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THE EFFECTS OF WILDFIRE ON SMALL MAMMALS AND LIZARDS IN THE SIMPSON DESERT, CENTRAL AUSTRALIA

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A thesis submitted in fulfilment of the requirements for the
degree of Doctor of Philosophy

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This thesis is dedicated to my dear great uncle,
Peter Montgomery Whyte. Throughout our time together,
you have inspired me, encouraged my inquiring mind and
never faltered in your belief in me. A large part of your
enthusiasm is in this thesis, and you will always be
present in my heart.

ABSTRACT

Animals in arid central Australia have undergone widespread declines and extinctions over the past century, particularly small and medium-sized mammals. These losses have coincided with what appears to have been a sharp shift in the fire regime, from one dominated by many small scale burns to one dominated by infrequent yet intense and widespread wildfires. Previous work in the region has reported conflicting effects of fire on small mammals and lizards, but there have been few manipulative investigations to explore the likely reasons for observed post-fire responses. In this thesis I investigate the processes by which fire affects small mammal and lizard populations in the Simpson Desert, central Australia. My study began shortly after one of the largest wildfires in recent history swept across more than 2500 km^2 of the region, creating an ideal situation in which to analyse the effects of fire on resident vertebrate communities.

To characterise the effects of fire on vertebrates in a range of habitats, I first conducted a meta-analysis on the effects of fire on vertebrate diversity at a global scale. I tested initially for the main effect of fire before investigating the potential influence of fire type (wildfire or prescribed burn), taxon, ecoregion, and geographical location (hemisphere and continent). To account for fire-effects on local patch diversity and community assemblage composition, I measured the influence of fire on both alpha and beta diversity. The study revealed that, when analysed at a global scale, prescribed burns significantly increase alpha diversity, whereas wildfires have no effect. However, the effect size associated with prescribed burns was low and considerable variation was evident in fire responses within taxonomic, habitat and geographical groupings. Species assemblage composition (beta diversity) was also influenced primarily by fire type, with species assemblages more similar between burnt and unburnt habitats after prescribed burns than after wildfires.

I next compared the effects of prescribed burns and wildfires on the alpha and beta diversity of plants, mammals and lizards in my study region in central Australia. Conducting these two studies in close temporal succession eliminated the usual interactive effects of study location, study taxon, geographic variation and climate and presented a unique opportunity to directly compare the effects of these two fire types. I live-trapped small mammals and lizards and undertook vegetation surveys in burnt and unburnt habitat before and after both the prescribed burns and the wildfire. In line with the global perspective, I found that prescribed burns and wildfires had contrasting effects on alpha and beta diversity, that prescribed burns did not universally benefit biodiversity, and that the effects were taxon-dependent. In particular, the wildfire did not have the predicted effects on either the alpha or beta diversity of lizards.

I next explored the effects of the wildfire specifically on lizard populations. I investigated the role of multi-scale processes such as rainfall, food availability and regional land use histories in driving differential lizard responses to fire across broad spatial scales. I predicted that a rainfall gradient within the region affected by the wildfire would influence lizard responses to the fire by encouraging post-fire succession to proceed more rapidly in high-rainfall areas, and would be enabled in turn by more rapid vegetation recovery. I live-trapped lizards, measured rainfall, undertook vegetation surveys and sampled invertebrate abundance across burnt and unburnt habitat ecotones within three regional areas situated along a gradient of long-term annual rainfall. The study revealed that lizard community responses to wildfire were influenced primarily by region, but also that the trends did not relate to differences in rainfall or habitat as I had predicted. Regional differences in lizard assemblages related instead to food availability, and were also likely influenced by biotic interactions with predators and changes in land use.

Lastly, I experimentally investigated how prey behaviour changes in the post-fire environment under different levels of predation risk. I used native small mammals and introduced predators, the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*), as my model system. I used a combination of live-trapping and tracking methods, simple predator exclusion cages, and assays of small mammal foraging behaviour and activity based on the giving-up density (GUD) approach to investigate prey and predator behaviour. The results indicated that fox and cat activity was concentrated on burn ecotones and that small mammals foraged for longer in burnt environments when their risk of predation was experimentally reduced.

My findings suggest that fire effects on vertebrate diversity are context-dependent and that there is no ‘one size fits all’ approach that can be incorporated into land management practices, either at a global scale or at the regional scale of the Simpson Desert. My results highlight instead the range of biotic and abiotic factors that can interact with fire to produce unexpected post-fire successional trajectories and animal assemblages. Rainfall variability, grazing, predation and interspecific competition can all influence species responses to fire, either by acting on the regenerating vegetation or via direct effects on recovering animal communities. My research also indicates the urgent need for predator control in recently burnt habitats.

My research also highlights the absence of a current model to help predict the short and longer term effect of wildfire on lizards. In response to this gap, I propose a new state-and-transition model to describe lizard recovery after fire in hummock grasslands. The model accounts for species functional traits, along with key aspects of a disturbance regime including the interacting effects of rainfall, predation, interspecific competition and commercial grazing on lizard assemblages at any stage of post-fire succession. Inherent regional specificity in species assemblages, characteristic species rarity and their joint effects on lizard assemblages at each stage, are also accounted for.

My research is unique as I have addressed several topic areas that have not been previously investigated. A world-wide meta-analysis of the effects of fire on vertebrate diversity has not yet been conducted. Similarly, the opportunity to directly compare the effects of wildfire and prescribed burns on plant, mammal and lizard diversity is rare. This study is also one of the first to have used experimental manipulations to investigate the effect of predation by feral cats and foxes in post-fire habitats and to determine how this may influence small mammal movement and survivorship.

DECLARATION

I hereby declare that this is my own original work and that it contains no material previously published or written by another person, except where due acknowledgement is made. This work was carried out while I was enrolled as a student for the degree of Doctor of Philosophy in the School of Biological Sciences, The University of Sydney. This thesis has not been previously submitted for examination at this, or any other, university.

Louise Pastro

28 March 2013

PREFACE

This thesis is written in the style of a thesis by manuscript and therefore some repetition of the study rationale, aims and the site descriptions occurs among chapters.

Chapters 3, 4, 5 and 6 have each been submitted, or written for submission, as Pastro, Dickman and Letnic, and thus the term ‘we’ has been used throughout. American spelling is also used in these chapters due to publication in American journals.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisors, Chris Dickman and Mike Letnic. Chris, when I first approached you all those years ago with the hope of researching in the desert, I could never have imagined the dream project that would ensue! Thank you for welcoming me into your dynamic team and for your support and time throughout the tenure of my project. Your passion for research, your deep knowledge and understanding of desert ecosystems, your dedication and enthusiasm for field work in such a remote and sometimes hostile environment, and your boundless good nature, even in some of the trickiest field situations imaginable, are an inspiration. You have taught me about so much more than my thesis research throughout my candidature; my life is certainly richer for the time that I have spent in your lab. Mike, you have also contributed so much to my project, particularly in recent years as I have been analysing data and writing up. Your crash courses on statistics, ideas for analyses, and perspectives on results have been valuable contributions to each chapter in this thesis. Your continued encouragement to publish as I go has also been a key driver in the publication of several of my thesis chapters.

Other members of the Dickman Lab also provided essential support and guidance, especially during the early planning stages and field work components of my research. Glenda Wardle was instrumental in the early stages of my research, providing much hands-on support, advice on experimental design and statistics, and many a conversation around the lab table (or camp fire!) Aaron Greenville, Bobby Tamayo and Chin-Liang Beh each provided advice and know-how on all things “desert”, on topics as varied as identifying an unknown plant to changing a tyre on the side of a sand dune. You three were instrumental in helping me set up and run my field trips, organise my equipment, recruit volunteers and help trap my sites when I couldn’t get to them. I simply could not have done it without you! Similarly, my co-students Anke Frank, Tim Parratt and Max Tischler provided much support and shared many good times in the field.

Funding from a variety of sources helped to make this thesis a reality. The Australian Research Council (to C.R.Dickman) provided the bulk of funding for much of the field work, and further funding for field work was received from the Wildlife Protection Society of Australia, the Zoological Society of New South Wales (Ethel Mary Read Research Award) and the University of Sydney Postgraduate Research Support Scheme. Funding from the Ecological Society of

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A big thank-you to Greg Woods, the manager of Carlo Station, and Australian Bush Heritage for allowing me to research on Ethabuka and Cravens Peak Reserves. All ABH station managers (Alistair Dermer and Karen Harrland, Mark and Nella Lithgow, Scott and Sajidah Morrison, Len and Jo Rule) provided great hospitality and many a cool drink to myself and my volunteers on many occasions.

A big thank-you also to members of the Bedourie Community. In particular, Jim Smith, owner of the Bedourie Hotel – you welcomed myself and my band of volunteers at all hours of the day and night, cooking us delicious meals, providing use of your shower, and an undercover area to sleep when it rained. The day you flew me over the desert in your light plane will stay etched in my mind forever, as will the many hours that I have spent in your pub partaking in John Denver sing-a-longs and juke-box country-and-western discos. Thank-you also to the many other kind and caring residents of Bedourie, for offering cold drinks, a clean bathroom or use of the internet on many occasions.

This research would not have been possible without the help of many volunteers, who braved 40-45°C temperatures for weeks at a time, flies, spiders, snakes, tyre punctures, spinifex spikes and very long periods between baths, to share some fantastic and memorable times in the field. The Simpson Desert is an amazing and special place, and I feel so lucky to have shared it with such a capable (and exceedingly good-natured!) group of volunteers. In particular, Jon Creenaune and Robin Roestart provided endless enthusiasm and help as ‘deputies’ on many trips to the field. A big thanks also goes to Liz Cameron who was irreplaceable in the lab - your keen knowledge of invertebrates, willingness to train myself and others, and weekly invertebrate sorting sessions were invaluable in helping me wade through a seeming mountain of invertebrate pitfall samples. Wendy Cheng and Jessica Low also provided much-needed assistance sorting invertebrates.

A big thanks also goes to the Hochuli Lab. Your weekly lab meetings kept me sane, stimulated, laughing, and thinking about something other than the desert for at least one hour a week! Dieter Hochuli, Fran van den Berg, Mat Crowther, Petah Low, Lizzy Lowe, James Schlunke and Shawn Wilder - not only did you provide feedback on earlier drafts of several chapters of this thesis, but I now have a very real interest in all things invertebrate, and a somewhat passable knowledge of soccer, which is entirely creditable to you! Jennifer Anson, Miguel Bedoya Perez, Lindsey Gray and many other Sydney Uni postgrads also provided support and camaraderie between trips, at conferences, and during the analysis and write-up stages.

Outside of Uni, there are also many people that helped to make this possible. My employer, Focus Press, and my endlessly patient and flexible bosses David Fuller and Alan Davis – your willingness to support me through many iterations of 2-day weeks, 3- day weeks, 4-day weeks and full time work was second to none. The support of a steady and predictable income stream took a lot of the stress out of the later stages of my thesis, and provided a very welcome distraction. The support of my friends, particularly in these past few months, has also been fantastic. Dina Bullivant, Adam Dalgarno, Kate Hancock, Lea Shea, Angela Sinnett and Zinate Wehbe – your endeavours to understand what it is that I do, your acceptance of my recent disappearance into 'PhD Land', and your ongoing encouragement have been wonderful.

My family have also been a key part of this journey. Mum and Dad, Emma and Tom – your continued support over the past eight years has been exceptional. From providing countless frozen dinners and other practical assistance in the early days, to Emma and my more recent Sunday night "debrief and prepare for the week ahead" sessions, your continued encouragement and belief in my ability to achieve my goals has been second to none. Even over the past few months when I have become the increasingly absent family member, you have continued to provide support from afar. Tom – you had a good solution to this when you decided to move in with me instead! To think that as I submit this thesis, mum will be celebrating my milestone with her colleagues in their own "thesis submission" event; it makes me realise that as far as family support goes, I could not have asked for anything more.

And lastly, I could not have done any of this without the love and support of my partner, Kim Lazzarini. You supported my decision to go back to the PhD after a mid-project break, you never faltered in your belief that I could, and would, finish, and you have brought me back down to Earth on so many occasions when the finish line seemed to be so far away. You have enabled this thesis in so many ways, taking on a myrid of roles including cook, housekeeper, shopper, dog walker and social coordinator (!) as I drew closer to handing in. You listened to my stories and rants and patiently reminded me time and again that there really is "life after PhD" ☺ This thesis would certainly not have been the same without you.

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CHAPTER 1

GENERAL INTRODUCTION

A dingo (*Canis lupis dingo*) camouflaged among the sandhills of the Simpson Desert (L. Pastro)

PREFACE

This thesis describes the effects of wildfire on mammal and reptile populations in the Simpson Desert, central Australia. Over the past 100 years, widespread extinctions and declines have been observed in many arid zone species, particularly small and medium-sized mammals (Johnson 2006, McKenzie et al. 2007, Saunders et al. 2010). These have co-occurred with a shift in fire patterns from a regime characterised by many small-scale burns to one dominated by intense and widespread wildfires (Burbidge and McKenzie 1989, McKenzie et al. 2007, Woinarski et al. 2010). Previous work has revealed conflicting effects of fire on small mammals and lizards in the region and there have been few manipulative investigations to explore the likely reasons for observed post-fire responses.

My thesis focuses on untangling the effect of wildfires on arid zone small mammals and lizards by investigating the direct effects of a broadscale wildfire in addition to the interacting effects of a range of biotic and abiotic processes such as predation, rainfall and regional heterogeneity. A broadscale wildfire affected a large portion of the study area shortly before this study commenced, providing ideal conditions to investigate subsequent community recovery.

In this first chapter I review the role of fire in the evolution of global vegetation communities and in the development of current day Australian vegetation biomes. I review historical fire regimes, particularly in the central deserts region, and discuss changes to these regimes following human settlement, European settlement, and the potential linkages between these changes and the widespread declines in small mammal fauna that have occurred throughout the region. I also review the potential interactions between these effects and processes such as rainfall, introduced predators, introduced herbivores, and climate change. I introduce the study region and review the known responses of plants, mammals and reptiles in the study region to wildfire. Lastly, I introduce the aims and scope of this thesis and the thesis structure. A detailed description of the study area, climate, animal assemblages and regional fire history is provided in Chapter 2.

1.1 FIRE AND THE EVOLUTION OF GLOBAL ECOSYSTEMS

Evidence of wildfire first appeared in the fossil record 420 million years ago, shortly after the evolution of terrestrial plants (Glasspool et al. 2004, Bowman et al. 2009). Since that time, wildfire has played a critical role in shaping the evolution and distribution of flora and fauna around the globe (Keeley and Rundel 2005, Beerling and Osborne 2006, Glasspool et al. 2006). For example, increasing incidence of fire in the late Miocene (6-8 MA) accelerated the replacement of forests and woodlands across much of the Americas, Africa and Asia with fire-prone communities such as C_4 grasslands, shrublands and boreal forests (Bond et al. 2005, Keeley and Rundel 2005).

Palaeo-fire records indicate that much of this historical burning was driven by fluctuations in climate and atmospheric oxygen levels (Scott and Glasspool 2006, Lynch et al. 2007, Daniau et al. 2010, Mooney et al. 2011, Mooney et al. 2012). Periods in which fires were frequent were typically characterised by a seasonally fluctuating climate that involved sequential periods of high biomass production, low rainfall, and monsoon weather (Keeley and Rundel 2005, Vanniere et al. 2008). These periods were also often characterised by reduced levels of atmospheric CO_2 that limited tree recruitment and allowed further ingress of flammable C_4 grasses (Beerling and Osborne 2006).

More recently, fire arising from anthropogenic origins has played a key role in shaping the structure and function of modern global ecosystems (Laris 2002, Sheuyange et al. 2005, Stephens et al. 2007), especially in the Southern Hemisphere (Bond et al. 2005, Bowman and Haberle 2010, McWethy et al. 2010, Fox 2011). For example, it is thought that Polynesian settlers in New Zealand transformed 40% of the original forest cover to grassland and fern-shrubland by using fire shortly after colonization around A.D. 1280 (Bowman and Haberle 2010). Today, grasslands dominate many regions that are climatically suitable for forests, particularly in the Southern Hemisphere (Bond and Keeley 2005, Bowman and Haberle 2010). Additional watershed changes instigated by frequent fires, such as erosion and the introduction of plant species, also further prevent the return of forest even in the absence of fire (McWethy et al. 2010). Figure 1.1 shows the global distribution of vegetation biomes a) at climate potential; and b) versus actual vegetation. The effect of frequent fire on vegetation distribution is evident when fire-suppressed high rainfall regions (dominated by forests) are compared with high rainfall regions where fire is frequent (dominated by C_4 grasses and shrubs).

Modern wildfires incur significant economic losses due to their impacts on forestry, non-timber forest products and agriculture. They can also have serious impacts on human health via soot and smoke hazes, which are thought responsible for increased hospital admissions, increased mortality and lowered infant and foetal survival in affected regions, particularly in the developing world (Kinnaird and O'Brien 1998, Lohman et al. 2007, Bowman et al. 2009).

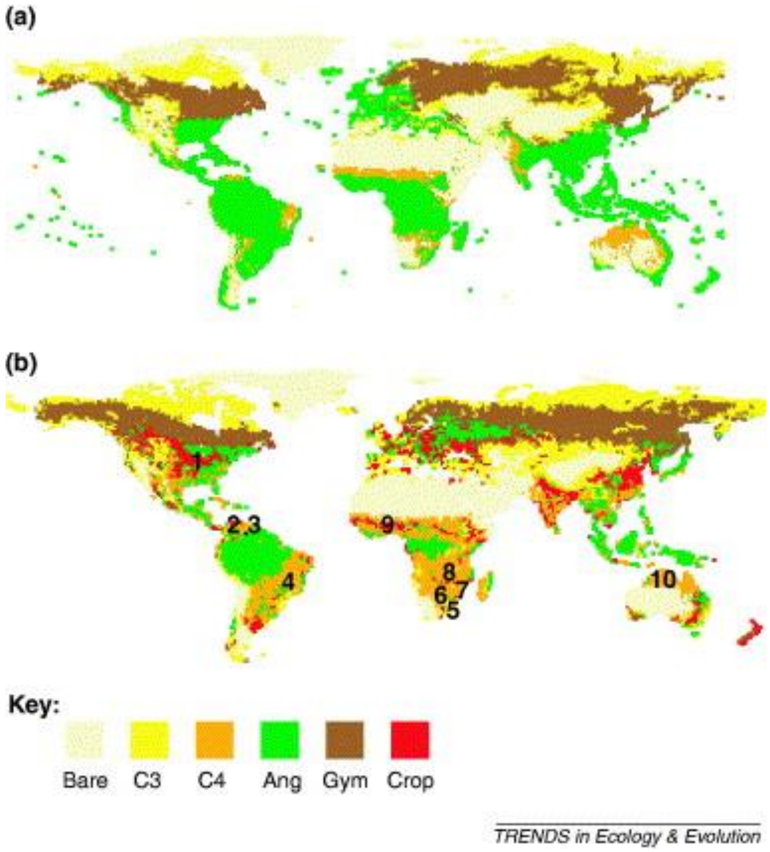

Figure 1.1 The global distribution of vegetation biomes a) at climate potential; and b) versus actual vegetation. Biomes are coded as follows: C3 grasses or shrubs; C4 grasses or shrubs; Angiosperm trees (Ang); Gymnosperm trees (Gym); Crops. The numbers indicate sites where fire has been excluded for several decades. Source: Bond and Keeley (2005).

1.2 FIRE AND THE EVOLUTION OF AUSTRALIAN ECOSYSTEMS

In Australia, charcoal and pollen extracted from paleoenvironmental records such as swamp, lake and marine sediments have allowed the construction of fire histories dating back to the start of the Tertiary (65 MA; Mooney et al. 2012). As with fire incidence around the globe, the occurrence of fire during the early Tertiary was linked closely to climatic fluctuations, with cold intervals characterised by less fire and warm intervals by more fire (Mooney et al. 2011). Accordingly, fire activity increased throughout the later part of the Tertiary as precipitation decreased and climatic variability increased (Kershaw et al. 2002, Lynch et al. 2007, Mooney et al. 2011). Very little fire activity occurred throughout the more recent Quaternary period (1.6 million years ago until present) until the most recent glacial/interglacial cycle (110,000 to 10,000 years ago). At this time, fire activity became particularly pronounced throughout drier interglacial periods and in times of extreme climate change (Power et al. 2008, Daniau et al. 2010, Mooney et al. 2011, Mooney et al. 2012).

Frequent fires throughout this time encouraged the evolution of fire-prone landscapes on all vegetated continents (Bradstock et al. 2002, Bond and Keeley 2005). These fires disrupted the reproductive rate of slow growing species and promoted species that were able to reproduce quickly and survive fires (Allan and Southgate 2002, Bowman et al. 2004, Bird et al. 2008). Adaptive traits such as fire tolerance and survival followed by resprouting, low flammability, rapid growth to reproductive maturity, fire-stimulated seed fall and fire-promoted germination were favoured and are now common features in many families of Australian plants (Hodgkinson and Griffin 1982, Bowman 1998, Enright et al. 1998, Pausas and Bradstock 2007).

Frequent fire events also influenced the distribution of vegetation communities. For example, a sharp increase in the number of fires between 5 and 8 MA corresponded with the contraction of *Nothofagus* rainforest and the expansion of Myrtaceae-dominated wet sclerophyll and open forest across much of Australia (Kershaw et al. 2002). Fire has since impacted on virtually all Australian ecosystems, with the close interrelationship between fire and climate interacting to create complex geographical and historical patterns in both vegetation and fire regimes across the continent (Gill et al. 1981, Sutherland and Dickman 1999, Orians and Milewski 2007, Bowman et al. 2012, Bradstock et al. 2012).

1.3 FIRE IN ARID AUSTRALIA

Suitable climatic conditions meant that much early burning in Australia occurred throughout the centre of the continent in arid and semi-arid grassland and shrublands (Suijdendorp 1981, Allan and Southgate 2002, Bradstock et al. 2002, Greenville et al. 2009, Mooney et al. 2011, Morton et al. 2011). Today, these regions cover close to one third of the Australian landmass and are characterised primarily by fire-prone ecosystems that coevolved closely with fire (Nano et al. 2012). The extent of the Australian arid zone and the major vegetation formations that characterise it are indicated in Figure 1.2.

As shown in Figure 1.2, the central Australian region is characterised primarily by fire-prone perennial grasses of the genus *Triodia*, which is commonly known as spinifex. Spinifex grasslands are highly combustible due to the dry, sclerophyllous construction of the individual plants, their flammable resin content, the retention of dead biomass and the close proximity of neighbouring hummocks in mature grasslands. Fire fronts in these regions move rapidly, consuming individual hummocks and jumping between neighbouring hummocks, resulting in some instances in the almost complete destruction of above-ground vegetation (Winkworth 1967, Burrows et al. 1991). Spinifex fires are largely wind-driven but are also influenced by temperature, humidity, precipitation and natural firebreaks (Burrows et al. 1991). High perennial biomasses, slow decomposition rates and high carbohydrate levels in plant tissues further render spinifex grasslands as particularly fire prone (Burrows and Christensen 1990, Lazarides 1997, Allan and Southgate 2002, Orians and Milewski 2007, Morton et al. 2011).

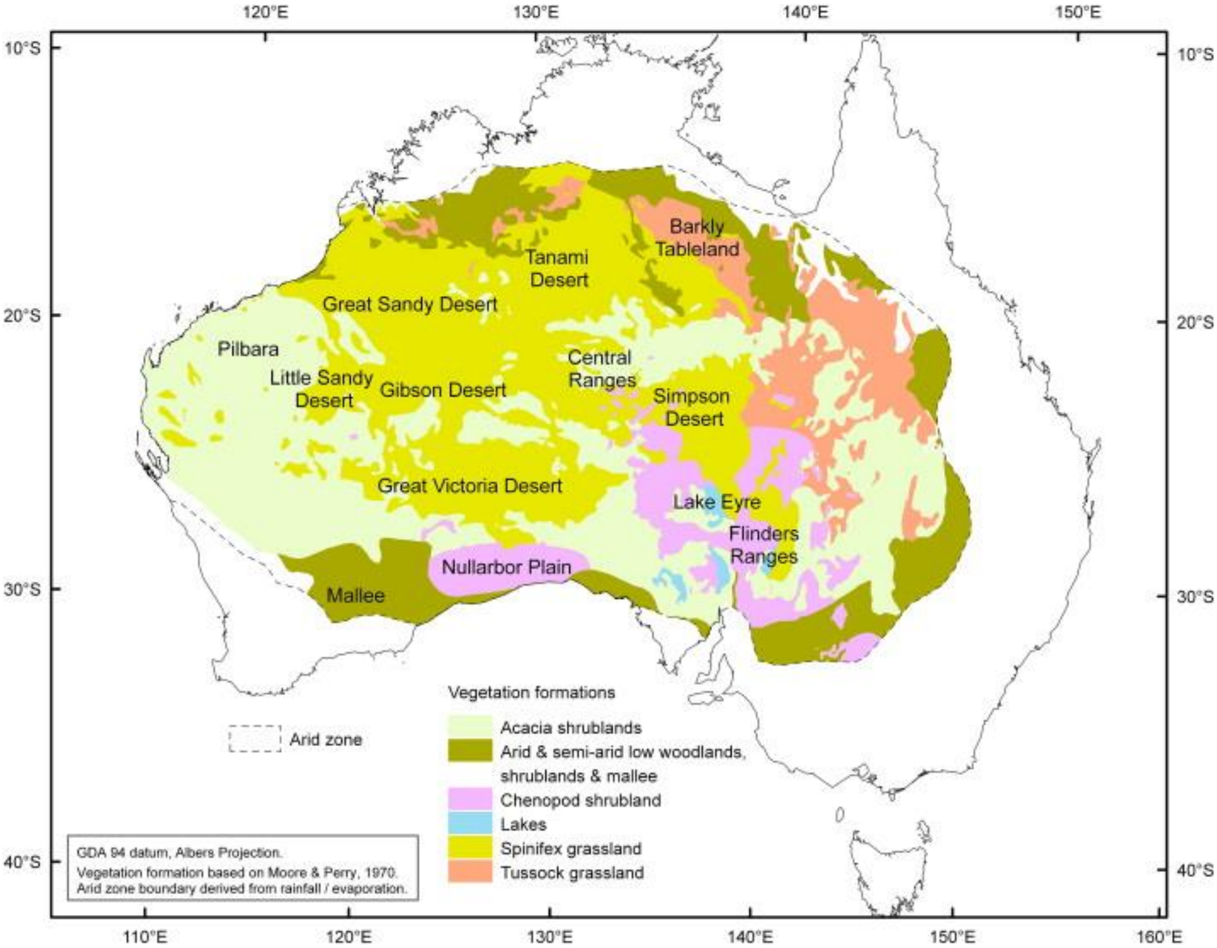

Figure 1.2 Major vegetation formations and desert locations in the Australian arid and semi-arid zone. Source: Morton et al. (2011).

1.3.1 Early anthropogenic burning

Peaks in charcoal at about the time of Aboriginal settlement (50 ±10 ka; Bird et al. 2004) have been long thought to indicate early Aboriginal burning practices (Singh et al. 1981, Kershaw 1986, Kershaw et al. 2007). This line of thinking also accords with hominid use of domestic fire in other parts of the world, which began 50,000-100,000 years ago (Bar-Yosef 2002).

Aboriginal settlement certainly provided a powerful new ignition source which changed the pattern of burnt and unburnt patches across the central Australian landscape (Bowman et al. 2012). Whilst pre-settlement wildfires were characteristically large and intense, burning under Aboriginal land tenure was characterised by smaller, less intense controlled fires. This burning regime created a heterogeneous landscape that was composed of a fine-grained mosaic of uniquely-aged vegetation patches (5 – 10 km^2). Figure 1.3 shows a graphical representation of the likely change in landscape heterogeneity instigated by Aboriginal burning practices. The change in the extent and patchiness of burnt habitat between historic wildfire regimes and subsequent Aboriginal burning practices is clear.

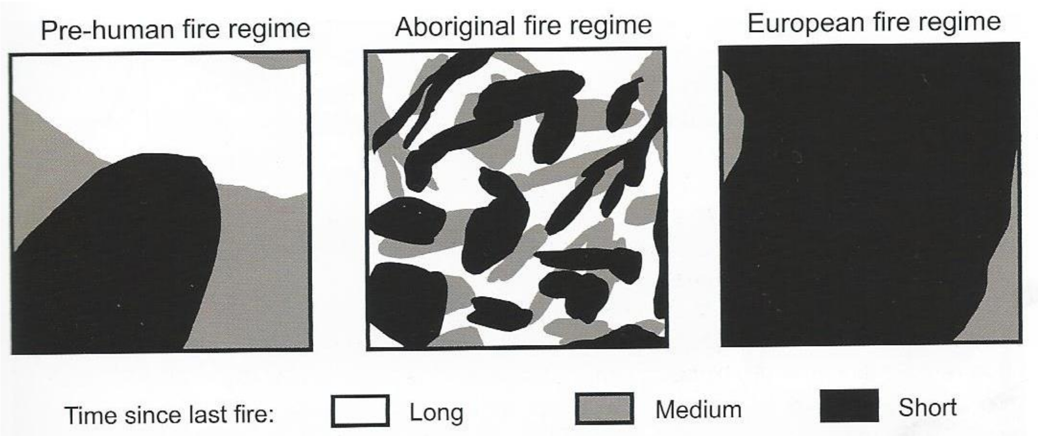

Figure 1.3 Graphical representation of the likely changes in the spatial scale and frequency of fires in a typical Australian landscape. In the pre-human period, fires were typically started by lightning, they were infrequent, and they burnt over large spatial scales. During Aboriginal land tenure, fires were frequent and small in scale, creating a fine-scale habitat mosaic. During the European fire regime, fires were of a frequency similar to the previous Aboriginal period however they burnt over much larger areas, thus eliminating any existing habitat mosaic. Source: Bowman et al. (2012).

The mosaics created by Aboriginal burning practices were both spatially and temporally dynamic. They are thought to have benefited plant and animal communities by increasing structural diversity and providing a variety of habitat and food resources that likely facilitated mammal and reptile diversity (Masters 1993, 1996, Pianka 1996, Letnic 2003, Letnic and Dickman 2005). Mammalian herbivores were able to forage on the palatable post-fire herbs and grasses (Suijdendorp 1981, Letnic et al. 2004) whilst remaining close to nearby long-unburnt spinifex habitat for shelter (Bolton and Latz 1978, Lundie-Jenkins et al. 1993). The fire mosaics are also thought to have benefited highly specialised lizard assemblages by providing a variety of habitat types at different stages of post-fire recovery (Pianka 1992, Pianka 1996).

Patch-burning also protected stands of fire sensitive vegetation such as mulga (*Acacia aneura*) through the creation of firebreaks (Allan and Southgate 2002).

Despite the prolific use of fire by Aborigines, recently analyses using novel techniques have suggested that this is unlikely related to changes in vegetation across the continent. Frequent use of fire by Aborigines has previously been thought to have encouraged the diversification of fire adapted species across the continent (Singh et al. 1981, Kershaw 1986, Turney et al. 2001b, Kershaw et al. 2002, Black and Mooney 2006, Kershaw et al. 2007, Lynch et al. 2007) and even to have helped drive the increasing aridification of the climate (Miller et al. 2005). However, recent analyses of the palaeo-fire record, combined with new techniques such as calibrated molecular phylogenies (e.g. Crisp et al. 2010) show no correlation between intervals of increased human activity and intervals of high biomass burning (Mooney et al. 2011, Bowman et al. 2012). In addition, a number of individual records (e.g. Stevenson and Hope 2005) have also shown that changes in vegetation at around this time are independent of either changes in fire or of human activity.

Thus although the Aborigines used fire skilfully and frequently, they likely did not have strong impacts on Australasian fire regimes or any bearing on ecological changes in the Late Pleistocene or the evolution and diversification of fire-adapted flora across the continent (Mooney et al. 2011, Mooney et al. 2012). However they may still have had some impact on vegetation distribution patterns and species' ranges (Bowman et al. 2012) and the mosaic of small-scale burns they created likely reduced the spread of wildfires (Bird et al. 2012).

1.3.2 20th Century wildfires and coincident animal declines

Aboriginal patch-burning practices largely ceased across much of the continent with the arrival of European pastoralists. In the absence of a fine scale habitat mosaic, the landscape increasingly had no protection from broadscale wildfires and the incidence of these events increased markedly. Ignited from lightning strikes during the spring and summer months, these wildfires burnt in excess of 1000 km^2 after adequate fuel buildup (Griffin et al. 1983, Griffin et al. 1993, Latz 1995, Allan and Southgate 2002). Evidence from the available literature and Landsat imagery indicates that extensive wildfires occurred throughout the central Australian arid zone in 1917/18, 1951, 1974/75 and 2001/02 (Letnic and Dickman 2006).

Wildfires homogenise the habitat mosaic that existed previously, replacing the matrix of vegetation with expansive burnt areas, which regenerate to become stands of similarly-aged spinifex (Burrows and Christensen 1990, Burrows et al. 1991, Letnic et al. 2004, Burrows et al. 2006, Edwards et al. 2008, Bird et al. 2012). In 1953, for example, the average size of burnt patches in the Western Desert was 34 ha. By 1973, some 11 years after Aborigines began to leave the land, the small-grained mosaic of burnt patches had been replaced by large tracts of burnt or unburnt land, and the size of the average fire scar had increased to over 32,000 ha (Burrows and Christensen 1990). Today, there is still a marked difference in burn patch size between anthropogenic and non-anthropogenic landscapes in the Western Desert, with the average patch size increasing significantly from 58 ha to 189 ha between Aboriginal-managed and non-managed landscapes (Bird et al. 2008).

This shift in fire regime was accompanied by widespread animal declines in arid and semi-arid regions. More than one third of mammal species in the arid zone has become extinct in the past fifty years and the region is now home to more than half of Australia's currently-endangered species (Burbidge et al. 1988). Many of these mammals were small- to medium-sized, weighing 35-5500 g; a weight range which has subsequently become known as the Critical Weight Range (CWR; Burbidge and McKenzie 1989). Mammals in the CWR include rodents, carnivorous dasyurids, omnivorous bandicoots and herbivorous kangaroos. Early European collecting expeditions, such as the Horn Expedition in the 1890s and Finlayson's expeditions in 1936 and 1940 were the last to collect many of these species, including the inland burrowing bettong (*Bettongia lesueur*) and the long-tailed hopping mouse (*Notomys longicaudatus*; Baynes and Johnson 1996, Gibson and Cole 1996, Kerle and Fleming 1996).

The increase in wildfire incidence is thought to have encouraged animal extinctions via the collapse of the fine-grained habitat mosaic across much of the landscape (Burbidge and McKenzie 1989, Dickman et al. 1993, McKenzie et al. 2007, Johnson and Isaac 2009, Woinarski et al. 2010). Many species, such as the rufous hare-wallaby (*Lagorchestes hirsutus*; Lundie-Jenkins 1993), utilised the habitat mosaic for foraging and shelter and, in the absence of a habitat mosaic, access to food and mates would have been limited (Letnic and Dickman 2005, Green and Sanecki 2006, Kodandapani et al. 2008, Pelegrin and Bucher 2010). The homogenised habitat would also no longer have provided for the highly specific habitat requirements of many arid zone lizard species, particularly where dense vegetation was required for shelter, thermoregulation and foraging (Pianka 1996, Letnic et al. 2004, Bird et al. 2012).

Despite such acute impacts, it is unlikely that wildfires alone caused the observed animal declines. Recent research has highlighted the importance of concomitant processes that influence arid ecosystems and have likely interacted with wildfire events to produce the observed animal declines. Three processes that have been identified as central to animal declines in arid land systems are variations in rainfall, introduced predators and introduced herbivores. I next discuss the relative interactions between wildfire and each of these processes, along with a review of the likely impacts of climate change on wildfire incidence and impacts.

1.4 INTERACTIONS BETWEEN WILDFIRE AND OTHER PROCESSES IN ARID AUSTRALIA

1.4.1 Rainfall

Rainfall is the overwhelmingly dominant driver of arid systems (Letnic and Dickman 2010, Morton et al. 2011) and is a key process influencing both the incidence of wildfire events and post-fire ecosystem recovery. Wildfire events in central Australia are tightly coupled with interannual- and decadal-scale climate oscillations and the related periods of drought and high rainfall (Swetnam 1993, Kitzberger et al. 2007, Le Page et al. 2008). In particular, a period of rainfall-stimulated productivity is a key precursor for broad-scale wildfire events (Greenville et al. 2009). In addition to this, the period immediately following high rainfall is critical for wildlife conservation as grazing pressure is often increased due to re-stocking (Letnic et al. 2004) and predators increase in numbers (Dickman et al. 2010). The two climatic systems that influence wildfire incidence in Australia and the broader Southern Hemisphere region are the El Niño Southern Oscillation cycle (ENSO) and the Indian Ocean Dipole (IOD).

The El Niño Southern Oscillation cycle (ENSO) exerts a significant influence on wildfire incidence as the heavy rainfall and subsequent vegetative growth stimulated by a strong La Niña event can fuel widespread, intense wildfires in the dry El Niño phase of the ENSO cycle (Nicholls 1991, Letnic and Dickman 2006, Greenville et al. 2009). The cycle has particularly strong effects in arid and semi-arid regions where productivity and fuel accumulation are strongly limited by rainfall (Holmgren et al. 2006). The strength of an ENSO event is measured by the Southern Oscillation Index (SOI) which is calculated from the difference in air pressure between Darwin and Tahiti. Sustained negative values of the SOI (< - 8) often indicate El Niño episodes and sustained positive values (> 8) are associated with La Niña episodes (BOM 2013) . This coupling between ENSO and wildfire incidence occurs throughout much of the rest of the Southern Hemisphere, including Asia (Page et al. 2002, Fuller and Murphy 2006, Taylor 2010) and South America (Nepstad et al. 1999, Block and Richter 2000, Gonzalez and Veblen 2006).

In the Northern Hemisphere, the reverse occurs and wildfire events correspond with the drought conditions experienced during La Niña (Swetnam and Betancourt 1990, Kitzberger et al. 2001, van der Werf et al. 2004).

The Indian Ocean Dipole (IOD) involves an irregular cycle of warming and cooling sea surface temperatures between the western and eastern equatorial Indian Ocean (Saji et al. 1999). A positive IOD is characterised by anomalous cooling of sea surface temperatures in the eastern Indian Ocean and anomalous warming of sea surface temperatures in the western Indian Ocean and is associated with severe droughts and forest fires in Australia and the Eastern Asian region and heavy rainfall over east Africa (Black 2005, Cai et al. 2009, Taylor 2010). A combination of a positive IOD and a low index phase of ENSO further interact to cause intense and widespread fires in the Southeast Asian and Australian regions (Taylor et al. 1999, Saji and Yamagata 2003, O'Donnell et al. 2011).

Small to moderate post-fire rainfalls in arid Australia stimulate germination and growth in a variety of grasses and herbs. Heavy rainfall stimulates widespread germination and growth of ephemeral, annual and perennial plant species and the recruitment of shrubs and trees (Stafford Smith and Morton 1990, Orians and Milewski 2007, Letnic and Dickman 2010). This boom in primary productivity provides ample plant food resources to stimulate the recovery of small mammals and lizards in burnt areas, and many of these early-regenerating plant species are highly palatable to mammalian herbivores (Letnic et al. 2004). Typically, rodents exhibit strong and rapid population increases in response to rainfall events, although the responses of insectivorous dasyurid populations are usually quite muted (Dickman et al. 2001, Letnic and Dickman 2010). This is likely a function of their fixed breeding cycles and the flooding of their burrows by rain. A prolonged post-fire drought can delay the onset of recovery for many years.

1.4.2 Introduced Predators

Historical records indicate that cats (*Felis catus*) reached the Simpson Desert by 1883 (Winnecke 1884) and that foxes (*Vulpes vulpes*) reached the area in the early 20th century (Letnic and Dickman 2006). Small mammals in the arid zone are thought to have been particularly susceptible to predation by these introduced predators given that many native species were relatively predator-naïve and of a suitable size for hunting by cats and foxes (Dickman et al. 2000, Johnson 2006, McKenzie et al. 2007). Extinctions and declines followed the arrival of these predators on the mainland and offshore islands (Burbidge and Manly 2002, Johnson 2006, Saunders et al. 2010), whereas remnant populations still remain on islands that are free of these predators (Burbidge 1999). Today, predation by cats and foxes is still having major effects on the population dynamics and conservation of arid-dwelling mammals (Pavey et al. 2008, Letnic et al. 2009b, Moseby et al. 2009a, Read and Cunningham 2010, Kutt 2012).

Both prescribed burns and wildfires may compound the effects of predation by cats and foxes. These predators are highly efficient hunters in the absence of shelter provided by mature spinifex hummocks (Haythornthwaite and Dickman 2000, Letnic et al. 2005, Johnson 2006, Letnic and Dickman 2010, Yang et al. 2010) and recent evidence suggests that cats and foxes may move purposefully towards recently burnt areas (Kutt and Woinarski 2007, Legge et al. 2011, Andersen et al. 2012). There is mounting evidence that interactions between fire and predation have been key to the sharp decline of native mammals in northern Australian savannahs (Fisher et al. 2013) and recent studies suggests that this may be the case in arid spinifex grasslands also (Letnic et al. 2004, Letnic and Dickman 2006, Letnic and Dickman 2010). For example, the brush-tailed mulgara (*Dasycercus blythi*) has been found to persist in burnt habitats after fire in Uluru-Kata Tjuta National Park only to undergo subsequent population declines due to predation by foxes and cats (Körtner et al. 2007). However, there remains a paucity of studies that experimentally investigate the effects of predation by cats and foxes in burnt habitats and the sensitivity of native populations to the increased predatory risk.

1.4.3 Introduced herbivores

Cattle, camels (*Camelus dromedarius*) and rabbits (*Oryctolagus cuniculus*) can have negative impacts on mammal and lizard abundance and diversity in arid and semi-arid land systems (Morton 1990, Landsberg et al. 1997, James 2003, Driscoll 2004, Frank 2010, Read and Cunningham 2010). These introduced herbivores trample on vegetation and disturb refuge habitats, reduce invertebrate food sources, and destroy burrows and cryptogamic crusts (Eldridge 1996, James et al. 1999, Letnic 2004, 2007, Read and Cunningham 2010, Legge et al. 2011). They compete with native herbivores for forage and can prevent plant regeneration by browsing on seedlings, thus changing the quality and quantity of food available to small mammals and lizards.

These effects may be magnified when combined with wildfire events. Regeneration following fire is slower in heavily grazed areas, and introduced predators are more efficient hunters in heavily-grazed areas that are denuded of shelter and in which burrows have been destroyed, especially after fire. Watering points for cattle can serve to attract predators to heavily grazed regions (Brawata and Neeman 2011) and overgrazing during drought has been suggested to be one of main contributors to the extinctions of many arid-dwelling animals (Ludwig and Tongway 1996, Lunney 2001).

1.4.4 Climate change

Global wildfire incidence has increased on all vegetated continents over the past decade, and this has been linked to changes in climate including earlier melt and warmer springs (Westerling et al. 2006, Forsyth and Wilgen 2008). For example, the frequency, duration and seasonality of large wildfires in western United States forests increased markedly in the mid - 1980s (Westerling et al. 2006), and wildfires in Africa now occur every 2 - 5 years, compared with a return interval of 18 years in 1970 (Forsyth and Wilgen 2008). The frequency of deforestation fires in Indonesia and Brazil has also increased, and this increase has been found similarly to be climate dependent (van der Werf et al. 2008).

Wildfires also account for a significant proportion of global carbon emissions. They equate to a third of fossil fuel combustion and are characterised by significant year to year variability, making the effects difficult to predict (Ito and Penner 2004, van der Werf et al. 2004, van der Werf et al. 2006). The global warming projected to occur due to deforestation fires in particular is thought to likely increase extreme fire weather (Westerling et al. 2006), which will cause further spikes in carbon emissions (Marston et al. 1991). Wildfires also influence climate by altering the Earth's planetary albedo and radiative budget. The black carbon aerosols released in many biomass burns have strong solar radiation absorption properties (Ramanathan and Carmichael 2008) and the occurrence of fire in boreal habitats may increase albedo over time (Randerson et al. 2006)

The incidence, severity and scale of wildfires are expected to increase further in many parts of the globe under current climate change scenarios (Bowman et al. 2009, Pechony and Shindell 2010). This is particularly so if global mean temperatures increase by several degrees as suggested by many models (Scholze et al. 2006, Krawchuk et al. 2009). Global climate change will likely increase the risk of extreme fire events (Solomon et al. 2007), driving a shift towards a temperature-driven global fire regime to create an unprecedented and highly fire-prone environment (Pechony and Shindell 2010). In Australia, palaeo-fire records indicate that the predicted increases in temperature during the 21st century (mean annual increases of ≥2° C with medium emission scenarios by 2070; CSIRO and Australian Bureau of Meterology 2007) will lead to a rapid increase in biomass burning (Mooney et al. 2012). There is no discernible lag between rapid climate changes during the last glacial period and the response of fire to these changes (Mooney et al. 2011) which provides an imperative for further research in this area. Figure 1.4 shows the potential aridification of the climate under three climate change scenarios over the coming six decades; each of these scenarios is likely to have serious effects on fire incidence, intensity and scale. The evolutionary consequences of the current rapid changes to fire incidence remain uncertain but the available evidence suggests that land managers should be preparing for broad scale ecological changes (Bowman et al. 2012).

