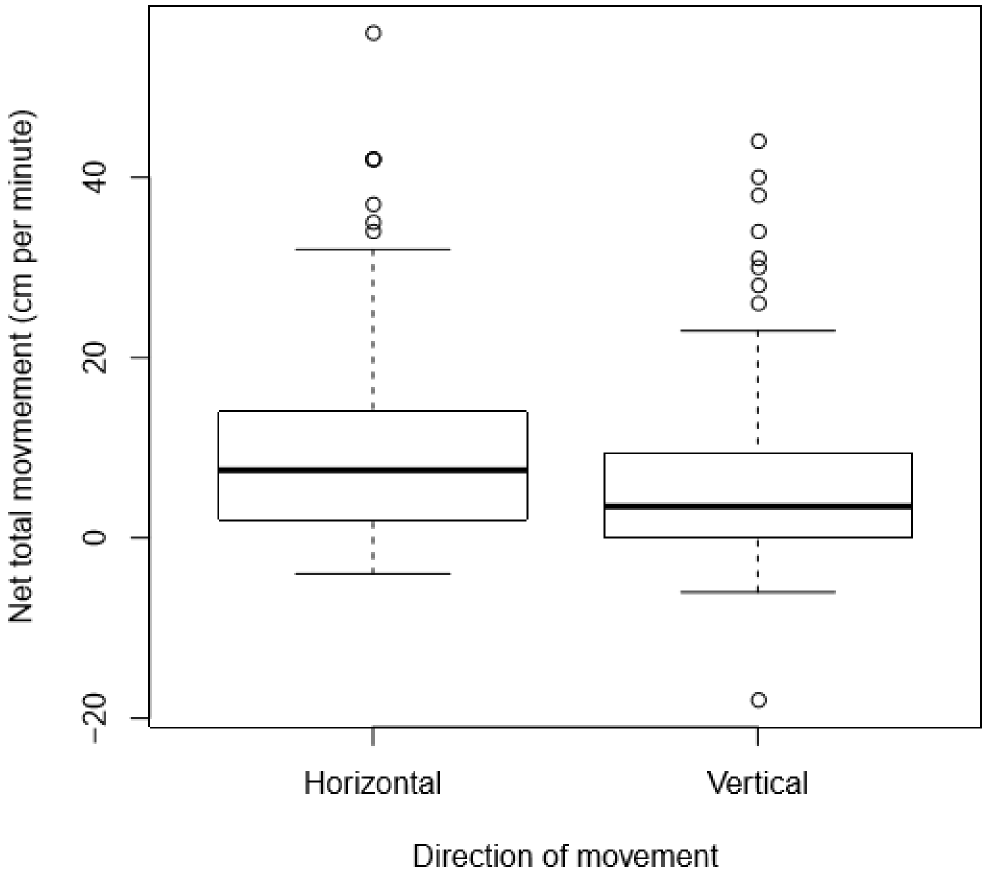

Figure Four: Showing the total net vertical and horizontal movement (in cm) by spiders following treatment with *Eucalyptus* smoke. Total net movement is defined as the total movement by all spiders in the minute following a treatment being added minus the total movement in the minute prior to the treatment being added. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

There was no significant difference between the rate of horizontal movement (median rate = 3 cm per minute, range= 0cm, to 48 cm per minute) and vertical movement (median rate = 2 cm per minute, range= -9cm, to 64 cm per minute) with paper smoke (see Fig. Five) , p>0.05.

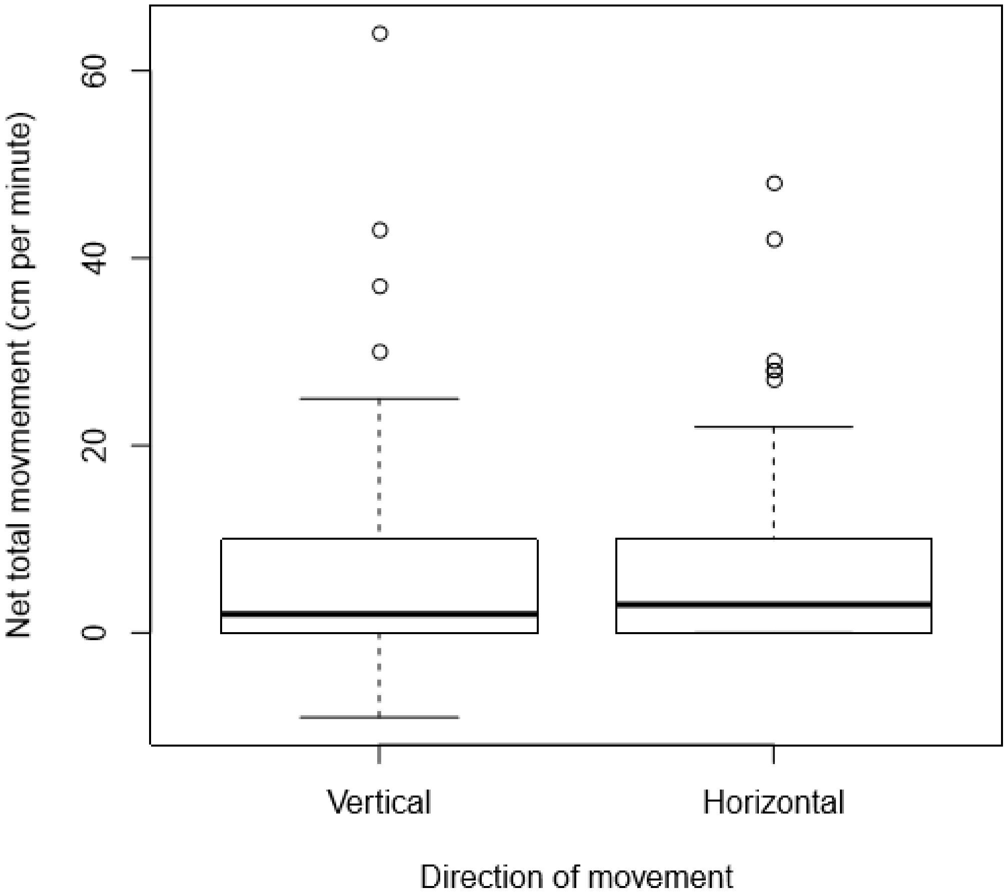

Figure Five: Showing the total net vertical and horizontal movement (in cm) by spiders following treatment with paper smoke. Total net movement is defined as the total movement by all spiders in the minute following a treatment being added minus the total movement in the minute prior to the treatment being added. Boxplots extend from the lower quartile (25% data point) to the upper quartile (75% data point). The whiskers indicate the minimum and maximum values, and outliers are indicated by dots.

Mann-Whitney U tests were conducted to test for inter-guild differences between web building and free running spider guilds in the rate of vertical and horizontal movement, following smoke treatment. We found free running spider guilds to exhibit a significantly higher rate of vertical movement (U=462.0, p=0.04) and horizontal movement (U=504.0, p=0.028) than web building spiders in the pre-treatment and control trials. However, these inter-guild differences in the rate of movement were not apparent following the application of *Eucalyptus* or paper smoke during which both guilds moved similar amounts.

Of the spiders exposed to paper and *Eucalyptus* smoke, 17% (n=13 individuals), initiated silk spinning activity and assumed a characteristic ballooning stance, with abdomen raised. This was activity was not seen in spiders that were given the control treatment. These spiders were all from the web-spinning spider guild. Of those spiders who performed this activity, 46% were Araneidae (n=6 individuals), 15% were Therididae (n=2 individuals), 15% were Linyphiidae (n=2 individuals) and 23% were Tetragnathidae, (n=3 individuals).

Discussion

This study demonstrates an apparent sensitivity of spiders to the presence of smoke. We found spiders to show changes in behaviour, in the form of an increase in the rate of movement, when exposed to a smoke stimulus. It also demonstrates that the source of the smoke is important, with a differentiation in the rate of movement when exposed to smoke from burning *Eucalyptus* leaves as compared to smoke from burning paper. An increase in the rate of motion following exposure to smoke may infer a survival advantage to individuals occupying bush fire prone ecosystems, via the emigration of spiders away from fire activity and lethal radiant heat. Thus, this would provide a mechanism behind the anecdotal observations of spiders emigrating from fire by the author (Pers. Obs) and for the emigration of spiders recorded by Brennan et al. (2011). Adaptations to surviving in a fire prone environment have been recorded in plants, for example some plants require fire, or the components of fire in order to produce seed, for example some *Banksia* and *Hakea* species, or for seeds to germinate, for example some *Acacia* species. Adaptations have also been recorded in invertebrates, for example pyrophillic beetles of the Burprestidae and Cerambycidae, which are attracted towards fire or to recently burnt areas. To date, adaptations to fire in spiders have not been recorded, however the findings of this study provides evidence for a possible mechanism for pyrophobic behaviour in spiders.

The finding of a significant difference between the net rates of movement following exposure to *Eucalyptus* smoke compared to smoke from paper suggests a specificity to burning vegetation, rather than to smoke *per se*. Spiders have a strong olfactory sense (Foelix, 2011; Jackson & Cross, 2011) and use chemoreception for a range of behaviours, such as the detection of airborne and contact kairomones and pheromones for prey detection and mate location (for example Clark et al., 2000; Jackson et al., 2002; Hostettler & Nentwig, 2006; Cerveira & Jackson, 2013) and the detection of habitat-related olfactory cues for selection of a foraging site and mate location (Heiling et al., 2004; Stellwag & Dodson, 2010; Dodson et al., 2013). Spiders can also detect pungent odours, such as acids and ammonia vapour (Foelix, 2011) and tobacco smoke (Keller, 1961; Dumpert, 1978). Chemo-reception of smoke has been recorded in invertebrates; for example, beetles of the family Cerambycidae and Buprestidae have smoke detecting receptors in their antennae with which they orientate towards smoke (Schutz et al., 1999; Alvarez et al., 2015).

Further research is needed to determine the mechanism behind the apparent detection of smoke recorded in this study, in particular to investigate the sensitivity of the tarsal organ to smoke. Also, the role of heat in the observed responses requires further testing. The tarsal organs of spiders react to tobacco smoke (Keller, 1961; Dumpert, 1978); however, more recent research suggests that these organs are primarily a hygroreceptor and are sensitive to changes in temperature and humidity (Ehn & Tichy, 1994; Foelix, 2011). Oils containing terpenes, which are found in *Eucalyptus* leaves, increase the flammability of vegetation, and so may increase the temperature at which they burn, compared to paper. The resultant smoke, when pumped through to the experimental chamber might have been hotter than paper smoke, which may have been responsible for the observed differences in responses. However, a study by Ormeno et al. (2009) found that leaf litter with a higher terpene concentration did not burn at a higher temperature than leaf litter with a lower terpene concentration, although overall flammability did increase with higher terpene levels. In order to address these issues it is suggested that further trials are conducted, where heat is independently manipulated as a variable. A further consideration is the possibility that spiders were sensitive to the oils produced by *Eucalyptus* leaves. In order to control for this it is recommended a trial be conducted where fire is absent, but the burn chamber is filled with *Eucalyptus* leaves.

As hypothesised, following the application of *Eucalyptus* smoke, the rate of horizontal movement of spiders was significantly greater than that of vertical movement. This is consistent with our theory that if movement in response to smoke (or heat) was an adaptation for survival then horizontal movement would infer a greater survival advantage than vertical movement and so we would expect the rate of horizontal movement to exceed that of vertical. Spiders exhibited a significantly higher rate of horizontal than vertical movement in control treatment trials. This mirrored the rate of pre-treatment movement for all treatment groups, and is explained by the larger rate of horizontal over vertical movement of wandering free running spiders, such as members of the Salticidae, that had a naturally high rate of movement around the chamber even in the absence of a smoke stimulus**.** When exposed to *Eucalyptus* smoke, the typical observed behaviour for most of the free running guilds and for some of the web building spider guilds was to drop to the base of the experimental chamber and move rapidly around the perimeter of the base. We found no significant difference between the rate of vertical and horizontal movement following treatment with paper smoke. Overall spider movement showed a significant increase, but this was not directional.

In pre-burn and control trials there was a significant difference in the rate of movement of web building and free running spider guilds. Spiders from free running guilds exhibited a higher rate of horizontal and vertical movement than spiders from web building guilds. This result was expected and reflects the greater mobility of free running spiders to web builders. However, following the application of *Eucalyptus* and paper smoke, this inter-guild difference disappeared and the rate of movement of both guilds increased and became equivalent. On exposure to a smoke stimulus web building spider guilds, which had been stationary, typically dropped from the places they had settled and started moving around the experimental chamber.

Consistent with our hypotheses, we recorded a small percentage of individuals showing increased silk spinning activity and ballooning-related stances on exposure to smoke. Posturing, or tip-toeing, with abdomen raised is a precursor to ballooning (Bell et al., 2005) and the presence of these behaviours in even a small number of individuals on exposure to a smoke stimulus is an interesting finding that warrants further research. In a laboratory experiment, Weyman (1995) identified moving air currents as being a key stimulus for Linyphiidae spiders to initiate ballooning behaviour, and it is conceivable that in a fire situation ballooning spiders could take advantage of the convection currents associated with fire. The movement of air currents and air pressure would likely have varied between the smoke trials and the control trial due to changes in pressure and/or air volume as a result of the fire. However, during control trials air was moved through the experimental chamber via the bellows, at a similar rate to the smoke treatments, but additional movement due to the fire was not controlled for. Air movement in the controls was not sufficient to stimulate ballooning behaviour. Further tests are needed to assess the role of smoke, air currents and air pressure and volume on initiating ballooning behaviour, especially given the small number of individuals showing this response in smoke trials. The spiders in this study were collected from Kangaroo Island, where other biota, such as plants, exhibit evolutionary adaptations to fire. Previous studies have found the rate of dispersal by ballooning in spiders to increase for spiders that have come from a disturbed habitat, whether that disturbance is anthropogenic, such as agricultural disturbance (for example Entling et al., 2011; Blandenier et al., 2013), or is natural, such as flooding (for example Lambeets et al., 2008; Lambeets et al., 2008).