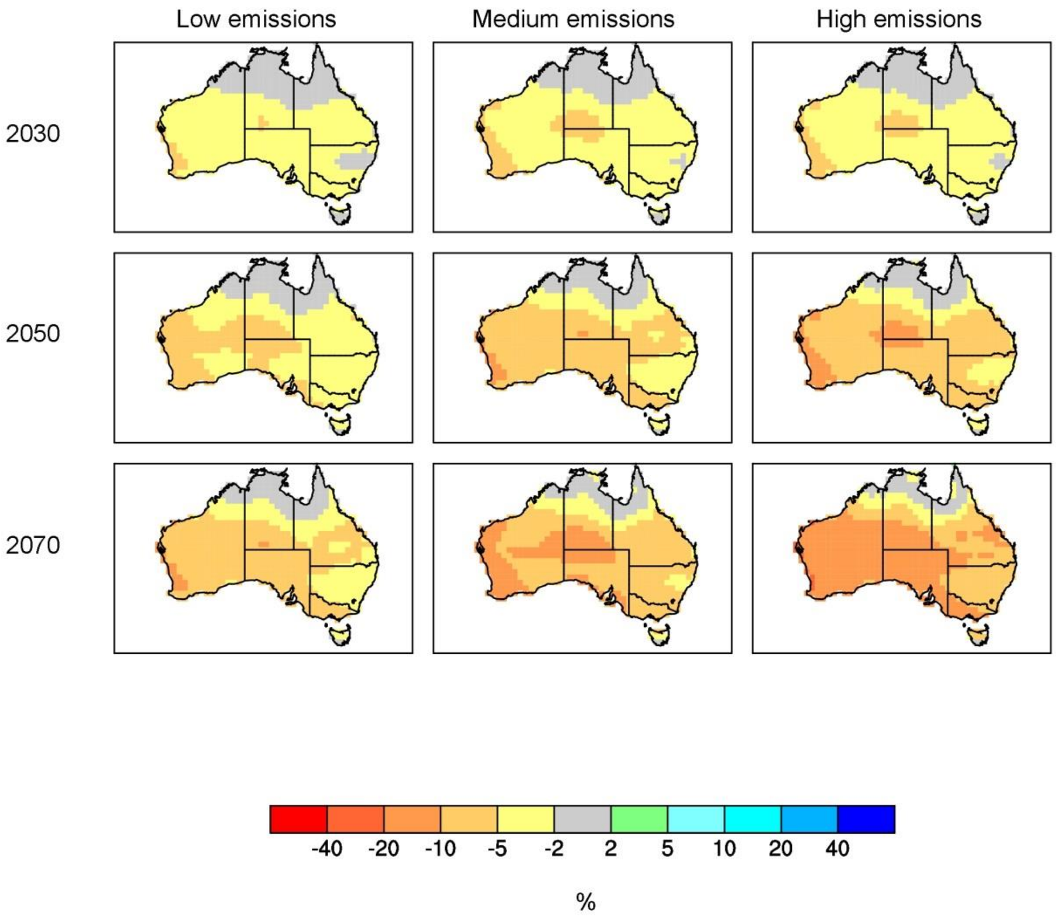

Figure 1.4 The effect of three potential climate change scenarios on rainfall (indicated as a percentage change) over the coming six decades. Projections are given relative to the period 1980–1999. Source: CSIRO and the Australian Bureau of Meteorology (2007).

1.5 MODERN DAY RESPONSES OF DESERT PLANTS, SMALL MAMMALS AND LIZARDS TO WILDFIRES

Given the prevalence of wildfire in Australian arid regions and its current and potential impacts on biological diversity, a sound understanding of the effects of fire on biota is essential. I next provide a summary of known facts and knowledge gaps relating to the effects of wildfire on desert plants, small mammals (< 150 g) and lizards. I have restricted my discussion of mammals to the small mammals group as this is a diverse group and species' responses to, and recovery after, wildfire are not well understood. Small mammals are also a focus of research for this thesis.

1.5.1 Plants

Fire in spinifex grasslands promotes plant diversity through space creation and nutrient release (Pausas and Bradstock 2007, Turner et al. 2008, Morton et al. 2011). New spinifex plants germinate readily from seed following the first effective post-fire rainfall (Suijdendorp 1981, Allan and Southgate 2002) or, depending on the species, re-sprout readily from their roots (Edwards et al. 2008). Before spinifex grows to become the dominant vegetation type, the vegetation in burnt areas is characterised by young spinifex plants along with a diverse range of annual grasses after summer rain and forbs after winter rain (Suijdendorp 1981). Common post-fire grasses include *Aristida contorta*, *Eragrostis eriopoda* and *Eriachne aristidea* (Letnic et al. 2004). These grasses can germinate and produce seed within two months of burning if substantial summer rainfall is received (>50 mm; Letnic et al. 2005). The time taken for spinifex to become the dominant vegetation post-fire depends on the species, location, cumulative rainfall since the last fire, and normally takes in excess of 5 years (Allan and Southgate 2002).

Wildfires can negatively affect fire-sensitive vegetation, such as mulga (*Acacia aneura*). Traditionally protected by Aboriginal burning practices, stands of mulga have no protection against wildfires now that small scale patch-burning has ceased in many regions. As a result, mulgas have been significantly impacted by the recent rises in wildfire activity. In one specific example, an area of 8.2 km^2 of mulga shrubland in the Tanami Desert subregion was reduced to 2.2 km^2 after wildfire activity between 1984 and 1996 (Allan and Southgate 2002).

1.5.2 Small mammals

Fire in hummock grasslands appears to cause little direct small mammal mortality, as animals are generally able to take cover in burrows (Reid et al. 1993, Southgate and Masters 1996, Letnic 2003). Studies conducted following summer wildfires demonstrate a general reduction in total mammal capture rate and species richness in the first year following fire (Southgate and Masters 1996, Letnic and Dickman 2005, Letnic et al. 2005).

Small mammal assemblages in the arid and semi-arid zones generally correlate poorly with structure variables indicative of vegetation succession or habitat type (Masters 1993, Southgate and Masters 1996, Paltridge and Southgate 2001). This offers little evidence for the existence of a predictable post-fire succession such as that observed in coastal woodland habitats of eastern Australia (Fox 1982). Although some species such as *Pseudomys desertor* and *Ningaui ridei* appear to prefer the dense spinifex of long-unburnt areas (Coventry and Dixon 1984, Masters 1993, Letnic et al. 2004, Letnic and Dickman 2005) other species such as *Notomys alexis*, *Sminthopsis youngsoni* and *Pseudomys hermannsburgensis* do not show a consistent preference for recently burnt or long unburnt habitats and their responses vary both within and between studies (Masters 1993, Letnic et al. 2004, Letnic and Dickman 2005, Kelly et al. 2011). *Sminthopsis hirtipes* is the only species that has been observed to consistently prefer regenerating areas (Masters 1993).

Recent research has indicated that the fluctuating post-fire responses of small mammals more likely indicate a life history that is focused towards the location and exploitation of resource-rich refuges (Predavec 2000, Dickman et al. 2010, Dickman et al. 2011, Letnic et al. 2011). Resource patches are transient and often scattered widely across the landscape, however many central Australian small mammal species are nomadic which facilitates their utilisation of habitat mosaics and ability to make long-distance movements towards areas of increased productivity (Dickman et al. 1995, Letnic 2002, Haythornthwaite and Dickman 2006b, Dickman et al. 2011). This transiency is supported further by life history characteristics such as the absence of permanent burrow construction in most small dasyurids (Dickman et al. 1995). In the post-fire environment, utilisation of resource-rich patches may interact with factors such as habitat type and regeneration age, rainfall, food resource availability and predation risk to determine the post-fire movements of many species (Masters 1993, Predavec 1994, Predavec and Dickman 1994, Southgate and Masters 1996, Letnic et al. 2004).

To account for this complex interplay of variables, Letnic et al. (2004) developed a state-and-transition model which does not assume a unidirectional response to fire. The model was developed further by Letnic and Dickman (2010) and is shown in Figure 1.5. The model starts with State 0, which occurs shortly after wildfire and in which all small mammals are rare. State I is reached as the numbers of insectivorous dasyurids such as *Sminthopsis* spp. and *Ningaui ridei* increase following rainfall-stimulated increases in their food sources. In State II, vegetation has begun to recover from fire to provide adequate food resources for rodents such as *Pseudomys* spp. and *Notomys alexis*, and in this State the numbers of dasyurids and rodents are approximately equal. In State III, rodents become dominant over the dasyurids in terms of numbers, which is assisted by the rise in numbers of the larger carnivorous dasyurid *Dasycercus blythii*, which preys on both the dasyurids and the rodents. Transitions between the defined States are driven by disturbances such as flooding rains, droughts, grazing and predation which together affect food resources, mortality, competition and interspecific interactions.

The predictions of the state-and-transition model in the post-fire environment have yet to be experimentally tested, and further research is needed to clarify interactions and key processes that influence arid-dwelling small mammal responses to wildfire.

1.5.3 Lizards

As with small mammals, direct mortality of reptiles from fire is low, as larger animals are able to disperse to fire-refugia and small species take cover in burrows (Reid et al. 1993). Post fire succession is thought to follow the “habitat accommodation model” of succession as proposed by Fox (1982) to describe the recovery of small mammals after fire in coastal heath (Masters 1996, Pianka 1996, Letnic et al. 2004, Pianka and Goodyear 2012). The model was first adapted for arid and semi-arid regions by Caughley (1985) and has since been developed further to form ‘habitat use’ models which match the habitat accommodation model with species traits related to vegetation (such as thermoregulatory or dietary requirements) to form ‘habitat use’ models (Driscoll and Henderson 2008, Lindenmayer et al. 2008, Nimmo et al. 2012a).

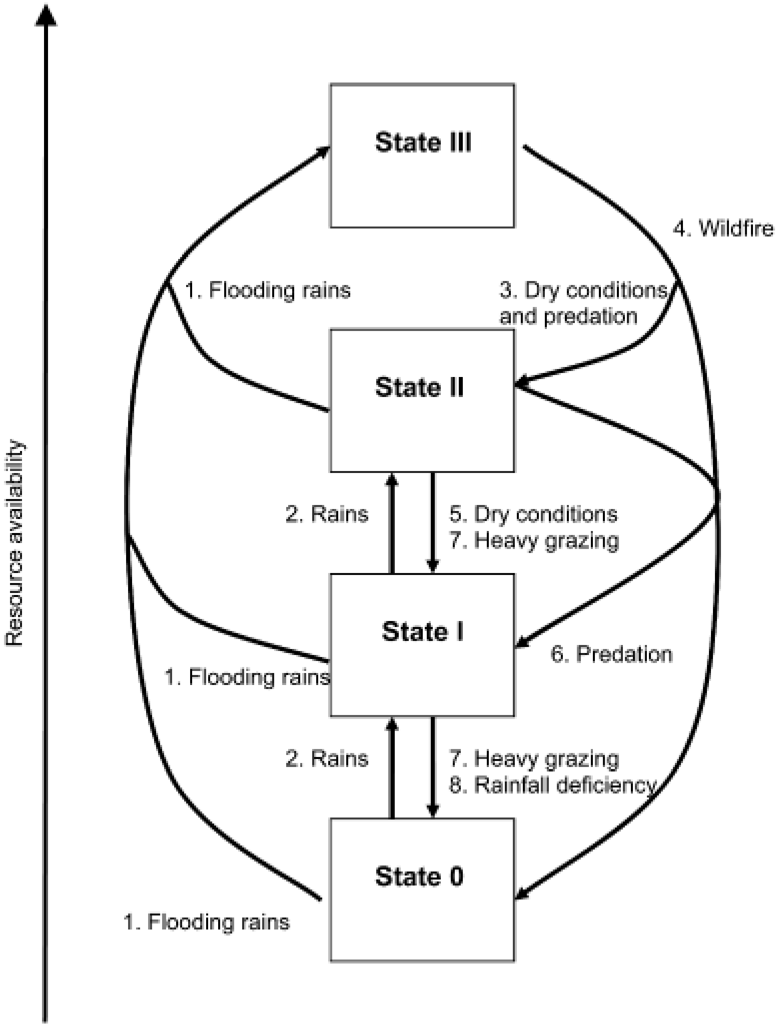

Figure 1.5 State-and-transition model proposed by Letnic et al. (2004) and modified by Letnic and Dickman (2010) to explain the population dynamics of small mammals in spinifex grasslands of central Australia. States are shown in the rectangles and transitions by arrows. Numbers indicate different transitions that drive the system from one state to another.

In these models, species that use similar vegetation structural attributes, such as spinifex cover, are grouped together and a discrete set of fire responses is assumed. Early successional specialists therefore typically consist of burrowing species that forage in open-areas and are tolerant of high daytime temperatures, such as the central netted dragon (*Ctenophorus nuchalis*; Pianka 1996, Letnic et al. 2004). Nocturnal lizards, such as the beaked gecko (*Rhynchoedura ornata*) are also likely to be abundant at this time as these species seek shelter underground during the day and emerge to forage in the cooler night time temperatures (Letnic et al. 2004). Species that require shade for thermoregulation and which have more complex habitat requirements, such as shuttling heliotherm skinks (*Ctenotus* spp.) and the military dragon (*Ctenophorus isolepis*) were predicted to be late-successional species which would not recolonize burnt habitat until the vegetation reaches the appropriate seral stage (Letnic et al. 2004, Daly et al. 2008, Gordon et al. 2010a). Abundant rainfall or drought conditions can moderate the succession of lizard species by enhancing or retarding vegetation growth (Dickman et al. 1999a, Letnic et al. 2004). Ample post-fire rainfall will encourage the start of lizard succession and will enable it to proceed more rapidly. A prolonged post-fire drought, however, can delay the start of succession by years.

Recent research, however, has questioned the utility of these models for predicting lizard recovery after fire. For example, in the semi-arid mallee woodlands of southern Australia, Driscoll and Henderson (2008) found that the habitat accommodation model of succession correctly predicted the fire responses of just three out of 16 lizard species, and that lizard responses to fire were structured by location rather than fire history. In another mallee study, habitat use models correctly predicted just three of 34 proposed reptile response curves (Nimmo et al. 2012a). A study in forest habitat in eastern Australia produced similarly little evidence to suggest that reptile responses to fire were predictable from life history attributes (Lindenmayer et al. 2008).

It is thought that lizards may be responding to a range of processes other than fire and fire-mediated vegetation succession in arid and semi-arid Australia, such as vegetation condition, rainfall, inter-specific interactions and land use history. Further research is required to experimentally test these factors and to develop models which better predict the observed responses of arid zone lizards to wildfire.

1.6 INTRODUCTION TO THE CURRENT STUDY

My study is located in the Simpson Desert in the north-eastern part of the Australian arid zone (Figure 1.2). A large wildfire swept throughout much of the desert in 2001/02 (Letnic et al. 2005), creating an ideal opportunity to study animal responses and ecosystem recovery. It was one of the largest wildfires to affect the central Australian arid zone since the mid 1970s and it created a typical post-fire landscape characterised by patches of unburnt refuge habitat nested within broader expanses of bare sand. Some research was already being conducted on the biota in the region, and this has provided a longitudinal dataset for further perspective.

As described above, the interactive role of processes such as rainfall, herbivory and predation in determining fire effects on animal assemblages are not well understood and for the most part have yet to be experimentally tested and quantified. In addition to this, the spatially explicit nature of many fire responses is not well covered in the literature and has so far been excluded from many predictive models (such as those described in Sections 1.6.2 and 1.6.3). This was acknowledged by Driscoll et al. (2010) in their recent review of key fire management research questions and the capacity of current research practices to answer them. In this review, Driscoll et al. (2010) identified three major gaps in existing fire knowledge. These were: (i) a mechanistic understanding of species' responses to fire regimes; (ii) knowledge of how the spatial and temporal arrangement of fire influences the biota; and (iii) an understanding of interactions of fire regimes with other processes.

In this thesis I focus specifically on the role of interacting factors such as rainfall, food availability, regional variability and predation in driving animal responses to fire. I measure and analyse the effect of these factors across several temporal and spatial scales and I report one of the first instances in which experimental manipulations have been used to test the role of predation in facilitating community recovery in burnt habitats. In addressing the role of interacting biotic and abiotic processes, in addition to the likely spatial and temporal variability of observed responses, I aim for my research to contribute to at least two of the three aforementioned key knowledge gaps.

1.7 THESIS AIMS AND SCOPE

The overall objective of my PhD research is to determine the effect of a broadscale wildfire on vegetation, mammal and reptile populations in the Simpson Desert, central Australia, focussing on the interactive roles of rainfall and predation. Based on the foregoing literature review, I developed five specific aims to meet this broad objective.

1. To investigate the effect of fire on vertebrate diversity at a global scale, and to identify the influence, if any, of fire type, taxon, habitat, and geographical location;
2. To compare the effects of a wildfire and prescribed burns on plant, mammal and lizard diversity in the Simpson Desert. Although it is anecdotally accepted that wildfires

affect animal populations more severely than prescribed burns, this has yet to be quantified;

3. To explore the effects of the 2001/02 Simpson Desert wildfire on lizard populations, with specific reference to the influence of multi-scale processes including rainfall, vegetation structure, food availability and regional land use histories;
4. To experimentally determine how perceived and actual predation risk affects small mammal recovery in burnt habitats after the 2001/02 Simpson Desert wildfire; and
5. To synthesise the results from these studies to develop effective fire management strategies and recommendations for land managers in arid regions.

1.8 THESIS STRUCTURE

In Chapter 1 I provide a general introduction to this thesis. I briefly overview the significance of wildfire in the development and management of global vegetation and animal communities and examine the role of fire in the evolution of Australian ecosystems and biota. I introduce fire as a key process in arid land systems and discuss its known effects on plant and animal communities. I summarise the secondary processes that may interact with fire and likely play a key role in driving animal recovery in burnt areas. Lastly, I introduce the aims and scope of the thesis.

In Chapter 2 I provide a detailed description of the study area including the topography, geography, climate, land use, fire history, vegetation and animal assemblages. The conservation significance for each of the mammal and reptile assemblages present in the study area is also described.

In Chapter 3 I investigate the effects of fire on vertebrate diversity at a global scale. This meta-analysis is the first to examine the effects of fire at such a broad scale and in doing so I am able to identify processes that influence the effects of fires across studies, such as fire type (wildfire or prescribed burn), study taxon, habitat and geographical location. The study provides a global perspective and allows me to identify processes in turn that may influence the effects of fire at the more localised scale of the Australian arid zone.

In Chapter 4 I compare the effects of the 2001/02 wildfire to the effects of prescribed burns conducted just prior to the wildfire. I analyse these impacts on plants, mammals and reptiles. Prescribed burns and wildfires are thought to have very different effects on diversity, but the opportunity rarely arises to compare these effects directly. To my understanding this is the first study to directly compare the effects of these two fire types within the same ecosystem and time scale.

In Chapter 5 I explore the effect of the 2001/02 Simpson Desert wildfire on desert lizard assemblages. I test the predictions of the habitat accommodation model of succession and explore the influence of multi-scale processes including rainfall, predation, food availability and regional variation in determining lizard responses to the wildfire.

In Chapter 6 I examine the role of the introduced predators feral cats (*Felis catus*) and foxes (*Vulpes vulpes*) in determining small mammal recovery after the wildfire. I quantify the post-fire movements of these predators in burnt, ecotone and unburnt habitats and experimentally manipulate the risk of predation for small mammals.

In Chapter 7 I summarise my results and discuss these with reference to the scientific literature. I discuss my key findings with respect to the effectiveness of the patch mosaic burn hypothesis as a management tool and the importance of rainfall and predation in determining the effects of fire. I review the current models for predicting post-fire small mammal and lizard population dynamics and propose a new state-and-transition model for lizards. Lastly, I make some management recommendations and identify opportunities for future research.

CHAPTER 2

STUDY SITE, SPECIES ASSEMBLAGES AND FIRE HISTORY

Parakeelya (*Calandrinia balonensis*) blooms on the crest of a sand dune after rain (L. Pastro)

2.1 THE SIMPSON DESERT

"A vast, howling wilderness of high, spinifex-clad ridges of red sand..."
(Carnegie 1898 pg 164)
"Sand and spinifex were the universal covering of the land" (Sturt I849 pg 279)

The Simpson Desert covers an area of approximately 200,000 km^2 and is located in eastern central Australia (Purdie 1984). The majority of the desert is placed in the Northern Territory and South Australia, with a smaller portion extending into south-western Queensland (Figure 2.1).

The predominant topography in the Simpson Desert is an extensive Quaternary aeolian dune field system, dated to be at least one million years old (Fujioka et al. 2009). The sand dunes are long, continuous and mostly parallel and run NNW-SSE in line with the prevailing south-southeasterly wind (Figure 2.1; Purdie 1984). The dunes extend for up to 200 km in some parts of the desert and are on average 8-10 m high, reaching to 35 m (Wopfner and Twidale 1967, Purdie 1984). The average spacing between the dunes is 100-1500 m, however this distance varies inversely with height and thus results in a uniform total volume of sand per unit area (Wopfner and Twidale 1967). The slope of the dunes is steeper on the eastern side due to the characteristic wind direction (Mabbutt et al. 1969, Buckley 1981). The northern, eastern and south-western margins of the Simpson Desert grade into stone-covered plains (gibber plains) and associated hills and tablelands (Purdie 1984).

2.2 STUDY SITE LOCATION AND TOPOGRAPHY

My study was conducted in the north-eastern part of the Simpson Desert, located in south-western Queensland (Figure 2.2). The study area covers 7000 km^2 and stretches across two pastoral properties: Carlo (23°29'S, 138°32'E) and Tobermorey (22°16'S, 137°58'E); and two conservation reserves: Cravens Peak (23°16'S, 138°17'E) and Ethabuka (23°45'S, 138°28'E; Figure 2.2). The conservation reserves are owned and managed by Bush Heritage Australia. Cravens Peak was purchased in 2006 and Ethabuka was purchased in 2004; prior to this both reserves operated as cattle stations.

Carlo covers an area of 211,000 ha and is located within both the Boulia and Diamantina Shires in south-western Queensland. About 90% of the property is covered by sand dunes, with the remainder characterised by ephemeral clay plans and Tertiary limestone country. It is crossed by numerous small creeklines.

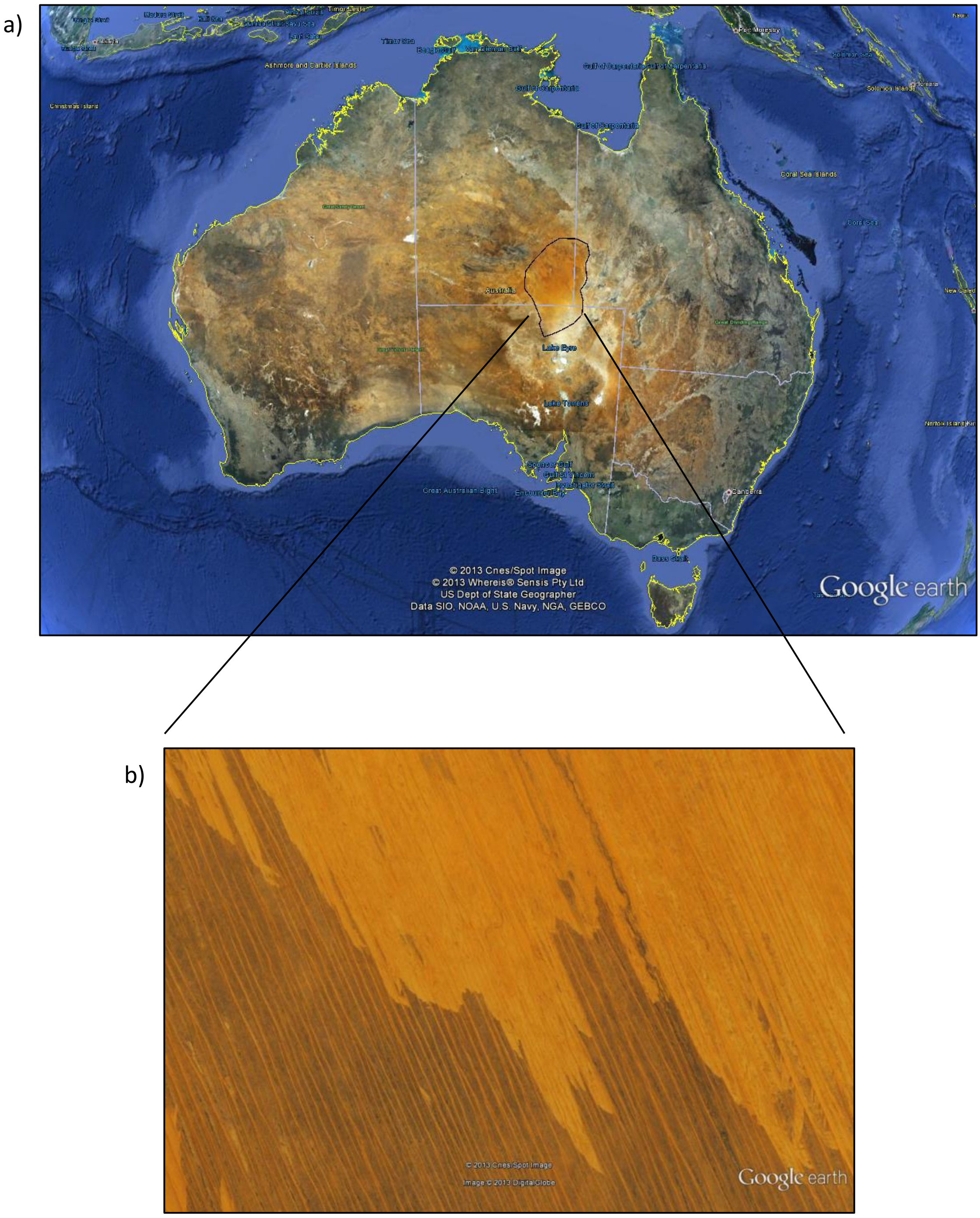

Figure 2.1 a) Location of the Simpson Desert (black line) within Australia; and b) detail of the Aeolian dune system. The NNW/SSW direction of the dunes is clear. The light orange dunes were burnt in the 2001/02 wildfire and the darker dunes remain unburnt and are stabilised by spinifex hummocks. Images were accessed from GoogleEarth© on March 5, 2013.

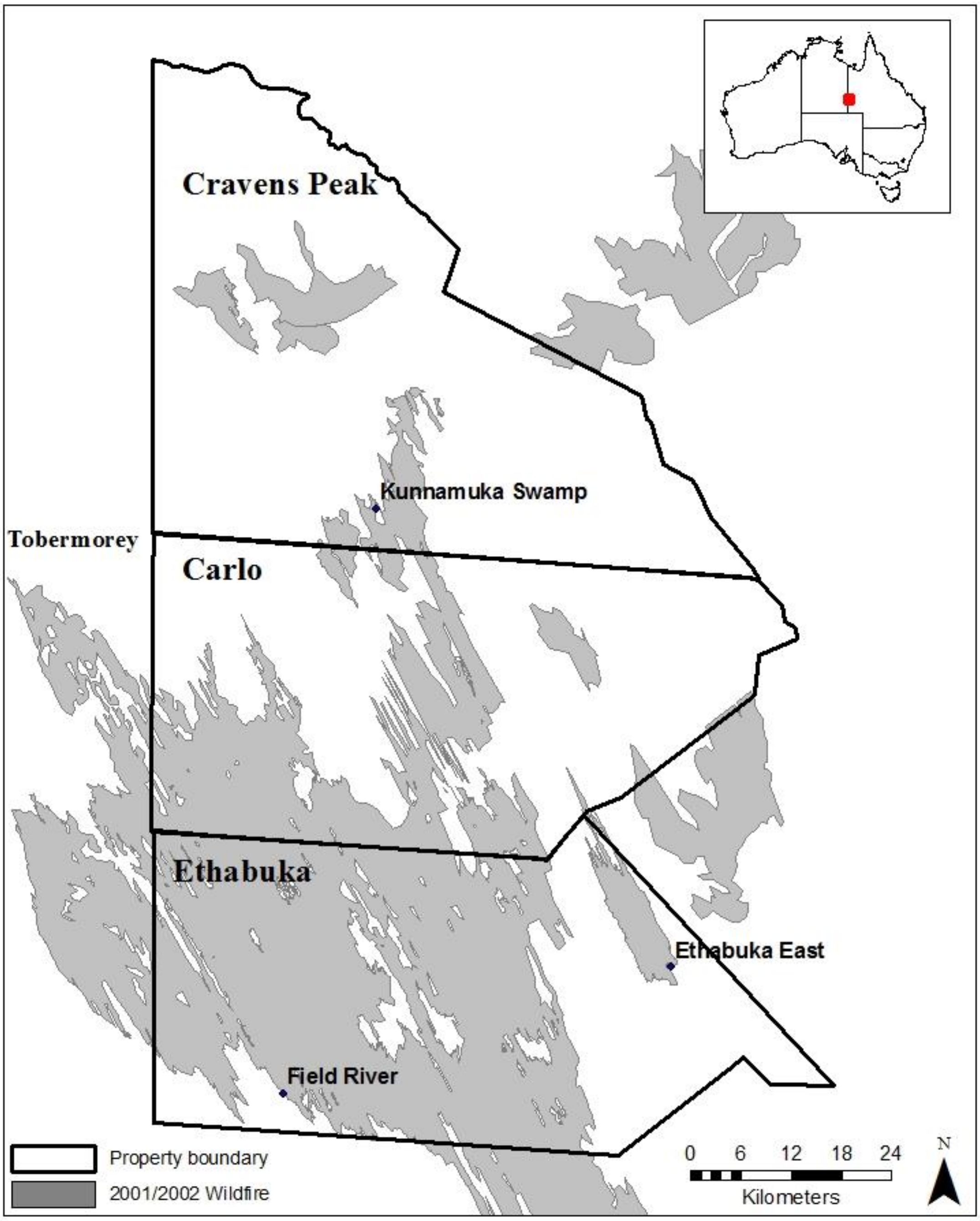

Figure 2.2. Map of the study region showing the four study properties . The black lines represent the property boundaries and the extent of the 2001/02 wildfire is shaded in grey. Projection: GDA 1994. Prepared with assistance from Aaron Greenville.

Tobermorey covers an area of 1,600,000 ha and is located within the Barkley Shire in the Northern Territory, adjacent to the Queensland border. It is characterised by sand dunes in the south and rocky country with some wetlands and associated grasslands in the north. Only a small, southern portion of the property was used in this study. Tobermorey is bounded to the east by the Field River.

Cravens Peak covers an area of 233,000 ha and is located with Boulia Shire. About 40% of the reserve is covered by sand dunes, which are concentrated in the southern part of the property. The north-eastern region is dominated by the Toko Range and associated rocky gorges and escarpments, and the western and south-western area is characterised by the Toomba Range and associated rocky country, mesas and gibber plains. The property also contains significant ephemeral wetlands. Cravens Peak is crossed by the Mulligan River in the north-east. I worked primarily in the southern dunefields on this property.

Ethabuka covers an area of 213,000 ha and is located within Diamantina Shire. About 80% of the property is covered by sand dunes, with the remainder (the south-eastern portion) covered by sparse herb fields. After high rainfall the herb fields are transformed into ephemeral wetlands which may persist for many months. The property is crossed by the Mulligan River in the east and by the Field River in the west.

All rivers and creeklines are dry in this part of the desert except in times of flooding rains.

2.3 SOIL CHARACTERISTICS

The sand dunes and swales throughout the study area are composed of red siliceous sand which is no more than 35 m deep at any point (Wopfner and Twidale 1967, Buckley 1982). Some swales contain up to 5% clay (Twidale 1972, Buckley 1982) which causes slow drainage after rainfall and can lead to extensive flooding for up to several months after major rainfall events. Although the soil moisture content decreases as the dune crest is reached, moisture is more available to plants on the crest due to greater evaporation and capillary action (Buckley 1982).

Nutrients including carbon and nitrogen occur in low concentrations, particularly on dune crests (Buckley 1982). Heavy minerals such as magnetite, zircon and tourmaline constitute only 0.5-1.5 % of the soil (Wopfner and Twidale 1967).

2.4 CLIMATE

"I consider that the irregular and excessive rains are the most characteristic fact of the climate of Australia" (Jevons 1859)

"During nearly four months there was not enough rain to wet a pocket handkerchief" (Horn 1896pg viii)

The Simpson Desert is classified as a hot desert (Williams and Calaby 1985). It has a mean annual temperature of 21-23°C, with summer maxima of 46-49°C and winter minima of -6°C (Purdie 1984). Environdata® automated weather stations (Environdata Australia Pty. Ltd. 44 Percy Street, Warwick, Queensland, Australia) are positioned at regular intervals across the study area. The mean monthly, minimum and maximum temperatures recorded by these weather stations throughout the study period are presented in Figure 2.3.

The study area lies between the 100 mm and 150 mm median annual rainfall isopleths (Purdie 1984) and there is a slight latitudinal rainfall gradient that decreases from north to south across the study area (Purdie 1984). There is a pronounced wet season during the austral summer; however, the occurrence of rainfall is both spatially and temporally unpredictable (Stafford Smith and Morton 1990, Dickman et al. 1999a). As indicated in Figure 2.4, rainfall incidence in the study region is amongst the most variable of all Australian regions.

As reviewed in the Introduction, the annual variation and intensity of rainfall in the study area are strongly influenced by the El Niño Southern Oscillation (ENSO) which is a natural, coupled atmospheric/oceanic cycle in the tropical Pacific Ocean (Nicholls 1991, Chiew et al. 1998, Diaz et al. 2001, Letnic et al. 2005). The system consists of two extremes, the El Niño and the La Niña, which are associated with below-average and above-average rainfall respectively (Nicholls 1991). The El Niño phenomenon dominates the Australian climate (Diaz et al. 2001) and, as such, the Simpson Desert is characterised mostly by prolonged periods of low rainfall which are interspersed by periods of flooding rains (La Niña). El Niño and La Niña events may both occur within short time periods, causing large inter-annual fluctuations in rainfall (Nicholls 1991). The strength of an ENSO event is measured by the Southern Oscillation Index (SOI) which is calculated from the difference in air pressure between Darwin and Tahiti. Sustained negative values of the SOI (< - 8) often indicate El Niño episodes and sustained positive values (> 8) are associated with La Niña episodes (BOM 2013).

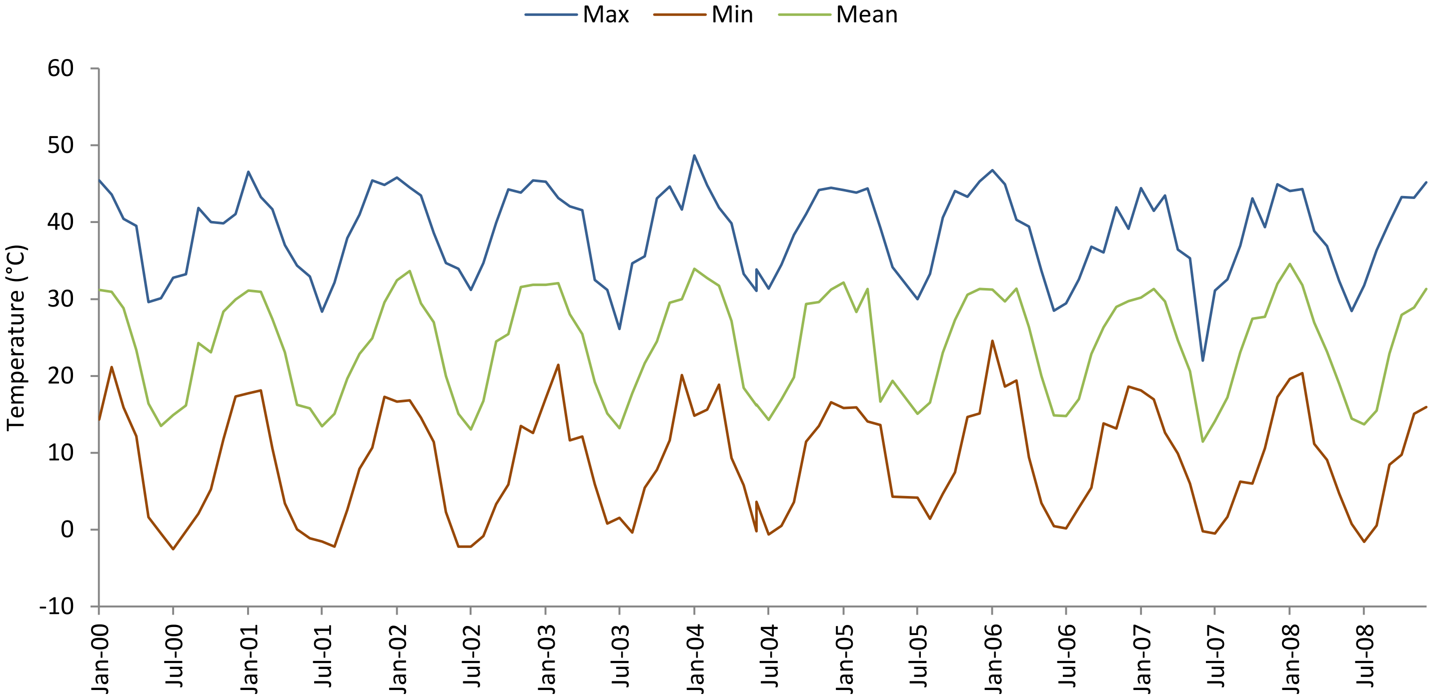

Figure 2.3 Monthly minimum, maximum and mean temperatures for the duration of the study. Temperatures are the means of data recorded by Environdata® weather stations at each study site.

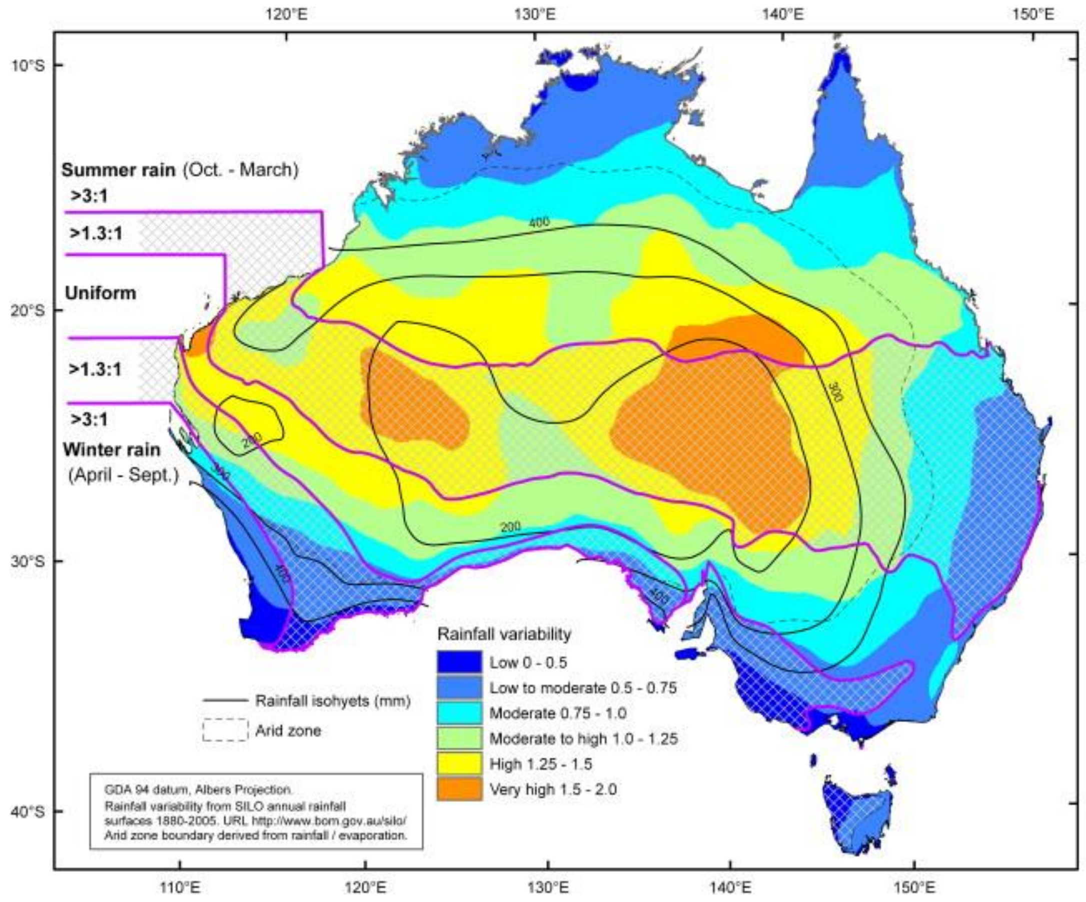

Figure 2.4 Rainfall means, variability and seasonality in Australia, calculated from annual and monthly rainfall surfaces for the continent over the period 1880‑2005. Isohyets show annual means; seasonality is calculated as the ratio of the long-term rainfall totals for October–March: April–September ('summer':'winter'); variability is calculated from deciles of annual rainfall as (9th decile–1st decile)/median. Source: Morton et al. (2011).

The long-term weather stations positioned closest to the study area are at Sandringham (24°03’S, 138°04’E), Marion Downs (23°21’S, 139°39’E), Glenormiston (22°55’S, 138°49’E) and Boulia (22°55’S, 139°54’E). They have recorded median annual rainfalls of 137 mm (n = 40 years), 149 mm (n = 86 years), 169 mm (n = 100 years) and 215 mm (n = 110 years), respectively. The mean localised rainfall across the study area as measured by the Environdata® weather stations and the associated mean SOI for the study period are presented in Figure 2.5.

2.5 VEGETATION ASSEMBLAGES

Spinifex: the “ideal pyrophyte” (Pyne 1991)

The swales and dune slopes across the study area are characterised by spinifex, or hummock grasslands. Hummock grasslands are a major Australian biome, covering 70% of the Simpson Desert and over one third of the Australian continent (Suijdendorp 1981, Purdie 1984, Allan and Southgate 2002). They are characterised by perennial grasses of the genus *Triodia* (Lazarides 1997), of which there are at least 69 species. The most common species in the Simpson Desert is *Triodia basedowii* (Purdie 1984).

Spinifex is constructed of sclerophyllous, pointed, cylindrical grass blades filled with a mixture of flammable resin and air (Winkworth 1967). The plants grow outwards in concentric oval rings, amassing new outer biomass during times of high rainfall and retaining dead biomass in the centre (Allan and Southgate 2002). Spinifex hummocks can be up to 2 m in diameter and 1 m high and in mature grasslands they are typically separated by only small areas of bare ground (Plate 2.1; Winkworth 1967, Allan and Southgate 2002). Depending on rainfall it may take more than 20 years for spinifex to reach maturity, and as it does so it competitively excludes other grasses, herbs and forbs, and thus overall plant species richness often decreases (Winkworth 1967, Wright and Clarke 2007). The accumulation of aboveground biomass in spinifex grassland can range up to 8000 kg/ha (Winkworth 1967).

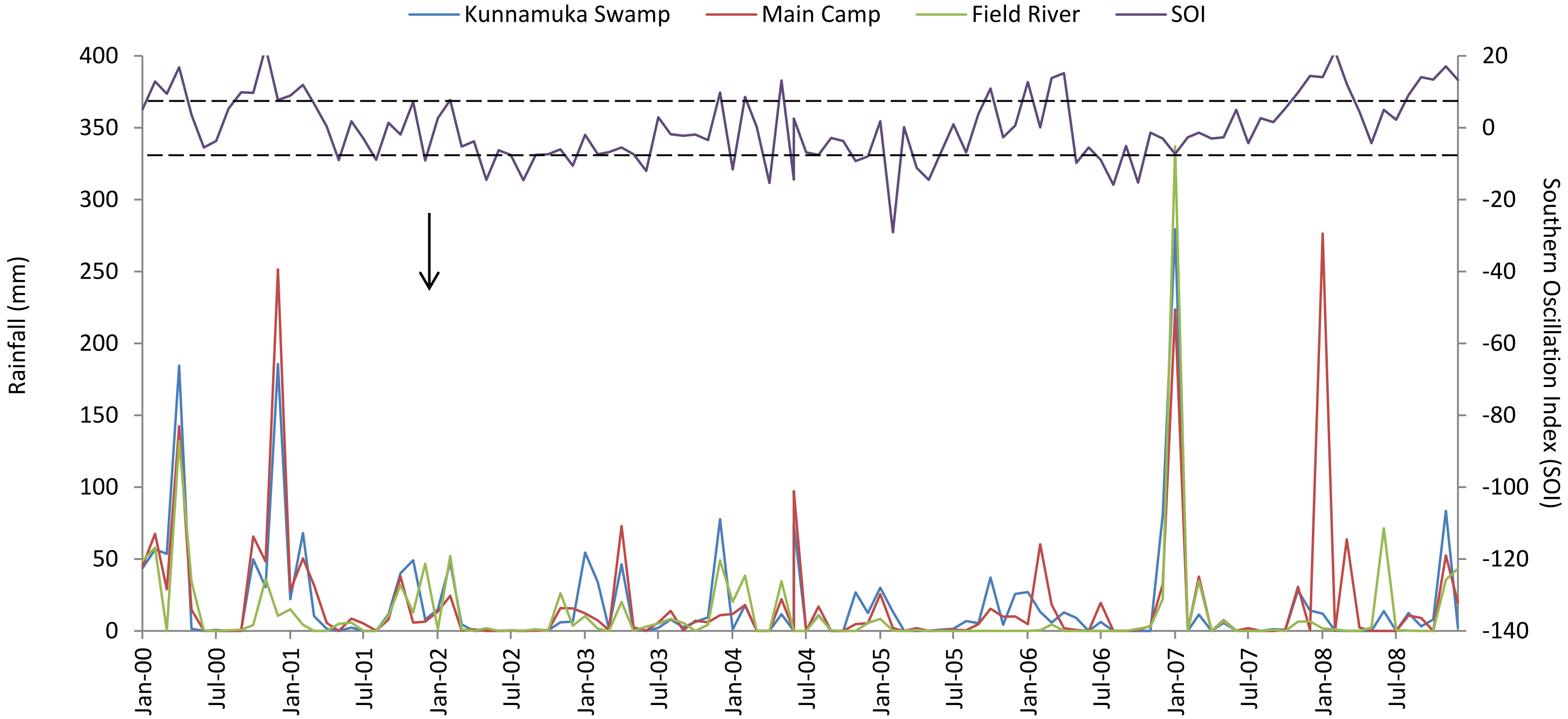

Figure 2.5 Accumulated monthly rainfall and the mean southern oscillation index (SOI) for the duration of the study period. Rainfall data were collected in each study region using Environdata® weather stations. The black arrow indicates the timing of the 2001/02 wildfire and the black dashed lines indicate the El Niño and La Niña SOI thresholds of -8 and +8 respectively.

The spinifex grasslands throughout the study area house a sparse overstorey of shrubs (Winkworth 1967, Buckley 1981). Common shrub species include *Acacia ligulata, Grevillea* spp. and *Eremophila* spp. Some mallee species (*Eucalyptus pachyphylla* and *E. gamophylla*) and trees (*Grevillea striata*, *Eucalyptus coolibah*) also occur in low densities along sand-based swales. Occasional stands of mulga shrubs (*Acacia aneura*) exist within the greater spinifex matrix, and the boundary between the two vegetation types is typically abrupt with each forming a monodominant stand (Nicholas et al. 2009).

Swales with a higher proportion of clay in the soil also often contain small (<5 ha) stands of gidgee trees (*Acacia georginae*; Plate 2.2; Purdie 1984). Perennial vegetation in these regions is negligible and is usually dominated by grasses (*Aristida contorta*, *Eragrostis* spp. and *Eriachne aristidea*) and chenopods (*Atriplex* spp. *Salsola kali* and *Sclerolaena* spp.) along with *Senna* spp. and emu bushes (*Eremophila macdonnellii*, *E. longifolia* and *E. obovata*) (Buckley 1982, Purdie 1984).

Vegetation on the dune crests is generally sparse, being characterised predominantly by cane grass (*Zygochloa paradoxa)* along with a range of herbs and small shrubs such as *Grevillea stenobotrya, Goodenia cycloptera, Crotalaria* spp. and *Sida* spp. (Buckley 1981, Purdie 1984).

Plant nomenclature throughout this thesis follows Jessop (1957), Urban (2006) and Moore (2005).

2.5.1 Rainfall-stimulated seed germination

The episodic flooding rains associated with the La Niña phase of ENSO stimulate the growth of a diverse range of ephemeral forbs and grasses and also allow tree and shrub recruitment to occur (Nicholls 1991, Holmgren et al. 2006, Letnic and Dickman 2010). The ephemeral waters that form in clay swales during these episodes can persist for many months, having a long-term positive effect on vegetation growth. Many species are able to persist in the seed bank during extended dry periods to await germination in times of flood.

During El Niño periods, rainfalls of just 12 mm are sufficient to trigger grass and forb germination in sand-based spinifex grasslands, especially on the dune crests where water is more available via greater capillary rise and evaporative loss (Grigg et al. 2008). Clay swales need at least 50 mm of rain to stimulate plant germination (Purdie 1990).

Plate 2.1 Long unburnt spinifex hummocks (*Triodia basedowii*), which are likely >30 years post-fire. A large growth ring of >3 m in diameter is evident, with newer spinifex hummocks present in the centre. A sparse shrubby overstorey is also evident (M. Simpson).

Plate 2.2 A patch of gidgee (*Acacia georginae*) nestled within a matrix of spinifex-stabilised sand dunes (G. Wardle).

2.6 VERTEBRATE ASSEMBLAGES

Spinifex grasslands are host to an unusual food web. Unlike other grasslands around the world, spinifex grasslands are mostly devoid of large mammalian herbivores and their corresponding predators as they are nutritionally poor (Ealey 1967, Newsome 1975, Kinnear and Main 1979, Mattson 1980). Instead, termites feed on the abundant supplies of cellulose and fill the herbivore niche (although the spinifex is often dead when ingested), and lizards are their main predators (Gay and Calaby 1970, Matthews 1976, Watson 1982, James 1991b). Spinifex seeds also provide important food resources for birds and mammals.

In this section I describe the assemblages and conservation significance of my two primary study taxa: reptiles and mammals.

2.6.1 Small mammals

The Simpson Desert is home to an extraordinarily diverse small mammal fauna (Dickman et al. 2001). The native mammal fauna of the study site consists of 30 species, including ten dasyurids, six rodents, two macropods and 11 bats. Common genera include *Pseudomys*, *Sminthopsis* and *Notomys* (Table 2.1). Complex interactions exist between these species, for example, the mulgara (*Dasycercus blythi*) facilitates the diversity of smaller insectivorous mammals by reducing rodent and other dasyurid species density (Dickman et al. 2013).

The study site also houses six species of introduced mammals including camels (*Camelus dromedarius*), cats (*Felis catus*), rabbits (*Oryctolagus cuniculus*), pigs (*Sus scrofa*), foxes (*Vulpes vulpes*) and house mice (*Mus musculus*; Table 2.1). No pigs were observed over the course of the study but cats, rabbits, camels, foxes and house mice were all present in low numbers.

Table 2.1 Mammal species trapped or observed in the study area of Ethabuka, Carlo, Cravens Peak and Tobermorey stations.

Order/Family	**Scientific name**	**Common name**
Monotremata	*Tachyglossus aculeatus*	Short-beaked echidna
Dasyuridae	*Dasycercus blythi*	Brush-tailed mulgara
	Dasycercus cristicauda	Brush-tailed mulgara
	Ningaui ridei	Wongai ningaui
	Planigale gilesi	Giles' planigale
	Planigale tenuirostris	Narrow-nosed planigale
	Pseudantechinus macdonnellensis	Fat-tailed pseudantechinus
	Sminthopsis crassicaudata	Fat-tailed dunnart
	Sminthopsis hirtipes	Hairy-footed dunnart
	Sminthopsis macroura	Stripe-faced dunnart
	Sminthopsis youngsoni	Lesser hairy-footed dunnart
Rodentia	*Leggadina forresti*	Forrest's mouse
	Notomys alexis	Spinifex hopping-mouse
	Notomys cervinus	Fawn hopping-mouse
	Pseudomys desertor	Desert mouse
	Pseudomys hermannsburgensis	Sandy inland mouse
	Rattus villosissimus	Long-haired rat
Macropodidae	*Macropus rufus*	Red kangaroo
	Macropus robustus	Wallaroo
Bats	*Chalinolobus gouldii*	Gould's wattled bat
	Mormopterus sp.	
	Nyctinomus (Tadarida) australis	White-striped freetail-bat
	Nyctophilus geoffroyi	Lesser long-eared bat
	Pteropus scapulatus	Little red flying-fox
	Saccolaimus flaviventris	Yellow-bellied sheathtail bat
	Scotorepens balstoni	Inland broad-nosed bat
	Scotorepens greyii?	Little broad-nosed bat
	Taphozous hilli	Hill's sheathtail bat
	Vespadelus finlaysoni	Inland cave bat
	Vespadelus baverstocki	Inland forest bat
Canidae	*Canis lupus dingo*	Dingo

Introduced mammals	*Camelus dromedarius*	One-humped camel
	Felis catus	Feral cat
	Mus musculus	House mouse
	Oryctolagus cuniculus	Rabbit
	Sus scrofa	Pig
	Vulpes vulpes	Red fox

2.6.1.1 Mammal conservation

Australian mammals have undergone three major extinction waves. The first occurred in the late Pleistocene with the loss of many very large (>44 kg) herbivores. There is now widespread agreement in the literature that human colonisation was a pivotal cause of these extinctions, however the mechanism by which they became extinct remains elusive (Johnson 2005, Brook et al. 2007, Rule et al. 2012). The second extinction event occurred in the Holocene (10,000-200 years ago) when the remaining large carnivores declined to extinction. The third event occurred much more recently, since the arrival of Europeans in the late 1700s. Of the 306 indigenous mammal species originally present when Europeans arrived, twenty-two species have become extinct, which includes thirteen marsupial species and nine rodents (Burbidge et al. 2008). This comprises 28% of the world's mammal extinctions in this time (McKenzie et al. 2007). A further ten species survive only on predator-free offshore islands and reserves, including Tasmania. The remaining species have suffered severe range contractions, with ninety-one species having become extinct from at least half of the bioregions in which they occurred before European settlement (DSEWPC 1999, Johnson 2006, McKenzie et al. 2007, Burbidge et al. 2008).

In this time period, thirteen mammal species have become extinct in the central deserts area, nine of which resided in the study area (DSEWPC 1999). Almost one in four marsupial species is now threatened with extinction (Maxwell et al. 1996) and more than half of Australia's endangered mammal fauna are from arid and semi-arid regions, as listed under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (Table 2; DSEWPC 1999). Many more species are considered to be rare or to have experienced substantial range decreases. In addition to changes in fire regimes, introduced predators and habitat loss have both been identified as key contributors to the continuing modern decline of

Australia's mammal fauna (Cole and Woinarski 2000, Dickman et al. 2000, Morris 2000, McKenzie et al. 2007).

The study area houses four species that are listed as Vulnerable under the *Environment Protection and Biodiversity Conservation Act 1999:* the mulgaras (*Dasycercus cristicauda* and *D. blythi*); the greater bilby (*Macrotis lagotis*) and the kowari (*Dasyuroides byrnei*; DSEWPC 1999). Of these three species, only the brush-tailed mulgara *D. blythi* was observed throughout the study period. Long term studies have indicated declines in the abundance of other species such as the desert mouse (*Pseudomys desertor*), and also large fluctuations in the abundance of others such as the spinifex hopping-mouse (*Notomys alexis*) and the sandy inland mouse (*Pseudomys hermannsburgensis*; Dickman et al. 1999b, Dickman et al. 2000, Dickman et al. 2001).

2.6.2 Reptiles

The celebrated mammalogist Hedley H. Finlayson referred to the vast interior deserts of Australia as "*a land of lizards*" (Finlayson 1943) and appropriately, the spinifex grasslands of arid Australia have since been identified as home to the world's richest reptile assemblages (Pianka 1969, Morton and James 1988). The study area houses over 60 species of native reptiles, including eight dragons, 11 geckos, 23 skinks and seven goannas. Common genera include *Ctenophorus*, *Ctenotus*, *Diplodactylus*, *Lerista* and *Varanus* (Table 2.2). The opposing forces of fire and rainfall and the dynamic spatial-temporal habitat mosaic that they create are thought to be a key reason for such diversity (Pianka 1989, Pianka 1992).

Most of these lizards survive in extremely low numbers across the landscape. The true reason for so many rare species remains unknown, but it is perhaps due to a long history of 'imperfect erasures', in which species have become incompletely extinct (Main 1982). The majority of species have evolved a high degree of habitat specificity such that small patchy populations arise only when patches of habitat meet their specific requirements, such as in a given seral stage after fire (Harrison 1991). It is common for many species to become temporarily and locally extinct when the surrounding habitat ceases to meet their requirements, only to periodically re-invade from a neighbouring area at some later time (Pianka 1992, Pianka 1996). Thus many of these species are at a high risk of local extinction during long droughts. So many rare species will most likely be vital to long-term ecosystem sustainability in the event of drastic future environmental changes (Main 1982)

Differences in substrate across the Simpson Desert also give rise to unique lizard communities via the different vegetation communities that they support. Lizard communities on sandy soils with *Triodia* spp. are generally distinct from communities on loam, clay, and stony soils without *Triodia* spp., and within each of the common *Ctenotus*, *Diplodactylus* and *Nephrurus* genera there are species that are confined to each of these substrates and species that are ubiquitous across all habitats (Pianka 1969, Cogger 1984).

2.6.2.1 Reptile conservation

No reptiles in the arid zone are yet known to have become extinct, but it has been suggested that they may soon follow a trajectory akin to that of arid zone mammals given that reptiles of concern are often associated with long-unburnt spinifex habitats (Recher and Lim 1990, Sadlier and Pressey 1994, Kerle et al. 2007). Fourteen reptile species are currently listed as endangered under the *Environment Protection and Biodiversity Conservation Act 1999* and 38 are listed as vulnerable (DSEWPC 1999). Genera on these lists that inhabit the study region include *Egernia*, *Diplodactylus*, *Lerista*, *Ctenotus* and *Nephrurus*. Three species that inhabit the study area are listed as threatened (‘rare’) for the State of Queensland: *Ctenotus ariadnae*, *Aspidites ramsayi* (Woma python) and *Oxyuranus microlepidotus* (Fierce snake; Wilson and Swan 2008).

Table 2.2 Reptile species trapped or observed in the study area of Ethabuka, Carlo, Cravens Peak and Tobermorey stations.

Order/Family	**Scientific name**	**Common Name**
Agamidae	*Ctenophorus clayi*	
	Ctenophorus isolepis	Military dragon
	Ctenophorus nuchalis	Central netted dragon
	Diporiphora winneckei	
	Lophognathus longirostris	
	Moloch horridus	Thorny devil
	Pogona vitticeps	Bearded dragon
	Tympanocryptis sp.	
Gekkonidae	*Crenadactylus ocellatus*	Clawless gecko
	Diplodactylus conspicillatus	Fat-tailed diplodactylus
	Diplodactylus stenodactylus	
	Strophurus ciliaris	Spiny-tailed gecko
	Strophurus elderi	Jewelled gecko
	Gehyra montium	
	Gehyra variegata	Tree dtella
	Heteronotia binoei	Bynoe's gecko
	Lucasium damaeum	Beaded gecko
	Nephrurus levis	
	Rhynchoedura ornata	Beaked gecko
Scincidae	*Ctenotus ariadnae*	
	Ctenotus brooksi	
	Ctenotus calurus	
	Ctenotus dux	
	Ctenotus helenae	
	Ctenotus lateralis	
	Ctenotus leae	
	Ctenotus leonhardii	
	Ctenotus pantherinus	Panther skink
	Ctenotus piankai	
	Ctenotus regius	
	Ctenotus schomburgkii	

	Cryptoblepharus sp.	
	Egernia inornata	Desert skink
	Eremiascincus fasciolatus	Narrow-banded sand swimmer
	Lerista aericeps	
	Lerista labialis	
	Lerista xanthura	
	Menetia greyii	
	Morethia ruficauda	
	Notoscincus watersi	
	Tiliqua multifasciata	Centralian blue-tongued lizard
Varanidae	*Varanus acanthurus*	Ridge-tailed monitor
	Varanus brevicauda	Pygmy goanna
	Varanus eremius	
	Varanus gilleni	
	Varanus giganteus	Perentie
	Varanus gouldii	Sand monitor
	Varanus tristis	
Pygopodidae	*Delma nasuta*	Sharp-snouted delma
	Delma tincta	
	Lialis burtonis	Burton's snake-lizard
	Pygopus nigriceps	Hooded scaly foot
Boidae	*Aspidites ramsayi*	Woma
	Liasis stimsoni	Stimson’s python
	Acanthophis pyrrhus	Desert death adder
Elapidae	*Demansia psammophis*	Yellow-faced whip snake
	Oxyuranus microlepidotus	Fierce snake
	Pseudechis australis	King brown snake
	Pseudonaja modesta	Ringed brown snake
	Pseudonaja nuchalis	Western brown snake
	Simoselaps fasciolatus	Narrow-banded snake
	Suta punctate	Little spotted snake
Typhlopidae	*Ramphotyphlops endoterus*	Interior blind snake

2.7 CURRENT AND HISTORICAL FIRE REGIMES AND LAND USE

2.7.1 Aboriginal use of fire

“Large tracts of burnt country had to be crossed from which clouds of dust and ashes were continually rising” (Carnegie 1898 pg 167)

“Nevertheless the natives were about burning, burning ever burning; one would think they were of the fabled salamander race and lived on fire instead of water”
(Giles 1889 Vol. 1 pg 81)

Aborigines arrived in Australia 50 ± 10 k years ago (Roberts et al. 1990, Turney et al. 2001a, Bowler et al. 2003) and radiated into the central deserts by at least 27,000 years ago (Smith 1987). It is likely that they remained there throughout the height of full glacial aridity around 18,000 years ago (Smith 1989). Their hunting and gathering economy was highly mobile and reflected the temporally and spatially variable nature of the available food resources, which in turn were driven by the unpredictable rainfall regime.

The first European records of Aboriginal use of fire came from the early European explorers, who commented on the frequency with which they observed smoke, ashes, or other evidence of burning. These observations were made across the expanse of the central deserts (e.g. Warburton 1858, Giles 1889, Winnecke 1894, Carnegie 1898) and specifically in the Simpson Desert (Hodgkinson 1877, Winnecke 1884, Sturt I849). Fire was subsequently mentioned frequently by anthropologists and ecologists studying Aborigines in central Australia (e.g. Finlayson 1943, Jones 1969, Calaby 1971, Gould 1971, Latz and Griffin 1978, Kimber 1983, Latz 1995, Bowman 1998). As summarised by Latz (1995); “*the judicious use of fire was, in the past, the single most important aspect of the desert economy*”. Letnic and Dickman (2006) estimated that half of fires observed by early European explorers could be attributed to Aborigines, with the remainder presumably being the result of lightning strikes.

2.7.2 "Looking after country"

"...patches of this country have been lately burnt by natives; some parts burnt less recently are beautifully green" (Gosse 1874)

"*In places where recent fires had burnt the porcupine large quantities of parakylia, herbage and good grass were met with*" (Winnecke 1897)

"The natives...seldom hunt without making perpetual grass or spinifex fires" (Giles 1889), regarding the Great Victoria Desert.

Aborigines used fire regularly to stimulate the growth of their preferred food plants, many of which appeared in the early regenerative phases after fire. This use of fire to assist food production has become known as "fire-stick farming" (Jones 1969, Latz and Griffin 1978, Latz 1995). Fires were typically low in intensity (Bowman et al. 2004) and small in scale (5-10 km^2) and were set in winter so that plant regeneration would be assisted by the spring and summer rains (Kimber 1983, Baker et al. 1993). Rains during this time of year promoted the regeneration of palatable grasses, whereas winter rains produced unpalatable forbs (Buckley 1986).

The frequency of burns created a landscape characterised by a fine-grained mosaic of vegetation in a diversity of successional stages (Burrows and Christensen 1990, Burrows et al. 2006, Bird et al. 2008). Country of this kind was perceived to be well managed country (Baker et al. 1993), ensuring a good, long-term food supply and helping to prevent the spread of lightning-ignited wildfires that could otherwise spread over very large areas (Latz and Griffin 1978, Baker et al. 1993, Bird et al. 2005, Bird et al. 2008). Frequent fires increased nutrient availability and removed climax vegetation which enhanced the short term productivity of herbaceous plants and within-patch diversity (Bird et al. 2008). Fire mosaics also protected fire-sensitive vegetation, such as *Acacia aneura* (mulga) shrublands (Bowman et al. 2008) and other fire-sensitive species (Yibarbuk et al. 2001).

The Aborigines also used fire for a range of other purposes. They were skilled hunters with fire, using a combination of fire and wind to kill, flush out or herd animals (Nicholson 1981, Kimber 1983, Reid et al. 1993). The small-scale habitat mosaics that resulted from their patch burning methods also reduced time spent foraging for small game, especially for burrowing prey such as goannas (Bird et al. 2005, Bird et al. 2008). Interestingly, they also reduce hunting time for feral cats (Bird et al. 2008), which are a significant predator of native small mammals.

Aboriginal people fire additionally to communicate, to clear country, and for a range of spiritual and sacred purposes (Gould 1971, Nicholson 1981, Kimber 1983, Baker et al. 1993). In a survey of Aboriginal fire patterns across the western deserts, Burrows and Christensen (1990) found high concentrations of fire scars around resource-rich areas such as rockholes, creeks, claypans and salt lakes, which is indicative of the high level of Aboriginal activity in these valuable locations.

2.7.3 European settlement and associated wildfires

"...*miles of country must have been burning, a greater extent than we have yet seen actually alight. Probably hot weather accounted for the spread of the flames*" (Carnegie 1898)

European exploration of the Simpson Desert began with Charles Sturt's expedition in 1844 (Sturt 1844), which came to within 100 km of the present study area's southern boundary (Sturt 1844). Subsequent expeditions were led by Hodgkinson (1877), Winnecke (1884) and Poepell (1879).

European colonisation of the eastern portion of the study area began with the establishment of short-lived pastoral enterprises in the early 1870s (Nolan 2003). By the 1950s, the majority of Aboriginal people had moved off the land to settle in European missions and outstations and regional centres such as Birdsville, Alice Springs and Mt Isa. The exodus was encouraged by Queensland laws and droughts (Hercus 1985).

Permanent cattle grazing (*Bos taurus* and *B. indicus*) commenced on all four study properties in the 1970s and during this time they were each subject to extensive pastoral development in the form of fencing and bore sinking (Letnic 2003). The northern part of Tobermorey Station, which does not form part of the study area, was likely settled much earlier and was called Allanjeer at that time. Historical stocking rates were slightly higher on Ethabuka than on Carlo and Tobermorey, and Craven's Peak was stocked more heavily in the south due to the rocky country in the north. Overall, it is unlikely that cattle densities on any of the study properties exceeded the recommended stocking rate of one beast per 250 ha for the dunefields and one beast per 80-100 ha for the gidgee woodlands (Wilson et al. 1990).

Many of these early pastoralists viewed fire as a threat to their plant resources and infrastructure and actively suppressed wildfire events (Griffin et al. 1983, Letnic 2003). Only a limited degree of prescribed burning was used by pastoralists to reduce fuel loads, stimulate vegetation growth and benefit biodiversity (Letnic et al. 2004, Edwards et al. 2008, Turner et al. 2008). As a result, large scale, lightning-induced wildfire events became the dominant feature of the fire regime by the mid 1900s.

2.7.4 Recent wildfire events in the Simpson Desert

The minimum wildfire return interval across the central deserts region varies from nine years in the Tanami Desert to 26 years for the Simpson desert, 30 years in the Great Victoria Desert and 32 years for Uluru (Haydon et al. 2000b, Allan and Southgate 2002, Greenville et al. 2009).

Evidence from the literature and from Landsat imagery indicates that the last four major wildfires in the Simpson Desert occurred in 1917/18, 1951, 1974/75 and 2001/02 (Anon. 1917, 1918, 1952, 1977, Letnic and Dickman 2006, Greenville et al. 2009). Available information for the two most recent fires indicates that they both burned disproportionately more spinifex than any other vegetation type (Greenville et al. 2009), indicating the high flammability of this vegetation.

The 1974/75 fire burnt 4561 km^2, or 55% of the study area (Greenville et al. 2009). The next major wildfire in 2001/02 burned 2544 km^2, or 31% of the study area (Letnic and Dickman 2005, Letnic and Dickman 2006, Greenville et al. 2009). This fire went on to burn in excess of 10,000 km^2 of the Simpson Desert and over 500,000 km^2 of the Northern Territory, in addition to parts of Western Australia and South Australia (Ellis et al. 2004). Historical records suggest that the 1917-1918 and 1951 wildfire events were of a similar scale, but no detailed information exists to confirm this.

In total, 49% of the study area has burnt once since 1972 and 20% has burnt twice. Less than 1% has burnt three times and 36% has remained unaffected by wildfire since 1972 (Greenville et al. 2009). Smaller fires also occurred in the study area between the 1974/75 and the 2001/02 wildfires and in each case they occurred in areas not burnt in the 1974/75 fires, a fact that underpins the effectiveness of patch-burning in retarding the spread of wildfires.

As discussed in the Introduction, fire events in arid Australia are closely related to climatic fluctuations and heavy rainfall events. In the study region, wildfire events are associated specifically with two years of heavy cumulative rainfall before a fire event, rainfall during the year of a fire event and the mean Southern Oscillation Index (SOI) from June to November in the year before a fire event (Greenville et al. 2009). Figure 2.6 shows the timing of the last 4

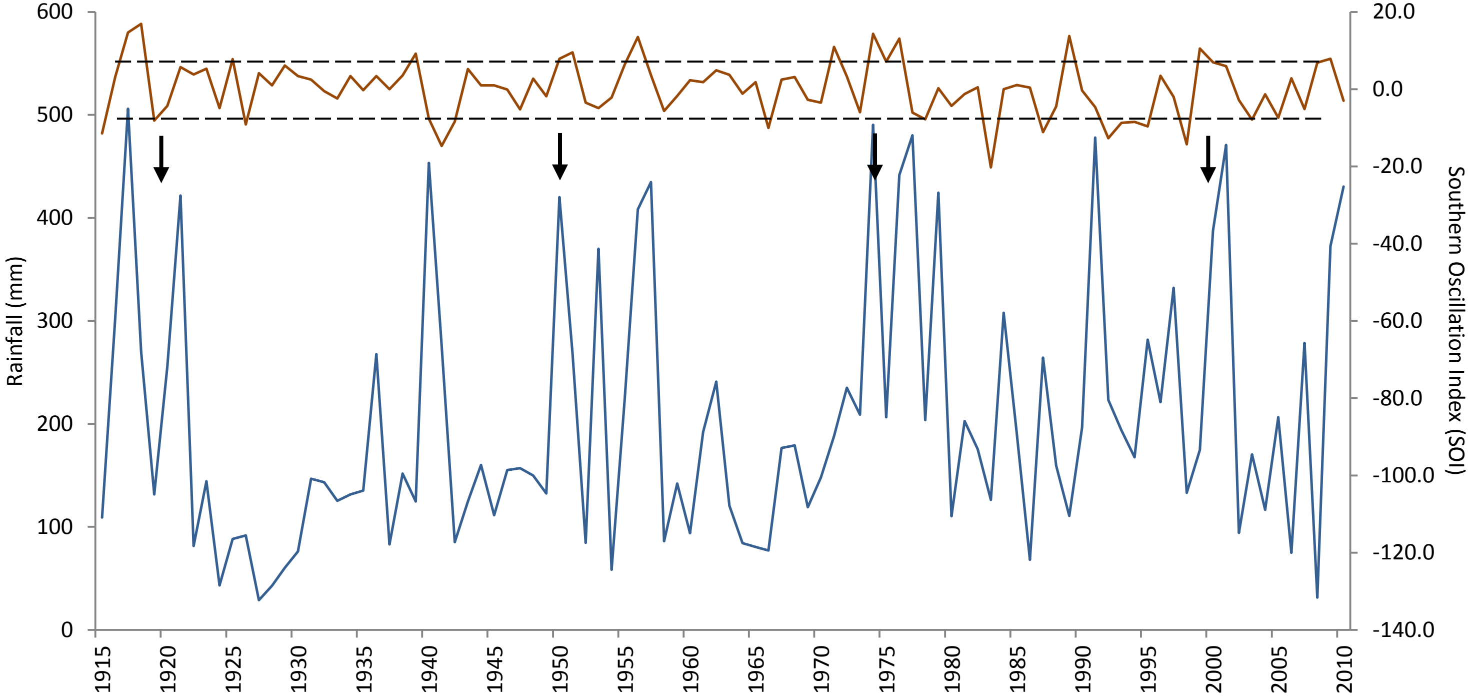

Figure 2.6 Rain-year (July-June) rainfall for the Marion Downs weather station over the past 100 years. The black arrows indicate the timing of the 1917/18, 1951, 1974/75 and 2001/02 wildfires. The orange line indicates the southern oscillation index (SOI) over this period. The black dashed lines indicate the El Niño and La Niña SOI thresholds of -8 and +8 respectively.

wildfire events with reference to the annual rain-year (July-June) rainfall and SOI over that period.

2.7.5 Limitations of fire knowledge

Although spatial databases describing fire incidence have been created from early aerial photography and Landsat satellite images from the mid-1970s to the present, these databases cover only a restricted spatial area. Despite the observations of early European explorers and naturalists we have little verified knowledge of the fire frequency, extent and seasonality of current and previous fire regimes in much of semi-arid and arid Australia. Current databases are limited both spatially and temporally and do not provide information about fire regimes prior to European land tenure (Burrows et al. 1991, Haydon et al. 2000a, Allan and Southgate 2002, Edwards et al. 2008, Greenville et al. 2009). Thus, much of the fine scale detail such as how often the early Aboriginal inhabitants burnt, the size of the burnt patches, and the precise effects of this, if any, on the flora and fauna has been lost.

2.7.6 Current fire management in the study area

Small-scale control burns (<1 km^2) are conducted by station managers on Carlo and Tobermorey stations to rejuvenate pastures and create fire-breaks. Limited fire management activities are carried out on Ethabuka and Cravens Peak Reserves and are confined largely to the maintenance of fire breaks along fences and tracks, or to the protection of infrastructure.

CHAPTER 3

FIRE TYPE AND HEMISPHERE DETERMINE FIRE EFFECTS ON ALPHA AND BETA DIVERSITY OF VERTEBRATES: A GLOBAL META-ANALYSIS

A knob-tailed gecko (*Nephrurus levis*) rests on a gidgee log

Publication Details

This chapter has been submitted to *Global Ecology and Biogeography*. Revisions were recommended, and they have been included in this Thesis. The final publication decision is pending.

We conducted a worldwide meta-analysis to investigate the effects of fire on vertebrate diversity, controlling for fire type, taxon, hemisphere, continent and ecoregion to identify trends across studies and locations. We collated studies on the effects of fire on amphibian, reptilian, avian and mammalian diversity. To account for effects on local patch diversity and community assemblage composition, we measured the influence of fire on both alpha and beta diversity. We tested first for the main effect of fire before investigating the potential influence of fire type (wildfire or prescribed burn), taxon, ecoregion, and geographical location (hemisphere and continent). One hundred and four studies were evaluated: 56 studies on birds, 26 on mammals, 17 on reptiles and 5 on amphibians. Comprehensive species lists were provided for 94 studies, with birds the most diverse taxonomic group studied and mammals the least. The studies fell into 14 ecoregions, with the three most common being temperate broadleaf and mixed forests; temperate grasslands and savannas; and shrublands and temperate coniferous forest. The effect of fire on patch diversity and community assemblage composition was not determined by taxon, ecoregion, or geographic location, but instead by fire type. Prescribed burns significantly increased alpha diversity, whereas wildfires had no effect. Fire-effects on alpha diversity were also more positive in the northern than southern hemisphere. Species assemblage composition (beta diversity) was influenced primarily by fire type. Here, however, species assemblages in between burnt and unburnt habitats were more similar after prescribed burns and generated lower levels of beta diversity than did wildfires. Our findings have ramifications for the application of prescribed burning programs because they show that fire effects on vertebrate diversity are context dependent and that there is no ‘one size fits all’ approach that can be incorporated into land management practices.

3.1 INTRODUCTION

Fire is a powerful force that has shaped the evolution and function of ecosystems in many parts of the world (Bowman et al. 2009). Frequent and widespread fires can transform entire ecosystems, as seen in the conversion of expansive tracts of forest into fire-adapted savannahs across South America, Africa, Australia and New Zealand (Keeley and Rundel 2005, Bowman and Haberle 2010). Fire-dependent ecosystems now cover a large proportion of the global land surface and contain primarily fire-tolerant and fire-adapted species, often at the expense of fire-sensitive species (Parr and Andersen 2006, Lohman et al. 2007, Bowman et al. 2009).

Fire also occurs frequently at smaller scales where it is often intentionally prescribed to benefit biodiversity (Letnic et al. 2004, Fuhlendorf et al. 2006). This technique is informed by the Intermediate Disturbance Hypothesis (Connell 1978) and the Patch Mosaic Burn Theory (Brockett et al. 2001) which each predict that a moderate level of disturbance, such as that produced by small scale burns, will promote local biodiversity (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006).

Despite the global prominence of natural and prescribed fires, the effects of fire on faunal diversity remain uncertain. In many instances, wildfires eliminate habitat and food resources and increase the hunting efficiency of predators in post-fire landscapes (Letnic et al. 2005, Green and Sanecki 2006, Kodandapani et al. 2008). In some cases, however, these effects are short-lived and no lasting effects on faunal diversity are evident (e.g. Pons and Prodon 1996, Cunningham et al. 2002). Similarly, increasing numbers of studies are reporting that prescribed burning does not provided the expected biodiversity gains over a wide range of mammal, reptile and plant taxa (Parr and Andersen 2006, Driscoll and Henderson 2008, Lindenmayer et al. 2008, Pastro et al. 2011).

In addition to the effect of fire type (wildfire or prescribed burn), the effect of fire on faunal diversity is influenced by factors such as study taxon, habitat and geographical location. For example, many C_4 arid and temperate grasslands have co-evolved with fire and biota in these habitats types are often fire-adapted and thus impacted less by fire events (Andersen et al. 2005). Regions such as the Mediterranean, central Australia and southern Africa are also particularly fire-prone and wildfires there can be more intense and widespread than in other parts of the globe. Fire regime can also strongly influence the effect of fire on biota, with factors such as fire interval, intensity, seasonality and spatial arrangement interacting to change community structure and either positively or negatively influence the survival of affected species (Charrette et al. 2006, Parr and Andersen 2006, Gill and Allan 2008, Fisher et al. 2009).

The choice of taxon studied can also determine the outcome of fire studies (Letnic et al. 2005). Birds, for example, are relatively mobile and are often able to escape fire. Consequently, mobile taxa may be less affected by fire than more sedentary taxa such as amphibians that frequently suffer higher mortality (Bury 2004, Cano and Leynaud 2010). These suites of interacting factors make it challenging to draw general conclusions about the effect of fire on biodiversity and to design appropriate fire management strategies and programs that are tailored towards different habitats and locations (Pastro et al. 2011).

In this study we use quantitative meta-analytic methods to investigate the effects of fire on biodiversity at a global scale. This approach allows us to control for variables such as fire type, taxon and vegetation type to identify trends across studies and locations. To obtain a comprehensive understanding of the effects of fire on faunal diversity, we examine the effect of fire on two components of biodiversity; alpha diversity (α: within sampling units) and beta diversity (β: between sampling units; Whittaker 1972, Crist et al. 2003). While alpha diversity measures the species richness of burnt and unburnt habitats, beta diversity reflects changes in assemblage or community composition after fire. Assemblage composition is frequently affected by fire as fire-induced habitat heterogeneity may benefit or adversely affect different species and hence influence assemblage composition at the landscape scale, depending on the size and intensity of the fire (Cleary et al. 2004, Pastro et al. 2011). For example, we might expect low beta diversity after prescribed fire, where patches are typically small and the landscape is heterogeneous in nature. Conversely, we might expect a large change in assemblage composition, or high beta diversity, after a wildfire, given the characteristically intense and widespread nature of these fires (Pastro et al. 2011).

Our specific aims were to (1) quantify the effect of fire on alpha and beta diversity; (2) determine the influence, if any, of fire type, study taxon (amphibians, reptiles, birds and mammals), ecoregion and geographical location on the effects of fire; and (3) use these results to guide future fire management programs and studies.

3.2 MATERIALS AND METHODS

3.2.1 Literature searches

We searched the electronic databases Web of Science, Biosis Previews, Zoological Record and Scopus using combinations of the search terms fire*, wildfire*, burn*, mammal*, rodent*, reptil*, lizard* herpeto*, avian*, bird*, vertebrate* and amphib*. The reference lists of earlier reviews (e.g. Sutherland and Dickman 1999, Kotliar et al. 2007, Fontaine and Kennedy 2012) and of relevant papers were also searched. Only published, peer-reviewed journal articles were included in the analysis and the end-date for literature inclusion was June 2011.

Papers were included if they addressed the effect of fire on the species richness of amphibians, birds, mammals or reptiles or at the community level. Studies that analyzed the effects of fire on only one or a selected number of species were excluded. We did not set a threshold of allowable species numbers for inclusion in the study; as long as a study endeavoured to sample all available species in a study area it was deemed suitable for inclusion.

Where studies investigated the combined effects of fire and other disturbances, only data pertaining to the effects of fire were extracted. To avoid influencing our conclusions with selection criteria that were not specifically a function of the relevance of the data, no other quality-based inclusion criteria were applied (Englund et al. 1999).

3.2.2 Variables

The following data were extracted from the text, tables and/or figures of each study: experimental methodology (treatment - control or before - after); replication (replicated or unreplicated); fire type (wildfire or prescribed burn); study taxon (amphibian, reptile, bird or mammal); study time length and spatial scale and geographical location (continent and hemisphere). Each study was also classified into one of 17 terrestrial ecoregions or one freshwater ecoregion based on the World Wildlife Fund (WWF) global classification system (Olson et al. 2001, Coetzee et al. 2013). Ecoregions were as follows: arid and semi-arid grassland; boreal forests/taiga; flooded grasslands and savannas; mangroves; Mediterranean coniferous forest; Mediterranean oak forest; montane grassland and shrubland; small lake ecosystems; subalpine woodland; temperate broadleaf and mixed forest; temperate coniferous forest; temperate grasslands, savannas and shrublands; tropical and subtropical grasslands, savannas and shrublands; tropical and subtropical coniferous forests; tropical and subtropical dry broadleaf forests; tropical and subtropical moist broadleaf forests; tundra; and xeric shrubland.

Data were collected at the end of each study. In the event that terminal data were not available the mean values obtained over the course of the study were used. Where studies included once-burnt or multiple-burnt habitats, data from the once-burnt areas were used to minimize the confounding factor of repeated burning. Where a study included sampling units that varied in spatial scale, the means of these were used to indicate the spatial scale of the study.

Our literature searches yielded 368 publications that addressed the effects of fire on vertebrates. Eighty-seven of these addressed the effect of fire on the alpha or beta diversity of amphibians, reptiles, birds or mammals and thus were included in the meta-analysis (Appendix 3.1). Some studies reported the independent effects of fire on more than one taxon and thus the total number of studies included in the meta-analysis was 104 (Appendix 3.1).

3.2.3 Statistical analyses: alpha diversity

Due to the limited data available in many published papers, we defined alpha diversity (α) as the species richness within a sampling unit. We calculated the effect size as $\ln(X_e/X_c)$ for each study to indicate the effect of the fire on alpha diversity, where X_e and X_c represent the species richness in post-fire burnt and unburnt habitat (treatment - control studies) or in habitat before and after a fire (before - after studies; Rosenberg et al. 2000, Salo et al. 2010). This metric was chosen over more traditional effect sizes such as Hedges' d or $\ln(R)$ because it does not require within-study variance and a large proportion of our data set consisted of unreplicated or pseudo-replicated studies in which within-study variance was not reported (Salo et al. 2010).

We tested first for the main effect of fire before investigating the potential influence of fire type, taxon, habitat, and geographical location (hemisphere and continent). An effect size $\ln(X_e/X_c)$ ± 95% confidence interval (CI) > 0 indicated that a fire event increased species richness, an effect size $\ln(X_e/X_c)$ ± 95% CI = 0 indicated that the fire event had no effect on species richness, and an effect size $\ln(X_e/X_c)$ ± 95% CI < 0 indicated that the event reduced species richness (Rosenberg et al. 2000).

Univariate tests were employed to compare alpha diversity effect sizes within and between variable groupings. Outliers were identified and removed prior to analysis. Relationships between the alpha diversity effect size and 1) study length; and 2) spatial scale were explored using Pearson correlations. The relationship between alpha diversity effect size and study replication was tested using the Mann Whitney U-test.

3.2.4 Beta diversity

The effect of fire on beta diversity was assessed using Sørensen's similarity index (Sørensen 1957). The formula for the index is $QS = 2C/(A + B)$, where A represents the species richness of the landscape prior to the burn or in control habitat and B represents the species richness of the landscape after the burn or in treatment habitat. C represents the number of species shared by both A and B. An increase in the Sørensen index signifies an increase in the similarity of species assemblages between burnt and unburnt habitats and thus a decrease in beta diversity. As with our alpha diversity metric, metrics such as the Bray-Curtis dissimilarity index (Oliver et al. 1998, Kessler et al. 2009) which take into account species abundances, could not be calculated given the limited quantitative information that was presented in many studies.

We tested first for the primary effect of fire before investigating the potential contribution of fire type, taxon, habitat and geographical location (continent and hemisphere). The effect of fire on beta diversity within and between variable groupings was investigated using univariate tests. Outliers were identified and removed prior to analysis.

Our measures of alpha and beta diversity were each free to vary independently as we chose not to calculate beta diversity as a multiplicative or additive function of gamma and alpha diversity (Jost 2007, Veech and Crist 2010). All statistical analyses were undertaken in SPSS (IBM SPSS 2010).

3.2.5 Publication bias

Publication bias can arise in meta-analyses as authors may choose to publish only statistically significant results (the "file-drawer problem"; Rosenthal 1979) or results that support currently popular theories (Simmons et al. 1999).

To check for publication bias, we plotted the sample size of each study against the alpha diversity effect size $\ln(X_e/X_c)$ to produce a funnel plot (Appendix 3.2; Gates 2002). This method was chosen over the more traditional normal quantile plot as our study contained many unreplicated studies for which the variance required by the normal quantile plot could not be calculated. The funnel plot produced no evidence of publication bias (Appendix 3.2).

3.3 RESULTS

Fifty-six studies investigated the effect of fire on birds, 26 on mammals, 17 on reptiles and 5 on amphibians. Seventy studies were replicated (i.e. they included at least two treatment and two control plots or a before-after design where the treatment was reversed between plots) and 34 studies were unreplicated. Fifty-three studies examined the effects of prescribed burns and 51 examined the effects of wildfires (Appendix 3.1).

The studies took place in 14 ecoregions. The three most commonly studied ecoregions were temperate broadleaf and mixed forest, temperate grasslands savannas and shrublands, and temperate coniferous forest (Table 3.1). Fifty-two studies were located in North America, 22 in Australia, 16 in South America, 7 in Europe, 5 in Africa and 2 in Asia. Overall, 61 studies were located in the Northern Hemisphere, 34 in the Southern Hemisphere, and 9 in equatorial regions (Figure 3.1).

Lists with scientific names for each species were provided for 94 studies (Appendix 3.1). Birds were the most diverse of the taxonomic groups evaluated, with a mean of 28.16 species per study (± 2.30 Standard Error). Reptiles were the next most species-rich group, with an average of 11.76 species per study (± 1.89 SE). Amphibians returned an average of 6.40 species per study (± 1.96 SE) and mammals were the least species-rich group, with an average of just 6.26 species per study (± 0.88 SE).

3.3.1 Alpha diversity

Ninety-six studies analyzed the effect of fire on alpha diversity (Appendix 3.1). The number of species in burnt and unburnt habitats, along with the alpha diversity effect size, is recorded for each study in Appendix 3.1.