Whilst exposure to smoke stimulated increased movement, this study did not find a direct aversion to smoke. On exposure to smoke spiders typically moved around the perimeter of the base of the experimental chamber, up and down the sides of the chamber, or around the perimeter of the top of the chamber and not directionally in relation to the source of the smoke. However, the shape of the experimental chambers was not optimum for detecting directional movement, being tall and thin. It is recommended that further research is conducted using a controlled directional smoke source in a horizontally elongated experimental chamber to further study aversion. An additional limitation with the experimental design was that due to poor visibility through the smoke, movement could not always be measured accurately when spiders moved towards the centre of the experimental chamber. In cases where this occurred estimates could be made based on the location of the spider when it could be viewed and its likely course. In order to correct for this it is suggested a new design of experimental chamber be used, which has a smaller volume of interior space.

For the purposes of this research spiders were categorised in to functional guilds. A recommendation for future study would be to analyse the response to smoke of spiders at the species level, in order to assess species specific reactions and to ascertain differences between species from geographical regions prone to fire, and those not.

This study investigated the mechanism driving emigration away from an area of fire activity. Our findings are novel and suggest a range of avenues for future research. We investigated the potential mechanisms behind emigration from a fire. Future research is needed to measure and quantify spider emigration during fire activity in real life situations, the survival advantages associated with such behaviour and the propensity of spiders for later recolonization.

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CHAPTER SIX
Thesis Conclusion

This thesis was dedicated to increasing knowledge of how spiders respond to fire, both at an individual and a community level. The fire ecology of spiders is a growing area of research. The role spiders play in the ecosystem, and their importance to ecosystem functionality is becoming increasingly acknowledged in the academic literature. The chapters in this thesis cover diverse elements of the fire ecology of spiders, which link together, building on the findings of previous studies and adding new and novel insights. The four empirical chapters cover aspects of spider community fire ecology with recommendations of management techniques, methodological suggestions for improving the use of spider data in ecological research and experimental analyses of behavioural responses by spiders to fire related stimuli.

In Chapter Two, the first empirical chapter of this thesis, we investigated the effect of burning on the taxonomic diversity and composition of spiders in fragmented patches of *Eucalyptus cneorifolia* vegetation. We showed that the composition and diversity of spider communities were significantly affected by fire and these findings were consistent with those of previous studies (Moretti et al., 2002; Koponen, 2005; Langlands et al., 2006; Pompozzi et al., 2011 and Podgaiski et al., 2013). We extended these findings and introduced novel research by including analyses on the effect of burn temperature, pre-burn vegetation treatment and post-burn changes in habitat structure on spider communities. The inclusion of habitat data in our analyses allowed us to show how spider communities in the post-burn ecosystem change with the changing structural complexity of vegetation communities. In doing so this study has highlighted the value of a multi taxa approach, which includes information on the nature and strength of responses from other groups, such as vegetation communities, in order to better understand the responses of a target group. By gaining accurate readings of burn temperature we were able to directly compare the effect it had on spider communities. This was interesting ecologically, but also allowed us to be able to advise decisions on the optimal methods for burning in order to conserve, or limit harm to the spider community. We showed how burn temperature significantly affected spider community composition. Burns of a high temperature, of above 450 °C, were associated with the greatest level of alteration to spider communities. These hot burns were also associated with the dominance of an exotic spider *Ostearius melanopygius* of the Linyphiidae. This finding supports those of Malumbres-Olarte et al., 2013 who recorded the association of an exotic Linyphiidae with burning in New Zealand. Linyphiidae are frequent ballooners, and are therefore able to travel large distances and colonise new habitat. *Ostearius melanopygius* is associated with disturbed habitat and bare ground, habitat qualities that characterise the high temperature burn plots in the initial year following burning. We also showed how some spiders were associated with unburnt habitat and increasing litter depth such as a gnaphosid spider that declined in abundance in burnt plots. This finding supports that of Buddle et al., (2000), who similarly recorded a decline in the abundance of a gnaphosid spider following burning. These findings are important and provide suggestions for informing management decisions on how to best conduct burns of fragmented, remnant vegetation. As a result we recommend that where burning of such vegetation is to be conducted, burns should be of a low intensity, and thus result in a patchy, heterogeneous post-burn environment with remnant standing vegetation and coarse woody debris. We investigated the effect of pre-burn vegetation treatments; coppicing vegetation prior to burning and burning of un-manipulated vegetation, on spider communities. Our findings indicate that that coppicing of vegetation prior to burning is detrimental to the conservation of spiders and therefore should not be conducted.

In this study we showed how all fires are not equal and that the response of organisms to burning can vary distinctly with temperature, with burn treatment and depend on the amount of vegetation and litter in the post-burn ecosystem (for both of which burn temperature and treatment are significant factors). This highlights the importance of considering the effects of fire-related variables, such as temperature, when making predictions on how a fire may effect a community and when assessing, and comparing analyses of data gathered from different fires.

The methodology developed in Chapter Two was a controlled, replicated design, with pre-burn spider data, accurate readings of burn temperatures and post-burn surveys of habitat variables which is rare in fire ecology studies. Prior to burning, all sites were matched for grazing, area, historic land use and vegetation type. This combination of qualities is rare in invertebrate fire ecology, where due to the costs and logistics of conducting multiple burns, studies are often based on smaller scale experimental burns with few replicas, on chronosequence studies comparing sites with different historical times since burning, or on single wild-fire events. In these cases it is not possible to control for factors that may affect community response to fire, such as the area of the site, the type of vegetation, or the pre-burn disturbance history. Whelan (2002) highlighted the need for increased, empirical research on the effects of fire on invertebrate communities and discussed the lack of an empirical approach in many invertebrate studies to date.