Fire had no overall effect on alpha diversity (see Appendix 3.3). Instead, the effect of fire was determined primarily by fire type, as prescribed burns significantly increased alpha diversity and wildfires had no effect (Figure 3.2a). Fire effects were not influenced by study taxon or habitat, and North America was the only continent in which fire had significant effects (Figure 3.2b, Figure 3.3a-c).

Ecoregion	Number of studies
Arid and semi-arid grasslands	9
Boreal forests/taiga	2
Flooded grasslands and savannas	5
Mediterranean coniferous forest	2
Mediterranean oak forest	5
Montane grassland and shrubland	1
Subalpine woodland	1
Temperate broadleaf and mixed forest	17
Temperate coniferous forest	12
Temperate grasslands savannas and shrublands	18
Tropical and subtropical grasslands, savannas and shrublands	7
Tropical and subtropical dry broadleaf forests	8
Tropical and subtropical moist broadleaf forests	7
Xeric shrubland	10
Total studies	104

Table 3.1 World Wildlife Fund (WWF) ecoregion classifications (Olson et al. 2001, Coetzee et al. 2013) and the number of studies that fell into each. The ecoregion classification for each individual study is included in Appendix 3.1.

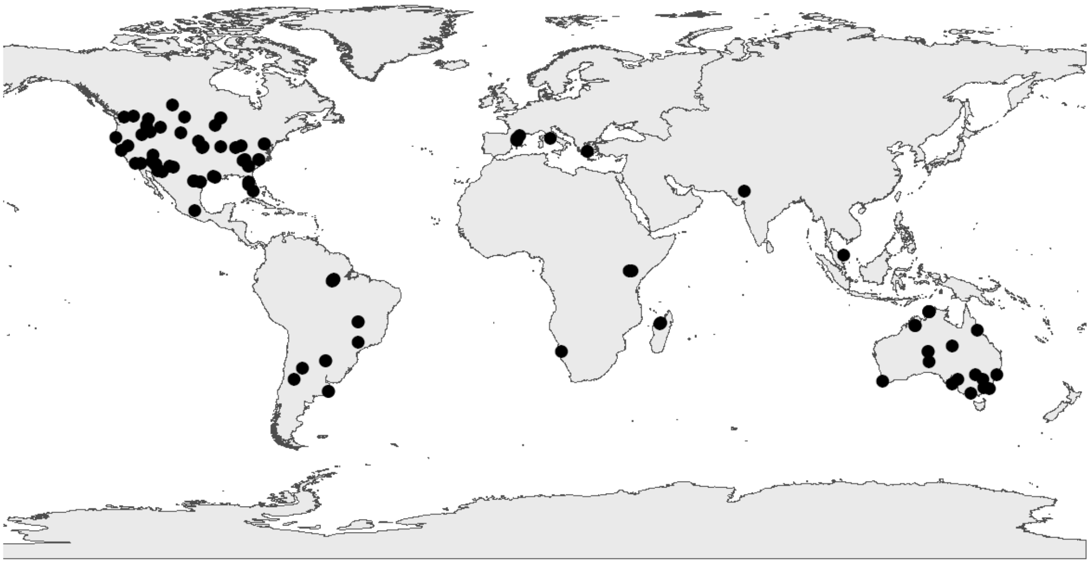

Figure 3.1 The location of each of the studies (represented by black circles) included in the meta-analysis.

The effect of fire in North America was not a generalized trend as it varied according to fire type and ecoregion. For example, prescribed burns increased alpha diversity but wildfires did not. However, prescribed burns increased the alpha diversity of birds in temperate grassland and shrubland but had no effect on bird alpha diversity in temperate coniferous forests (Figure 3.2c and 2d).

Hemisphere was also an important determinant, as fire significantly increased alpha diversity in the northern hemisphere (>10°N) and had a generally negative effect on alpha diversity in the southern hemisphere (<10°S; Figure 3.4). This held for both prescribed burns and wildfires. The effect of prescribed burns in the northern hemisphere was also significantly greater than in the southern hemisphere (t = -3.312, d.f. = 46, P < 0.001).

There was no correlation between alpha diversity effect size and study length, study spatial scale or replication.

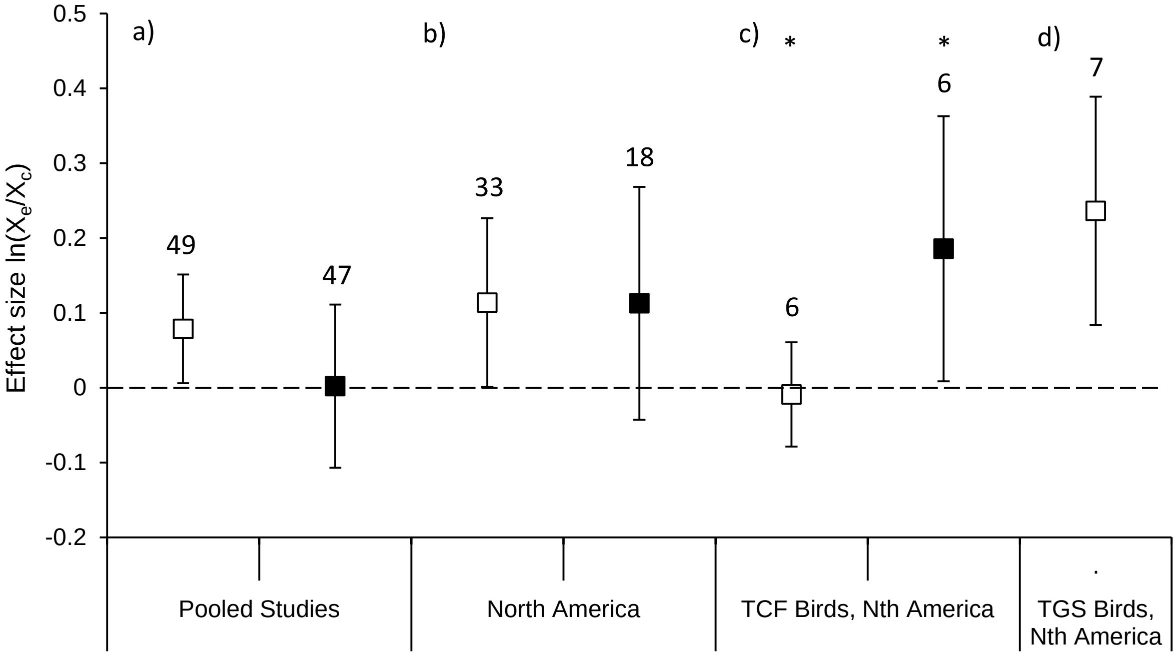

Figure 3.2 Effect size ln(Xe/Xc) ± 95% confidence interval (CI) of prescribed burns (open symbols) and wildfires (closed symbols) on the alpha diversity of terrestrial vertebrates a) Across all studies; b) In North America; c) For birds in temperate coniferous forests in North America; and d) For birds in temperate grassland and shrubland in North America. X_e and X_c represent the mean species richness in post-fire burnt and unburnt habitat (treatment - control studies) or in habitat before and after a fire. The number of studies in each analysis is indicated above each bar. A significant effect is obtained if $\ln(X_e/X_c) \pm 95\%$ CI > 0 or $\ln(X_e/X_c) \pm 95\%$ CI < 0. A significant difference between the prescribed burn and wildfire effect size in a given grouping is indicated by * ($P \leq 0.05$).

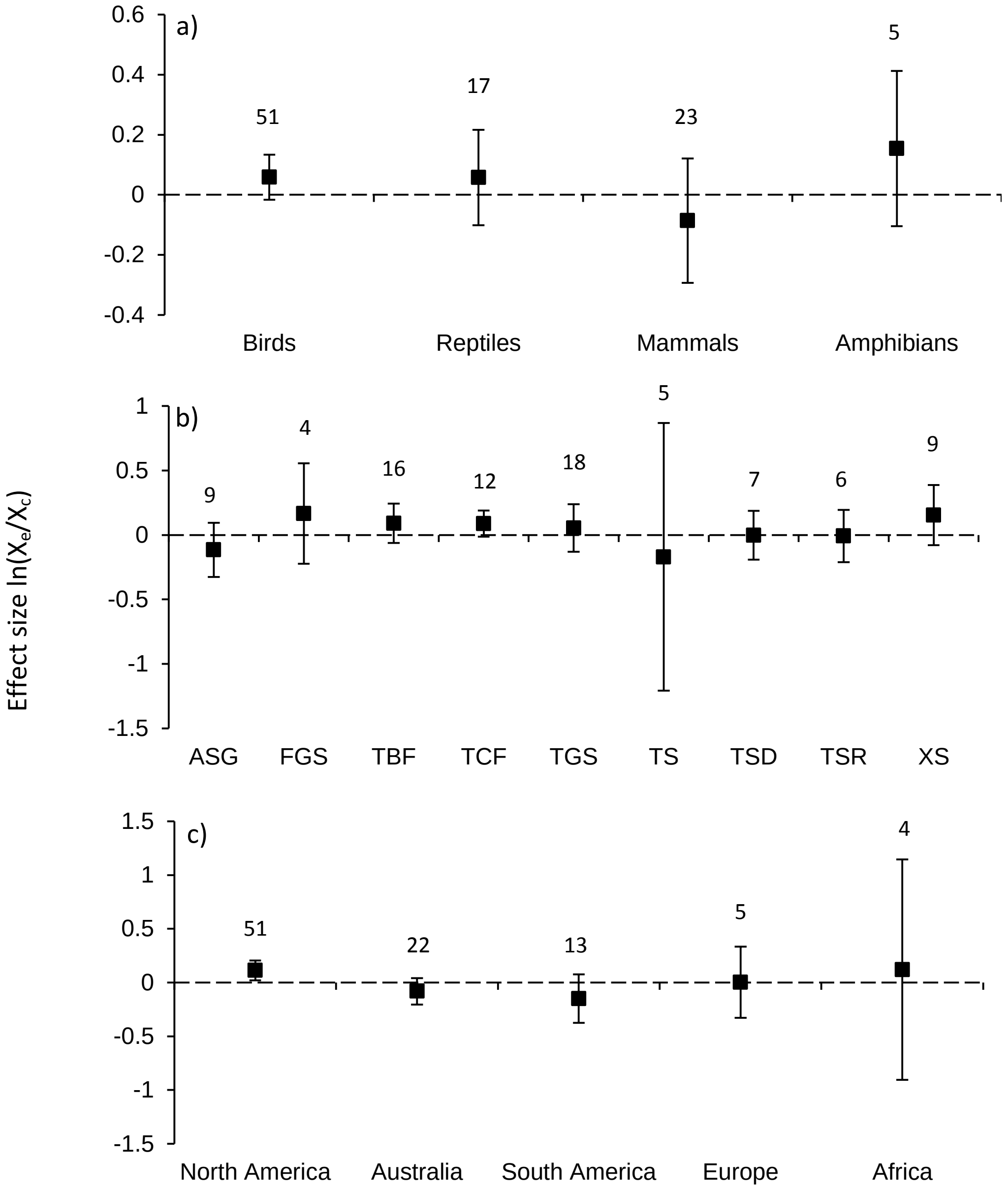

Figure 3.3 Effect size ln(Xe/Xc) ± 95% confidence interval (CI) of fire on alpha diversity grouped by a) taxon; b) ecoregion and c) continent. Xe and Xc represent the mean species richness in post-fire burnt and unburnt habitat (treatment - control studies) or in habitat before and after a fire. The number of studies in each analysis is indicated above each bar. A significant effect is obtained if ln(X_e/X_c) ± 95% CI > 0 or ln(X_e/X_c) ± 95% CI < 0. Ecoregion codes are as follows: ASG (arid and semi-arid grasslands); FGS (flooded grasslands and savannas); TBF (temperate broadleaf and mixed forests); TCF (temperate coniferous forests); TGS (temperate grasslands, savannas and shrublands); TS (tropical and subtropical grasslands, savannas and shrublands); TSD (tropical and subtropical dry broadleaf forests); TSR (tropical and subtropical moist broadleaf forests); and XS (xeric shrublands). Groupings without sufficient replication were excluded.

3.3.2 Beta diversity

Ninety-seven studies reported the effect of fire on the similarity of species assemblage composition between burnt and unburnt habitats (beta diversity). As with alpha diversity, these effects were not influenced by study taxon, study habitat or continent (Figure 3.5a-c). Instead, the effect of fire on beta diversity was influenced primarily by fire type, as species assemblages between burnt and unburnt habitats were less similar after wildfire (higher beta diversity) when compared with prescribed burns (Figure 3.6). Wildfires increased beta diversity when compared with prescribed burns across all studies (t = 3.049, d.f. = 88, P = 0.0015) and within the groupings of birds (t = 1.798, d.f. = 44, P = 0.040), lizards (t = 1.753, d.f. = 14, P = 0.050), North America (t = 2.378, d.f. = 45, P = 0.011), North American birds (t = 2.165, d.f. = 23, P = 0.020) and birds in North American temperate coniferous forests (t = 4.981, d.f. = 10, P = 0.00028). Studies in the northern hemisphere (t = 2.693, d.f. = 42, P = 0.0005) and southern hemisphere (t = 1.707, d.f. = 37, P = 0.048) showed a similar trend. Analysis was limited to these particular habitat and continent groupings as there was not adequate replication in other groupings for analysis (Appendix 3.1).

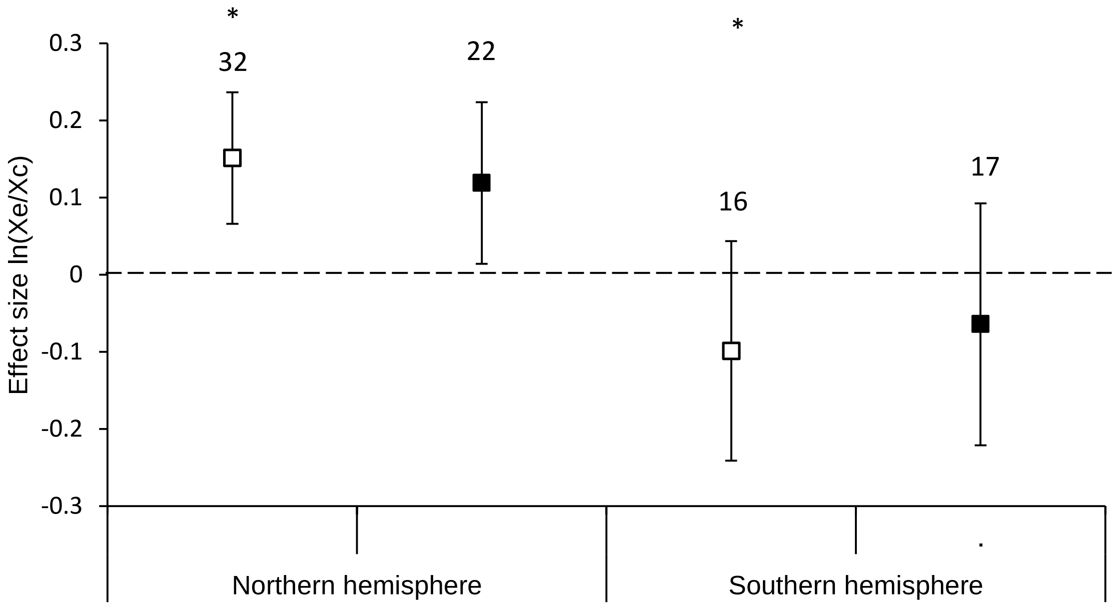

Figure 3.4 Effect size ln(Xe/Xc) ± 95% confidence interval (CI) of prescribed burns (open symbols) and wildfires (closed symbols) on alpha diversity in the northern and southern hemisphere. X_e and X_c represent the mean species richness in post-fire burnt and unburnt habitat (treatment - control studies) or in habitat before and after a fire. The number of studies in each analysis is indicated above each bar. A significant effect is obtained if $\ln(X_e/X_c) \pm$ 95% CI > 0 or $\ln(X_e/X_c) \pm$ 95% CI < 0. A significant difference between the effect of prescribed burns in the northern and southern hemisphere is indicated by * ($P \leq 0.05$).

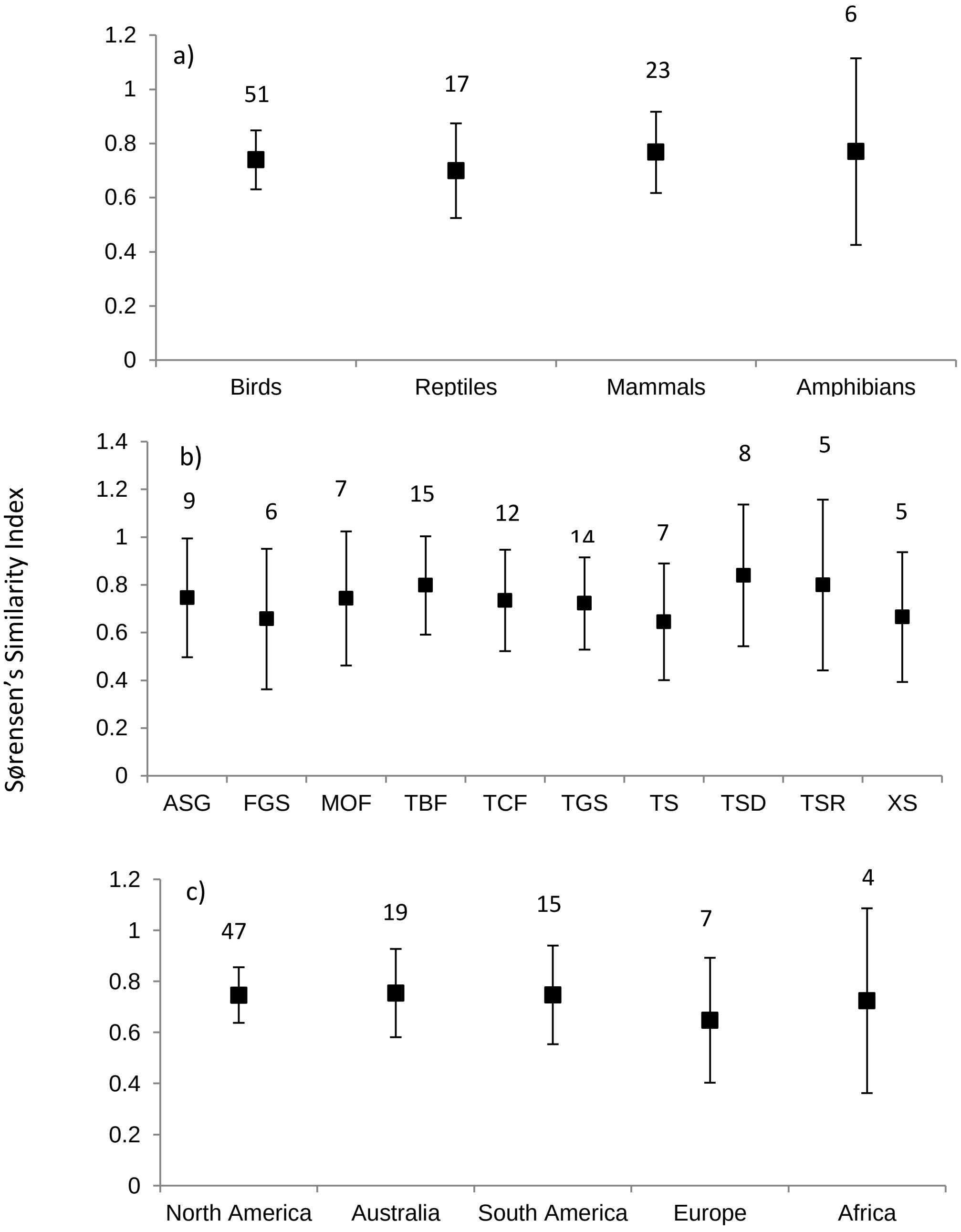

Figure 3.5 Sørensen's Similarity Index ± SE grouped by a) taxon; b) ecoregion; and c) continent. The number of studies in each analysis is indicated above each bar. Ecoregion codes are as follows: ASG (arid and semi-arid grasslands); FGS (flooded grasslands and savannas); MOF (montane forest); TBF (temperate broadleaf and mixed forests); TCF (temperate coniferous forests); TGS (temperate grasslands, savannas and shrublands); TS (tropical and subtropical grasslands, savannas and shrublands); TSD (tropical and subtropical dry broadleaf forests); TSR (tropical and subtropical moist broadleaf forests); and XS (xeric shrublands). Groupings without sufficient replication were excluded.

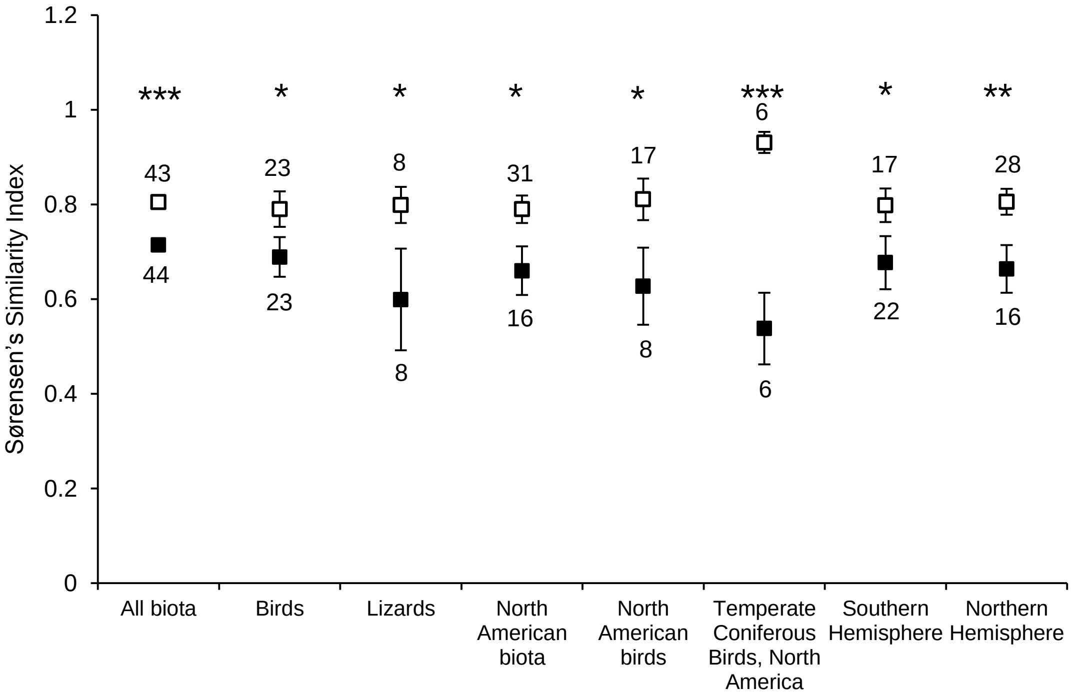

Figure 3.6 Sørensen's Similarity Index between burnt and unburnt habitats ± SE after prescribed burns (open symbols) and wildfires (closed symbols) across all studies and grouped according to fire type, taxon, continent, ecoregion and hemisphere. The number of studies in each analysis is indicated above each bar for prescribed burn studies and below each bar for wildfire studies. A significant difference between the prescribed burn and wildfire Sørensøn Similarity Index is indicated by * ($P \leq 0.05$), ** ($P \leq 0.01$), and *** ($P \leq 0.001$).

3.4 DISCUSSION

Across all our studies, fire had no overall effect on alpha diversity (Aim 1). Instead, fire effects were determined primarily by fire type (prescribed burn or wildfire) and hemisphere (Aim 2). Prescribed burns increased alpha diversity but wildfires had no effect (Figure 3.2a), and fires in the northern hemisphere increased alpha diversity whereas fires in the southern hemisphere did not (Figure 3.4). The effect of fire on beta diversity was also influenced primarily by fire type as prescribed burns decreased and wildfires increased beta diversity (Figure 3.6).

3.4.1 Alpha diversity

Small scale prescribed burns are often thought to promote alpha diversity by creating local habitat heterogeneity, as the resulting habitat matrix provides for species with varying habitat requirements (Fuhlendorf et al. 2006, Fuhlendorf et al. 2009, Pastro et al. 2011). However, recent studies have found that this effect is not widespread and is influenced by factors such as habitat type and the taxon studied (e.g. Cleary et al. 2004, Driscoll and Henderson 2008, Lindenmayer et al. 2008, Pastro et al. 2011). In our study, the positive effect of prescribed burning on alpha diversity was relatively small and associated with a large confidence interval. We suggest that this result was driven by a high proportion of habitat- and species-specific responses within the data set.

In support of this interpretation, the meta-analysis further revealed that taxon was a poor predictor of fire effects on alpha diversity (Figure 3.3a). In addition, North America was the only continent where prescribed burns significantly increased alpha diversity (Figure 3.3c); however, the effect differed between ecoregions (Figure 3.2c and 3.2d). The absence of a broadscale 'wildlife response' to prescribed burning has been identified in other recent studies (e.g. Fuhlendorf et al. 2006, Kotliar et al. 2007, Pastro et al. 2011, Fontaine and Kennedy 2012) which have similarly highlighted the importance of variables such as habitat, fire severity and species in determining fire responses. These findings have important ramifications for the application of the Patch Mosaic Burn Hypothesis and the Intermediate Disturbance Hypothesis because they suggest that a mosaic of habitat in different seral stages, as produced by patchy prescribed burns, does not as a general rule enhance alpha diversity within specific vertebrate taxa. Recent research suggests that fire-sensitive species could be further adversely affected by such practices (Haslem et al. 2011, Kelly et al. 2012).

In our study, wildfires did not significantly affect alpha diversity. Neutral responses such as this may represent a true ecological insensitivity to the variable of interest, or can be the product of inconsistency among studies. We suggest that the latter is more likely the cause of this result. Wildfires in the study occurred in a range of locations and ecoregions (Figure 3.1) and it is likely that ecoregion-specific and location-specific responses produced contrary variations within the data set that contributed to the overall neutral result. For example, ecoregions in which wildfires both occur frequently and are well studied, such as parts of the Mediterranean, South Africa and Australia, may be more adapted to severe fire events and thus resilient to the effects of fire (Andersen et al. 2005). Species-specific responses may have also contributed to the neutral effect, particularly in regions where severe-burn specialists, such as the Black-backed Woodpecker (*Picoides arcticus*), are common (Hutto 2008).

Differing severities among wildland fires, and the varying animal responses that they engender, also may have masked species responses to wildfire. Fire severity can be a key factor influencing the effect of wildfires on terrestrial biota, as vertebrates respond differently to low-intensity fires as compared with stand-replacing, high-intensity fires (Smucker et al. 2005, Kotliar et al. 2007, Fontaine and Kennedy 2012). The effect of low-, mid- or high-severity fires may vary further according to habitat type. For example, the effect of a low intensity grassland fire on animal communities may differ substantially from a low intensity shrubland or forest fire, and the three fires may result in quite different proportional changes in habitat structure. While a high intensity forest fire will likely create a heterogeneous post-fire environment of severely burnt and less burnt vegetation, a high intensity arid grassland fire will more likely create a homogeneously burnt habitat as grass hummocks will more readily burn to the ground. Even a low-intensity fire can lead to slow regrowth and long standing effects in a non fire-adapted arid shrubland (Vamstad and Rotenberry 2010) or kill a large number of large trees and dramatically alter the post-burn light environment in a tropical rainforest (Peres et al. 2003).

In addition, while high-severity, stand-replacing fires occur to the detriment of species diversity in many instances it is likely that high-severity fires are also an important habitat component for a small subset of species by providing habitat conditions not found in unburned or lightly-burned forests (Letnic et al. 2004, Fontaine and Kennedy 2012). These effects may also occur over very long time scales. For example, high-severity fire adversely affects Northern Spotted Owls (*Strix occidentalis occidentalis*) in northwestern California, but creates suitable habitat after approximately 20 years and high quality habitat after about 60 years (Franklin et al. 2000). Analysis of wildfires as a single category may therefore preclude the detection of finer-scale responses to differing fire severities. In addition to this, many high-severity fires contain complex mixtures of burn severities which may further confound the detection of species responses (Kotliar et al. 2007, Halofsky et al. 2011, Fontaine and Kennedy 2012). Analysis at this finer scale may allow the identification of positive and negative species- and community-responses to fire that are masked by a single ‘high-severity’ analysis. Of our wildfire studies, 23 reported a high severity fire, 10 reported a low severity fire, and 14 studies did not report fire severity (Appendix 3.1). Given that each fire type affected a range of habitats, we did not have an adequate number of observations to test for the independent effects of fire severity within the wildfire grouping.

Hemisphere had a strong influence on the effect of fire on alpha diversity. On average, fire increased alpha diversity in the northern hemisphere and somewhat decreased it in the southern hemisphere across all fire types, ecoregions and taxa (Figure 3.4). It is interesting to note here that the effect of fire type disappeared when studies were grouped by hemisphere. The northern hemisphere effect was most likely influenced by the high proportion of North American studies in that grouping (51 of 58 northern hemisphere studies) and the generally positive effect of North American fires on alpha diversity. Many North American studies involve the introduction of prescribed fire into fire-suppressed or excluded habitats (Allen et al. 2006) or the effects of wildfire in fire-suppressed forests (Mendelsohn et al. 2008). These fires thus may not have the same devastating effects on biodiversity that often accompany similar fires across parts of the southern hemisphere. For example, high-severity wildland fire in southwestern montane forests did not have long term negative ecological effects on bird communities (Kotliar et al. 2007). Further to this, Fontaine and Kennedy (2012), in their meta-analysis of bird responses to fire in fire prone habitats across the US, found that while many bird species responded negatively to high-severity fires (predominantly canopy-nesting and foliage-foraging species), many other did not.

The southern hemisphere effect is likely due to regional processes including threatening processes and climate. The prescribed burns grouping was dominated by Australian studies (22 of the 32 southern hemisphere studies) and prescribed burns are known to interact in complex ways on that continent. The significant pressure that Australian fauna experience from invasive predators and changing fire regimes (McKenzie et al. 2007) means that prescribed burns may not produce the expected benefits to alpha diversity (e.g. Woinarski 1990, Masters 1996). Debate is currently high over what constitutes a ‘correct’ fire regime in various parts of the continent (Bradstock et al. 2005, Driscoll et al. 2010, Andersen et al. 2012), and in some regions too-frequent prescribed burns are thought to be negatively affecting diversity (Driscoll and Henderson 2008). In addition to this, introduced predators such as the feral house cat (*Felis catus*) and European red fox (*Vulpes vulpes*) may preferentially hunt on newly burnt habitats and can have catastrophic effects on recolonizing biota in the bare habitat (Letnic et al. 2005, Kutt and Woinarski 2007, Legge et al. 2011, Andersen et al. 2012).

Wildfire incidence across the southern hemisphere is largely climate-driven, with various stages of both the El Niño Southern Oscillation (ENSO) cycle and the Indian Ocean Dipole (IOD) linked to intense and widespread wildfires (Black 2005, Gonzalez and Veblen 2006, Cai et al. 2009). These ENSO and IOD-induced wildfires are increasingly being found to have strongly negative effects on alpha diversity in affected areas (Cleary et al. 2004, Letnic and Dickman 2006, Cai et al. 2009, O'Donnell et al. 2011).

3.4.2 Beta diversity

The effect of fire on community similarity between burnt and unburnt habitats was influenced primarily by fire type, as wildfires consistently increased beta diversity when compared with prescribed burns (Figure 3.6). This effect occurred equally in both hemispheres and held for most variable groups including birds, lizards, North American biota, North American birds and birds in temperate coniferous forests. Our results concur with Cleary et al. (2004) who found that different taxa can show largely independent patterns of alpha diversity in response to fire but that beta diversity remains convergent.

Prescribed burns and wildfires each create different scales of landscape heterogeneity which are likely the drivers behind the divergent patterns of beta diversity (Pastro et al. 2011). Animals are often able to move between the typically smaller burnt and unburnt patches after a prescribed burn and thus species turnover between the two habitat types is low. In contrast, wildfires often burn intensely and affect larger areas of habitat. By profoundly altering habitat structure, often across large tracts of land, wildfires typically promote the beta diversity of vertebrate fauna by producing distinctive burnt and unburnt habitats that support unique species assemblages (Holdsworth and Uhl 1997, Pastro et al. 2011). For example, Kotliar et al. (2007) reported that in a study in southwestern montane forests in North America, the greatest species turnover of birds occurred after high-severity fires, and that the number of species absent post-fire was balanced by the number of species that only occurred post-fire.

The typically large area of burnt habitat created by wildfire likely enhances the high species turnover associated with these fires, as species recolonizing burnt areas must travel further to reach burnt patches (Pastro et al. 2011).

3.4.3 Methodological considerations

It should be noted that, as is the nature of meta-analyses, our results are average effects of all studies tested. Although comprehensive species lists were provided for 94 of the studies included in the meta-analysis, the examination of fire responses of individual species or groups of species, or the investigation of habitat use associations and how they may influence species responses to fire, was outside the scope of this study. Many prescribed burns are undertaken to protect IUCN Red List species, particularly in southwestern North America, and a post-fire analysis of just IUCN Red List species and changes in their density or abundance may yield substantially different findings.

Replicated studies of animal responses to fire regimes have been identified as a major research gap (Whelan et al. 2002) and remain a research priority in fire-prone communities (Bradstock and Cohn 2002, Parr and Chown 2003, Bury 2004). Our results support this, as we found that many studies were either unreplicated or pseudoreplicated as they were replicated only once at the landscape scale. Poor design is a problem inherent in unplanned natural ecological experiments, with other researchers acknowledging the difficulties inherent when single fires occur over large spatial areas with varying degrees of intensity (Kotliar et al. 2002, Kotliar et al. 2007). In these situations, multiple studies are needed to fully characterize species response patterns, and data collection along burn gradients will help to identify spatiotemporal variation. In addition, sampling methodology such as sample unit size, the count/detection metric that is used, and granularity of habitat classification may also contribute to variation among studies (Kotliar et al. 2007).

Also worth considering is the effect that differing species detection probabilities may have on data quality. Easier detection of species in newly simplified burnt environments or increased post-fire movements of some species may artificially inflate estimates of species numbers in these habitats (e.g. Hossack and Corn 2007, Driscoll et al. 2012). This effect is known to occur after fire in many Australian ecosystems, for example, where introduced terrestrial predators such as cats and foxes exploit the open burnt habitat to become extremely efficient hunters of native small mammals (Letnic et al. 2005, Kutt and Woinarski 2007, Legge et al. 2011, Andersen et al. 2012). While differing detection probability is certainly an issue in many fire studies, we believe that the landscape scale of our study, and the focus on assemblage composition and species richness rather than population-level abundance and indices, provide some degree of protection from the effects of differing detection probabilities. However, this potentially confounding factor should still be accounted for in the interpretation of our results.

Another important factor that could not be addressed by our study is the effect of fire regime on fire effects, including variables such as fire severity, frequency and size. Despite an abundance of research, the ecological significance of fire regimes remains contentious or poorly understood (Parr and Andersen 2006). The effect of repeated fires is also likely to have quite different results between prescribed burns, low-severity wildfires and high severity wildfires, and the effect of repeated high severity wildfires in particular is not well understood (Thompson et al. 2007, Fontaine et al. 2009).

3.4.4 Conclusions

Our study has returned the intriguing result that the effect of fire on patch diversity and landscape scale species assemblages cannot be grouped by taxon, ecoregion, or geographic location. Instead, fire type is the primary determinant of fire effects on both aspects of diversity, although the two diversity metrics studied here were affected in opposite ways. These results highlight the important fact that there is no ‘one size fits all’ approach that can be incorporated into land management practices and that the effects of management practices based on the Intermediate Disturbance Hypothesis (Connell 1978) and the Patch Mosaic Burn Theory (Brockett et al. 2001) are context dependent, especially in parts of the southern hemisphere. Small scale prescribed burns will almost definitely not produce the desired benefits to alpha diversity across all habitats, taxa and locations. Our results also suggest that fire management programs need to consider the effect of management actions at both the patch and landscape scale if they are to be truly effective. Our study identifies the need for more replicated, landscape scale studies of fire effects on terrestrial animal communities, especially of lizards and amphibians. Further research on the effects of fire on community assemblage composition is also needed in montane, alpine and boreal habitats, in tropical forests and in wetland environments. The incidence, severity and scale of wildland fire is expected to increase in many ecoregions and locations of the globe under current climate change scenarios (Bowman et al. 2009, Pechony and Shindell 2010), which underlines the necessity to understand better the community-wide effects of fire on biodiversity.

CHAPTER 4

BURNING FOR BIODIVERSITY OR BURNING BIODIVERSITY? PRESCRIBED BURN VS. WILDFIRE IMPACTS ON PLANTS, LIZARDS AND MAMMALS

A spinifex hummock erupts in a ball of flames (A. Greenville)

Publication details

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Fire is a large-scale phenomenon that affects ecosystems in many parts of the world. Wildfires can have highly destructive effects on habitats and the biota they support, and land managers frequently use prescribed burning to reduce the extent of wildfires and to benefit biodiversity. Underpinned by the predictions of the Intermediate Disturbance (IDH) and Patch Mosaic Burn (PMBH) Hypotheses, small-scale prescribed fires are thought to maximize biodiversity by creating heterogeneous mixes of early, mid and late-successional habitats across the landscape. However, evidence supporting the positive effects of prescribed burning for biodiversity is mixed. We conducted a before-after-control-impact study assessing the effect of prescribed burns and a wildfire on the alpha and beta diversity of plants, mammals and lizards in hummock grassland in arid central Australia. Diversity was assessed for up to one year after each fire. Applying the IDH and PMBH we predicted that 1) small scale, patchy, prescribed burns, by increasing habitat heterogeneity, would increase the alpha diversity and decrease the beta diversity of our study taxa in burnt patches, and 2) wildfire, by creating large, homogeneous burnt patches, would reduce the alpha diversity of the study taxa in burnt patches but promote beta diversity at the landscape level due to the differing assemblages expected to inhabit the burnt and unburnt areas. In accordance with our predictions, we found that fires of differing spatial scale and heterogeneity affected alpha and beta diversity in different ways, but also that the effects were taxon-dependent. In contrast to our predictions, we found a surprisingly high level of congruence between alpha and beta diversity within taxa. Our results provide little support for the application of the Intermediate Disturbance and Patch Mosaic Burn Hypotheses, and highlight instead the importance of stochastic events such as rainfall in influencing biodiversity over the immediate post-fire period in arid environments. We suggest that prescribed fire is of little utility for the broad-scale conservation of biodiversity due to taxon-dependent and unpredictable species responses, but that it may be useful in creating fire breaks that serve to protect the habitats of fire-sensitive species from the effects of broad-scale wildfire.

4.1 INTRODUCTION

Fire is a key process influencing the structure and function of many of the world's ecosystems. Uncontrolled wildfires frequently burn large tracts of land across the dry parts of North America, the Mediterranean, Africa and Australia and have been a key process shaping the evolution of flora and fauna in these regions (Keeley and Rundel 2005, Beerling and Osborne 2006). Such wildfires can have devastating effects on biodiversity via the removal of vegetation, refuge habitat and food sources and by increasing the subsequent vulnerability of surviving animals to predation (Letnic et al. 2005, Green and Sanecki 2006, Kodandapani et al. 2008, Pelegrin and Bucher 2010). Larger, more intense and more frequent wildfires are predicted to occur in many parts of the world in the future due to climate change (McKenzie et al. 2004, Pitman et al. 2007, Hemp 2009, Wilson et al. 2010, Wotton et al. 2010), providing an imperative to better understand and mitigate their impacts.

Smaller, controlled fires are used frequently as a tool to manage vegetation. They are prescribed to clear vegetation, improve the forage value of pastures, reduce wildfire hazard (Letnic et al. 2004, Valentine and Schwarzkopf 2008) and, more controversially, promote the conservation of biodiversity (Noble et al. 1997, Parr and Brockett 1999). This latter use rests on two tenets. The first derives from the Intermediate Disturbance Hypothesis (IDH), which predicts that species diversities will be highest in areas that are subject to moderate levels of disturbance (Connell 1978), and assumes that the habitat heterogeneity created by such disturbance is the precursor of biodiversity (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). The second is that small scale, controlled fire is an effective means of producing heterogeneity (Martin and Sapsis 1992, Parr and Brockett 1999, Parr and Andersen 2006); this idea has been formalized in the Patch Mosaic Burn Hypothesis (PMBH; Brockett et al. 2001). These concepts form the basis for the management of vegetation and biodiversity more broadly in many parts of the world; however, supporting evidence is contradictory (e.g. Short and Turner 1994, Dublin 1995, Schwilk et al. 1997, Mooney et al. 2011) and confined to a limited range of taxonomic groups (Whelan et al. 2002).

In some landscapes there is considerable evidence that habitat heterogeneity created by burning small patches of vegetation can increase biodiversity. For example, in temperate grasslands of the United States patch burning facilitates an increase in species richness of plants and birds, particularly when coupled with the additional disturbance of grazing (Fuhlendorf et al. 2006, 2009). Similarly, fire-induced habitat heterogeneity in African grasslands increases faunal diversity by providing a suite of habitats that provide resources for many species (Fuhlendorf et al. 2006). In the spinifex grasslands of central Australia, fire increases mammal and reptile diversity and may indirectly benefit small mammals (<200 g body weight) by reducing the likelihood of occurrence of damaging wildfires (Masters 1993, 1996, Letnic 2003, Letnic and Dickman 2005).

In contrast, there are many instances where fire-induced habitat heterogeneity has either not provided the expected benefits to biodiversity or in fact has been detrimental for biodiversity by increasing species' extinction risks (Driscoll and Henderson 2008). In the tropical savannas of Africa and Australia many elements of the flora and fauna are resilient to fire, and consequently there is often little differentiation between the assemblages inhabiting burnt and unburnt habitats (Andersen et al. 2005, Parr and Andersen 2006). Similarly, in the heath and forest habitats of eastern Australia no relationship has been observed between reptile species richness and fire characteristics such as the number of fires or time elapsed since the last fire; burning also does not always produce predictable responses by fauna to fire (Sutherland and Dickman 1999, Lindenmayer et al. 2008). No relationship was observed between burning frequency and species richness of understory flowering stems in a Florida pine savanna (Beckage and Stout 2000). In the spinifex grasslands of central Australia, mammal diversity may be unaffected, positively affected (Masters 1993, Letnic 2003, Letnic et al. 2004) or negatively affected by fire (Kelly et al. 2010), with additional factors such as rainfall and grazing also interacting with fire to influence biodiversity (Yarnell et al. 2007).

In this study we compare the impacts of wildfire and prescribed burns on the diversity of plants, mammals and lizards in arid Australia. Perennial hummock grasses, or spinifex (*Triodia* spp.), form the structural backbone of habitat in the region and also provide important foraging reserves for mammals and lizards (Figure 4.1a). Spinifex grasslands cover about 25% of the Australian landmass, and are particularly fire-prone (Allan and Southgate 2002). Aboriginal management of the vegetation using fire was once widespread throughout the spinifex deserts of central Australia, and entailed the burning of relatively small areas of land so that there was a mosaic of both burnt and unburnt patches in the landscape (Burrows and Christensen 1990). Where hummock grasslands are held under pastoral tenure or as conservation reserves, patch-burning is often advocated as a management tool to enhance biodiversity, to improve pastures for cattle, and to create fire-breaks to prevent the spread of broadscale wildfires (Gould 1971, Suijdendorp 1981, Bird et al. 2008). Wildfires in these grasslands are linked to high rainfalls associated with the La Niña phase of the El Niño Southern Oscillation (ENSO) and the mean return interval of wildfires increases with decreasing annual rainfall (Allan and Southgate 2002, Letnic and Dickman 2006, Greenville et al. 2009). They have a devastating impact on the landscape, removing all vegetation across vast tracts of country and leaving remaining animals highly susceptible to predation (Fig. 1b: Letnic et al. 2005). An increase in the extent of wildfire has been hypothesized as a driver of the decline and/or extinction of several mammal species in a 'critical weight range' (35-5500 g) in central Australia (Bolton and Latz 1978, Burbidge and McKenzie 1989); however, this theory is not supported by field data. The intensity and spatial scale of wildfires and of prescribed burns, and the degree of habitat heterogeneity they produce, differ markedly. Relatively cool prescribed burns create a patchy landscape characterized by a mosaic of burnt patches (1-50 ha each) nestled within a matrix of unburnt habitat (Figure 4.1a). Conversely, wildfires create large, mostly homogeneous intensely-burnt areas that can cover >100,000 ha (Allan and Southgate 2002) (Figure 4.1b).