The use and interpretation of spider community data in fire ecology is currently associated with a range of taxonomic and methodological limitations, which have necessitated researchers to use alternatives to species for categorising spider communities. The most common alternatives are family level taxonomic classifications, morphospecies and guilds. Guilds can offer additional functional information compared to a purely taxonomic approach, allowing interpretation of how environmental variables associated with burning affect functionality in the post-burn ecosystem. In Chapter Three we showed how the RGS, a novel morphological guild system, could be used to categorise the spider community, thus creating a replicable, quantifiable system based on measurable morphological and developmental traits. The RGS is a complete guild system that combines the use of two complimentary functional techniques; a guild approach, where spider communities are categorised into discrete guilds based upon their function and a trait based approach in which individual traits are analysed to assess their correlation with environmental variables. Ecological studies of spiders conducted in areas where there are a large number of unidentified species, such as in Australia, are subject to the same taxonomic limitations. These limitations mean that species identification is often not possible and therefore any biological information that may be gleaned from species data is not available to researchers. The use of higher taxonomic surrogacy for species identification and for replacing species information used to assign guilds and traits, is therefore common. As discussed in Chapters Three and Four the use of information from higher level classifications is associated with a series of limitations, both to the accuracy and resolution of the data and also the inter study comparability of results. We showed how by categorising spiders into guilds based upon measurable morphological traits we could bypass the use of taxonomy, and its associated limitations. The benefits associated with this are multiple; the RGS is replicable and quantifiable, therefore is a standardised, comparable system, which defines spiders in to guilds based upon a set of defined, measurable morphological traits. Guilds are therefore defined based on function as defined by spider morphology and not on a researcher’s interpretation of the function of a large group. Thus much of the ambiguity in the decisions made by researchers in how to assign spider guilds, how many guilds to use and where to make the cut off between guilds is removed. Where there is variation in the limits used to categorise spiders into guilds and where the groupings are, in some cases, arbitrary, there is a risk that the patterns being detected are a result of the decision making process, rather than reflecting actual patterns in the spider community. By bypassing the need for taxonomy and by grouping guilds based upon scores from a set of measurable, morphological traits the RGS removes much of this ambiguity. This means the RGS may be used by different researchers to enable direct comparisons of different ecosystems. It also means that researchers can bypass the need to identify the spider community taxonomically prior to guild groupings, therefore saving time. The use of traits to investigate spider community response to fire has been investigated by Langlands et al. (2011), Podgaiski et al. (2013) and Malumbres-Olarte et al. (2014), our findings from this Chapter continue on from the findings of these studies and offers a non-taxonomic alternative.

In our analyses in Chapter Three we found RGS guilds to be sensitive to burning. Guild community composition and diversity were affected by burn treatment, time since burn and mean burn temperature. This finding supports those of other studies that have recorded a change in the functional composition of spider communities following burning (Buddle et al., 2000; Moretti et al., 2002; Koponen, 2005; Podgaiski et al., 2013). Fourth corner analyses revealed significant positive correlations between eye size and time since burn and negative correlations between the presence of false tufts and mean burn temperature. These traits were not found to be associated with burning by Langlands et al. 2011, by Podgaiski et al., 2014, or by Malumbres-Olarte et al., 2013. However, of these three papers, which have used a trait based approach, the only duplicated finding was the positive link between body size and fire recorded by Malumbres-Olarte et al., 2013 and Langlands et al., 2011. This lack of consensus might indicate that spider traits are perhaps not good factors for detecting change following burning, that the traits selected are too variable and interacting making it difficult to distinguish the role of individual traits in shaping the distribution of spiders, or it may be a result of limitations in the methods of categorisation and analysis. We have already discussed the limitations of assigning traits based upon inferences made using higher taxonomic classifications. Additional factors that may have influenced the lack of consensus in the findings could be based upon the methods used to analyse the data. Adjusting the data to correct for multiple comparisons and control for the Type One error is a contentious issue. Moran (2003) argued against using adjustments for multiple comparisons. This approach was followed by Langlands et al., 2011 in their study investigating the link between spider morphological traits and burning, where they did not adjust data for multiple comparisons when running fourth corner analyses. Garcia (2004), however argued for the importance of adjusting for multiple comparisons in order to control the Type One error rate, but favoured using less conservative approaches, such as the “fdr” (Benjamini & Hochberg, 1995). This was the initial approach taken in this study. Dray (2013) recommended using a high number of permutations when running fourth corner analyses in order to maintain sufficient statistical power on data that had been adjusted for multiple comparisons. The data used in this study were large and complex, with a high number of individual guilds and traits, the combination of this and computers with insufficient memory meant that we had to use less than the recommended number of permutations, thus reducing statistical power. When data were adjusted for multiple comparisons we failed to detect any significant relationships between traits and environmental variables. When the adjustment was removed we did detect significant findings. The lack of consensus between the study by Langlands et al., 2011 and this study might be an artefact from an increased Type One error rate, or as a result of insufficient statistical power due to too few permutations. In this study we used n=999 permutations; Langlands et al. (2011) used n=9999 and Dray (2013) recommended n=49999. This requires further research, using adjusted data and the recommended permutations. To be a useful analytical technique of invertebrate data, the fourth corner technique needs to be able to cope with the large, complex data sets, such as are gained from surveys of invertebrates. There is a need for further research into the interaction of spider guilds, traits and environmental variables and this will improve the understanding of the effect of fire on spider communities. This should include the use of trait based approaches, such as the fourth corner technique, but there is also a need for alternative approaches, such as a general linear mixed model approach (Jamil et al., 2013), which will allow complex invertebrate datasets to be more accurately analysed.

Whilst bypassing taxonomy in order to assign guilds is associated with benefits, it also presents some challenges and limitations. Essentially, during taxonomic classification a set of morphological traits and characteristics are grouped and these groupings are used in order to classify an individual to a species. The conventions on which set of traits and characteristics combine to define each species are well defined and have been subject to much research. The RGS removes this set of conventions and attempts to classify spiders based on a whole new, functional viewpoint. The removal of taxonomic groupings means that the boundaries defining one group of specimens from another and the way groups of traits relate to those groups are removed. Therefore we recommend further research is conducted to investigate which traits are used and to determine where best to meaningfully draw the boundaries on classifications within a trait. We have shown that the RGS may be used to assess community change following burning, however it requires further testing in a range of ecosystems to a number of disturbances, to assess its suitability as an alternative to morphospecies.

Our findings from Chapter Four continue from the findings of Chapter Three and support the use of the RGS as an alternative to species classification. We revealed similarities in the responses of the composition and diversity of RGS guilds and morphospecies to burning and to the key variables of mean burn temperature, burn treatment and time since burn. In Chapter Four we illustrated how the use of common spider community categorisation methods, family, morphospecies and guild, affect the outcomes of analyses of our data assessing how composition and diversity of communities change following burning. We showed that categorisation method significantly affected the outcome of interpretations of spider community data. Additionally we illustrated how the removal of immature specimens from the RGS dataset, as is required for species or morphospecies data, affected the outcome of analyses of spider data. This is an important finding. Species identification is often seen as the ideal in ecological studies. However, even in a known ecosystem, where 100% of the species are identifiable, only a proportion will be included in analyses. Where mature and immature specimens have different habitat requirements, as is the case with some spiders, and where habitat management decisions are based upon the outcomes of ecological surveys, it is essential that those surveys do not under-represent a sector of the community. The findings of this chapter supported those of Timms et al. (2013) that the significance of treatment effects on spiders were stronger for classifications that had a higher community resolution (i.e. species and morphospecies) as compared to those that had a lower resolution (i.e. family), and those of Cardoso et al., (2004), that spider families are inappropriate surrogates for species.