Given the very different spatial scales of habitat heterogeneity created by the fires in our study (Greenville et al. 2009), we predicted that they would have different effects on the diversity of our study taxa. We measured two components of diversity: alpha diversity (α: local diversity within homogeneous sampling units or habitats) and beta diversity (β: derived from differences in species composition between homogeneous sampling units or habitats; Whittaker 1960, Whittaker 1972, Crist et al. 2003). Patterns of alpha and beta diversity do not always vary in a similar manner; congruency is linked closely with habitat heterogeneity as it is mediated by ecological factors such as dispersal and habitat isolation (Oliver et al. 1998, Gering and Crist 2002, Wagner and Wildi 2002, Mandl et al. 2010). Thus alpha and beta diversity are often highly congruent across similar, proximate habitats (Clough et al. 2007), but may differ substantially across dissimilar and/or distant habitats as two sites with equal species richness may share few of their species in common (Tylianakis et al. 2005).

We predict that alpha and beta diversity will have low congruence in our study due to the differing nature of burnt and unburnt habitats, and that fire-type (prescribed burn and wildfire) will influence alpha and beta diversity in different ways due to the markedly different spatial scales of habitat heterogeneity they produce. We use a conceptual model (Figure 4.2) to formalize the differing effects on alpha and beta diversity that we predict to arise from wildfire and prescribed burns, and derive the following two *a priori* hypotheses to test it.

1) Prescribed burns, and the fine scale, heterogeneous landscapes they create, will increase the alpha diversity of burnt patches as these patches will be accessible to early successional species as well as to species dependent on the unburnt grassland habitat that surrounds them.

Animals will be able to move between adjacent burnt and unburnt patches and seeds will be readily dispersed by wind between the two habitats (Jurado et al. 1991), leading to low species turnover between habitats and hence decreased beta diversity (Figure 4.2).

2) Wildfire, and the extensive, homogeneous tracts of burnt land that it produces, will decrease alpha diversity in burnt areas. Surviving animals will be restricted to unburnt or refuge patches of grassland habitat and early successional species will recolonize burnt land only as the vegetation recovers to an appropriate seral stage. The considerable distances between burnt and refugia habitats will slow the transport of seeds to burnt habitats. Beta diversity of the landscape will increase due to the markedly differing species assemblages inhabiting the burnt and unburnt areas and the large distances between them (Figure 4.2).

4.2 MATERIALS AND METHODS

4.2.1 Study area

The study was conducted in the north-eastern part of the Simpson Desert, Queensland, central Australia (Figure 4.3a). The study area covered 360 km^2 and stretched across four pastoral properties: Carlo (23°29'S, 138°32'E), Cravens Peak (23°16'S, 138°17'E), Ethabuka (23°45'S, 138°28'E) and Tobermorey (22°16'S, 137°58'E).

The major landforms in the region are longitudinal, parallel sand dunes running NNW-SSE in line with the prevailing southerly wind. The dunes are 8-10 m high and are spaced 100-1000 m apart (Purdie 1984). The soil is predominantly red siliceous sand of varying composition from the dune crests to swales (Buckley 1982). The swales and dune slopes are characterized primarily by the hummock grass spinifex (*Triodia basedowii*). Common shrubs in the swales include *Acacia ligulata*, *Grevillea* spp. and *Eremophila* spp., and common shrubs on the dune crests include *Grevillea stenobotrya, Goodenia cycloptera, Crotalaria* spp. and *Sida* spp. Some swales contain clay soils and are dominated by gidgee trees (*Acacia georginae*), forbs and short grasses. After heavy rain clay pans fill with water and an abundance of ephemeral forbs and grasses spring up on the surrounding dunes and swales. The mean return interval of wildfires in the study area is 26 years (Greenville et al. 2009).

a)

b)

Figure 4.1 Two photographs indicating the different effects of a prescribed burn and a wildfire on habitat composition and heterogeneity in the Simpson Desert, central Australia.

a) A prescribed burn nestled within a matrix of surrounding spinifex.

b) An example of the vast area of land burnt in the 2001-2002 wildfire in the Simpson Desert. This photo was taken approximately one year after the fire and a very small amount of shrub regeneration is evident.

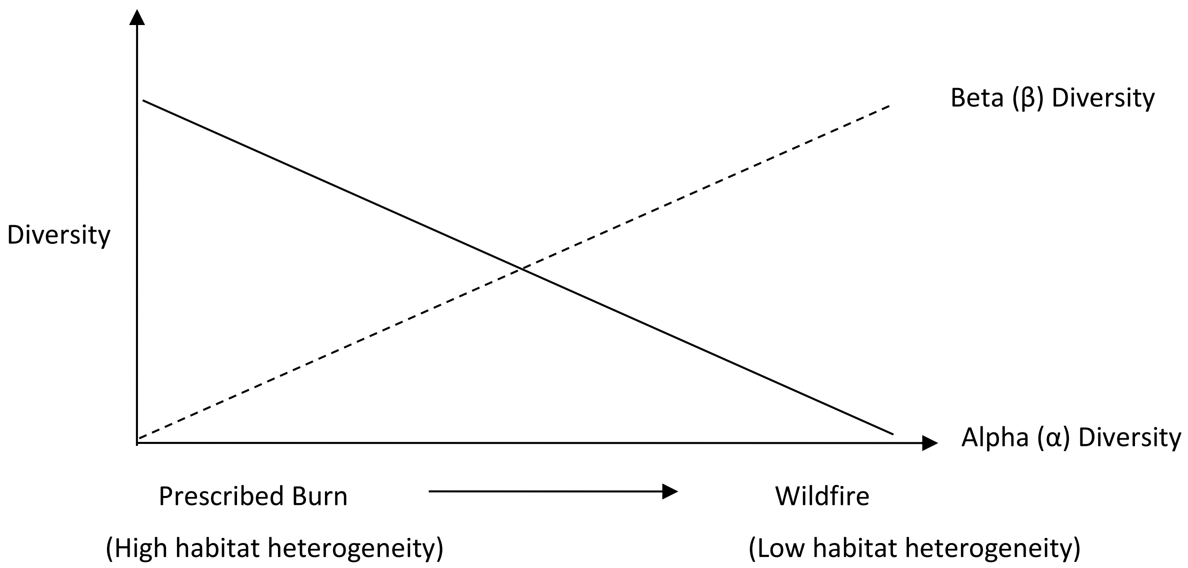

Figure 4.2 Conceptual model describing the relationship between fire-induced habitat heterogeneity and alpha and beta diversity.

4.2.2 Climate

The Simpson Desert is classified as a hot desert with a mean annual temperature of 21-23°C. Summer maxima are 46-49°C and winter minima descend to -6°C (Purdie 1984). The study area lies along a north-south rainfall gradient between the 100 mm and 150 mm median annual rainfall isopleths (Purdie 1984). Rainfall is both spatially and temporally variable and highly unpredictable (Dickman et al. 1999a). The closest long-term weather stations are located at Sandringham (24°03’S, 138°04’E), Marion Downs (23°21’S, 139°39’E), Glenormiston (22°55’S, 138°49’E) and Boulia (22°55’S, 139°54’E) and have median annual rainfalls of 137 mm (*n* = 40 years), 149 mm (*n* = 86 years), 169 mm (*n* = 100 years) and 215 mm (*n* = 110 years) respectively. There is a pronounced wet season during summer, although rain can fall throughout the year, and the wet season does not necessarily bring heavy rainfall each year. Mean monthly rainfall experienced across the study area during the study is presented in Figure 4.4. Rainfall in the study area is more temporally than spatially variable (Letnic et al. 2005).

At the time of the study, the entire region was pastoral land used to graze cattle (*Bos taurus* and *Bos indicus*) and had been subject to extensive pastoral development from fencing and the sinking of bores since the 1970s. Prior to this time few watering points existed and pastoral activity was limited largely to the mustering of feral cattle from natural waters.

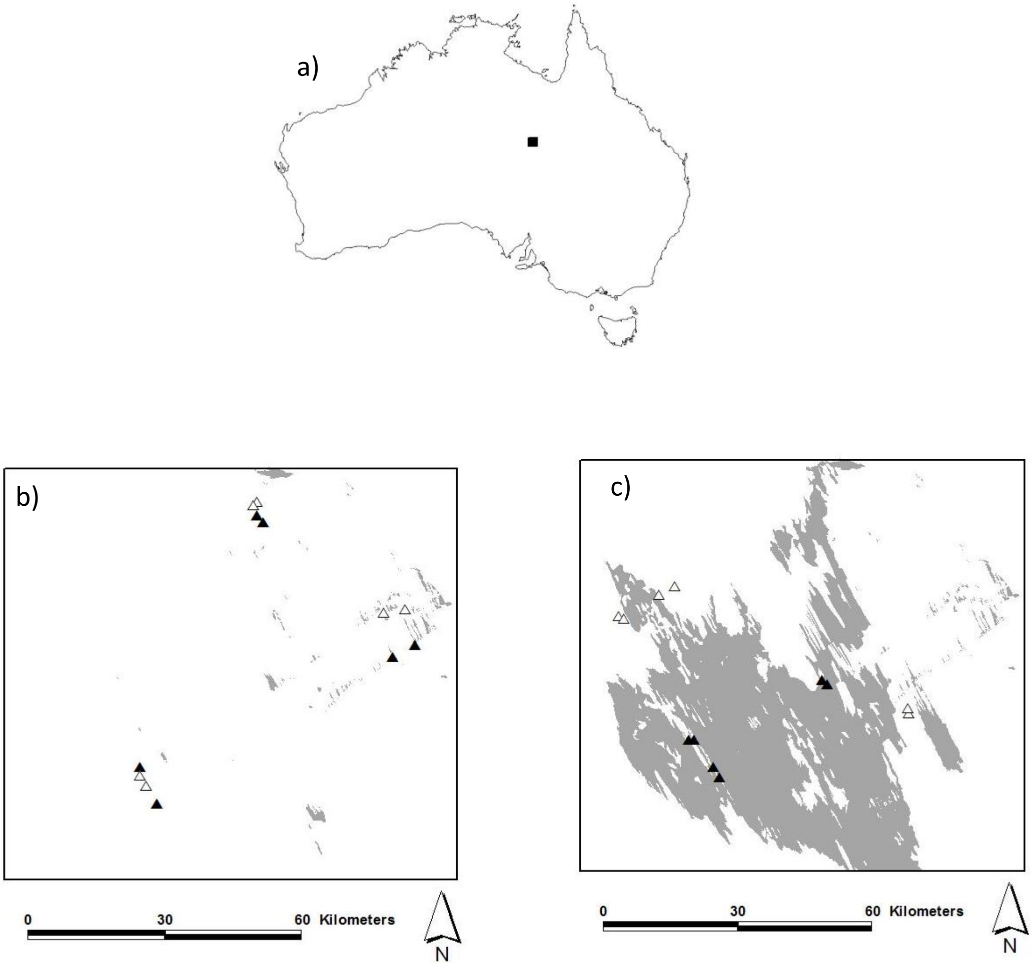

Figure 4.3 Map of the study area indicating a) the location of the study area in the Simpson Desert, central Australia; and the area burnt (grey) by fire within the previous 3 years in (b) June 2001 and (c) June 2002. The triangles show the location of the burnt (shaded) and unburnt (unshaded) sampling plots in the prescribed burn (b) and wildfire (c) studies. The burnt areas in (b) stem largely from prescribed burns. The large area burnt in (c) was primarily due to wildfires that occurred between November 2001 and March 2002.

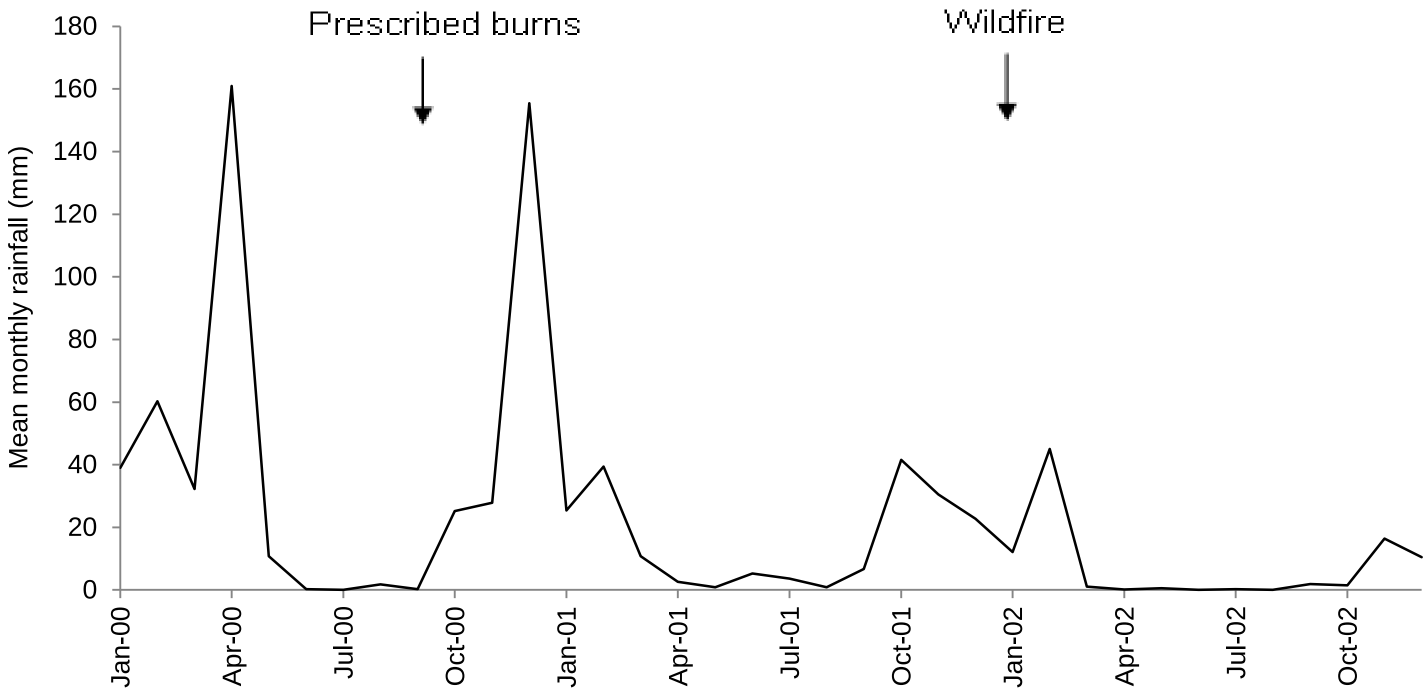

Figure 4.4 Monthly rainfall averaged over six rainfall gauges located across the study area in the Simpson Desert, central Australia. The arrows indicate the timing of the prescribed burns and the wildfire.

4.2.3 Hypothesis 1: Prescribed burn study design

The prescribed burn experiment was conducted across 12 sampling plots that were established in long-unburnt vegetation aged more than 25 years post-fire (Figure 4.3b). To minimize the effects of cattle grazing, the plots were located >2 km from bores that were active at the beginning of the study. Following rainfall received in the summer of 1999/2000, cattle activity decreased across the study area (unpublished data) as pastoralists moved cattle to other areas of the stations. Cattle activity on the sampling plots was minimal throughout the study.

In August 2000, six randomly-chosen plots were burnt, giving a total of six treatment plots and six controls. The size of the burnt areas ranged from 0.9-3.0 ha, with a mean size of 1.7 ha, which is comparable to the sizes of patches burnt by pastoral managers. The sizes of such burns frequently are limited by topography, insufficient fuel loads or lack of wind, and were constrained here by the presence of dune tops and roads. The fires were lit in winter and were relatively “cool” when compared with summer wildfires. The burns were patchy at the western-most plots and the dune crests remained unburnt on all plots except the northern-most plots (see Figure 4.3b for plot locations).

Sampling was carried out across three time periods: prior to the burns (Pre-burn), immediately after the burns (Post-burn I) and nine months after the burns (Post-burn II). To achieve sufficient sampling effort, especially for trapping (see below), the results of two sampling sessions were combined for each time period. Pre-burn sampling was conducted in April and August 2000, Post-burn I sampling in October and December 2000, and Post-burn II sampling in March and June 2001.

4.2.4 Hypothesis 2: Wildfire study design

From November 2001 – January 2002 a wildfire burnt about 254,000 ha of the study area. Some pre-existing sampling plots that were being used as part of a separate study were burnt, allowing pre-fire data to be collected. Six of these burnt plots and six unburnt controls were used (Figure 4.3c). The unburnt plots were located in vegetation aged more than 25 years since fire (Greenville et al. 2009). The wildfire was "hot" when compared with the prescribed burns and all six treatment plots were burnt entirely except for one that was only partially burnt. Cattle activity on the study plots was minimal throughout the study.

Sampling was conducted across three time periods: prior to the fire (Pre-burn), within 3 months of the fire (Post-burn I) and nine months after the fire (Post-burn II). The results of two sampling sessions were again combined for each time period to achieve sufficient sampling effort. Pre-burn sampling was conducted in April and August 2001, Post-burn I sampling in February and April 2002 and Post-burn II sampling in September and November 2002.

4.2.5 Vertebrate trapping procedure

A trapping grid covering 1 ha was established on each sampling plot and comprised six lines of six pitfall traps spaced 20 m apart (Dickman et al. 2001). The grids were located along the sides of sand dunes so that the top row of traps ran along the crest and the bottom row ran parallel along the swale. Grids were located >1.2 km apart. Each pitfall trap consisted of a length of PVC pipe (16 cm diameter and 60 cm in length) buried flush with the ground. A 5 m length of aluminum flywire drift fence was positioned over the top of each trap to improve capture efficiency and a smaller piece was placed underneath the pipe to prevent captured animals from escaping (Figure 4.5). Upon capture, mammals were given a unique ear-clip and lizards a unique toe-clip for identification purposes. When not in use, traps were closed with lids. Most trapping sessions were conducted for three consecutive nights (Dickman et al. 1999a, Dickman et al. 1999b, Dickman et al. 2001), with some variation in the wildfire study due to floods and sandstorms. In the prescribed burn study we completed a total of 216 grid nights, giving a total of 7776 trap nights. In the wildfire study we completed 206 grid nights, giving a total of 7416 trap nights.

Abundance indices for lizards and mammals were calculated using catch-per-unit-effort methods (Caughley 1977, Letnic et al. 2004) rather than indices based on capture-mark-recapture or minimum numbers known to be alive. This was due to the very low recapture rates (0-10%) of all species both within and between trapping sessions. Trapping effort was standardized for each grid for each trapping session by dividing the number of captures by the number of nights that the grid was open. Standardized trap data (captures/grid night) for abundance were used in all analyses.

Figure 4.5 A pitfall trap located in unburnt habitat, indicating the flywire drift fence and proximity to nearby quality food and shelter (A. Greenville).

4.2.6 Vegetation assessment

Vegetation cover was assessed by visual estimation of the percentage cover of each plant species present within a 2.5 m radius around six randomly-chosen pitfall trap stations on each trapping grid (Dickman et al. 2001). Each trap was located on a different row and the same six traps were assessed throughout the study. The area covered by each species was calculated as the mean of the six measurements taken on each grid. Assessments were made once during each sampling session for the small vertebrates, giving a total of 432 plant surveys for each of the prescribed burn and wildfires studies.

4.2.7 Analyses

Alpha diversity–Alpha diversity was calculated for each sampling plot for each taxonomic group using the Shannon-Wiener index. This is a preferable metric when compared with species richness as it includes a measure of species evenness (Magurran 1988). A two-factor repeated measures analysis of variance (ANOVA) was used to determine if the alpha diversity of mammals, lizards and plants on each grid differed over time in each fire treatment (Green 1993). The factors were Treatment (Burnt, Unburnt) and Time (Pre-Burn, Post-Burn I and Post-Burn II). A significant interaction term (time*fire) indicated that the alpha diversity between burnt and unburnt habitat changed differentially over time due to the effects of the fire. Assumptions of analysis of variance were checked by examining residual plots, and analyses were performed using Super Anova (Abacus Concepts Inc. 1989).

Unplanned one degree of freedom contrast analyses were used to test the specific hypothesis that treatment and control alpha diversity differed during a given sampling period (Pre-burn, Post-burn I and Post-burn II: Green 1993). The number of contrasts performed was restricted to the number of error degrees of freedom for the effect being tested. Because of correlated error structure in repeated measures designs, contrasts may be valid even when time-related interaction effects are not (Green 1993). Thus contrasts were performed when interaction effects were not significant. Probability values for time-related *F*-tests in ANOVA were adjusted for correlation between observations using the Hunyh-Feldt epsilon (Green 1993).

Beta diversity–The effect of each of the fire-types on beta diversity was assessed using two techniques. Firstly, we used non-metric multi-dimensional scaling (nMDS) within Primer 5 to investigate changes in the assemblages of plants, mammals and lizards across the burnt and unburnt habitats (Clarke and Gorley 2001). An ordination was performed for each taxonomic group for each sampling period (Pre-burn, Post-burn I and Post-burn II) after both the wildfire and the prescribed burns. The ordinations were based on Bray-Curtis similarity matrices which take into account species abundances (Quinn and Keough 2002). Abundances were square-root transformed prior to analysis to down-weight the contribution of dominant species. New starts of the nMDS procedure were undertaken until the stress value had not been reduced for 100 successive iterations. The Bray-Curtis coefficient could not be defined for mammal captures in the wildfire Post-burn II sampling period as no mammal captures were recorded at two of the sampling plots. To allow ordination, the data were transformed by adding a constant of 1 to the denominator of the Bray-Curtis coefficient (the zero-adjusted Bray-Curtis coefficient: Clarke et al. 2006). This effectively adds a 'dummy species' to the original abundance matrix with value 1 for all samples. Analysis of similarities (ANOSIM) was used to determine if species assemblages in the burnt and unburnt trapping grids differed (Quinn and Keough 2002). If a significant result (*P*<0.05) was obtained, similarity percentages (SIMPER) analysis was undertaken to determine which species contributed most to the separation (Clarke 1993). A significant result was taken to indicate an increase in beta diversity as it signified different species assemblages between the burnt and unburnt habitats and thus an increase in species turnover between the habitats.

As nMDS can indicate only an increase in beta diversity, our second assessment of beta diversity employed the Bray-Curtis Index to identify when beta diversity had decreased. A Bray-Curtis dissimilarity matrix was constructed for each taxon in each sampling period and mean measures of dissimilarity were then calculated to produce the Bray-Curtis Dissimilarity Index for each matrix (Oliver et al. 1998, Ellingsen 2002, Kessler et al. 2009). The data were square-root transformed prior to analysis. Ranging from 0-100, high values of the index occur when sites share few species (high species turnover) and low values occur when sites share many species (low species turnover). In studies of fire-effects on diversity it is useful to combine the Bray-Curtis Index with nMDS and ANOSIM as the latter analyses confirm that any dissimilarity identified by the Bray-Curtis measure is grouped into burnt and unburnt clusters. That is, nMDS confirms that any change in beta diversity indicated by the Bray-Curtis Index is caused by the fire event in question and not by an overall change in beta diversity across the landscape.

We chose not to calculate beta diversity as a function of gamma and alpha diversity (through either multiplicative or additive partitioning), and as a result our measures of alpha and beta diversity are each free to vary independently (Jost 2007, Veech and Crist 2010).

4.3 RESULTS

Full results of the repeated measures ANOVA, contrast analyses, ANOSIM and SIMPER results are presented in Appendices 4.1, 4.2, 4.3 and 4.4 respectively.

4.3.1 Hypothesis 1: Prescribed burns

4.3.1.1 Vegetation

In total, 68 plant species were identified during the study. These consisted of 10 grasses, 45 forbs, 11 shrubs and two trees. Plant alpha diversity increased markedly following prescribed burns ($P = 0.0113$; Figure 4.6a, Appendix 4.1), as predicted by our model, and the magnitude of the difference continued to increase from the Post-burn I ($P = 0.007$) into the Post-burn II ($P < 0.001$) sampling periods (Appendix 4.2). Contrary to predictions, plant beta diversity also increased in the Post-burn I ($P = 0.002$, Figure 4.7a, 4.8a) and Post-burn II ($P = 0.002$; Figure 4.7b, 4.8a) periods (Appendix 4.3). Assemblage differences were driven primarily by the absence of spinifex and the increased abundance of annual grasses such as *Aristida contorta, Yakirra australiensis* and *Eriachne aristidea* on burnt grids (Appendix 4.4.1, 4.4.2).

4.3.1.2 Mammals

Overall, 862 individuals of 10 mammal species were captured over the course of the study, giving a capture success rate of 11.1%. Contrary to our predictions prescribed burns had no effect on mammal alpha diversity ($P = 0.357$; Figure 4.6b); however, significant main effects of Time ($P = 0.022$) and Fire ($P = 0.001$) indicate that mammal alpha diversity varied over time regardless of the fire treatment and varied intrinsically between the burnt and unburnt sites regardless of the timing of the fire (Appendix 4.1). This trend is evident in Figure 4.6b and is supported by the results of the contrast analyses which indicate that the alpha diversity of burnt and unburnt sites differed significantly before the fire ($P = 0.001$) and in the Post-burn II sampling period ($P = 0.017$, Appendix 4.2). This result reflects high levels of stochastic population variability. Prescribed burns lowered the beta diversity of mammals (Figure 4.8a), in line with our predictions.

4.3.1.3 Lizards

Four hundred and thirty-one individuals of 35 lizard species were captured during the prescribed burn study, giving an overall trap success of 5.5%. Lizard alpha diversity increased after the prescribed burns (*P* = 0.025; Fig 5c), as predicted, and continued to increase over the course of the study (Appendix 4.1). The alpha diversity of burnt sites peaked in the Post-burn II time period and was significantly greater than the alpha diversity of unburnt sites in this sampling period (*P* = 0.013, Appendix 4.2). Contrary to our predictions the beta diversity of lizards increased in response to the prescribed burns in the Post-burn I (*P* = 0.002; Figure 4.7c, 4.8a) and Post-burn II (*P* = 0.009; Figure 4.7d, 4.8a) sampling periods (Appendix 4.3). SIMPER analysis revealed some inconsistent patterns of habitat use. In Post-burn I beta diversity effects were driven primarily by the abundance of open area specialists such as *Ctenophorus nuchalis* and *Varanus brevicauda* in burnt areas and shuttling heliotherms such as *Ctenotus ariadnae*, *Ctenophorus isolepis* and *Ctenotus dux* in unburnt areas (Appendix D5). However, in Post-burn II shuttling heliotherms such as *Ctenotus dux, Ctenophorus isolepis* and *Ctenotus pantherinus* were driving species assemblages in the burnt habitat as well as in the usually preferred unburnt habitat (Appendix 4.4.6).

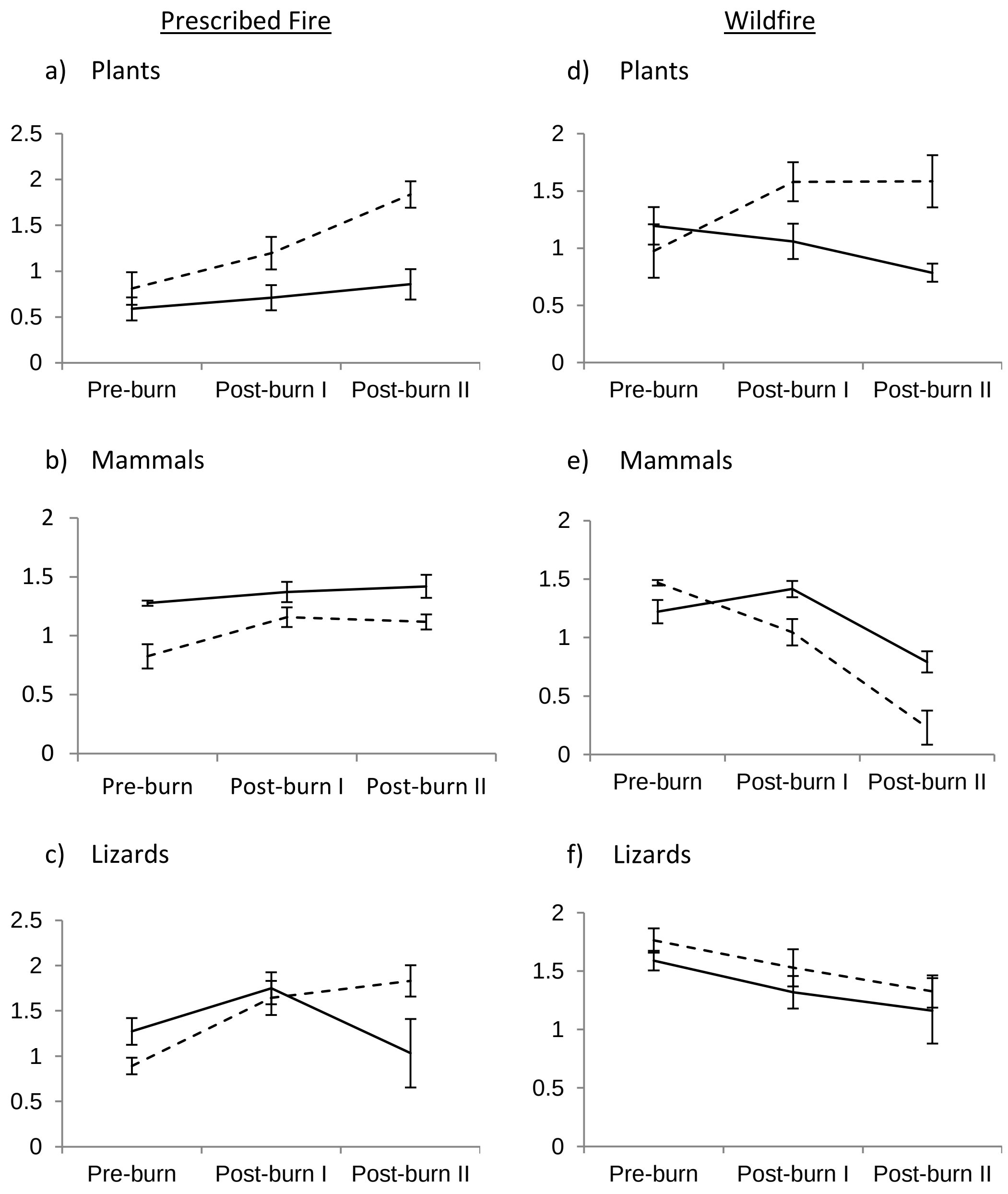

Figure 4.6 Alpha diversity (mean ± SE) of plants, mammals and lizards in each time period (pre-burn, post-burn I and post-burn II) at sites subjected to prescribed burns and wildfire in the Simpson Desert, central Australia. Solid lines represent the alpha diversity of unburnt sites and dashed lines represent the alpha diversity of burnt sites.

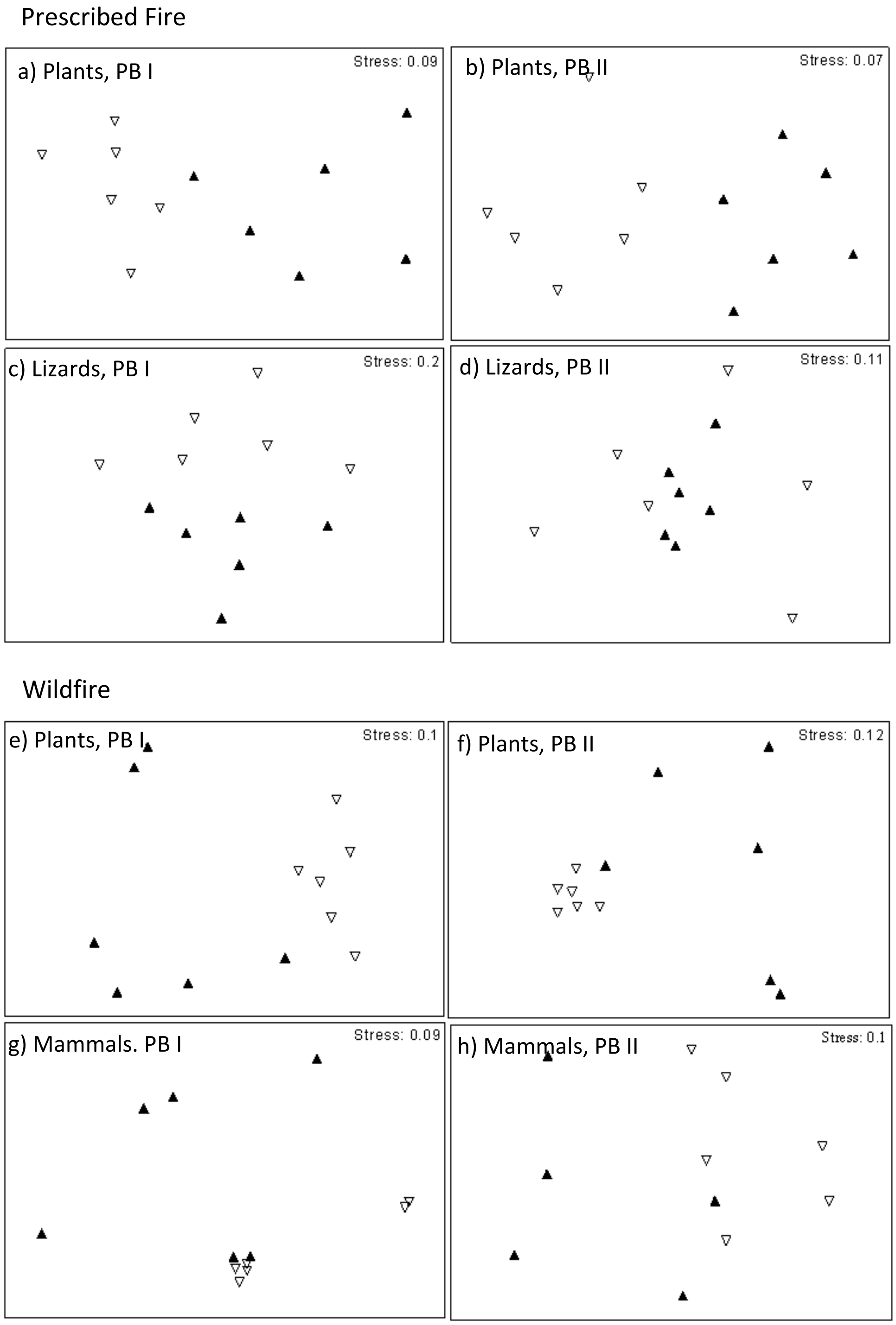

Figure 4.7 nMDS (non-metric multi-dimensional scaling) plots for taxa with significantly different species assemblages between burnt (closed symbols) and unburnt (open symbols) sites in the Post-burn I (PB I) and Post-burn II (PB II) sampling periods after a prescribed burn and wildfire in the Simpson Desert, central Australia. Plots are based on Bray-Curtis similarity matricies, with significance taken at P ≤ 0.05 (Appendix C). All plots were generated in Primer v. 5.

4.3.2 Hypothesis 2: Wildfire

4.3.2.1 Vegetation

We identified a total of 54 plant species over the course of the wildfire study; eight grasses, 33 forbs, 11 shrubs and two trees. Contrary to our predictions, wildfire led to an increase in the alpha diversity of plants ($P = 0.0015$; Figure 4.6d: Appendix 4.1). This effect continued to magnify from the Post-burn I ($P = 0.007$) to the Post-burn II ($P < 0.001$) sampling periods (Appendix 4.2), as the alpha diversity of unburnt areas steadily declined (Figure 4.6d). As predicted, plant beta diversity also increased after the wildfire in both the Post-burn I ($P = 0.002$, Figure 4.7e, 4.8b) and Post-burn II ($P = 0.002$, Figure 4.7f, 4.8b) sampling periods (Appendix 4.3). SIMPER analysis revealed that these differences were driven primarily by the reduction in spinifex and an increase in the cover of annual grasses such as *Aristida contorta* and *Eriachne aristidea* on burnt grids (Appendix 4.4.7, 4.4.8).

4.3.2.2 Mammals

In total, 927 individuals of 10 mammal species were captured throughout the wildfire study, giving a capture success rate of 12.5%. In accordance with our model, the alpha diversity of mammals decreased markedly after wildfire ($P = 0.0007$, Figure 4.6e) in both the Post-burn I ($P = 0.010$) and Post-burn II ($P < 0.001$) time periods (Appendix 4.1, 4.2). Beta diversity increased after wildfire in both the Post-burn I ($P = 0.004$; Figure 4.7g, 4.8b) and Post-burn II ($P = 0.009$; Figure 4.7h, 4.8b) time periods (Appendix 4.3), which was also in line with our predictions. SIMPER analysis revealed that the rodents *Pseudomys hermannsburgensis*, *P. desertor* and *Notomys alexis* were the primary contributors to differences in the Post-burn I time period (Appendix 4.4.9), while the dasyurid marsupial *Ningaui ridei* along with the rodents *P. hermannsburgensis* and *P. desertor* contributed to observed differences in the Post-burn II time period (Appendix 4.4.10). These species all preferred the unburnt habitat.

4.3.2.3 Lizards

We captured 399 individuals of 34 lizard species during the wildfire study, giving a capture success rate of 5.3%. Contrary to prediction, wildfire had no effect on the alpha diversity of lizards ($P = 0.989$; Figure 4.6f); however, there was a significant main effect of Time ($P = 0.035$) that arose from a consistent decline in alpha diversity in both the burnt and unburnt sites over the course of the study (Figure 4.6f, Appendix 4.1). The wildfire also had no effect on lizard beta diversity in either the Post-burn I (*P* = 0.238) or Post-burn II (*P* = 0.074) time periods (Appendix 4.3) despite the relative increase in the Bray-Curtis Index throughout the study (Figure 4.8b). The increase in this index indicates increased turnover among all the sites, unrelated to the fire event; that is, the increase in beta diversity was not restricted to a group of burnt or unburnt sites.

4.4 DISCUSSION

Our results provide clear support for our primary hypothesis that wildfires and prescribed burns differentially affect patterns of alpha and beta diversity of desert biota via the different spatial scales of habitat heterogeneity that they each create. However, neither fire-type consistently influenced patterns of diversity in the directions we had predicted in our model (Figure 4.3) for all taxa. Thus our results provide only mixed support for our *a priori* hypotheses. Our expected and observed results are summarized in Table 4.1. Below we examine the responses of the studied taxa to prescribed burning and wildfire in the context of the two hypotheses raised in the introduction and the influence of other factors, particularly rainfall.

The literature is divided on the influence of taxon in biodiversity studies, with some studies citing a clear divergence in alpha and beta diversity across taxa (Oliver et al. 1998, Negi and Gadgil 2002, Heino et al. 2009, Mandl et al. 2010, Marsh et al. 2010) and others finding that beta diversity in particular tends to remain congruent between taxa, particularly at higher levels of beta diversity (Cleary et al. 2004, McKnight et al. 2007, Kessler et al. 2009). In our study we found a high degree of divergence between taxa, with only two of the three taxa we measured responding in a similar direction for the prescribed burn alpha and beta diversity and the wildfire beta diversity (Table 4.1). For wildfire, the alpha diversity responses of all three taxa were dissimilar (Table 4.1). Despite these inconsistencies, our results accord with some post-fire studies in northern Australia (Woinarski et al. 2004) and on the continent’s south-eastern coast (Lindenmayer et al. 2008), where researchers have found that the impact of a given fire on biodiversity varies according to the taxon being observed. Cleary et al. (2004) found no alpha diversity congruence but a high level of beta diversity congruence between taxa in a fire-affected habitat mosaic in Indonesia, which concurs with our results as we also found a slightly higher congruency between taxa for beta diversity (Table 4.1).

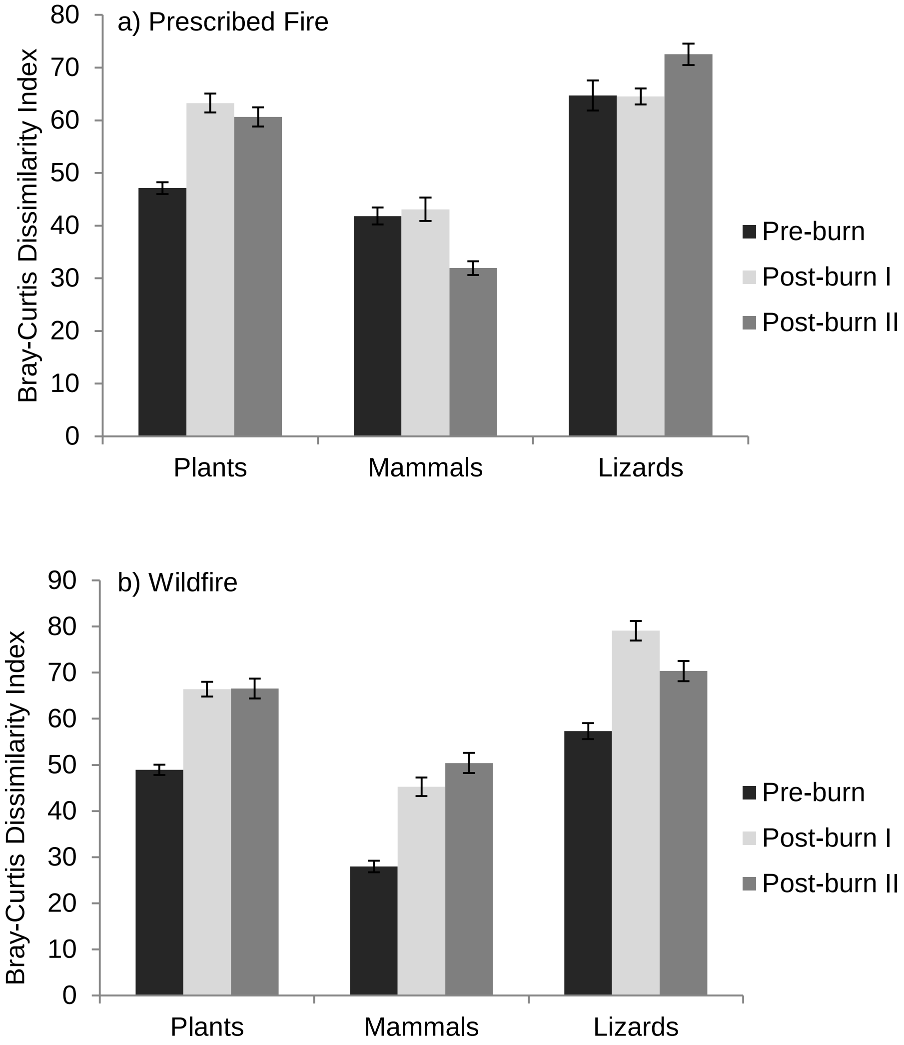

Figure 4.8 Bray-Curtis Dissimilarity Index indicating changes in plant, mammal and lizard beta diversity across the Pre-burn, Post-burn I and Post-burn II sampling periods after prescribed burns and a wildfire in the Simpson Desert, central Australia. A high Bray-Curtis dissimilarity Index indicates high species turnover between sites. As the baseline (Pre-fire) beta diversities differ between taxa, the relative change in beta diversity across the three sampling periods is the most informative assessment of the effect of the fire on beta diversity. The index range is 0-100, and error bars represent ± 1 SE.

	Prescribed burns				Wildfire			
	Alpha diversity		Beta diversity		Alpha diversity		Beta diversity	
	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs
Plants	↑	↑	↓	↑	↓	↑	↑	↑
Mammals	↑	0	↓	↓	↓	↓	↑	↑
Lizards	↑	↑	↓	↑	↓	0	↑	0

Table 4.1 A summary of the expected (Exp) and observed (Obs) changes in the alpha and beta diversity of plants, mammals and lizards after prescribed burns and a wildfire in the Simpson Desert, central Australia.

Unexpectedly, we found a high level of congruency between alpha and beta diversity within the taxa studied. In particular, alpha and beta diversity varied congruently in the plant and lizard taxa after both the prescribed burns and the wildfire (Table 4.1). These results contrast with those reported in the literature, where it is well established that within-taxon congruency is strongly linked with habitat heterogeneity (Oliver et al. 1998, Gering and Crist 2002, Wagner and Wildi 2002, Mandl et al. 2010); as such, highly heterogeneous habitats such as burnt and unburnt habitats would be expected to produce low levels of alpha and beta congruency. This assumption has held true in burnt and unburnt habitats in North American tallgrass prairie (Martin et al. 2005), African grassland (Uys et al. 2004) and in parts of the Mediterranean (Capitanio and Carcaillet 2008). We explore these findings in more detail with respect to the different taxon categories, below.