In this thesis we demonstrated how spider communities from native vegetation fragments on Kangaroo Island showed a clear sensitivity to fire or to smoke, both at a community level where we recorded significant changes to the structure and diversity of spider communities following burning, and at the individual level where spiders showed significantly increased rates of movement in response to smoke. Our findings of increased movement rates by spiders and of an instigation in ballooning behaviour on exposure to smoke, are significant and novel and suggest a potential mechanism for the emigration of spiders away from fire, recorded by Brennan et al., 2011. Further research will improve our understanding on how individual spiders respond to smoke. Recommendations for such research include empirical studies researching emigration by spiders from fire and the reaction of spiders to heat and a combination of heat and smoke.

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Appendix

Chapter Two

Table A1: A list of Families, abbreviations for family name, the collection method used to collect the family, morphospecies attached to those families (where one exists) and the sex of the morphospecies.

Family	**Abbreviation**	**Collection Method**	**Morphospecies**	**Sex**
Amaurobiidae	Amaurobiid	Pitfall / Sweep	A1	
Araneidae	Araneid	Pitfall / Sweep	Ar2	Male
			Ar12	Female
			Ar13	Female
xClubionidae Clubioninae	ClubClub	Pitfall		
Clubionidae Eutichurinae	ClubEut	Sweep		
Corinnidae	Corinnid	Pitfall / Sweep	Co1	Female
			Co3	Male
			Co5	Female
Desidae	Desid	Pitfall / Sweep	De2	Female
Dictynidae	Dictyni	Pitfall / Sweep		
Gallienellidae	Gallien	Pitfall		
Gnaphosidae Drassodinae	GnaphDras	Pitfall / Sweep	G1	Female
			G2	Male
			G3	Male
			G5	Male
			G6	Female
			G7	Male
			G8	Male
			G9	Female
			G10	Male
			G11	Female
			G13	Female

Family	**Abbreviation**	**Collection Method**	**Morphospecies**	**Sex**
			G26	Female
			G27	Male
			G28	Female
			G30	Female
			G31	Male
			G32	Male
			G33	Female
			G34	Female
			G35	Female
			G36	Male
Gnaphosidae Hemicloeinae	GnaphHemi	Pitfall	G21	Male
Gnaphosidae Laroniinae	GnaphLa	Pitfall	G19	Female
Hahniidae	Hahn	Pitfall	Ha1	Female
			Ha2	Female
			Ha3	Male
			Ha4	Female
Hersiliidae	Hersiliid	Sweep		
Idiopidae	Idiop	Pitfall	Id1	Male
Lamponidae Centrothelinae	LampCentro	Pitfall		
Lamponidae Lamponinae	Lamplamp	Pitfall	La1	Male
			La2	Male
			La3	Male
			La4	Female
			La5	Male
			La6	Male
			La7	Male
			La8	Male
Linyphiidae	Liny	Pitfall / Sweep	Li5	Male

Family	**Abbreviation**	**Collection Method**	**Morphospecies**	**Sex**
			Li6	Female
			Li7	Female
			Li8	Male
			Li10	Male
			Li13	Female
			Li14	Female
			Li17	Male
Liocranidae	Liocran	Pitfall		
Lycosidae	Lycos	Pitfall / Sweep	Ly1	Female
			Ly2	Female
			Ly4	Female
			Ly5	Female
			Ly6	Male
			Ly9	Female
			Ly10	Female
			Ly13	Male
			Ly14	Female
			Ly15	Female
			Ly16	Female
			Ly18	Male
			Ly20	Female
			Ly22	Male
Micropholcommatidae	Microphol	Pitfall	Mi1	Female
			Mi2	Male
			Mi3	Female
			MI4	Male
Mimetidae	Mimetidae	Sweep		
Miturgidae	Miturgid	Pitfall	Mit1	Male
			Mit2	Male
			Mit4	Female
			Mit5	Female
Mysmenidae	Mys	Pitfall	My2	Male

Family	**Abbreviation**	**Collection Method**	**Morphospecies**	**Sex**
			My3	Male
Nemesiidae	NemAna	Pitfall	N1	Male
Oonopidae Gamasinae	OonoGamas	Pitfall	Oo1	Male
			Oo2	Male
			Oo3	Female
			Oo4	Female
			Oo5	Male
			Oo6	Female
Oonopidae Oonopinae		Pitfall		
Oxyopidae	Oxyopid	Sweep		
Pholcidae	Pholcid	Pitfall		
Prodidomidae	ProdMol	Pitfall	Pr1	Male
			Pr2	Female
			Pr3	Male
			Pr4	Female
			Pr5	Female
Salticidae	Salt	Pitfall / Sweep	Sa2	Male
			Sa3	Male
			Sa12	Female
Segestriidae	Segest	Pitfall		
Sparassidae	Sparass	Pitfall / Sweep		
Stiphidiidae	Stiphidiid	Pitfall / Sweep	St3	Male
			St4	Female
			St5	Female
Symphytognathidae	Symphytognathid	Sweep		
Tetragnathidae	Tetragnath	Sweep		
Theridiidae	Therid	Pitfall / Sweep	Th1	Male
			Th3	Female
			Th5	Male
			Th20	Female

Family	**Abbreviation**	**Collection Method**	**Morphospecies**	**Sex**
			Th21	Female
Theridiidae Hadrotarsinae	TheridHadro	Pitfall	Th22	Male
Thomisidae	Thom	Pitfall / Sweep	Tho	Female
			Tho5	Male
Toxopidae		Sweep		
Zodariidae	Zodariid	Pitfall / Sweep	Z1	Male
			Z2	Male
			Z3	Female
			Z4	Male
			Z6	Male
			Z8	Female
			Z10	Female
			Z12	Male
			Z13	Male
			Z14	Female
			Z15	Male
			Z16	Male
			Z18	Male
			Z19	Male
			Z20	Male
			Z23	Female
			Z24	Female
			Z25	Male
			Z27	Male
Zoridae	Zori	Pitfall	Zr2	Female
			Zr3	Female
			Zr4	Female
			Zr7	Female
			Zr8	Male
			Zr13	Male

Figure A1: NMDS plot of cursorial spider data from Chapter Two, showing skewed distribution with plot DA1, standing plot, survey year 2011 included.

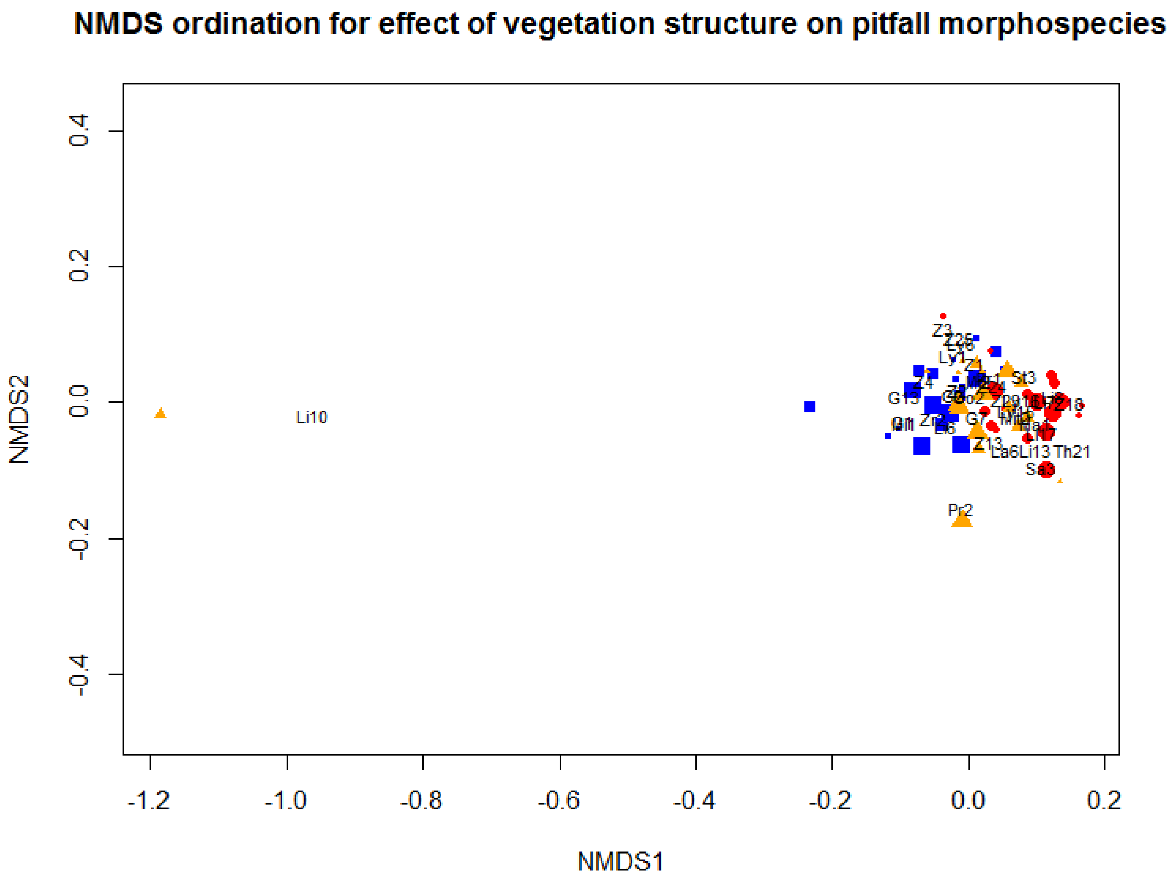
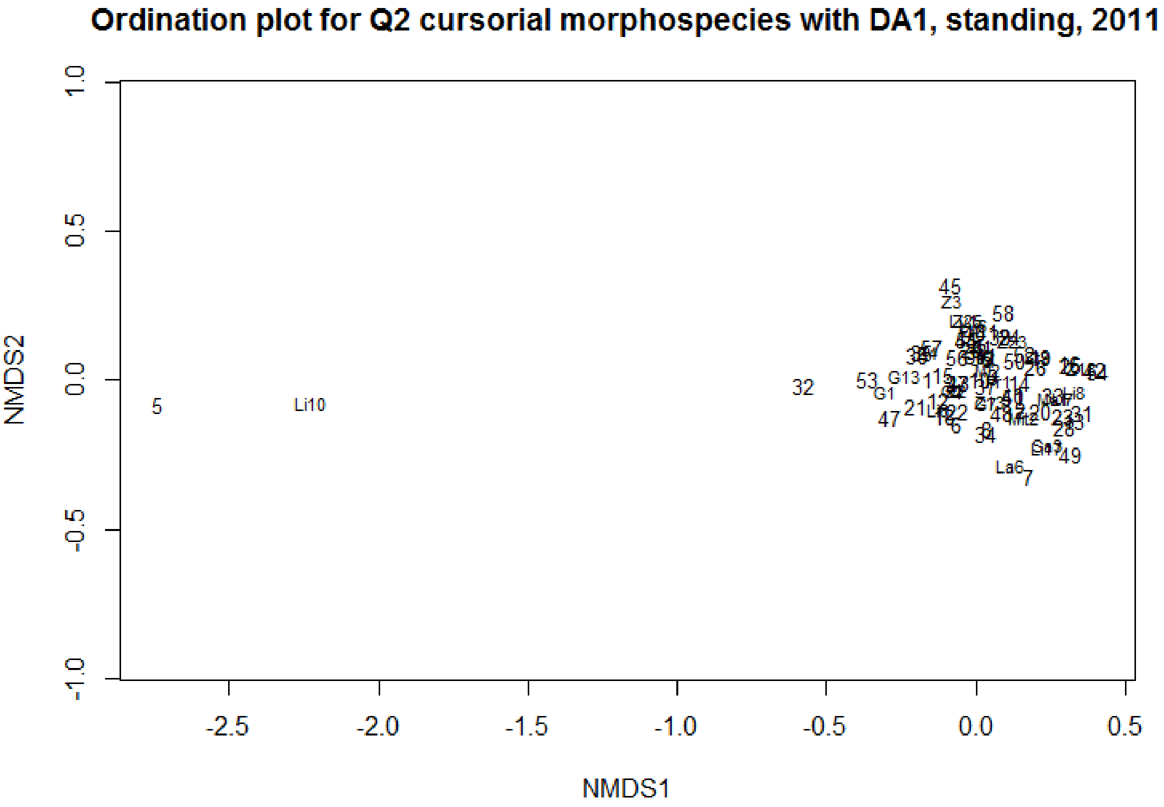


Figure A2: NMDS ordination from pitfall trapped surveys of the vegetation survey years with plot DA1, standing plot, survey year 2011 included.



Chapter Three

Table A2: Spider RGS guilds with corresponding traits. Table Q in Fourth corner analysis. Abbreviations used in the maturity columns denote; m- mature, nm- immature and abbreviations used in the tuft column denote; t- tuft, ft- false tuft, n-no tufts.