4.4.1 Vegetation responses

Our results demonstrate that fire increases both the alpha and beta diversity of plants in the arid zone regardless of the size of the fire and the spatial scale of the resulting habitat heterogeneity. In accordance with previous research (Burbidge 1944, Noble 1989, Letnic 2004), the patchy, low-intensity prescribed burns and the intense, broadscale wildfire both stimulated rich assemblages of early-successional grasses and herbs. The extra space and light created by the removal of the dominant spinifex grass most likely encouraged this flush of new growth, and species diversity in the burnt patches increased rapidly. Species assemblages in recently burnt areas contrasted sharply with the spinifex-dominated assemblages of the unburnt habitat, increasing species turnover between the two habitats.

The effect of fire on plants is strongly influenced by rainfall, with the episodic flooding rains associated with the La Niña phase of ENSO driving primary productivity in arid grasslands by stimulating an abundance of grasses and herbs and the recruitment of shrubs and trees (Nicholls 1991, Holmgren et al. 2006). Our study further indicates that both pre-fire and post-fire rainfall is similarly effective in stimulating an immediate post-fire increase in alpha and beta plant diversity. Our prescribed-burn study was conducted during an unusually wet period associated with the La Niña phase of ENSO (Letnic and Dickman 2006) and, soon after burning in August 2000, substantial rain fell in October and again in December (Figure 4.4). Conversely, the November-January 2001-2002 wildfire was preceded by moderate rainfall in October 2001 through February 2002 but was followed by a period of extended El Niño-associated drought (Figure 4.4). Despite these differing rainfall regimes, each of the fires stimulated an immediate increase in the alpha diversity of burnt patches and increased beta diversity throughout both the Post-Burn I and II sampling periods.

The effect of the drought on vegetation recovery after the wildfire was reflected in the alpha diversity values for plants. Alpha diversity increased sharply in burnt areas immediately after the wildfire (and shortly after heavy rainfall) but stabilized after this point, whereas the alpha diversity of plants in unburnt sites continued to decline throughout the study (Figure 4.6d). This was in contrast to the La Niña-inundated Post-burn II period that followed the prescribed fires when the alpha diversity of plants in both the burnt and unburnt habitats continued to increase with time since burning (Figure 4.6a). It is likely that the effect of the wildfire and prescribed burns on alpha and beta plant diversity may have been quite different if no rainfall had been received prior to or after either of the fires, particularly in the Post-burn I period. For example, in a study of vegetation recovery after fire which commenced during relatively dry conditions, Letnic (2004) observed no vegetation recovery in burnt spinifex grassland for up to four months post-fire.

4.4.2 Prescribed burn effects – mammals and lizards

Lizard recovery after fire in arid habitats has been well documented to follow the habitat accommodation model of succession (Masters 1996, Pianka 1996, Letnic et al. 2004, Pianka and Goodyear 2012), with early successional open-area specialists such as *Ctenophorus nuchalis* and *Rhynchoedura ornata* predictably recolonizing extensive, open burnt habitat soon after fire (Letnic et al. 2004). Late-successional species such as shuttling heliotherm skinks (*Ctenotus* spp.) and the military dragon (*Ctenophorus isolepis*) require shade for thermoregulation and generally do not recolonize burnt habitat until the vegetation reaches the appropriate seral stage (Letnic et al. 2004, Daly et al. 2008, Gordon et al. 2010b). Rainfall or lack of it can moderate the succession of lizard species by enhancing or retarding vegetation growth, respectively (Dickman et al. 1999a, Letnic et al. 2004). In our study, even though the species turnover between burnt and unburnt patches was enough to produce distinct assemblages (Figure 4.7c, 4.7d), shade-loving species such as *C. isolepis* and *Ctenotus pantherinus* were unexpectedly present in burnt patches, reflecting the additional shelter provided by the rapid growth of grasses and herbs (Appendix 4.4.6). It is likely then that the increase in alpha diversity following prescribed fire was due to the movement of animals across the burn ecotone into the burnt habitat. These movements were likely facilitated by the rain-induced increase in shade and food resources in the burnt area.

Unlike the lizards, and contrary to our predictions, the prescribed burn had no effect on the alpha diversity of mammals. Mammals in many arid habitats of central Australia are characterized by unpredictable fire responses, with species preferences for burnt and unburnt areas being inconsistent both between and within studies (Letnic and Dickman 2010). Similar results have been recorded in semi-arid African grasslands (Yarnell et al. 2007). After the wildfire in our study, for example, *Ningaui ridei* preferred the burnt habitat in the Post-burn I sampling period and the unburnt habitat in the Post-burn II sampling period (Appendix 4.4.9, 4.4.10). The open habitats created by prescribed burning were not recolonized by any clear suite of early successional mammal species; animals appeared to utilize both the burnt and unburnt patches to the degree that beta diversity actually decreased relative to the pre-fire time period (Figure 4.8a). The failure of mammals to respond to the burning treatment may have been due to the plentiful growth of annual grasses, and thus availability of food, in the newly burnt habitat (Letnic and Dickman 2010). It was only in the Post-burn II period that any species showed a preference for the burnt habitat (the spinifex hopping mouse: *Notomys alexis*: Appendix 4.4.4).

The weak responses of mammals to prescribed burning in our study supports the results of Oliver et al. (1998) who found that highly mobile taxa are able to use multiple habitat patches in a heterogeneous environment and thus tend to exhibit low beta diversity. Arid zone mammals can travel long distances during a single night's foraging, with species such as dunnarts (*Sminthopsis* spp.) and spinifex hopping mice (*Notomys alexis*) traveling distances of over 400 m within a night's foraging (Letnic 2002, Haythornthwaite and Dickman 2006b) and >10 km over periods of several weeks (Dickman et al. 1995). They are also able to identify and selectively exploit resource-rich areas within the patchy landscape and move towards these areas (Letnic 2002, Haythornthwaite 2005).

4.4.3 Wildfire effects – mammals and lizards

Although the beta diversity of mammals increased after the wildfire, as we had predicted in Figure 4.3, the responses of lizards to the wildfire were not as we had predicted and may be better understood with reference to the heavy pre-fire rainfall events and following El Niño-associated drought. In our study the habitat burnt in the wildfire was recolonized by a mixture of open area specialists such as *C. nuchalis* and *Egernia inornata* along with shade-loving species such as *C. isolepis* (Appendix 4.4.11, 4.4.12). This most likely occurred because of the shelter provided by the rain-stimulated recovery of vegetation in burnt areas. We believe that the presence of vegetation in recently burnt areas was the reason why the fire did not increase the beta diversity gradient across burnt and unburnt habitats. The heavy pre-fire rainfall probably also influenced the abundance of the main food source of lizards, arthropods, which may have further drawn lizards into the newly-burnt habitat.

The effect of the extended drought after the wildfire was also reflected in the alpha diversity values for mammals and lizards over the course of the study. Alpha diversity values for both these taxa showed strong declines in burnt and unburnt habitats, from the Pre-burn period through to Post-burn II (Figure 4.6e, f). This is indicative of the effect of the drought on population numbers, irrespective of fire (James 1991a, Yarnell et al. 2007).

4.4.4 General considerations

One aspect of fire that was not tested in our study is the effect on biota of the fire-return interval. Certain life history characteristics make some plants and animals particularly vulnerable to a short fire-return interval, an effect that is not always detected during short-term surveys. Slow growing plant species such as spinifex (*Triodia* spp.), which may take over five years to re-establish after fire (Winkworth 1967), are particularly vulnerable to short fire-return intervals, as are slow-growing obligate seeders with no persistent seed bank (Bowman and Panton 1993, Russell-Smith 2006). Animals with limited mobility and small home ranges (Friend and Taylor 1985, Woinarski et al. 2001, Williams et al. 2002, Woinarski et al. 2005) and animals that are reliant on fire-sensitive vegetation (Noske 1992, Woinarski 1992) are also at risk in areas where the fire-return interval is short. Conversely, other species may require the habitats created by intense fires for their long-term survival (Hutto 2008).

Another consideration is the spatial complexity of habitat mosaics generated by prescribed burning. This study addressed a simple mosaic of discrete and isolated burnt habitat patches surrounded by homogeneous, unburnt habitat. In areas subject to a higher frequency of burning, the spatial and temporal structure of fire mosaics may be far more complex (Burrows and Christensen 1990, Haydon et al. 2000a) and may consist of many adjacent areas burnt at several different times and with different frequencies. Further study is required to examine the response of small mammals and lizards to fire mosaics in more detail, particularly complex mosaics. Such studies could consider factors omitted from the present study including patch size, patch shape and arrangement, and the effect of fire frequency.

The effect of fire on threatened fauna and flora was not addressed in our study, but also needs to be considered. Animal and plant species that occur in just one or a few remnant populations are particularly vulnerable to extinction from fire events. For example, in tropical Australia small populations of various species of rock rats (*Zyzomys* spp: Begg et al. 1981, Legge et al. 2008) have been adversely affected by single fires primarily because of fire-induced depletion of food. In addition, some taxa have complex habitat requirements that need to be identified prior to burning. For example, the fine-scale habitat heterogeneity that benefits many species following a patchy fire may be perceived by others as fragmentation and thus have a negative effect on their populations (Sullivan and Sullivan 2001).

The metric used to measure diversity is a further factor that should be considered in any biodiversity assessment. Even within single taxonomic groups different metrics can lead to quite different outcomes. Orme et al. (2005), for example, found little congruence between avian diversity hotspots measured according to species richness, endemic richness or threat richness. Similarly, Péru and Dolédec (2010) found that species richness varied greatly across ecoregions while Simpson’s diversity index varied little across the same regions. With regard to beta diversity, Heino et al. (2009) and Ellingsen (2002) found that the beta diversity of given taxa differed depending on the metric used. We found a high level of congruence between the two metrics of beta diversity that we used, but it can be supposed that the outcomes may have differed if we had used alternative biodiversity metrics. This needs to be considered when comparing results across biodiversity studies.

4.4.5 Management implications

Our study has demonstrated that fires of differing spatial scales have contrasting effects on short-term alpha and beta diversity through the different scales of habitat heterogeneity that they each create. These effects were taxon-dependent and, as such, the generality of our primary model (Figure 4.3) appears to be quite limited. We also found an unexpectedly high correlation between alpha and beta diversity within taxa; this contrasts with the findings of other studies that have revealed a high divergence of alpha and beta diversity in heterogeneous habitat such as those created by fire (Uys et al. 2004, Martin et al. 2005, Capitanio and Carcaillet 2008).

An important management implication of our study is that the fire responses of lizards may not be as well understood as previously thought. Lizard assemblages responded in a manner contrary to the predictions of post-fire succession models (Mushinsky and McCoy 1985, Mushinsky 1992, Greenberg et al. 1994, Taylor and Fox 2001a, b, Pianka and Goodyear 2012) after both the wildfire and the prescribed burns. The response of lizard assemblages may have been due to effects of unusually high and low rainfall after the prescribed burning and wildfires, respectively (Dickman et al. 1999a, Letnic et al. 2004). Other studies have also reported that the response of lizard assemblages to fire could not be predicted using either the habitat accommodation model of succession or by using life history attributes (Driscoll and Henderson 2008, Lindenmayer et al. 2008). Collectively, these findings suggest that further work is required to develop conceptual models to explain lizard responses to fire.

Given that our results indicate that post-fire responses are taxon-dependent and are also influenced by rainfall or the lack of it, we propose that prescribed fire has little value for the maintenance of general “biodiversity” in the hummock grasslands of central Australia, as predicted by either the Intermediate Disturbance or Patch Mosaic Burn Hypotheses. When species within a given taxon respond differentially to fire it also becomes more difficult to use any single taxon as a surrogate for biodiversity or to predetermine with any level of reliability the potential response of a species group to a fire event. Despite these problems, we contend that fire may be used as a tool to conserve biodiversity if it is used to protect habitat rather than to create it. Relatively small prescribed burns can act as effective fire breaks to prevent the spread of wildfire (Letnic et al. 2005) and, in this role, prescribed burning may contribute to overall biodiversity protection even when the direct biodiversity benefits of prescribed burning remain unclear.

We suggest that a more useful approach to conserving biodiversity through the use of fire is to identify high priority, fire-sensitive, species or groups of species and to focus subsequent fire management accordingly. Designing fire management plans to incorporate the needs of such species requires a detailed knowledge of their habitat and food requirements (Bradstock et al. 2005), but minimizes the potentially damaging effects of fires. Identification of keystone structures that drive animal distribution and abundance in management areas (Tews et al. 2004) should also contribute to the efficacy of fire management plans.

CHAPTER 5

EFFECTS OF WILDFIRE, RAINFALL AND REGION ON DESERT LIZARD ASSEMBLAGES: THE IMPORTANCE OF MULTI-SCALE PROCESSES

A central bearded dragon (*Pogona vitticeps*) catching the early morning sun (A. Chen)

Publication details

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Vertebrate populations are influenced by environmental processes that operate at a range of spatial and temporal scales. Wildfire is a disturbance that can affect vertebrate populations across large spatial scales, although vertebrate responses are frequently influenced by processes operating at smaller spatial scales such as topography, interspecific interactions and regional history. Here, we investigate the effects of a broad scale wildfire on lizard assemblages in a desert region. We predicted that a rainfall gradient within the region affected by the wildfire would influence lizard responses to the fire by encouraging post-fire succession to proceed more rapidly in high-rainfall areas, and would be enabled in turn by more rapid vegetation recovery. To test our prediction, we censused lizards, measured rainfall, undertook vegetation surveys and sampled invertebrate abundance across burnt and unburnt habitat ecotones within three regional areas situated along a gradient of long-term annual rainfall. Lizard diversity was not affected by fire or region and lizard abundance was influenced only by region. Lizard assemblage composition was also only influenced by region, but this did not relate to differences in rainfall or habitat as we had predicted. Regional differences in lizard assemblages related instead to food availability. The observed differences also likely reflected regional differences in the strength of biotic interactions with predators and changes in land use. Our study shows that assemblage responses to a disturbance were not uniform within a large desert region and instead were influenced by other environmental processes operating simultaneously at multiple temporal and spatial scales.

5.1 INTRODUCTION

The distributions and abundances of animals often are influenced by a range of drivers that operate at different spatial scales (Harte et al. 2005, Haythornthwaite and Dickman 2006a). At the largest scale, factors such as climate and geography are most important. These in turn interact with processes operating at smaller scales, such as food and habitat availability, disturbances such as fires and storm events, interspecific interactions and human land-use, so that the same global drivers will have different effects in different regions (Peters et al. 2004, Bestelmeyer et al. 2011). Wildfires in particular are an important determinant of animal distributions and the effects of these fires can be influenced by a range of multi-scale processes such as climate and rainfall patterns, fire history, habitat characteristics and predation pressure (Nimmo et al. 2012a). Climate change is predicted to drive shifts in rainfall regimes and increase the occurrence and intensity of wildfire events in many regions around the globe, providing an imperative to further understand the effects of fire on animal communities (Krawchuk et al. 2009).

The effect of wildfires on lizard populations is often thought to be highly predictable, with lizards showing characteristic responses to fire that are determined by their foraging modes and life history traits. This regular pattern of response accords with the predictions of the “habitat accommodation model” of succession as proposed by Fox (1982) to describe the recovery of small mammals after fire in coastal heath. According to the model, open-area specialists and burrowing species are likely to be early colonists after fire, followed by species with more complex habitat requirements that cannot recolonise until the vegetation recovers to the necessary seral stage (Pianka 1992). The model has subsequently been applied to lizards in various habitats around the world (Driscoll and Henderson 2008, Santos and Poquet 2010) including the species-rich deserts of central Australia (Masters 1996, Letnic et al. 2004).

Despite the wealth of empirical support for the habitat accommodation model, recent research suggests that for lizards, post-fire recovery in many regions does not follow the expected linear trajectory (Driscoll and Henderson 2008, Lindenmayer et al. 2008, Nimmo et al. 2012a, Pianka and Goodyear 2012). Instead, multi-scale biotic and abiotic processes such as habitat, species composition and regional history can affect lizard recovery. In the fire-prone savannah forests of northern Australia for example, a moisture gradient was found to have a stronger influence than the direct effects of fire in structuring lizard communities (Trainor and Woinarski 1994). In semi-arid mallee (*Eucalyptus* spp.) woodlands in southern Australia, the fine scale influence of study location causes greater differences between reptile assemblages than fire history (Driscoll and Henderson 2008). In other parts of the world, rainfall similarly influences both plant (Pugnaire and Lozano 1997, Heelemann et al. 2008) and arthropod (Uys and Hamer 2007, Vasconcelos et al. 2009) responses to fire, which in turn provide important habitat and food resources for lizards. In African savannahs, for example, termites respond most strongly to fire events in regions with high rainfall, as fire-induced vegetation changes are more significant in regions of high primary productivity (Davies et al. 2012a).

One region in particular where large discrepancies exist between expected and observed lizard responses to fire is arid Australia (Driscoll and Henderson 2008, Pastro et al. 2011, Pianka and Goodyear 2012). Fire has been an integral process shaping the structure and species composition of the arid interior of Australia for millennia. Fire-prone perennial hummock grasses (*Triodia* spp.) dominate the habitat and have burnt frequently under Aboriginal land tenure over the last 40,000-50,000 years. The region supports the world's richest desert reptile assemblages (Pianka 1969) and these appear to be facilitated indirectly by the long history of fire in the region, as many species are habitat specialists that reach their peak population densities only when post-fire habitat has regenerated to the necessary seral stage (Pianka 1992). Since the cessation of Aboriginal land management over much of arid Australia in the early to mid 20th century, large scale wildfire events have become more widespread and may pose major threats to lizards that require dense vegetation for shelter, thermoregulation and foraging (Letnic et al. 2004, Bird et al. 2012).

The central Australian arid regions are critically moisture-limited and rainfall is the dominant factor driving productivity (Letnic and Dickman 2006). Recent studies suggest that rainfall may exert a strong enough influence over lizard communities to drive regionally-differing lizard responses to fire, via rainfall-stimulated differences in vegetation and arthropod recovery rates (Letnic et al. 2004, Pastro et al. 2011, Schlesinger et al. 2011, Nimmo et al. 2012a). Other local and regional scale factors that are important in structuring lizard communities in arid Australia and elsewhere and that may influence lizard responses to wildfire include soil composition (Driscoll 2004), cattle grazing (James 2003, Driscoll 2004), vegetation differences, climate and interspecific interactions (Daly et al. 2008, Driscoll and Henderson 2008, Nimmo et al. 2012a, Pianka and Goodyear 2012, Read et al. 2012).

In this study we investigate the influence of multi-scale processes on the medium-term recovery of lizards following a wildfire in the Simpson Desert, Australia. The study was located in three regions, which allowed us to examine how the regional effect of differing rainfall regimes interacts with local-scale processes to determine lizard responses to wildfire (Figure

5.1). To guide our investigations, we constructed a simple conceptual model that predicts how differing levels of rainfall should drive lizard responses to wildfire (Figure 5.2). Our conceptual model is informed by previous studies showing that rainfall stimulates post-fire recovery of vegetation and food resources of lizards (Pugnaire and Lozano 1997, Uys and Hamer 2007, Heelemann et al. 2008, Vasconcelos et al. 2009, Davies et al. 2012a) and that lizard abundance and species richness increase with these (Masters 1996, Letnic et al. 2004, Read and Cunningham 2010, Nimmo et al. 2012a, Pianka and Goodyear 2012). Habitats on the edge of burnt areas – ecotones – can be expected to show recovery characteristics that lie between those of the burnt and unburnt habitats. We measure lizard abundance, diversity and assemblage composition along with a range of vegetation and food indicators in burnt, ecotone and unburnt sites in each of our three regions.

Using the model, we derived three *a priori* hypotheses:

1) Lizard abundance and diversity will be highest in regions receiving more rainfall due to greater rain-stimulated recovery of vegetation and food resources (Figure 5.2);
2) Lizard abundance and diversity will be most similar between burnt, ecotone and unburnt habitats in high-rainfall regions as the rainfall will facilitate faster recovery in burnt habitats (Figure 5.2); and
3) Lizard assemblage composition in high-rainfall regions will recover more rapidly after wildfire than assemblages in low-rainfall regions, facilitated by the accelerated vegetation and arthropod recovery in these regions. Lizard assemblage composition will therefore be most similar between burnt, ecotone and unburnt habitats in high-rainfall regions.

Following Letnic et al. (2004) we assumed that medium-term recovery of lizards would occur in the study region about five years post-fire and hence tested our hypotheses at this time.

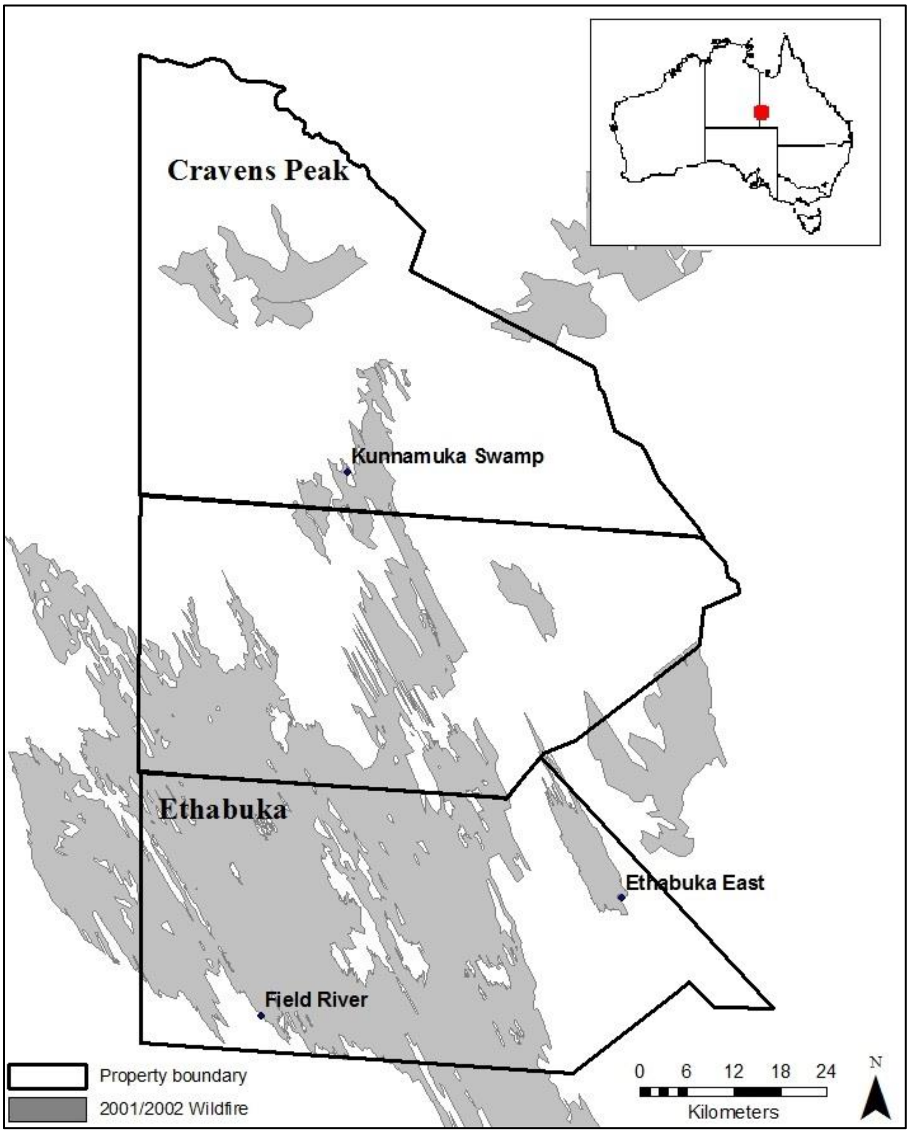

Figure 5.1 Map of the study region showing the two study properties (Cravens Peak and Ethabuka) and the three study regions (Ethabuka East, Field River and Kunnamuka Swamp). The black lines represent the property boundaries and the extent of the 2001/02 wildfire is shaded in grey. Kunnamuka Swamp received the most rainfall since the wildfire (661.7 mm) followed by Ethabuka East (465.8 mm) and the Field River sites (367.2 mm)

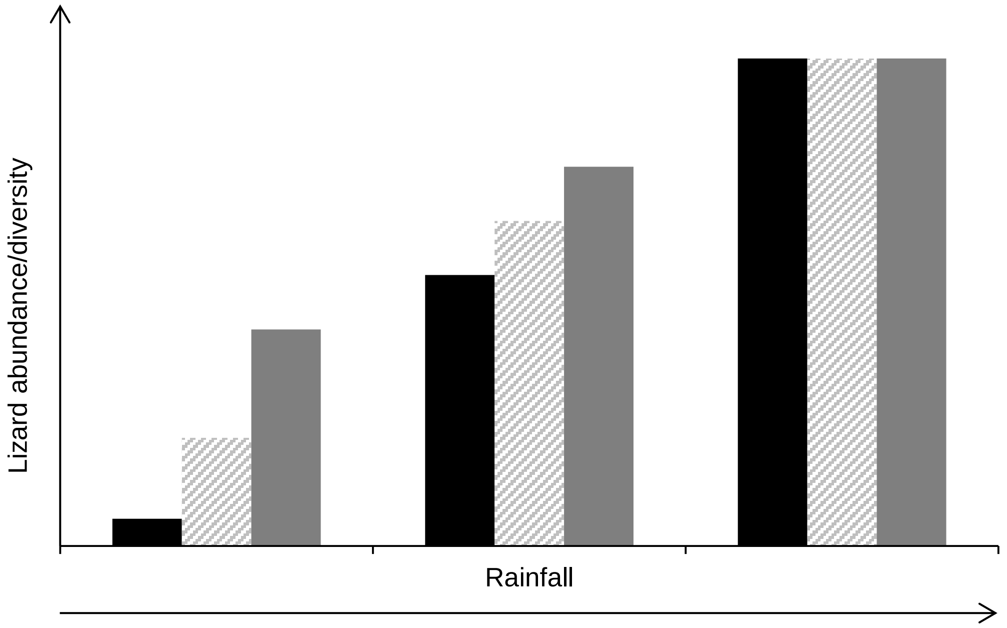

Figure 5.2 A conceptual model of the recovery of lizard abundance and diversity in burnt (black bars), ecotone (stippled bars) and unburnt (grey bars) habitats after wildfire in desert environments. The model is relevant to medium-term responses rather than those that occur immediately post-fire or long after fire when successional trajectories have been completed. The X-axis is a spatial axis that represents the change in annual rainfall along a rainfall gradient (from low to high). The Y-axis represents lizard abundance and diversity. The model predicts that lizard diversity and abundance will be highest in the region receiving most rainfall. It also predicts that diversity and abundance will be more similar between burnt, ecotone and unburnt habitats in this region as the high rainfall has facilitated faster recovery of burnt habitats

5.2 MATERIALS AND METHODS

5.2.1 Study area and species

Our study was conducted in the Simpson Desert, Australia, which is classified as a hot desert. Mean annual temperatures are 21-23°C, with summer maxima of 46-49°C and winter minima of -6° (Dickman et al. 1999a). There is a north-south rainfall gradient between the 100-150 mm median annual rainfall isopleths with a pronounced wet season during the austral summer; despite this seasonality, rainfalls are spatially and temporally variable (Dickman et al. 1999a). Inter-annual variation and intensity of rainfall are influenced strongly by the El Niño Southern Oscillation (ENSO) cycle, and in particular the La Niña phase which is associated with above-average rainfall events (Letnic and Dickman 2006).

Longitudinal dunes of red siliceous sand are the dominant landforms; they are 8-10 m in height and spaced 100-1000 m apart (Dickman et al. 1999a). The dune swales and slopes are stabilized by spinifex (*Triodia basedowii*), a needle-leaved hummock grass, and by sparsely-distributed low shrubs. Common shrubs in the swales include *Acacia ligulata*, *Grevillea* spp. and *Eremophila* spp., while shrubs on the dune crests include *Grevillea stenobotrya*, *Crotalaria* spp. and *Sida* spp. Some swales contain clay soils and are dominated by gidgee trees (*Acacia georginae*), forbs and short grasses. Associated clay pans usually fill with water after heavy rainfall which stimulates the germination of an array of ephemeral forbs and grasses.

Our study was conducted in three spatially-independent regions situated on two conservation reserves in the north-eastern part of the Simpson Desert in central Australia (Figure 5.1). The southern reserve, Ethabuka (23°45’S, 138°28’E), was managed as a cattle station until it was purchased in 2004 by Bush Heritage Australia; all cattle were removed in that year. The northern reserve, Cravens Peak (23°16’S, 138°17’E), also ran cattle until purchased by Bush Heritage Australia in 2006. Cattle remained on this property in very low densities throughout our study.

A wildfire burnt over 2500 km^2 of the Simpson Desert in the summer of 2001/02, including over 30% of our study region (Figure 5.1; Greenville et al. 2009). Broadscale fires such as this have a mean return interval of 26 years (Greenville et al. 2009). Their incidence is linked closely to La Niña episodes, as the associated rainfall stimulates widespread germination of grasses, herbs, shrubs and trees, providing ample fuel for fires after the vegetation has dried (Letnic and Dickman 2006).

The north-eastern Simpson Desert provides habitat for over 70 species of native reptiles, including 10 species of Agamidae, 15 species of Gekkonidae, 30 species of Scincidae and seven species of Varanidae, with the majority occurring in spinifex grassland. Common genera include *Ctenophorus*, *Ctenotus*, *Diplodactylus*, *Lerista* and *Varanus* (Letnic et al. 2004).

5.2.2 Study design and sampling methodology

Five years after the 2001/02 wildfire, we established two replicate sampling sites along burnt habitat edges in each study region (Plate 5.1). At each site, three parallel transects with 20 pitfall traps were set up. The centre transect was placed along the burn ecotone, the second was located parallel and 100 m away in burnt habitat and the third transect was located parallel and 100 m distant from the centre transect in unburnt habitat. With the possible exception of the sand goanna, *Varanus gouldii*, none of the lizard species known to occur in the study region were considered likely to be able to move more than 100 m, so we assumed that this distance would be sufficient to avoid any edge effects that might otherwise occur. We set traps along each transect at intervals of 20 m; each transect crossed through both swale and dune crest habitat.

Plate 5.1 The location of an ecotone transect (with a pitfall trap and drift fence circled in black). Unburnt habitat is located on the left and burnt habitat, with a small amount of spinifex regeneration, is located on the right (L Pastro).

Pitfall traps consisted of PVC pipe (16 cm diameter, 60 cm long) buried flush with the ground surface. A 5 m length of aluminium flywire drift fence was positioned over the top of each trap to improve capture efficiency and a smaller piece was placed underneath the pipe to prevent captured animals from escaping. Upon capture, animals were identified, weighed, measured and given a unique toe-clip for identification. Traps were closed with lids when not in use.

Two trapping sessions took place, in each of October and November 2006. Each trapping session lasted three consecutive nights (Dickman et al. 2001) and the data were pooled over both trapping sessions for each site to ensure adequate captures for analysis. Abundance indices were calculated using a catch-per-unit-effort method (Letnic et al. 2004) to account for low within- and between-session recapture rates (0-10%). The pooled data were standardised by dividing the number of captures by the number of nights that the site was open to obtain captures/site night. Within trip recaptures were excluded to retain independence of data. A total of 36 site nights, giving 2160 trap nights, were completed over the course of the study. Regeneration of vegetation in the burnt areas between the fire event and the start of data collection was minimal due to a period of prolonged drought.

5.2.3 Rainfall, habitat and food resources

Monthly cumulative rainfall totals were measured in each region using an Environdata® automated weather station (Environdata Australia Pty Ltd, 44 Percy Street, Warwick, Queensland, Australia). The monthly totals were then summed over the five year period between the wildfire and data collection. Sites in the northern-most region, at Kunnamuka Swamp, received the most rainfall (661.7 mm) followed by sites at Ethabuka East (465.8 mm) and the Field River sites (367.2 mm).

To indicate the available shelter at each site, the percentage cover of each plant species was estimated visually in a 2.5 m circular quadrat around eight randomly-chosen pitfall trap stations on each transect (Dickman et al. 2001). The area covered by each species was calculated as the mean of the eight measurements taken on each transect. For analysis, each plant species was classified as spinifex, other grass (all species in the families Poaceae and Cyperaceae except *T. basedowii*), forb (ephemeral herbs with non-woody stems or woody at the base only), shrub or tree. The percentage area of lying dead wood was also estimated for each quadrat. An estimate of total plant coverage was calculated by combining estimates for all vascular plant species.

We undertook invertebrate sampling to assess food availability, as invertebrates comprise >95% of the diets of lizards in our study area (Gordon et al. 2010a). Six 125 mL pitfall traps filled with 3% formalin solution were buried flush with the ground within a 2.5 m radius of one randomly selected vertebrate pitfall trap in the swale and one pitfall trap on the dune crest on each transect and left open for three days in both October and November 2006. In the laboratory arthropod samples were rinsed, identified to order, counted and sorted into 2.5 mm size classes. The overall abundance of arthropods was used in final analyses. Although this sampling method fails to adequately sample groups such as aerial insects and fossorial arthropods, the species captured comprise a large proportion of the diet of the lizards in the study area (Greenville and Dickman 2005, Daly et al. 2008, Greenville and Dickman 2009, Gordon et al. 2010b). Thus we believe that our method provides an adequate indication of food availability for the study species.

Cumulative rainfall 0-9 months prior to data collection was measured to provide an indication of the productivity of conditions influencing lizard assemblages at the time of data collection. This time period incorporated rainfall over the previous summer, which has been shown to influence hatchling survival of several species in the region (Dickman et al. 1999a, Greenville and Dickman 2005). Rainfall was measured as monthly cumulative totals using Environdata® automated weather stations (Environdata Australia Pty Ltd). In accordance with the longer-term rainfall trends of both the present study and that of Haythornthwaite and Dickman (2006a), Kunnamuka Swamp received the most rainfall in the nine months prior to sampling (99.7 mm), followed by Ethabuka East (83.1 mm) and Field River (14.4 mm).

5.2.4 Statistical analyses

5.2.4.1 Abundance and diversity

A 2-factor analysis of variance (ANOVA) was used to explore the effect of fire and region on a) lizard abundance and b) lizard diversity (Shannon-Wiener diversity index; Magurran 1988). The factors were Fire (Burnt, Ecotone, Unburnt) and Region (Ethabuka East, Field River, Kunnamuka Swamp). A significant interaction term (Fire*Region) indicated that the effect of fire on lizard abundance or diversity differed according to region. Assumptions of analysis of variance were checked by examining residual plots and analyses then performed using IBM SPSS Statistics v19 (IBM 2010).

5.2.4.2 Assemblage composition and factors driving observed trends

Canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) was used to model changes in the lizard community along the fire gradient. CAP is a discriminant procedure based on principal coordinates that is designed to find axes through a multivariate cloud of points. Thus it is ideal for situations where the existence of two or more distinct groups has been predicted *a priori*. The *a priori* factors that we hypothesised would influence our data were fire history (burnt, ecotone and unburnt) and region (Ethabuka East, Field River and Kunnamuka Swamp).

A zero-adjusted Bray-Curtis dissimilarity matrix (Clarke et al. 2006) was constructed and species abundances were square-root transformed prior to analysis to down-weight the contribution of dominant species. All analyses were conducted using the PERMANOVA+ add-on package for PRIMER v6 (Anderson et al. 2008).

The final number of ortho-normal Principal Coordinate Analysis (PCO) axes (*m*) used in the CAP model was assessed using a leave-one-out residual sum of squares cross validation method (Anderson et al. 2008). This procedure maximised the predictive capability of the model whilst minimising the number of axes (*m*) that were included in the final model, helping to prevent identification of false trends. The strength of the association between the multivariate data cloud and the hypothesis of group differences is indicated by the size of the first two canonical correlations (δ), which varies between 0 and 1.

The CAP procedure is also able to draw axes through multivariate data clouds that have the strongest correlation with a second set of variables, such as habitat variables. The habitat and resource variables that we included in our analysis were mean spinifex cover, grass cover, forb cover, shrub cover, total vegetation cover, rainfall 0-9 months prior to sampling, and total arthropod abundance.

If the CAP model identified distinguishable groups within the data cloud, we calculated Pearson correlations (r) of the individual species or habitat variables with the model CAP axes. Variables with $r > 0.5$ were taken as contributing to observed group differences and were superimposed on the plot as vectors to form a biplot. The length and direction of each vector indicated the strength and sign of the relationship between that variable and each of the CAP axes. The central position of the vector's circle is arbitrary with respect to the underlying plot (Anderson et al. 2008).

The CAP procedure provides a permutation test to check for significant differences among the groups in multivariate space. The test statistic is a “trace” that represents the sum of the canonical eigenvalues or the trace of the matrix $\mathbf{Q^0{}_m{}'HQ^0{}_m}$. Significance testing was carried out using 9999 permutations (Quinn and Keough 2002).

5.3 RESULTS

We caught a total of 323 lizards representing 21 species. These included ten Scincidae, four Agamidae, five Gekkonidae and two Varanidae. For a full list of species caught refer to Appendix 5.1, Table A5.1). One hundred and eight individuals were caught in the burnt habitat, 133 in the ecotone and 82 in the unburnt habitat.

5.3.1 Lizard abundance and diversity

Lizard abundance was not affected by the fire ($F_{(2,4)} = 1.688$, $P = 0.30$) but was influenced by region ($\mathrm{F}_{(2,4)} = 8.126$, $P = 0.039$, Appendix 5.2, Table A5.2.1). Fewer lizards were captured at the Kunnamuka Swamp sites compared with the Field River and Ethabuka East sites (Figure 5.3a). There was no interaction between fire and region ($\mathrm{F}_{(4,9)} = 1.750$, $P = 0.22$).

Lizard diversity was not affected by fire ($\mathrm{F}_{(2,4)} = 0.331$, $P = 0.74$), region ($\mathrm{F}_{(2,4)} = 3.040$, $P = 0.16$), or any interaction between these factors ($\mathrm{F}_{(4,9)} = 2.922$, $P = 0.084$, Figure 5.3b, Appendix 5.2, Table A5.2.2).

5.3.2 Lizard assemblage composition

5.3.2.1 Effects of fire

When data from the three regions were pooled, there was no effect of fire on the lizard assemblages ($\mathrm{Q^0{}_m{}'HQ^0{}_m} = 0.402$, $P = 0.35$, $m = 3$). The first canonical axis had a canonical correlation of $\delta = 0.62$ and slightly separated the unburnt assemblages from the ecotone and burnt assemblages. The second canonical axis had a canonical correlation of $\delta = 0.15$ and played no role in separating the assemblages (Figure 5.4, Appendix 5.3, Table A5.3).

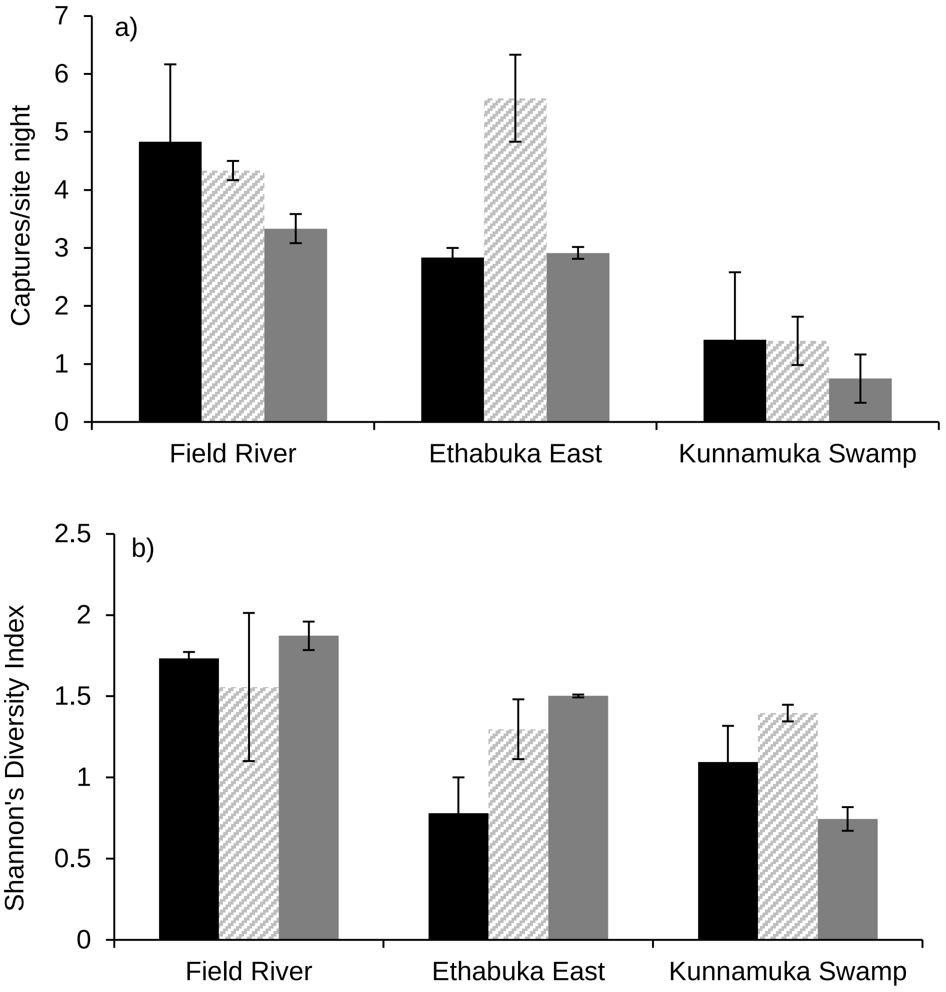

Figure 5.3 a) Mean lizard abundance (± SE) in burnt (black bars), ecotone (stippled bars) and unburnt (grey bars) habitats in three sampling regions in the Simpson Desert, expressed as captures / site night.

b) Mean lizard diversity (± SE) in burnt (black bars), ecotone (stippled bars) and unburnt (grey bars) habitats in three sampling regions in the Simpson Desert, expressed as the Shannon-Weiner Diversity Index.

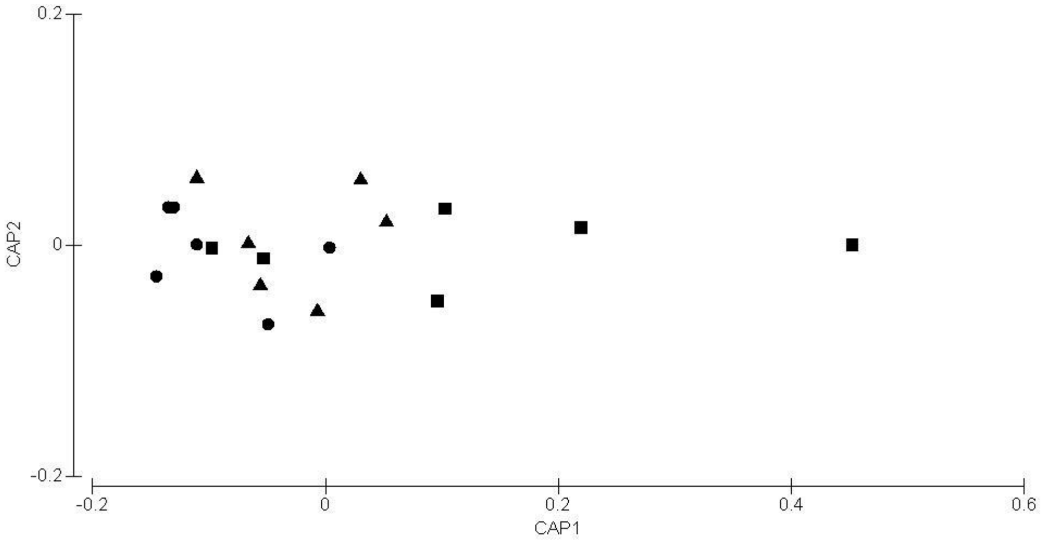

Figure 5.4 Results of canonical analysis of principal coordinates (CAP) analysis to model the effect of wildfire on lizard assemblage composition in burnt (triangles), ecotone (circles) and unburnt (squares) habitats in the Simpson Desert. The analysis is based on a zero-adjusted Bray-Curtis dissimilarity matrix and species abundances have been square-root transformed. Axes represent Principal Coordinate Analysis (PCO) axes (*m*) as determined using a leave-one-out residual sum of squares cross validation method.

5.3.2.2 Effects of region

The lizard assemblages were influenced by the region in which they were located ($Q^0_m{}'HQ^0_m$ = 1.228, *P* = 0.0001, *m* = 3). The first canonical axis had a canonical correlation of δ = 0.90 and separated the assemblages at Field River from those at Ethabuka East and Kunnamuka Swamp. The second canonical axis had a canonical correlation of δ = 0.64 and separated the assemblages at Ethabuka East from those at Field River (Figure 5.5, Appendix 5.3, Table A5.3).

The vector overlay procedure indicated that the Kunnamuka Swamp (high rainfall) assemblages were characterised by a high abundance of *Ctenophorus isolepis*. Assemblages at Field River (low rainfall) were characterised by *Egernia inornata*, *Ctenophorus clayi, Ctenophorus nuchalis, Diporiphora winneckei* and *Eremiascincus fasciolatus.* Assemblages at Ethabuka East were characterised by *Lerista labialis, C. nuchalis* and *Menetia greyii* (Figure 5.5, Appendix 5.4, Table A5.4.1).

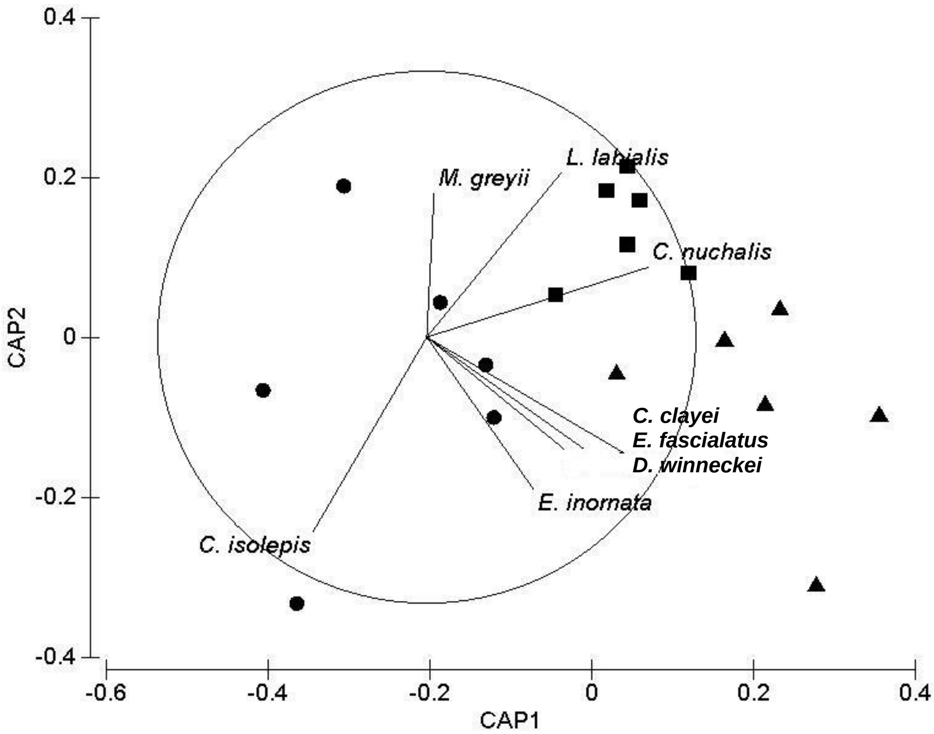

Figure 5.5 The effect of region on lizard assemblage composition in the Simpson Desert, as determined by CAP analysis. Field River sites are represented by triangles, Kunnamuka Swamp sites are represented by circles and Ethabuka East sites are represented by squares. The analysis is based on a zero-adjusted Bray-Curtis dissimilarity matrix and species abundances have been square-root transformed. To visualise which species contribute to observed group differences, vectors corresponding to the Pearson correlations (*r*) of individual species with the CAP axes are superimposed on the plot. The length and direction of each vector indicate the strength and sign of the relationship between that variable and the CAP axes. The central position of the vector circle is arbitrary with respect to the underlying plot.

The position of the study sites relative to each other in the biplot gives an indication of the similarity or dissimilarity of the lizard assemblages they contain. Thus the biplot also indicated that, contrary to our predictions, lizard assemblages were most similar across the Ethabuka East sites and least similar across the Kunnamuka Swamp sites (Figure 5.5).

5.3.2.3 Effects of food, habitat and recent rainfall

A CAP analysis using the external matrix of food, habitat and resource variables indicated that the lizard assemblages were influenced by grass cover, arthropod abundance and rainfall 0-9 months prior ($Q^0_m{}'HQ^0_m = 1.999$, $P = 0.020$, $m = 3$). CAP Axis 1 had a canonical correlation of $\delta = 0.92$ and separated the assemblages along a gradient of high arthropod abundance and forb cover vs high rainfall and lying wood. CAP Axis 2 had a canonical correlation of $\delta = 0.85$ and separated assemblages along a gradient of grass cover (Figure 5.6a, Appendix 5.3 and 5.4, Table A5.3 and Table A5.4.2).

The analysis also indicated that these habitat variables were separated according to region. In Figure 5.6a, CAP Axis 1 separates the assemblages at Ethabuka East and Field River from Kunnamuka Swamp and CAP Axis 2 also separates the Field River from the Ethabuka East lizard assemblages. The Kunnamuka Swamp assemblages were associated with high rainfall, as expected, and with high grass coverage and lying wood. Assemblages at Ethabuka East and Field River were associated with high arthropod abundance and forb coverage. Spinifex and total plant cover were not identified in the analysis because they occurred in relatively equal proportions in all regions.

Projecting the Pearson correlations of the original species variables (suitably transformed) onto the biplot indicated the association of the lizard species with the characteristic habitat and climatic variables at each site (Figure 5.6b, Appendix 5.4, Table A5.4.3). *Ctenotus pantherinus* was associated negatively with grasses and *Ctenophorus isolepis* and *Ctenotus helenae* positively with grasses and negatively with arthropod abundance. *Ctenotus pantherinus* and *C. nuchalis* were associated positively with arthropod abundance. *Egernia inornata*, *D. winneckei*, *C. clayi* and *E. fasciolatus* were all associated negatively with rainfall.

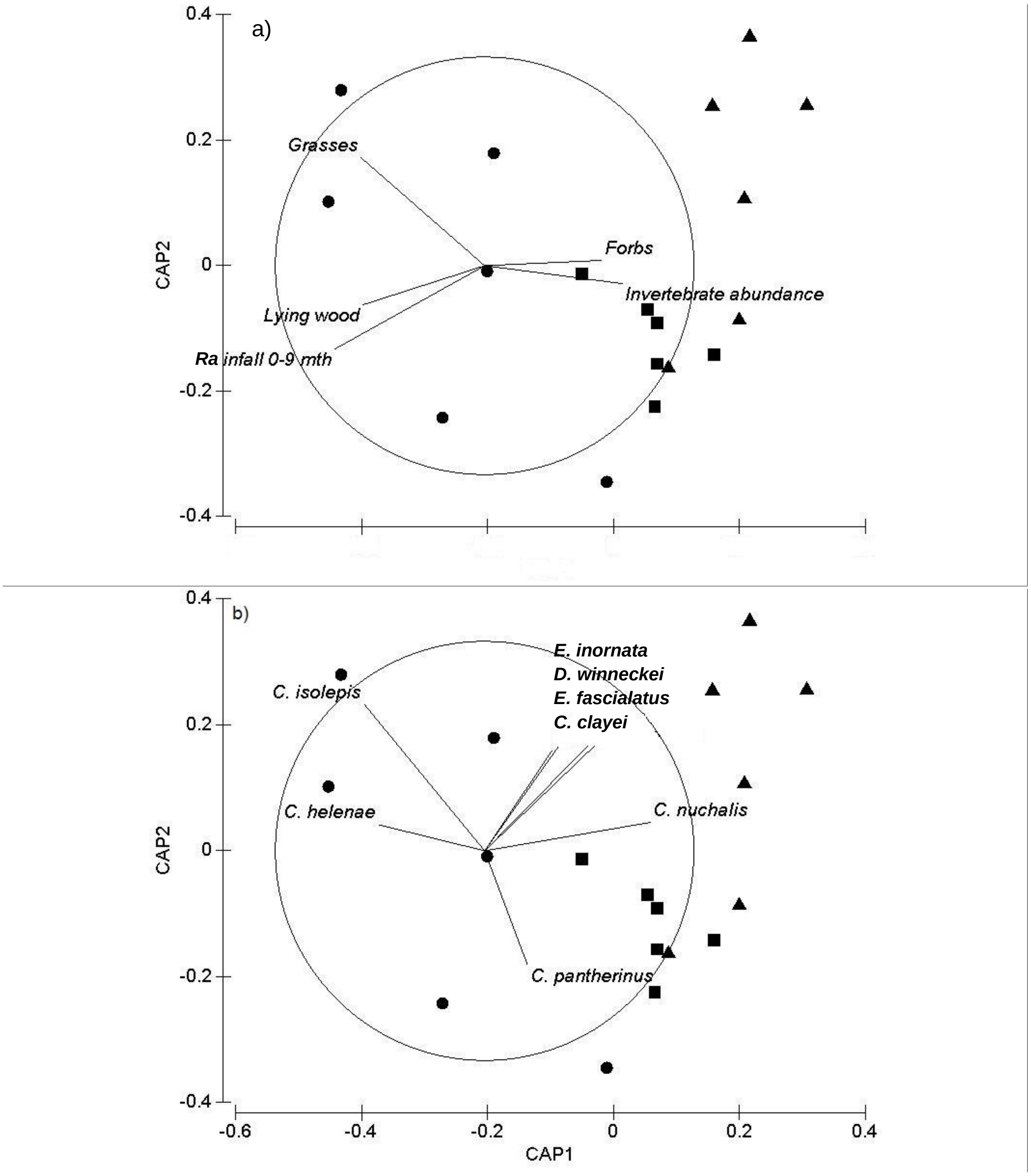
a)
Grasses
Forbs
Invertebrate abundance
Lying wood
Rainfall 0-9 mth
CAP2
0.4
0.2
0
-0.2
-0.4
b)
E. inornata
D. winneckei
E. fascialatus
C. clayei
C. isolepis
C. helenae
C. nuchalis
C. pantherinus
-0.6
-0.4
-0.2
0
0.2
0.4
CAP1

Figure 5.6a) (opposite page) The effect of habitat and resource variables on lizard assemblage composition in the Simpson Desert, as determined by CAP analysis. Field River sites are represented by triangles, Kunnamuka Swamp sites are represented by circles and Ethabuka East sites are represented by squares. The analysis is based on a zero-adjusted Bray-Curtis dissimilarity matrix and species abundances have been square-root transformed. Of the habitat variables measured, grasses, lying wood, rainfall 0-9 months prior, forbs and invertebrate abundance are identified as contributing to observed group differences between the study regions

Figure 5.6b) (opposite page) The effect of habitat and resource variables on lizard assemblage composition in the Simpson Desert, as determined using CAP analysis. Field River sites are represented by triangles, Kunnamuka Swamp sites are represented by circles and Ethabuka East sites are represented by squares. Lizard species overlays show which lizards are associated with the habitat and resource variables identified in Figure 5.6a. The analysis is based on a zero-adjusted Bray-Curtis dissimilarity matrix and species abundances have been square-root transformed.

5.3.3 Food, habitat and climatic variables

5.3.3.1 Effects of fire

CAP analysis indicated that the food, habitat and climatic variables were affected by the fire and were distributed along the fire gradient ($Q^0_m{}'HQ^0_m = 0.907$, $P = 0.0005$, $m = 2$). The canonical correlation of CAP Axis 1 was $\delta = 0.95$ and it separated the variables along the gradient of fire history. The clumping of sites in the burnt, ecotone and unburnt groupings along this axis indicates their similarity to each other. CAP Axis 2 had a canonical correlation of $\delta = 0.05$ and did not distinguish any of the observed groups (Figure 5.7, Appendix 5.3, Table A5.3).

As expected, the variables contributing most to the separation were a high cover of spinifex, total plant cover, lying wood and shrubs in the unburnt sites (Figure 5.7). Arthropod abundance and rainfall were not influenced by fire history (Appendix 5.4, Table A5.4.4).

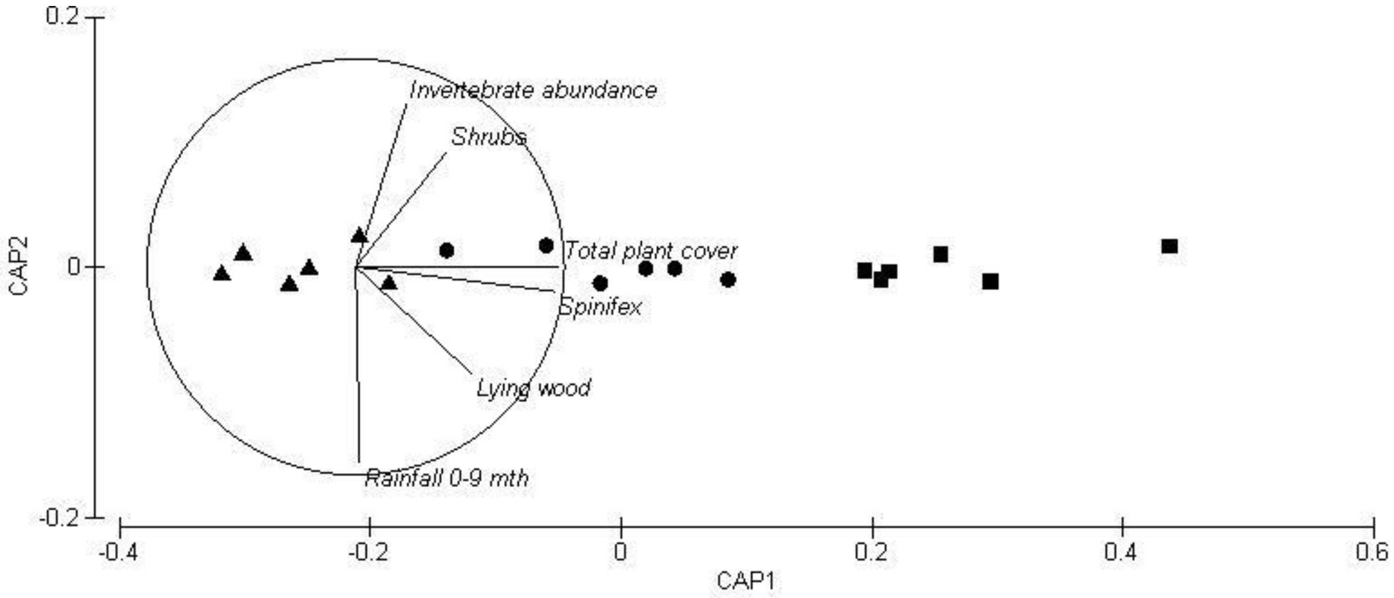

Figure 5.7 The effect of fire on vegetation and resource variables in burnt (triangles), ecotone (circles) and unburnt (squares) habitats in the Simpson Desert, as determined using CAP analysis. The analysis is based on a zero-adjusted Bray-Curtis dissimilarity matrix and species abundances have been square-root transformed.

5.3.3.2 Effects of region

The food, habitat and climatic variables were also separated according to region ($Q^{0}_{m}{}'HQ^{0}_{m} = 0.937$, $P = 0.0004$, $m = 2$). This was expected given the separation of lizard assemblages by region. CAP Axis 1 had a canonical correlation of $\delta = 0.97$ and separated the Field River sites from the Kunnamuka Swamp and Ethabuka East sites. CAP Axis 2 had a canonical correlation of $\delta = 0.058$ and did not separate any sites (Figure 5.8, Appendix 5.3, Table A5.3).

The variables contributing to the separation were consistent with the results in the Lizard CAP (Figure 5.6a), with high rainfall and lying wood associated with the Kunnamuka Swamp sites and high arthropod abundance at the Field River sites. Spinifex and total plant cover were equally distributed among all regions. The Kunnamuka Swamp sites were most closely clumped, indicating the similarity of the food, habitat and climatic variables across the sites in this region (Figure 5.8, Appendix 5.4, Table A5.4.5).

5.4 DISCUSSION

5.4.1 Influence of fire

Based on previous work in similar arid sandridge habitats, we predicted that wildfire would drive decreases in lizard diversity and abundance and that, five years post-fire, recovery would be strongest in productive areas receiving most rainfall (Masters 1996, Letnic et al. 2004, Read et al. 2012). Contrary to our expectations, however, fire history had no effect on diversity and the converse effect on abundance to that predicted (Figure 5.3a and 5.3b). The CAP analysis of lizard assemblage responses to the fire (Figure 5.4) also provided no evidence of post-fire lizard succession, again contradicting much prior work.

In central Australia, lizards previously have been found to exhibit a unidirectional trajectory post-fire that closely follows the successional recovery of burnt vegetation (Masters 1996, Pianka and Goodyear 2012). Letnic et al. (2004) proposed a similar single-axis post-fire trajectory for lizards in the study region, but with a moderator: they suggested that lizard succession could move in either direction in response to changes in vegetation structure and resource availability that are influenced by fluctuations in rainfall. Early successional colonists typically consist of *Ctenophorus nuchalis*, *Rhynchoedura ornata, Lerista labialis* and other species that can tolerate or even prefer expanses of open, burnt land (Masters 1996). Late-successional species include shuttling heliotherm skinks (*Ctenotus* spp.) and the military

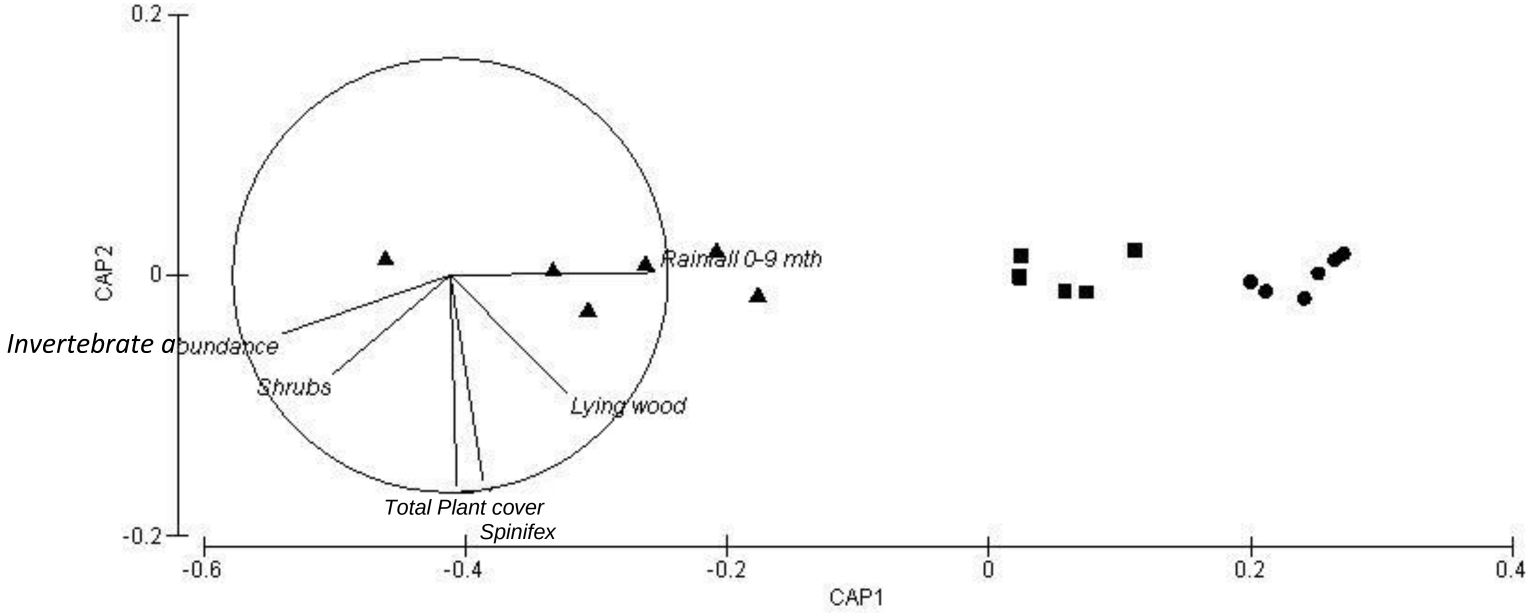

Figure 5.8 The effect of region on vegetation and resource variables in the Simpson Desert, as determined using CAP analysis. Field River sites are represented by triangles, Kunnamuka Swamp sites are represented by circles and Ethabuka East sites are represented by squares. The analysis is based on a zero-adjusted Bray-Curtis dissimilarity matrix and species abundances have been square-root transformed.

dragon (*Ctenophorus isolepis*) that require shade for thermoregulation (Masters 1996, Dickman et al. 1999a, Letnic et al. 2004, Daly et al. 2008).

The absence of lizard responses to wildfire in our study was particularly unexpected given that vegetation was undergoing marked post-fire succession and lizard assemblages were richest at the sites that received the least rainfall (Figure 5.3). However, the result is not unique. For example, in the arid chaco forest in Argentina, vegetation assemblages were distinctly different between burnt and unburnt areas 14 years after a wildfire, but there were no differences in lizard diversity (Pelegrin and Bucher 2010). Elsewhere, lizard abundance and diversity increased following wildfire in montane habitat in central Arizona and in Mediterranean forest (Cunningham et al. 2002, Santos and Poquet 2010), but showed decreases in the same metrics after wildfire in chaparral and sage scrub habitats with no effects of wildfire in grassland (Rochester et al. 2010).

Lizard assemblages are commonly affected by food availability, and our analyses of post-fire arthropod abundance suggest that this food source may have contributed to the post-fire lizard distributions we observed. Arthropods are the primary food source for most lizards in central Australian grasslands (Gordon et al. 2010a) and in our study they were distributed equally across the burnt, ecotone and unburnt habitats in each region (Figure 5.7). Thus although the available shelter differed between the three habitats, food resources were similar.

The absence of any obvious arthropod response to fire is supported by a body of literature that details varied and inconsistent responses of arthropods to fire. In savannahs and other grasslands, fire has been found to increase the density of ants (Andersen 1991) and grasshoppers (Evans 1984). Fire also increases (Letnic et al. 2004) or decreases (Benzie 1986) termite abundance, depending on the study and location. In post-fire spinifex grasslands in Western Australia, rainfall was more important than fire history in determining the composition of spider assemblages (Langlands et al. 2006). At an ordinal level, fire has been found to have little long-term effect on arthropod abundance in spinifex grasslands (Letnic et al. 2004), in southern Australian temperate woodlands and open forests (Friend and Williams 1996) and in tropical savannah woodlands and open forest (Andersen and Muller 2000). In view of these studies it seems plausible that the lack of post-fire response of lizards in our study followed the similarly muted response of arthropods; however, detailed dietary analyses are needed to confirm this.

5.4.2 Influence of region

Our results indicate that lizard abundances and assemblages were determined by factors operating at a regional scale, but regionally-differing rainfall patterns were not the key driver as we had predicted. Lizards were least abundant at the highest rainfall sites (Kunnamuka Swamp) and most abundant at the Field River sites which received the least rain since the wildfire and the lowest rainfall in the nine months prior to sampling (Figure 5.3a). As summer rainfall boosts hatchling success, we expected that high rainfall in the summer would increase lizard numbers during subsequent sampling (Dickman et al. 1999a).

The Kunnamuka Swamp assemblages were also the least similar to each other in terms of the lizard assemblages they housed (Figure 5.5). This was unexpected as we had predicted that higher rainfall in this region would accelerate lizard recovery in burnt habitats which would increase the similarity of the assemblages inhabiting the burnt, ecotone and unburnt sites. This prediction is supported by the work of Dickman et al. (1999a) and Letnic et al. (2004) who found that rainfall-stimulated vegetation growth affects lizard assemblage composition in this region. The dissimilarity between the Kunnamuka Swamp sites was most likely caused by the very low lizard numbers captured across these sites combined with a remarkably high local population of *C. isolepis* at one site. Our results concur with Read et al. (2012) who found similarly that rainfall did not affect lizard abundance in arid Australia as expected. Instead, local scale processes such as vegetation conditions and inter-specific interactions were key influencing factors. Driscoll and Henderson (2008) also found that lizard responses to fire in arid Australia were structured by location rather than fire history. Further analysis indicates that such factors, in addition to regional history, likely affected lizard assemblages in our study also.

The vegetation attributes of the sites were strongly grouped by region, with the sites demonstrating high similarity in these characteristics within each region. The Kunnamuka Swamp (high rainfall) sites were the most similar to each other in terms of habitat, and were characterised by having higher coverage of lying wood and spinifex. The Field River (low rainfall) sites were characterised by the most shrub cover and the least amount of lying wood. The Ethabuka East sites were characterised by moderate presence of most types of vegetation (Figure 5.8). These regional distinctions in vegetation characteristics do not help to explain the regionally distinct lizard assemblages, however, as the characteristic species in each region cannot be placed readily into functional groups that require the specific habitats shown to occur in that region. For example, the dominant species at the Field River sites (*E. inornata*, *C.*

clayi, C. nuchalis, D. winneckei and *E. fasciolatus*) have no clear association with the high forb cover that was present at the Field River sites (Letnic et al. 2004).

The regional variation observed in lizard abundance and assemblage composition can instead be explained by food availability and perhaps by differences in predation pressure and regional grazing history. The abundance of arthropods varied regionally and corresponded with the variation in lizard abundance, as the Field River sites yielded the most arthropods, followed in turn by the Ethabuka East sites and the Kunnamuka Swamp sites (Figure 5.8). Lizard communities in arid Australia often survive in extremely low numbers across much of the landscape and reach peak abundances only when the necessary resources, such as food, allow them to do so (Pianka 1992). Thus it is likely that the abundance of food resources at the Field River sites, perhaps supported by a higher water table and riparian vegetation lining the banks of the usually-dry Field River (Free 2009) contributed to the high abundance of lizards in this region.

The regionally distinct lizard abundances were also likely to have been influenced by regional differences in predation pressure. The pitfall trapping methods used in this study captured small dasyurid predators also (5-15 g body weight, Marsupialia: Dasyuridae). In *post-hoc* analyses of the mammalian predator by-catch, Kunnamuka Swamp yielded the highest mean capture rate (2.2 captures/site night; *Ningaui ridei*, *Sminthopsis hirtipes* and *S. youngsoni*) compared with Field River (1.4 captures per site night) and Ethabuka East (0.9 captures/site night). Dasyurids are predators of arthropods and also lizards and hence may be capable of suppressing lizard abundances through both competition for food and direct predation (Woolnough and Carthew 1996). Densities of foxes (*Vulpes vulpes*) and cats (*Felis catus*) were not measured but appeared to be low across all regions. Avian predators were not sampled.

Lastly, differences in historical cattle grazing pressure also likely contributed to the regional variation in lizard communities. Livestock grazing in arid and semi-arid land systems can have strongly negative impacts on lizard communities (James 2003, Driscoll 2004) via impacts on vegetation and refuge habitats, invertebrate food sources, burrows and cryptogamic crusts (Eldridge 1996, Letnic 2007). In our study, the sites at Kunnamuka Swamp were under light cattle grazing pressure at the time of sampling, and even though grazing at Ethabuka East and Field River had ceased 2-3 years prior, Ethabuka East experienced considerably higher historical grazing pressure than Field River (Letnic and Dickman 2006, Frank et al. 2012). This historical grazing pressure gradient corresponds strongly with the lizard abundance gradient observed in our study and may also have further contributed to the reduced abundance of invertebrates at the lightly grazed Kunnamuka Swamp sites.

5.4.3 Conclusion

Our results demonstrate the importance of a multi-scale approach when measuring the effects of wildfire and disturbances more generally. Wildfire did not initiate a unidirectional succession of lizards as predicted by the habitat accommodation model of succession, and the regionally-distinct assemblages were not linearly related to the effects of rainfall. Instead they appeared to be influenced by a range of factors operating at different temporal and spatial scales including food availability, predation pressure and grazing history. Our study has implications for land- managers because it shows that wildlife responses to fire cannot always be predicted. Hence we caution that management strategies which aim to create habitat through the use of fire or predict the occurrence of wildlife species based on age since fire may not produce the expected outcomes. We recommend that future studies measuring the effects of wildfire on lizard populations in arid and semi-arid regions consider a range of influencing factors including (where possible) climate, fire history, vegetation condition, food resources, predation pressure, grazing history and inter-specific interactions.

CHAPTER 6

PREDATION RISK INFLUENCES SMALL MAMMAL RECOLONIZATION OF BURNT HABITATS

Clockwise from top left: A lesser hairy footed dunnart (*Sminthopsis youngsoni*; A. Chen), spinifex hopping mouse (*Notomys alexis*; A. Chen), sandy inland mouse (*Pseudomys hermannsburgensis*; A. Chen) and feral cat (*Felis catus*; L. Pastro).

After wildfire, surviving animals are frequently restricted to patches of unburnt refuge habitat. Predation is often purported to be a key factor influencing animal recovery in burnt areas; however, few studies have attempted to test this idea. Here, we experimentally investigate how prey behavior changes in the post-fire environment under different levels of predation risk. We use native small mammals and introduced predators, the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) in arid central Australia as our model system. We predicted that, if predators actively exploit prey populations in burnt habitats, then 1) predator activity would be focused on the burn ecotones; 2) small mammal abundance would be highest in unburnt habitat; and 3) small mammal activity would increase in burnt habitats if the risk of predation there was reduced. Our studies were set up in an environment that had experienced wildfires at least four years before our work began, and were designed to sample small mammals and their predators in burnt habitat, along burnt-unburnt ecotones, and in unburnt habitat. We used a combination of live-trapping and tracking methods, simple predator exclusion cages, and assays of small mammal foraging behavior and activity based on the giving-up density (GUD) approach. In line with our predictions, fox and cat activity was concentrated on burn ecotones and small mammals foraged for longer in burnt environments when their risk of predation was experimentally reduced. Our study indicates that foxes and cats selectively exploit burn ecotones and that this heightened risk of predation is likely a key determinant of small mammal recovery in burnt habitats. Together with recent research indicating the deleterious effects of foxes and cats on native Australian mammals, our study highlights the need for either an integrated fire management program to reduce the frequency of broadscale wildfire events in arid Australia, or a landscape-level program of predator control that can be mobilized in the wake of such wildfires. With climate change predicted to increase the frequency and intensity of wildfires in arid environments, there is a clear imperative to plan ameliorative measures now.

6.1 INTRODUCTION

Fire is a common phenomenon in many terrestrial ecosystems and can have dramatic effects on the structure and dynamics of ecological communities. On the one hand, fires quickly kill some organisms on and above the ground surface by raising temperatures above lethal limits or by direct immolation (Gerson and Kelsey 1997, Koprowski et al. 2006). Other organisms may fail to survive the loss of habitat and key resources (Banks et al. 2011) or succumb to attacks by parasites, pathogens or predators (Keyser et al. 2006, Körtner et al. 2007). On the other hand, fires provide opportunities that many organisms exploit. For example, fires can trigger germination in buried seeds either by weakening the seed coat or by providing chemical signals that stimulate activation of the embryo (Letnic et al. 2000, Finch-Savage and Leubner-Metzger 2006). Adult plants may resprout via epicormic growth or from underground storage organs or respond by releasing seed into the nutrient-rich ash bed (Vesk and Westoby 2004, Ooi et al. 2006). Animals can survive fires by fleeing from the flames or by seeking refuge as the flames pass (Whelan et al. 2002). Herbivores and granivores then may exploit the pulse of productivity in the post-fire environment and in turn provide prey for secondary consumers (O'Dowd and Gill 1984, Fox 2011).

Disparate species responses to fire often arise because of interactions between the fire event and additional factors such as changes in micro-climatic conditions or shifts in biotic interactions (Sutherland and Dickman 1999, Driscoll et al. 2010, Morris et al. 2011b). For example, fires may leave the soil surface with too little cover for shade-loving species but ameliorate conditions for heliotherms (Daly et al. 2007, 2008), or reduce litter cover so that surface-dwelling organisms are subject to desiccation (Vasconcelos et al. 2009). Post-fire trajectories of particular species may depend on the presence or absence of competitors, or engineer species that facilitate the recovery of others (Dickman 1992, Higgs and Fox 1993). In addition, the arrival of invasive species in fire-prone environments can alter the trajectory of post-fire recovery (Letnic et al. 2005).

Of the biotic factors that interact to shape species' recovery trajectories after fire, predation appears to be particularly pervasive and important. A process that can reduce animal densities and survival, delay reproduction, and stimulate changes in habitat use and activity levels (Lima and Dill 1990, Salo et al. 2010, Morris et al. 2011a), the effects of predation may be magnified further in denuded post-fire habitats (Russell et al. 2003, Körtner et al. 2007, Wilgers and Horne 2007, Morris et al. 2011b). In these situations, the effects of predation may interact with the need for prey to find food in the newly burnt habitat (Letnic et al. 2004, Letnic and

Dickman 2010). The reduction in shelter and food resource availability may cause prey to increase their searching activities and hence make them more continuously available, and conspicuous, to visually hunting predators (Letnic and Dickman 2005, Letnic et al. 2005).

Recent research indicates that prey in burnt habitats may be sensitive to the increased risk of predation posed by the open post-fire environment, deliberately selecting more sheltered refuge sites in burnt habitats when predators are present (Letnic et al. 2005, Derrick et al. 2010). This accords with evidence in other systems that shows there is likely to be strong selection pressure for behaviors that reduce the risk of predation (Berger and Gese 2007, Schmitz et al. 2008). Fire may also stimulate predators to move temporarily into burnt areas to take advantage of easier hunting in the newly-open and simplified habitat (Kutt and Woinarski 2007, Legge et al. 2011, Andersen et al. 2012). These increases in predator numbers and activity can profoundly influence ecosystem dynamics. For example, the rapid explosion in predator numbers that follows rare flood rains and coincides with wildfire events in Australian arid grasslands can exert enough population pressure to create strong but transitory top-down trophic pathways in systems that are traditionally dominated by bottom-up forces (Letnic et al. 2005, Letnic et al. 2011). Conversely, fires may reduce predator activity or predation risk and result in elevated prey populations (Zwolak et al. 2012).

In this paper we investigate how prey behavior changes in the post-fire environment under different levels of predation risk, using native mammals in the central Australian arid zone as model prey species. Several species of native mammals have been extirpated by altered levels of predation in Australia over the last 200 years, with losses being focused primarily in the continental deserts (Johnson 2006, McKenzie et al. 2007, Saunders et al. 2010). Predation can have major effects on population and assemblage dynamics of arid-dwelling mammals (e.g. Newsome et al. 1989, Read 1997, Risbey et al. 2000, Kinnear et al. 2002, Letnic et al. 2009a, Letnic et al. 2009b, Moseby et al. 2009a, Read and Cunningham 2010) and native Australian species are affected more negatively by introduced predators such as the red fox (*Vulpes vulpes*) and feral house cat (*Felis catus*) than are equivalent prey in other parts of the world (Salo et al. 2007, Salo et al. 2010). Both foxes and cats prey selectively on small mammals in arid Australia, and are able to consume up to six individuals, or 200 g of prey, in a night of foraging (Pavey et al. 2008, Kutt 2011, 2012). There is mounting evidence that native mammals in northern Australian savannas are disappearing due to the interactive effects of fire and introduced predator activity (Fisher et al. 2013) and increasing concern also that mammals of the arid inland may be at risk (Letnic and Dickman 2006, Letnic and Dickman

2010). As large and intense fires are predicted to occur more frequently in many regions (McKenzie et al. 2004, Wilson et al. 2010), including Australia (Pitman et al. 2007, but see also Bradstock 2010), there is some urgency to better understand the interactive effects of these events on native species.

Our studies were set up in an environment that had experienced wildfires at least four years before our work began, and were designed to sample small mammals and their predators in burnt habitat, along burnt-unburnt ecotones, and in habitat that had not been burnt in the wildfire event. Based on the observations and studies cited above, we predicted that:

1. Predator activity would be focused on ecotones where prey could be most readily intercepted;
2. Small mammals would be more abundant in unburnt than in burnt habitat; and
3. Small mammal activity would increase in burnt areas if their risk of predation was reduced.

Prey responses to changing predation pressure can be gauged in the short term using assays of behavior or in the longer term via demographic performance (Corbett et al. 2003). The interactive effects of fire and predation are most readily teased apart using manipulative experiments, either by changing levels of predator activity or by elevating cover for prey in the post-fire environment (Arthur et al. 2005, Arthur et al. 2012). In our study, we used a combination of live-trapping and tracking methods, simple predator exclusion cages, and assays of small mammal behavior and activity based on the giving-up density (GUD) approach pioneered by Brown (1988) to test our predictions.

6.2 MATERIALS AND METHODS

6.2.1 Study area and climate

The study was conducted on Ethabuka Reserve in the northeastern part of the Simpson Desert, central Australia (23°46’S, 138°28’E; Figure 6.1) between August 2005 and September 2008. The region is characterized by parallel sand dunes spaced 600 – 1000 m apart and rising on average 8-10 m high (Purdie 1984). The swales and dune sides are stabilized primarily by a needle-leaved hummock grass, spinifex (*Triodia basedowii*), and the dune crests support occasional stands of cane grass (*Zygochloa paradoxa*), herbs and small shrubs including *Grevillea stenobotrya, Goodenia cycloptera, Crotalaria* spp. and *Sida* spp. The grasslands support a sparse overstorey of shrubs with common species including *Acacia ligulata, Grevillea* spp. and *Eremophila* spp. Some mallee shrub species (*Eucalyptus pachyphylla* and *E. gamophylla*) and low trees (*Grevillea striata*, *Eucalyptus coolibah*) also occur. Swales with a higher proportion of clay in the soil also often contain small (<5 ha) stands of gidgee trees (*Acacia georginae*; Purdie 1984). Annual grasses and herbs are diverse and abundant after rainfall but persist in the seed bank during dry periods.

A wildfire burnt over 254 000 ha of the study region in the summer of 2001/02 (Figure 6.1; Greenville et al. 2009). The annual average rainfall is 206 mm a year, as recorded at Marion Downs, 128 km distant, over a period of 98 years. Except for a storm event in January 2007 when 211 mm of rain fell, the study region received rainfall equivalent to 17% - 84% of the annual average each year from 2002 to 2008 when the study concluded (Dickman et al. 2010, Greenville et al. 2012). Hence, there was very little recovery of vegetation over the study period, and overall ground cover remained < 5% in the burnt areas compared with 15 - 35% cover in unburnt areas throughout (Dickman et al. 2013). The Simpson is classified as a hot desert; mean annual temperatures are 21 - 23°C, with summer maxima of 46 - 49°C and winter minima of - 6° (Dickman et al. 1999a).

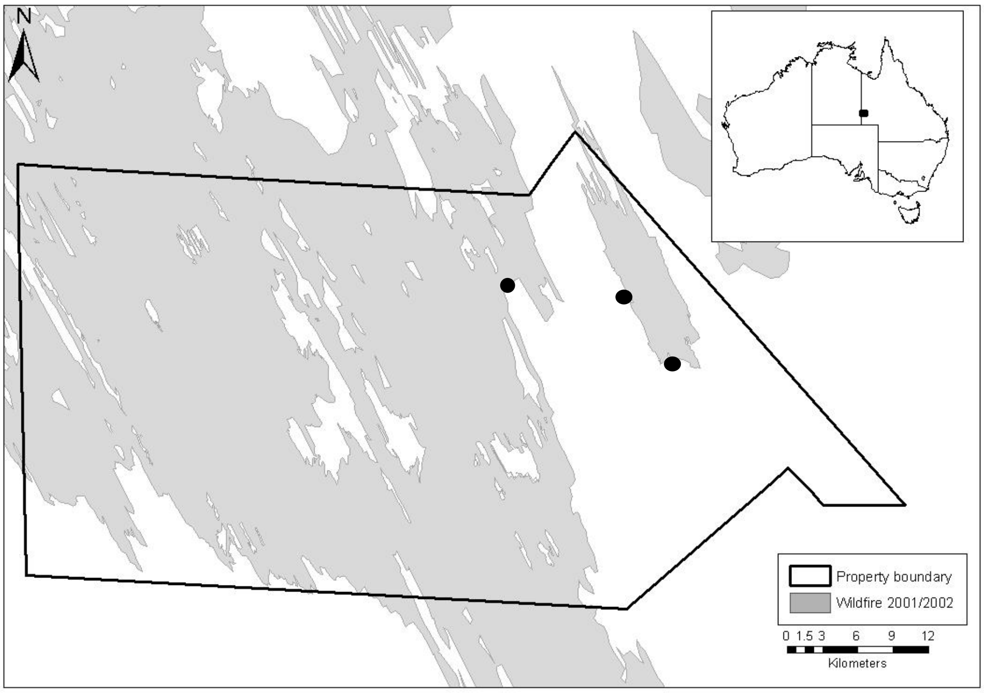

Figure 6.1 Map of the study area showing the location of the study area in the Simpson Desert, central Australia (inset), the study property boundary (solid line), the study sites (black circles) and the area burned (grey) by wildfires that occurred between November 2001 and March 2002.

6.2.2 Study species

Because of the ‘boom’ and ‘bust’ nature of Australia’s desert systems, small mammals were scarce during most of the study period and native mammalian and avian predators were virtually absent (Dickman et al. 2011, Dickman et al. 2013). However, three species of small mammals were sampled consistently. The spinifex hopping-mouse *Notomys alexis* (~30 g) and sandy inland mouse *Pseudomys hermannsburgensis* (~12 g) are omnivorous murid rodents that are widespread in spinifex grasslands. The hopping-mouse is bipedal and primarily exploits open sand between spinifex hummocks, whereas *P. hermannsburgensis* is quadrupedal and is found more commonly in hummocks or within a few centimetres of their edges (Murray and Dickman 1994). The hairy-footed dunnart *Sminthopsis hirtipes* (~16 g), by contrast, is an insectivorous dasyurid marsupial that prefers areas with sparse spinifex cover (Fisher and Dickman 1993, Haythornthwaite and Dickman 2006a). Introduced red foxes and feral cats were the major predators during our experiments and were present throughout. Both species occur widely in arid Australia and can exert strong predatory pressure on native small mammals (Risbey et al. 2000, Letnic and Dworjanyn 2011).

6.2.3 Experimental design

The wildfires in 2001/02 mostly burnt spinifex within dune valleys and stopped near dune crests, producing a situation where burnt-unburnt comparisons potentially could be confounded by dune position. To avoid this, we used satellite imagery to identify ecotones between burnt and unburnt habitat that covered both dune valleys and dune crests (Greenville et al. 2009), and then checked that potential sites were accessible on subsequent visits. We selected three sites that were separated by ~15 km and located in areas burnt by different wildfires during the 2001 - 2002 fire season.

To measure predator activity (Prediction 1) we established six footprint transects at each of nine distances relative to the ecotone at each of the sites: at the ecotone, and then at distances of 10 m, 250 m and 500 m away from the ecotone in both the burnt and unburnt habitat, with two additional distances set in burnt habitat at 750 m and ≥ 1000 m. Following the protocol of Mahon et al. (1998), each transect was 40 m long × 0.75 m wide and created by smoothing the sand surface; transects were set in random positions at each distance with the proviso that they were ≥ 100 m apart. The transect plots were run in August 2005, June 2006, September 2007 and February 2008.

To gauge the abundance of small mammals (Prediction 2), we set pitfall traps at one of the three sites where predators were sampled. Pitfall traps were constructed from PVC pipes (16 cm diameter, 60 cm deep) and were set with a drift fence of aluminum wire screening (flywire) across the top of each trap to increase trap success. The fence was 30 cm high and ran for 2.5 m on each side of the pitfall opening to intercept and guide surface-active animals into the trap (Friend et al. 1989). The bottom ends of the pits were provided with a floor of wire screening to prevent captured animals from digging their way out, and all pits were capped with metal lids when not in use. Twenty pitfall traps were set at 20 m intervals along the ecotone and on parallel lines at distances of 100 m away in both the burnt and unburnt habitat. Sampling was undertaken in April 2008.

We constructed predator exclusion cages to test Prediction 3. Since the cages were designed to provide absolute protection from foxes and cats, we expected that small mammals would perceive their risk of predation to be reduced when using them and thus their activity within or near the cages would increase. Two cage designs were used. The first employed a modular cage structure that was intended to manipulate the risk of predation that small mammals would experience in burnt and unburnt habitats. Cages measured 2 m × 3 m × 0.5 m high and were made from 1 mm woven steel mesh (Whites Wires Pty Ltd, Huntingwood, New South Wales, Australia). The bottom of the mesh was dug 10 cm into the soil so that cages stood 0.4 m above ground level upon completion; cages were secured in place further using metal pegs. The mesh had 5 cm gaps between the wires, allowing all species of small mammals to enter and exit without hindrance but preventing access by foxes and cats. Within days of establishment, wind-blown litter and other debris had begun to pile up around the mesh. To control for cage effects, we constructed and set further cages that were identical to the exclusion cages except for large holes that were cut in the cage sides to allow predator ingress. We also established open control stations that had no associated cage structure. We set up 21 stations comprising seven each of the three cage treatments (exclusion cage, cage control, open control) in two lines 100 m away from a burn ecotone; one line in burnt habitat and the other in unburnt. Stations were ~20 m apart, with the order of cage treatment randomized along each line. This cage design was used at the study site with the pitfall traps and operated in February, April and June 2008.