Guild	**maturity**	**cara**	**3rd.claw**	**tuft**	**acc.hair**	**crib**	**comb**	**eye**	**scutes**	**scop**	**leg**
A10	nm	10	n	ft	n	n	n	<0.5	n	n	1
A10m	M	10	n	ft	n	n	n	<0.5	n	n	1
A15	nm	15	n	ft	n	n	n	<0.5	n	n	1
A15m	m	15	n	ft	n	n	n	<0.5	n	n	1
A20	nm	20	n	ft	n	n	n	<0.5	n	n	1
A20m	m	20	n	ft	n	n	n	<0.5	n	n	1
A25	nm	25	n	ft	n	n	n	<0.5	n	n	1
B10	nm	10	n	ft	n	n	n	<0.5	n	y	1
B15	nm	15	n	ft	n	n	n	<0.5	n	y	1
B15m	m	15	n	ft	n	n	n	<0.5	n	y	1
B20	nm	20	n	ft	n	n	n	<0.5	n	y	1
B20m	m	20	n	ft	n	n	n	<0.5	n	y	1
B25	nm	25	n	ft	n	n	n	<0.5	n	y	1
B25m	m	25	n	ft	n	n	n	<0.5	n	y	1
B30	nm	30	n	ft	n	n	n	<0.5	n	y	1
B30m	m	30	n	ft	n	n	n	<0.5	n	y	1
B35m	m	35	n	ft	n	n	n	<0.5	n	y	1
B40m	m	40	n	ft	n	n	n	<0.5	n	y	1
C15	nm	15	n	ft	n	n	n	<0.5	y	y	1
D15m	m	15	n	ft	n	n	n	>0.5	n	n	1
E10	nm	10	n	n	n	n	n	<0.5	n	n	1
E15	nm	15	n	n	n	n	n	<0.5	n	n	1
E20	nm	20	n	n	n	n	n	<0.5	n	n	1
E5	nm	5	n	n	n	n	n	<0.5	n	n	1
F15	nm	15	n	n	n	n	n	<0.5	n	y	1
F20	nm	20	n	n	n	n	n	<0.5	n	y	1
F80m	m	80	n	n	n	n	n	<0.5	n	y	1
G10	nm	10	y	n	n	n	n	>0.5	n	n	1
G15	nm	15	y	n	n	n	n	>0.5	n	n	1
G20	nm	20	y	n	n	n	n	>0.5	n	n	1
G25	nm	25	y	n	n	n	n	>0.5	n	n	1
G30	nm	30	y	n	n	n	n	>0.5	n	n	1
G30m	m	30	y	n	n	n	n	>0.5	n	n	1
G35	nm	35	y	n	n	n	n	>0.5	n	n	1

Guild	maturity	cara	3rd.claw	tuft	acc.hair	crib	comb	eye	scutes	scop	leg
G35m	m	35	y	n	n	n	n	>0.5	n	n	1
G55m	m	55	y	n	n	n	n	>0.5	n	n	1
H40	nm	40	y	n	n	n	n	>0.5	n	y	1
H50	nm	50	y	n	n	n	n	>0.5	n	y	1
H70	nm	70	y	n	n	n	n	>0.5	n	y	1
H80	nm	80	y	n	n	n	n	>0.5	n	y	1
I20	nm	20	y	n	n	y	n	<0.5	n	n	1
I25	nm	25	y	n	n	y	n	<0.5	n	n	1
I25m	m	25	y	n	n	y	n	<0.5	n	n	1
I30m	m	30	y	n	n	y	n	<0.5	n	n	1
J10	nm	10	n	n	n	n	n	<0.5	y	n	1
J10m	m	10	n	n	n	n	n	<0.5	y	n	1
J15m	m	15	n	n	n	n	n	<0.5	y	n	1
J5	nm	5	n	n	n	n	n	<0.5	y	n	1
J5m	m	5	n	n	n	n	n	<0.5	y	n	1
K15	nm	15	n	t	n	n	n	<0.5	n	y	1
K15m	m	15	n	t	n	n	n	<0.5	n	y	1
K20	nm	20	n	t	n	n	n	<0.5	n	y	1
K20m	m	20	n	t	n	n	n	<0.5	n	y	1
K25	nm	25	n	t	n	n	n	<0.5	n	y	1
K30	nm	30	n	t	n	n	n	<0.5	n	y	1
K30m	m	30	n	t	n	n	n	<0.5	n	y	1
K35m	m	35	n	t	n	n	n	<0.5	n	y	1
K40m	m	40	n	t	n	n	n	<0.5	n	y	1
K50	nm	50	n	t	n	n	n	<0.5	n	y	1
K80m	m	80	n	t	n	n	n	<0.5	n	y	1
M30m	m	30	n	t	n	n	n	<0.5	y	y	1
N10	nm	10	n	t	n	n	n	>0.5	n	n	1
N10m	m	10	n	t	n	n	n	>0.5	n	n	1
N15	nm	15	n	t	n	n	n	>0.5	n	n	1
N20	nm	20	n	t	n	n	n	>0.5	n	n	1
N20m	m	20	n	t	n	n	n	>0.5	n	n	1
O10	nm	10	y	ft	n	n	n	<0.5	n	n	1
P10	nm	10	y	n	n	n	n	<0.5	n	n	1
P10m	m	10	y	n	n	n	n	<0.5	n	n	1
P15	nm	15	y	n	n	n	n	<0.5	n	n	1
P20	nm	20	y	n	N	n	n	<0.5	n	n	1
P20m	m	20	y	n	N	n	n	<0.5	n	n	1
P25	nm	25	y	n	N	n	n	<0.5	n	n	1
P25m	m	25	y	n	N	n	n	<0.5	n	n	1
P30m	m	30	y	n	N	n	n	<0.5	n	n	1
P40	nm	40	y	n	N	n	n	<0.5	n	n	1

Guild	maturity	cara	3rd.claw	tuft	acc.hair	crib	comb	eye	scutes	scop	leg
P40m	m	40	y	n	N	n	n	<0.5	n	n	1
P45m	m	45	y	n	N	n	n	<0.5	n	n	1
P5	nm	5	y	n	N	n	n	<0.5	n	n	1
P5m	m	5	y	n	N	n	n	<0.5	n	n	1
Q30	nm	30	y	n	N	n	n	<0.5	n	y	1
Q35	nm	35	y	n	N	n	n	<0.5	n	y	1
S5m	m	5	y	n	N	n	n	<0.5	y	n	1
W20m	m	20	y	n	Y	n	n	<0.5	n	n	2
X10	nm	10	y	n	Y	n	y	<0.5	n	n	2
Y20m	m	20	y	n	Y	n	y	<0.5	y	n	2
Y5	nm	5	y	n	Y	n	y	<0.5	y	n	2
Y5m	m	5	y	n	Y	n	y	<0.5	y	n	2

Table A3: Table R, showing environmental variables by site. Time since burn is in months and temp refers to the mean temperature of the burn in °C.

site	treatment	burnt	time	temp
AMD	control	unburnt	6	30.5
AMD	standing	burnt	6	219.8
CAMD	coppiced	burnt	6	338
DA1	control	unburnt	6	27.2
DA1	coppiced	burnt	6	381.6
DA1	standing	burnt	6	280
RA2	control	unburnt	6	44.4
RA2	coppiced	burnt	6	442.2
RA2	standing	burnt	6	64.5
RLCL	control	unburnt	6	20.7
RLCL	coppiced	burnt	6	377.6
RLCL	standing	burnt	6	179.5
RS1	control	unburnt	6	48.5
RS1	coppiced	burnt	6	353
RS1	standing	burnt	6	291.2
WR2	control	unburnt	6	31.1
WR2	standing	burnt	6	57.9

site	**treatment**	**burnt**	**time**	**temp**
WR2	coppiced	burnt	6	177.8
AMD	control	unburnt	18	30.5
AMD	standing	burnt	18	219.8
AMD	coppiced	burnt	18	338
DA1	control	unburnt	18	27.2
DA1	coppiced	burnt	18	381.6
DA1	standing	burnt	18	280
RA2	control	unburnt	18	44.4
RA2	coppiced	burnt	18	442.2
RA2	standing	burnt	18	64.5
RLCL	control	unburnt	18	20.7
RLCL	coppiced	burnt	18	377.6
RLCL	standing	burnt	18	179.5
RS1	control	unburnt	18	48.5
RS1	coppiced	burnt	18	353
RS1	standing	burnt	18	291.2
WR2	control	unburnt	18	31.1
WR2	standing	burnt	18	57.9
WR2	coppiced	burnt	18	177.8
AMD	control	unburnt	30	30.5
AMD	standing	burnt	30	219.8
AMD	coppiced	burnt	30	338
DA1	control	unburnt	30	27.2
DA1	coppiced	burnt	30	381.6
DA1	standing	burnt	30	280
RA2	control	unburnt	30	44.4
RA2	coppiced	burnt	30	442.2
RA2	standing	burnt	30	64.5
RLCL	control	unburnt	30	20.7
RLCL	coppiced	burnt	30	377.6
RLCL	standing	burnt	30	179.5
RS1	control	unburnt	30	48.5
RS1	standing	burnt	30	291.2

site	treatment	burnt	time	temp
WR2	control	unburnt	30	31.1
WR2	standing	burnt	30	57.9
WR2	coppiced	burnt	30	177.8

Table A4: Table L for the RGS, showing guilds by sites. This is a very large data set, therefore for the purposes of this appendix it has been abbreviated by removing the data for the inner 78 guilds.

site	A10	A10m	A15	A15m	A20		W20m	X10	Y20m	Y5	Y5m
AMD	1	3	0	0	0	. . .	0	0	0	1	3
AMD	0	1	0	0	0	. . .	0	0	0	0	0
AMD	0	0	0	1	0	. . .	0	0	0	0	0
DA1	0	1	1	1	0	. . .	0	0	0	0	0
DA1	0	0	0	0	0	. . .	0	0	0	0	0
DA1	1	0	1	0	0	. . .	0	1	0	0	0
RA2	0	3	1	1	0	. . .	0	0	0	0	0
RA2	0	0	2	0	1	. . .	0	0	0	0	0
RA2	0	1	0	0	0	. . .	0	0	0	0	0
RLCL	0	0	0	0	0	. . .	0	0	0	0	0
RLCL	0	0	1	0	0	. . .	0	1	0	0	0
RLCL	0	0	2	0	0	. . .	0	1	0	0	0
RS1	1	0	0	0	0	. . .	0	0	1	0	0
RS1	1	0	0	0	0	. . .	0	0	3	0	0

site	A10	A10m	A15	A15m	A20		W20m	X10	Y20m	Y5	Y5m
RS1	0	0	0	0	0	. . .	0	0	0	0	0
WR2	0	1	0	0	0	. . .	0	0	0	0	0
WR2	0	0	0	1	0	. . .	0	0	0	0	0
WR2	2	0	0	0	0	. . .	0	0	0	0	0
AMD	5	1	0	0	0	. . .	0	0	0	0	0
AMD	2	0	2	0	0	. . .	0	0	0	0	1
AMD	1	0	1	0	0	. . .	0	0	0	0	0
DA1	1	0	1	0	0	. . .	0	0	0	0	1
DA1	0	0	1	0	0	. . .	0	0	0	0	0
DA1	0	0	1	0	0	. . .	0	0	0	0	0
RA2	0	1	0	0	0	. . .	0	0	0	0	0
RA2	0	0	1	0	0	. . .	0	0	0	0	0
RA2	0	0	2	0	0	. . .	0	1	0	0	0
RLCL	2	1	0	0	1	. . .	0	0	0	0	0
RLCL	5	0	6	2	0	. . .	0	0	0	0	0
RLCL	4	0	2	0	0	. . .	0	1	0	0	0
RS1	0	0	0	0	0	. . .	1	0	0	0	0
RS1	0	0	0	0	0	. . .	0	0	0	0	0
RS1	1	0	0	0	0	. . .	0	0	0	0	0
WR2	0	1	0	2	0	. . .	0	0	0	0	0

site	A10	A10m	A15	A15m	A20		W20m	X10	Y20m	Y5	Y5m
WR2	3	1	0	0	0	. . .	0	0	0	0	0
WR2	0	0	1	0	0	. . .	0	0	0	0	0
AMD	2	0	1	0	0	. . .	0	0	0	0	0
AMD	0	0	0	0	0	. . .	0	0	0	0	0
AMD	0	0	0	0	0	. . .	0	0	0	0	0
DA1	0	0	0	0	0	. . .	0	0	0	0	0
DA1	2	0	2	0	0	. . .	0	0	0	0	0
DA1	2	0	0	0	0	. . .	0	0	0	0	0
RA2	1	0	0	0	0	. . .	0	0	0	0	0
RA2	1	0	0	0	0	. . .	0	0	0	0	0
RA2	8	0	2	0	0	. . .	0	0	0	1	0
RLCL	0	0	1	0	0	. . .	1	0	0	0	0
RLCL	1	0	2	0	0	. . .	0	0	0	0	0
RLCL	1	0	1	0	1	. . .	0	0	0	0	0
RS1	0	0	0	0	0	. . .	0	0	0	0	0
RS1	0	0	1	2	0	. . .	0	0	0	0	0
RS1	0	0	0	0	0	. . .	0	0	0	0	0
WR2	0	0	0	2	0	. . .	0	1	0	0	0
WR2	0	1	1	0	0	. . .	0	0	0	0	0
WR2	0	0	1	0	0	. . .	0	0	0	0	0

Table A5: A list of spider families, their abundances, and guild used in the smoking spider experiments of Chapter Five. Guilds were assigned based on the system of Uetz, 1977.

Family	**Abundance**	**Guild**
Araneidae	13	Web
Araneidae (*Phonognatha graeffei)*	3	Web
Clubionidae	3	Free running
Corinnidae	2	Free running
Desidae	9	Free running
Gnaphoside	1	Free running
Lamponidae	1	Free running
Linyphiidae	1	Web
Lycosidae	6	Free running
Oxyopidae	4	Free running
Pholidae	3	Web
Salticidae	12	Free running
Sparrassidae	1	Free running
Tetragnathidae	4	Web
Theridiidae	15	Web
Thomisiidae	1	Free running
unknown	1	Free running