The second type of exclusion cage was constructed in the form of a tunnel. This design was intended to determine whether small mammals would move from unburnt into burnt habitat if their risk of predation was reduced. Tunnels were 200 m × 0.5 m × 0.4 m high. These used the same gauge wire mesh as the first cage design and thus excluded introduced predators but allowed free access to small native mammals. Tunnels were secured to the ground by pegs and positioned so that one end of each tunnel began in unburnt vegetation and ran at 90° across an ecotone to terminate almost 200 m distant in burnt habitat. As before, we established tunnel controls that had holes cut along the length of the mesh, and open controls that were 200 m lines with no mesh structure. We constructed three of each of the three types of tunnel treatment, setting them 200 - 500 m apart in random order at a site without pitfall traps, and applied the treatments in February 2008.

6.2.4 Sampling protocol

The predator transects were checked for cat or fox footprints for 3 - 4 consecutive mornings and scored if prints were present to give a binary count of activity for each distance for each species. The sand was smoothed again each morning. Other species were noted if present (e.g. dingo *Canis lupus dingo*, goannas *Varanus* spp.), but these were infrequent and data are not presented here.

The pitfall traps were checked in the mornings and left open for 3 nights. Captured animals were identified, weighed, inspected for reproductive condition, and marked uniquely by ear-notching before release.

Giving-up density trials (GUDs; Brown 1988) were used to test the effect of the predator exclusion cage and tunnel treatments. GUDs create small patches where food is locally enriched for the target species. They indicate the trade-off between foraging returns and foraging costs (such as energetic, predation, and missed opportunity costs) and thus provide a quantitative measure of perceived predation risk (Brown 1988). The residual food after a night's foraging is the giving-up density (GUD). Low GUDS are indicative of an animal staying longer to forage at a resource patch, which likely indicates a low perceived risk of predation. Alternatively, we would expect GUDS to be higher under conditions of heightened perceived predation risk such as in open habitats, due to the presence of predators such as the barn owl (*Tyto alba*), red foxes and feral cats that occur in the study area.

To measure GUDs we established a food patch within each of the modular cages and at every 25 m along the length of the longer tunnel-cages. The food patches were plastic bowls (15 cm diameter, 4 cm deep) that were provisioned with either 20 peanut quarters or 10 live mealworms (larvae of *Tenebrio molitor*) mixed into 200 ml of sifted sand. The peanuts were expected to provide high quality food for the rodents (Kotler et al. 1998), whereas the mealworms were intended for the dunnart. We half-buried the bowls in the sand and coated the undersurfaces with a mixture of Vaseline and Coopex insecticide powder (Bayer Ltd., Pymble, New South Wales, Australia) to prevent ants from accessing the food source (Dickman et al. 2010). In general, trials targeting the rodents and the dunnart were carried out at different times so that either peanuts or mealworms were offered, but not both.

We pre-baited the food patches for a night to allow animals to encounter them, and then ran them for 3 - 4 consecutive nights. In the late afternoons, the 20 peanut quarters or 10 mealworms were added to each food patch and the surrounding sand was smoothed so that foot tracks could be read. The food patches were checked at dawn after each night and the numbers of peanut quarters or mealworms remaining per bowl were counted to obtain the GUD. Any tracks surrounding the bowls were identified. The tracks of *P. hermannsburgensis* could be identified by their small size (pes < 20 mm) and imprint of 5 hind toes. *N. alexis* tracks could be confirmed by their length (pes < 30 mm), imprint of the heel, and the impression of usually just 3 toes. Tracks belonging to *S. hirtipes* could be confirmed by the length of the rear pes (>15 mm) and the pattern of front and rear imprints (Triggs 1996). It is unlikely that *P. hermannsburgensis* tracks were confused with either of two other sympatric species of rodent, the desert mouse (*Pseudomys desertor*) and introduced house mouse (*Mus musculus*), as trapping conducted in this and other concurrent studies showed that these rodents were very rare throughout the course of the study (Dickman et al. 2013).

6.2.5 Analyses

To test our first prediction we calculated an index of activity for each predator species at each sampling distance by dividing the number of transects on which tracks were present by the number of sampling nights. Data were pooled across the three sites for each distance owing to many zero values. We then conducted a one-factor analysis of variance (ANOVA) on the predator activity index for each predator species (i.e. cat and fox). The factor was Distance (transect distance from the ecotone). Levene’s test was used to check for variance equality prior to analysis. Equal variances could not be obtained for cat data in 2006 or fox data in 2005, 2006 or 2008 even when data were transformed. We therefore used untransformed data and accepted significance at ≤ 0.01 for these analyses (Underwood 1997). Significance was set at ≤ 0.05 for all other analyses. Significant results were subjected to *post hoc* testing to identify the distances at which predator activity differed. Tukey's HSD tests with Bonferroni-adjusted *P* - values were used.

Small mammals were seldom recaptured (recapture rates were < 10%) which prevented us from modelling estimates of their abundance in burnt and unburnt habitats. Instead, we used simple counts of numbers of individuals captured to test Prediction 2, using chi-squared tests (χ^2) to compare the frequencies of each species captured in each habitat type.

To test our third prediction, we averaged the GUD data over the food patches that had been foraged for each species over the 3 - 4 nights that the patches were set. GUDs were included in analyses if the patches had been visited by the study species, as judged by foot tracks in the sand matrix of the bowls, even if no food had been removed. If both of the rodents *N. alexis* and *P. hermannsburgensis* had foraged at a patch, we used the GUD for that patch only if we could distinguish by the over-printing of tracks which species had been the last forager; if in doubt, data for that patch were discarded. Similarly, for *S. hirtipes*, we occasionally found bowls where other species of dasyurids (*Ningaui ridei* or *Dasycercus blythi*) had also foraged. Data were then included only if we could confidently see the tracks of *S. hirtipes* overprinting the others. Patches that had been visited by other foragers, such as Australian ravens (*Corvus coronoides)*, or disturbed by larger animals such as camels (*Camelus dromedarius)* or emus (*Dromaius novaehollandiae)*, or had not been visited, were omitted from analyses.

We used a two-factor ANOVA to detect differences in GUDs between cage treatments and habitats for each sampling session for the experiment using modular cages. The factors were Fire (burnt, unburnt; fixed) and Cage (exclusion, cage control, and open control; fixed). Levene's test was used to check for variance equality prior to analysis. Equal variances could not be obtained for the June 2008 sampling session for *Notomys alexis* and we therefore used untransformed data, accepting significance at $P \leq 0.01$ for this analysis (Underwood 1997). Significance was taken at $P \leq 0.05$ for all other analyses.

Differences in GUDs between the tunnel treatments were tested using a nested two-factor ANOVA. The factors were Tunnel (exclusion, tunnel control and open control) and Distance (distance of the food patch from the ecotone). Distance was nested within Tunnel. Analyses were conducted for *P. hermannsburgensis* and *N. alexis* only, as a lack of replication precluded analysis for *S. hirtipes*. Variances for *N. alexis* were not homogeneous (using Levene's test) and homogeneity could not be achieved via transformation. Untransformed data were therefore used and significance was accepted at $P \leq 0.01$ for these analyses. Significance was set at $P \leq 0.05$ for all other analyses (Underwood 1997). Significant results for Tunnel were subjected to *post hoc* testing to identify the distances at which small mammal foraging activity differed. Tukey's HSD tests with Bonferroni-adjusted *P* - values were used. All analyses were performed in SPSS (IBM SPSS 2010).

6.3 RESULTS

6.3.1 Prediction 1

The number of transects with cat prints differed between the nine transect positions in 2005 ($F_{(8,18)} = 11.152$, $P < 0.001$), 2007 ($F_{(8,18)} = 9.936$, $P < 0.001$) and 2008 ($F_{(8,18)} = 12.340$, $P < 0.001$; Figure 6.2a; Appendix 6.1). Pairwise comparisons indicate that these results were driven by significantly higher numbers of cat prints on the ecotone transects than on transects further away from the fire boundary (Figure 6.2a, Appendix 6.2).

The presence of foxes differed significantly between the nine transect positions in 2005 ($F_{(8,18)} = 8.386$, $P < 0.001$), 2007 ($F_{(8,18)} = 14.785$, $P < 0.001$) and 2008 ($F_{(8,18)} = 3.692$ $P = 0.01$; Figure 6.2b; Appendix 6.1). Again, pairwise comparisons indicated that these results were driven by significantly more fox prints on ecotone transects when compared with transects further from the fire boundary (Figure 6.2b, Appendix 6.3)

6.3.2 Prediction 2

In total, 32 *Pseudomys hermannsburgensis* were caught in pitfall traps over the three nights. Seven of these were caught on the burnt transect, 12 on the ecotone and 13 on the unburnt transect. The chi-squared test indicated that this was not a significant difference ($\chi^2 = 1.938$, $P = 0.380$).

Captures of *Sminthopsis hirtipes* (3 individuals) and *Notomys alexis* (6 individuals) were too low for analysis, violating the chi-squared test assumption that expected frequencies should be more than five (Quinn and Keough 2002).

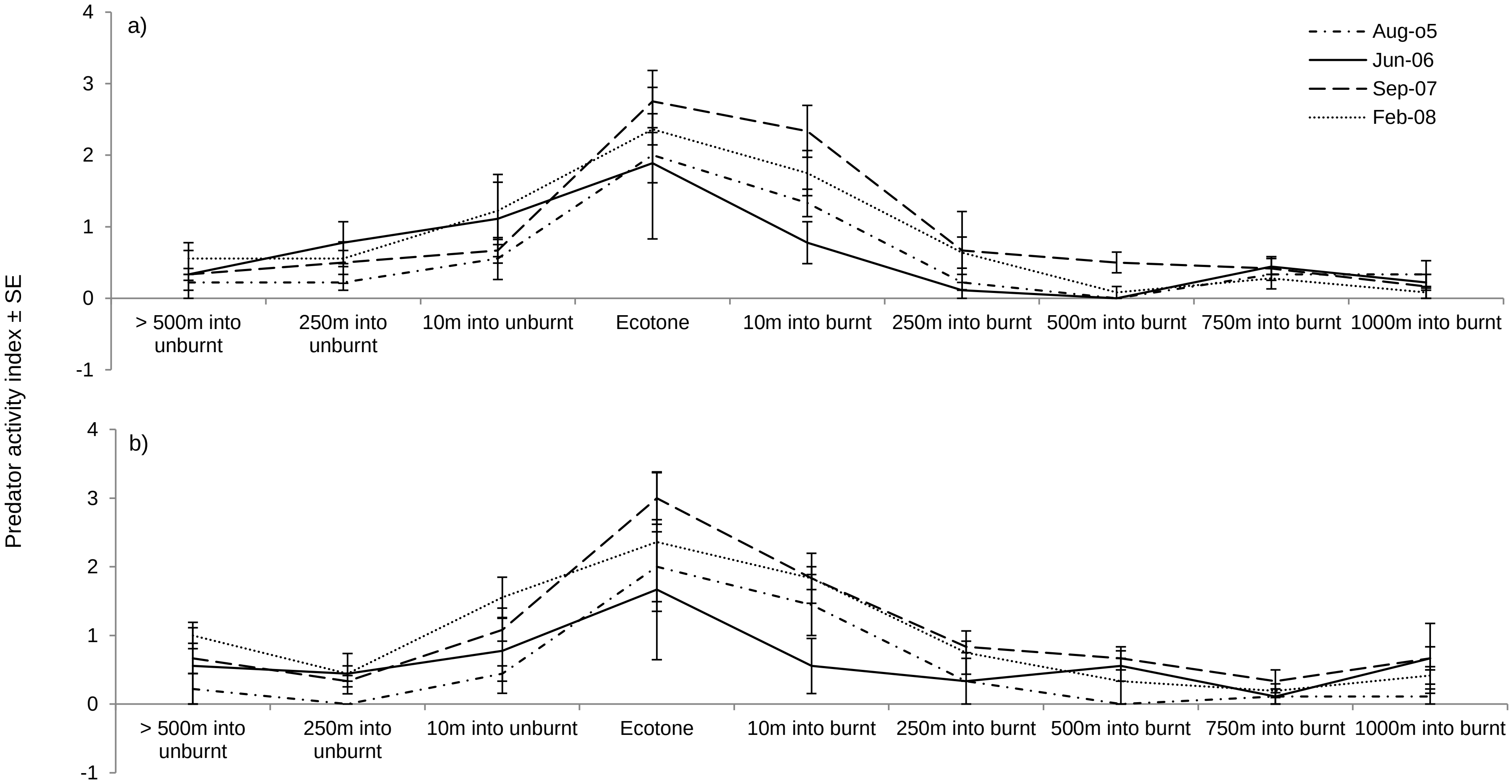

Figure 6.2 Predator activity index (± SE) for a) cats; and b) foxes across three sites and four years in the Simpson Desert, central Australia. The activity index was measured on a wildfire burn ecotone and at eight locations distant into the burnt and unburnt habitat.

6.3.3 Prediction 3

6.3.3.1 Cage treatment

Each of the three study mammals showed a significant foraging response to the Cage treatment in most sampling sessions (Figure 6.3). *Pseudomys hermannsburgensis* foraged to a lower GUD in the unburnt habitat when compared with the burnt habitat in the February ($F_{(1,85)}$ = 47.186, $P < 0.001$), April ($F_{(1,85)}$ = 17.629, $P < 0.001$) and June ($F_{(1,85)}$ = 43.527, $P < 0.001$) sampling sessions and under the predator exclusion cages when compared with the cage control and open control treatments also in February ($F_{(2,85)}$ = 9.390, $P = 0.001$), April ($F_{(2,47)}$ =9.805, $P < 0.001$) and June ($F_{(2,38)}$ = 9.844, $P < 0.001$). The significant interaction term Fire*Cage in February ($F_{(2,85)}$ = 16.145, $P < 0.001$), April ($F_{(2,47)}$ = 6.685, $P = 0.003$) and June ($F_{(2,38)}$ = 10.766, $P < 0.001$) indicates that *P. hermannsburgensis* responded differentially to the cage treatment between fire treatments in each sampling session. While GUDs were uniformly low across all three cage treatments in the unburnt habitat, GUDs were only significantly lower under the predator exclusion cages in the burnt habitat (Appendix 6.4).

Notomys alexis foraged to a lower GUD in the unburnt habitat when compared with the burnt habitat in the February ($F_{(1,28)}$ = 6.512, $P < 0.001$), April ($F_{(1,35)}$ = 10.719, $P = 0.002$) and June ($F_{(1,37)}$ = 16.141, $P < 0.001$) sampling sessions and under the predator exclusion cages when compared with the cage control and open control treatments in the February ($F_{(2,28)}$ = 2.925, $P = 0.007$) sampling session. There was a significant Fire*Cage interaction in the February ($F_{(2,28)}$ = 9.809, $P = 0.001$) and June ($F_{(2,37)}$ = 3.497, $P = 0.041$) sampling sessions (Appendix 6.4).

Sminthopsis hirtipes also foraged to significantly lower GUDs in the unburnt habitat in the February ($F_{(1,60)}$ = 34.807, $P < 0.001$), April ($F_{(1,14)}$ = 25.394, $P < 0.001$) and June ($F_{(1,22)}$ = 12.981, $P = 0.002$) sampling sessions and under the predator exclusion cages in the February ($F_{(2,60)}$ = 16.076, $P < 0.001$) and April ($F_{(2,14)}$ = 14.684, $P < 0.001$) sampling sessions. The interaction term Fire*Cage was significant in the February sampling session ($F_{(2,60)}$ = 9.382, $P < 0.001$; Appendix 6.4).

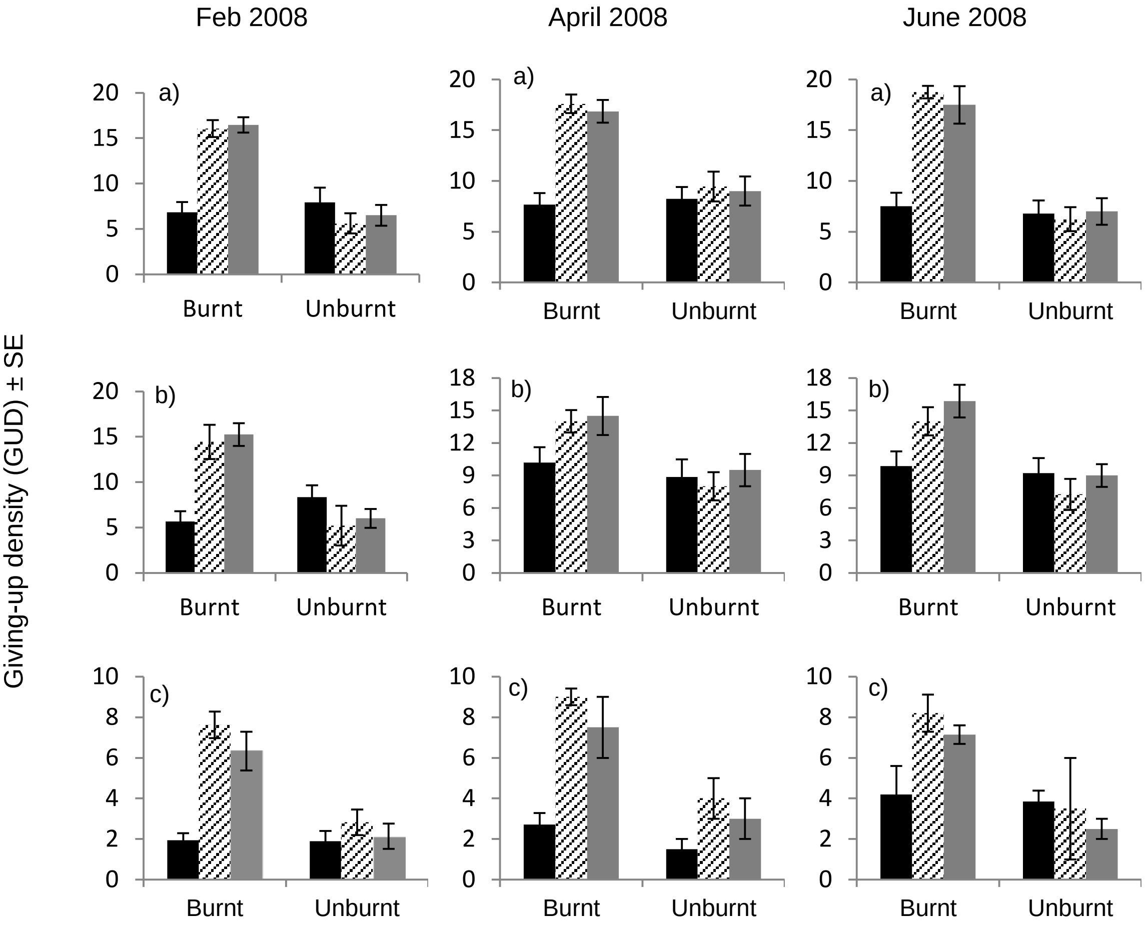

Figure 6.3 Giving-up densities (means ± SE) of a) *Pseudomys hermannsburgensis*; b) *Notomys alexis*; and c) *Sminthopsis hirtipes* under three predator manipulation treatments and sampling sessions in burnt and unburnt habitat in the Simpson Desert, central Australia. The three treatments are a predator exclusion cage (black), cage control (stippled) and open control (grey).

6.1.1.1 *Tunnel treatment*

Pseudomys hermannsburgensis foraged to significantly lower GUDs under the predator exclusion tunnels when compared with the tunnel control and open control treatments ($F_{2,44)}$ = 8.084, P 0.002; Figure 6.4a; Appendix 6.5) and foraged to higher GUD with increasing distance from the unburnt habitat ($F_{27,44)}$ = 2.808, P 0.001). Pairwise comparisons indicated that food patches were foraged to significantly lower GUDS under the Exclusion tunnels when compared with the Tunnel Control treatment and the Open treatment (Appendix 6.6).

Notomys alexis did not show the predicted foraging responses to the tunnel treatment ($F_{2,43)}$ = 52.308, *P* = 0.118) or to patch distance from the ecotone ($F_{27,43)}$ = 1.455, *P* = 0.133; Figure 6.4b; Appendix 6.5).

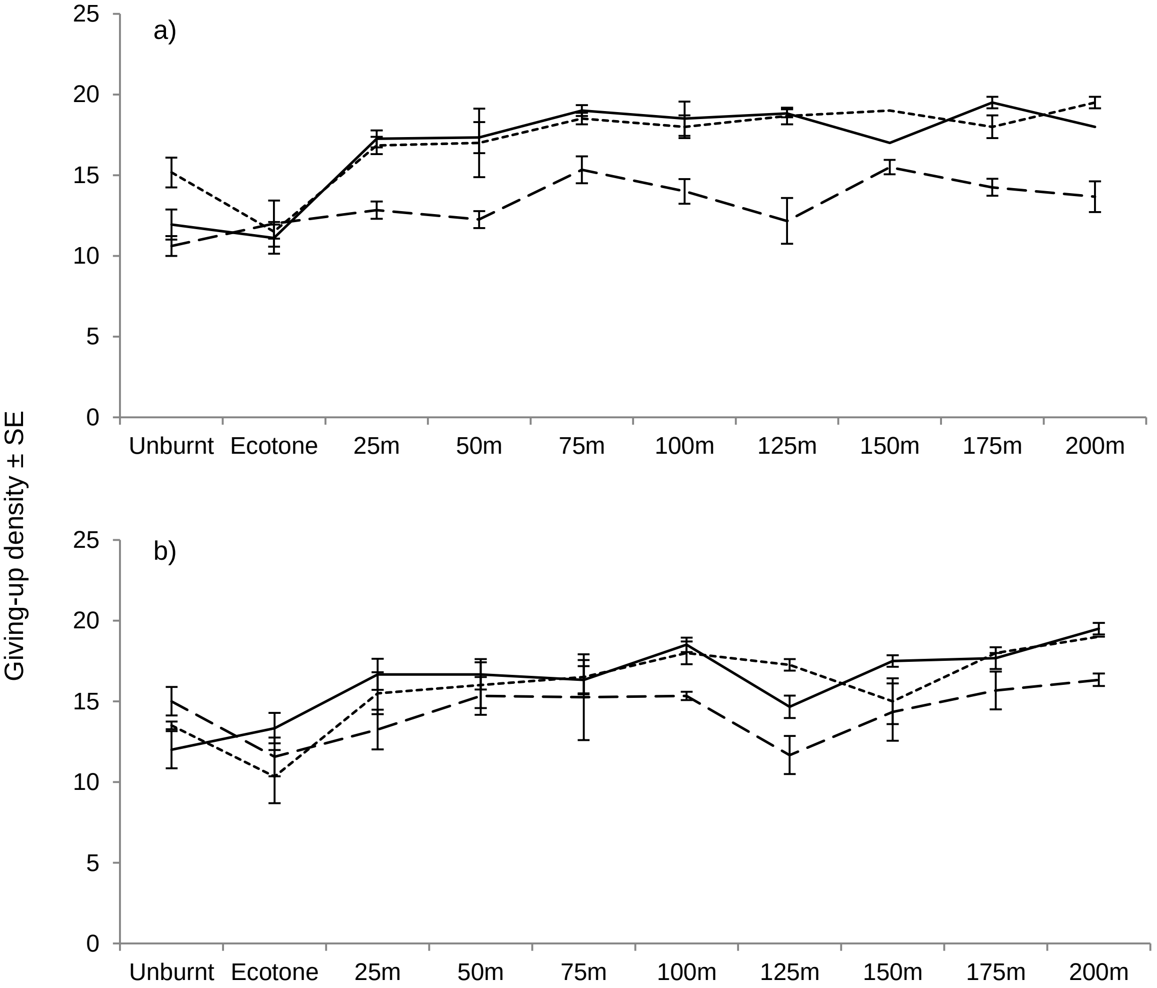

Figure 6.4 Giving-up densities (means ± SE) of a) *Pseudomys hermannsburgensis*; and b) *Notomys alexis* under three predator manipulation tunnel treatments and at varying distances from a wildfire ecotone in the Simpson Desert, central Australia. The three treatments were a predator exclusion tunnel (dashed line), tunnel control (dashed dots) and open control (black line). The tunnels were positioned in 225m transects running perpendicular to a wildfire burn ecotone and the food patches were located at 25m intervals along each tunnel. Apart from the Unburnt and Ecotone patches, all food patches were located in the burnt habitat.

6.4 DISCUSSION

Our study is the first to experimentally test the role that predation risk plays in the recovery of mammal populations in burnt desert habitat. It provides strong support for our predictions that small mammals in recently burnt grassland in arid Australia perceive a high risk of predation from foxes and cats and adjust their foraging behavior accordingly. Our study also indicates that the two species of introduced terrestrial predators actively exploit recently burnt habitats where their chances of hunting success presumably are highest.

6.4.1 Prediction 1

In Prediction 1 we proposed that predator activity would be focussed along burn ecotones. The results support this prediction as the activity of both cats and foxes was highest on the ecotone transect and on transects 10 m either side in most sampling years (Figure 6.2a and Figure 6.2b). Our prediction was based on a wealth of research indicating that foxes and cats are highly efficient hunters in arid environments (e.g. Risbey et al. 2000, Read and Bowen 2001, Kinnear et al. 2002, Pavey et al. 2008, Read and Cunningham 2010, Moseby et al. 2011, Kutt 2012) and that they additionally exploit the increased prey accessibility provided by newly-open and simplified burnt environments (Letnic et al. 2005, Kutt and Woinarski 2007, Legge et al. 2011, Andersen et al. 2012). Focussing activity on burn ecotones likely increases the opportunity for these predators to improve their hunting success by providing camouflage in the unburnt habitat combined with a short distance for movement into optimal hunting areas. Cats and foxes were also likely attracted to the structural boundary or “trail” provided by the fire ecotone, as these predators are known to preferentially follow landscape structures such as roads, dune tops and ridges (Mahon et al. 1998, Moseby et al. 2009b) .

The efficiency of cats and foxes as predators of small mammals in arid environments may be assisted by the paucity of larger native or introduced predators that could exert any meso-predator control. The only predator in the study region able to exert suppression over cat and fox populations is the dingo, but this species was not present in high numbers throughout the study (unpublished data). Recent evidence suggests that, when present in sufficient numbers, dingoes facilitate increases in the abundance and diversity of native small mammals due to their lethal or sub-lethal suppressive effects on foxes (Johnson et al. 2007, Letnic et al. 2009b, Letnic and Dworjanyn 2011). Although the effects of dingo presence on cats, and in turn on small mammals, is less clear (Letnic et al. 2009a), recent evidence suggests that dingoes may exert strong suppressive effects on these mesopredators also (Brook et al. 2012, Kennedy et al. 2012).

The patterns of activity of cats and foxes varied to a small degree between years (Figure 6.2a and 6.2b). The observed variation showed a time-lagged response to rainfall, in accordance with previous research indicating that these predators show density increases in response to rainfall-driven increases in prey abundance (Read and Bowen 2001, Letnic et al. 2005, Letnic and Dickman 2010). In our study for example, predator numbers were lowest in the June 2006 sampling period, which occurred during a drought period, compared with the September 2007 period which was preceded by a heavy rainfall event. The low abundance in 2006 is most likely responsible for the lack of significant results in this year.

6.4.2 Prediction 2

Our second prediction was based on two separate bodies of research. In the first instance, small mammals generally retreat to unburnt habitat after wildfire in hummock grasslands, especially before the burnt habitat has regenerated sufficiently to provide cover and foraging opportunities (Letnic et al. 2005, Pastro et al. 2011). In times of severe drought, habitat burnt in a wildfire can remain open with sparse coverage for several years and, under these circumstances, unburnt habitat affords opportunities for shelter and foraging that may not be available in open, recently burnt land (Pastro et al. 2011). Secondly, small mammals in the study region often associate more closely with dense spinifex habitats after fire when predators are common (Letnic et al. 2005) compared with periods of low predator abundance when many species exhibit few strong habitat preferences (Haythornthwaite and Dickman 2000, Letnic and Dickman 2005).

As small mammals were trapped in low numbers in burnt and unburnt habitats in our study, it is possible that their populations had been depressed generally by the activity of cats and foxes. If present in sufficient numbers, these predators are able to suppress small mammal activity and recovery in burnt habitats (Letnic et al. 2005, Pavey et al. 2008, Moseby et al. 2009a). Extreme levels of predation pressure after periods of high primary productivity can even reverse the usually bottom-up (food limited) trophic pathways to create transitory periods when top-down, predator-controlled prey dynamics prevail (Letnic et al. 2005, Letnic et al. 2011). The rarity of dingoes in our study area may have also contributed to the muted number of small mammals owing to mesopredator release (Letnic et al. 2009a, Letnic et al. 2009b).

6.4.3 Prediction 3

Previous research has indicated that small mammals retreat to unburnt refuge habitat after wildfire in arid hummock grasslands, and that they generally do not recolonize burnt areas until the vegetation starts to recover (Letnic et al. 2005, Pastro et al. 2011). The exploitation of burnt habitats by predators, particularly cats and foxes (e.g. Letnic et al. 2005, Kutt and Woinarski 2007, Legge et al. 2011, Andersen et al. 2012), has often been proposed as a key reason behind animal declines and slow population recovery in burnt areas; however, these ideas are for the most part not yet supported by experimental evidence. This provided the basis for Prediction 3, which stated that if animal declines in burnt areas were due to increased predation risk as we suggest, then small mammal activity would increase in burnt areas if we experimentally reduced their risk of predation.

The results from both our cage and tunnel experiments support this prediction, as animals consistently foraged to lower GUDs under the protection provided by the predator exclusion treatment when compared with the control and open treatments. In the cage experiment, this response was stronger in the more exposed, burnt habitat when compared to relatively safer unburnt habitat, which provides strong support for our prediction.

The foraging responses of *N. alexis* were muted when compared with the other two study species in the cage experiment, and were not significant in the Tunnel experiment. This is likely due to the enhanced predator awareness of *N. alexis*. This species possesses large ears which allow animals to audibly detect predators from a greater distance (Watts and Aslin 1981) and bipedal motion which allows them to escape predators more quickly when compared with both the quadrupedal *P. hermannsburgensis* and *S. hirtipes*. These capabilities likely mean that *N. alexis* will forage for relatively longer even in an ‘unsafe’ foraging patch, trading off its ability to detect and escape predators with the rewards of foraging.

Our results accord with a growing body of research that indicates that small mammals throughout central Australia are at certain times subject to intense predation from cats and foxes (Pavey et al. 2008, Letnic and Dworjanyn 2011). During these times, cat and fox activity can suppress small mammal populations and prevent the reestablishment of populations in areas where they have declined (Risbey et al. 2000, Read and Cunningham 2010, Moseby et al.

2011). Similarly strong effects of predation on small mammal survival have also been observed elsewhere, such as on snowshoe hares (*Lepus americanus*) in North American boreal forests (Krebs et al. 1995) and on Arctic ground squirrels (*Spermophilus parryii plesius*) in southwestern Yukon (Hubbs and Boonstra 1997).

Salo et al. (2010) proposed that the results of predator manipulation experiments depend largely on the quality of the treatment. Given that our predator exclusion treatments excluded all of the target mammalian predators in addition to reptilian and avian predators, we are confident that the manipulation was effective in achieving our aim. We can also be confident that the heightened foraging responses we observed in the exclusion treatment food patches were not due to the addition of the supplementary food itself, as equal food patches were also supplied under the cage control and open control treatments.

6.4.4 Conclusion

Our study indicates that predation risk is a key factor driving animal declines in burnt hummock grasslands in central Australia and that high levels of predation by cats and foxes may be instrumental in delaying subsequent population recovery in these habitats if arid-dwelling small mammals are to be retained. Our study further suggests that cats and foxes actively exploit recently burnt habitats where their chances of hunting success are highest. Given the role that these predators are thought to have played in previous and current small mammal declines and extinctions (Johnson 2006, Woinarski et al. 2011), our study highlights the need for urgent predator control in recently burnt habitats. Our study additionally highlights the need for integrated fire management programs in which small scale burns are used to reduce the frequency of broadscale wildfire events (Bird et al. 2012). Wildfires are predicted to occur more frequently and at higher intensities in arid environments with the onset of climate change (Pitman et al. 2007), which provides an imperative to better understand post-fire species interactions.

CHAPTER 7

SYNTHESIS AND GENERAL CONCLUSIONS

After rainfall, the desert takes on the hues of a lush meadow (L. Pastro)

This thesis investigated the roles of rainfall and predation in determining animal responses to wildfire in the Simpson Desert, central Australia. Animals in this arid region, particularly small and medium-sized mammals, have undergone widespread declines and extinctions over the past century (Johnson 2006, McKenzie et al. 2007, Saunders et al. 2010). These losses have coincided with what appears to have been a sharp shift in the fire regime, from one dominated by many small scale burns to one dominated by infrequent yet intense and widespread wildfires (Burbidge and McKenzie 1989, McKenzie et al. 2007, Johnson and Isaac 2009, Woinarski et al. 2010). Previous work in the region has reported conflicting effects of fire on small mammals and lizards (e.g. Masters 1993, 1996, Letnic et al. 2004, Driscoll and Henderson 2008, Kelly et al. 2010, Nimmo et al. 2012a) and there have been few manipulative investigations to explore the likely reasons for observed post-fire responses.

My study began shortly after one of the largest wildfires in recent history swept across a broad swathe of the Simpson Desert. This included a large study region of some 7000 km^2, of which 2540 km^2 was burnt in the wildfire (Greenville et al. 2009). Several years of pre-fire records exist for the region and these have contributed a long-term perspective and breadth to my findings.

The broad objective of my study was to investigate the processes by which wildfires affect small mammal and lizard populations in the Australian arid zone. I aimed to use this information to suggest better management of future wildfire events in the region and to develop strategies to aid in the effective management of affected flora and fauna. I developed five specific aims to meet this broad objective.

These were as follows:

1. To investigate the effect of fire on vertebrate diversity at a global scale, and to identify the influence, if any, of fire type, taxon, habitat, and geographical location. This was to establish global patterns to provide the setting for my next, more localised studies;
2. To compare the effects of a wildfire and prescribed burns on plant, mammal and lizard diversity in the Simpson Desert. Although it is anecdotally accepted that wildfires affect animal populations more severely than prescribed burns, this was yet to be quantified at the time of study;
3. To explore the effects of the 2001/02 Simpson Desert wildfire on lizard populations, with specific reference to the influence of multi-scale processes including rainfall, vegetation structure, food availability and regional land use histories;

4. To experimentally determine how perceived and actual predation risk affects small mammal recovery in burnt habitats after the 2001/02 Simpson Desert wildfire; and
5. To synthesise the results from these studies to develop effective fire management strategies and recommendations for land managers in arid regions.

This study is the first of its kind as I addressed several areas that have not been previously investigated. To address Aim 1, I conducted a global meta-analysis of the effects of fire on vertebrate diversity. Building on the key finding of this analysis—that fire type is a primary factor influencing the effects of fire on biota—I next compared the short-term effects of prescribed burning and a coincident wildfire in a fire prone region of the Australian arid zone, the Simpson Desert (Aim 2). Conducting these two studies in close temporal succession eliminated the usual interactive effects of study location, study taxon, geographic variation and climate and presented a unique opportunity to directly compare the effects of these two fire types. To address Aim 3, I investigated the medium-term (5-years post-fire) effects of the 2001/02 wildfire on lizard populations, focussing specifically on the role of multi-scale processes such as rainfall and food availability in driving differential lizard responses to fire across broad spatial scales. To address Aim 4, I studied the medium-term (5-years post-fire) responses of small mammals to the 2001/02 wildfire and experimentally manipulated the risk of predation in burnt habitats to determine the role of this process in driving small mammal recovery in burnt areas. I also investigated cat and fox movements in fire-ecotonal habitat to understand further how they use this habitat type and how this may influence small mammal movement and survivorship.

In this final chapter (Aim 5), I begin by summarising the key results from each of my Chapters. I next discuss each of my main findings with reference to the aims of my study and interpret them alongside contemporaneous research and current theories of post-fire succession. I review current predictive models of post-fire succession in light of my results and propose a new model to describe the post-fire succession of lizards in the Australian arid zone. Lastly, I discuss the implications of my results for conservation and fire management practitioners and identify opportunities for further research.

7.1 SUMMARY OF KEY FINDINGS

Chapter 3 consisted of a global investigation of the effects of fire on vertebrate alpha and beta diversity, including the potential influence of fire type, study taxon, habitat, geographical location, study replication, study length and spatial scale. For alpha diversity, I found that across all studies, fire had no effect. Instead, the effect of fire depended on fire type, as prescribed burns increased alpha diversity and wildfires had no effect. The variance associated with the prescribed burn result was large, indicating that much variation existed in fire responses when analysed at a global scale. Geographical location was also an important predictor of fire effects on alpha diversity, as fires significantly increased alpha diversity in the northern hemisphere and had a generally negative effect in the southern hemisphere. Taxon and habitat both emerged as poor predictors of fire effects on alpha diversity and species-specific responses appeared to be nested within spatially-determined groups. Notably, wildfires were not identified as having either a positive or negative effect on alpha diversity. For beta diversity, I found that effects were determined only by fire type, with wildfires increasing beta diversity compared with prescribed burns across all studies and within the groupings of lizards, birds, latitude and some habitats.

In Chapter 4 I investigated the influence of fire type and taxon on alpha and beta diversity at a more localised scale. Here, I focused on a single model study system in the Simpson Desert in arid central Australia. Using the predictions of the Patch Mosaic Burn Hypothesis (PMBH) and the Intermediate Disturbance Hypothesis (IDH), I predicted that small scale, prescribed burns would increase the alpha diversity of burnt patches as these patches are readily accessible from nearby refuge habitat. For this reason I also predicted that the beta diversity between burnt and unburnt patches would be low. Conversely, I predicted that a wildfire would decrease alpha diversity in burnt patches as these patches are typically large, intensely burnt and far from refuge habitat. I predicted that beta diversity between the burnt and unburnt habitat would be high after a wildfire due to the differing assemblages expected to inhabit the burnt and unburnt areas. The results provided moderate support for my predictions, highlighting that, as with the meta-analysis, prescribed burns and wildfires have very different impacts on alpha and beta diversity, and that prescribed burns do not always benefit alpha diversity as predicted by the PMBH and IDH. The study indicated further that the effects of fire on alpha and beta diversity are taxon-specific, as plants, small mammals and lizards each responded uniquely to the two fire events.

While the prescribed burns in Chapter 4 did not have the expected effects on alpha diversity, the wildfire also yielded some unexpected results. In particular, the wildfire did not have the predicted effects on either the alpha or beta diversity of lizards. In Chapter 5 I investigated the processes that may have caused these unexpected effects. A rainfall gradient existed within the area affected by the wildfire and I predicted that this would influence lizard responses to the fire by encouraging post-fire succession to proceed more rapidly in high-rainfall regions, as enabled by more rapid vegetation recovery. I also measured structural vegetation attributes, food availability, and rainfall immediately prior to sampling. I found that the vegetation was undergoing the expected post-fire succession but that lizard communities in the burnt, ecotone and unburnt habitats were not aligned to these vegetation attributes (as predicted by the habitat accommodation model of succession) and nor were they aligned with the rainfall gradient. Instead, lizard communities were grouped by the region in which they occurred and lizard abundance was correlated with food availability, which also varied regionally. The observed patterns also likely reflected the strength of biotic interactions with mammalian predators and the effects of previous grazing regimes, as the abundance of mammalian predators (dasyurids and rodents) was highest in the region with the lowest abundance of lizards, and that region had also experienced the highest historical grazing pressure.

In Chapter 4 I also observed that the abundance and alpha diversity of small mammals decreased dramatically following the wildfire and remained low over the course of the study. An increase in predation in burnt areas has previously been suggested as a potential reason for small mammal declines in burnt habitats (Kutt and Woinarski 2007, Firth et al. 2010, Woinarski et al. 2010, Andersen et al. 2012); however, this suggestion had yet to be experimentally tested. In Chapter 6 I experimentally tested this hypothesis by investigating how prey behaviour changes in the post-fire environment under different levels of predation risk. I used native small mammals in the central Australian arid zone as my model prey species. In this novel study, I found that both foxes (*Vulpes vulpes*) and cats (*Felis catus*) selectively exploit burn ecotonal habitat, which presumably provides them with shelter in the unburnt habitat close to the optimal foraging conditions provided by the open burnt land. Small mammals appeared to be sensitive to this increased risk of predation in burnt habitats, as when their predation risk was experimentally reduced in these areas, they ventured farther from refuge habitat and spent longer foraging there. They showed no response to the same manipulation in the unburnt habitat, in which ample shelter was already provided by mature spinifex hummocks.

7.2 DISCUSSION AND SYNTHESIS OF KEY FINDINGS

The implications of my research can be categorised into two key discussion areas: 1) a review of the patch mosaic burn hypothesis for arid environments; and 2) the importance of interactions between fire and other processes in arid Australia. I next discuss the implications of my research in the context of the broader literature in each of these topic areas.

7.2.1 Implications for the Patch Mosaic Burn Hypothesis

The first key finding of my research is with regards to the effects of prescribed burning and the effectiveness of the patch mosaic burn hypothesis (PMBH; Parr and Brockett 1999) as a means to benefit biodiversity. My research provides little evidence that "pyrodiversity begets biodiversity" as suggested by the PMBH. Instead, my results concur with a growing body of research that emphasises the importance of factors that interact with a spatial vegetation mosaic to influence animal responses to fire (e.g. Short and Turner 1994, Parr and Andersen 2006, Lindenmayer et al. 2008, Driscoll et al. 2010, Kelly et al. 2012, Nimmo et al. 2012a).

There has long been no formal definition of fire frequency or intensity that should be applied to patch burning to benefit biodiversity (Bradstock et al. 2005, Parr and Andersen 2006, Clarke 2008, Driscoll et al. 2010). This omission becomes particularly important in fragmented or modified landscapes where habitat fragments tend to be smaller, and in ecosystems where other threatening processes exist (Driscoll et al. 2010). In these situations, the inappropriate use of small scale burns can potentially increase extinction risk by eliminating areas of key habitat or by causing changes in community structure (Fisher et al. 2009). This highlights the need to develop more prescriptive and targeted fire management programs.

As indicated in Chapters 3 and 4, many species groups and ecological communities do not exhibit generalised responses to a prescribed burn, either at a localised scale or across broad geographic regions. This has important implications for the PMBH as it is contrary to a fundamental tenet of the concept; that patch burning will increase diversity in any given affected ecological community. Although the meta-analysis indicated that prescribed burning increased alpha diversity at a global scale, the effect size was small and the variance associated with the effect was large. Thus although the overall effect was positive, there was substantial variation in the effect of prescribed burns within and between taxa, geographic locations and habitats. Species' fire responses could not be grouped further into habitat or taxonomic groupings, and the study highlighted instead the importance of geographical location in determining fire outcomes: prescribed burns in North America tended to have more positive effects compared with prescribed burns in Australia. These effects were in turn likely due to climatic and regionally-specific factors, including historic fire frequencies and levels of current fire suppression.

In arid Australia, patch burning began under Aboriginal land tenure and is purported to have benefitted biodiversity by providing habitat for multiple species in a suite of seral stages and by preventing the spread of wildfires (Letnic and Dickman 2005). In more recent times, prescribed fire in arid and semi-arid habitats has increased small mammal and reptile diversity in some instances (Masters 1993, 1996, Letnic 2003) but animal communities have been unaffected by small scale burns in others (Driscoll and Henderson 2008, Kelly et al. 2010). Chapter 4 indicated that even though taxon was a better predictor of prescribed burn effects in an arid Australian ecosystem than at a global scale, considerable variation still existed within and between taxonomic groups. In this ecosystem, prescribed burns increased the alpha diversity of plants and lizards but had no effect on small mammal alpha diversity. A similar result has been found in semi-arid mallee country in southern Australia where it was found that a diversity of fire age-classes, as promoted by the PMBH, had no effect on small mammal diversity (Kelly et al. 2012).

When the effects of fire on small mammals in arid grasslands were investigated further in Chapter 4, inconsistent responses within species groups were identified. After the wildfire, for example, *Ningaui ridei* preferred the burned habitat in the immediate post-burn period but preferred the unburned habitat 9-12 months later. Other small mammal species have been found to exhibit similarly unpredictable or inconclusive fire responses in other parts of arid and semi-arid Australia (Letnic and Dickman 2010, Kelly et al. 2011), which further supports my findings.

Similarly for lizards, while prescribed burns did increase the alpha diversity of lizards in Chapter 4, their post-fire assemblage composition was not as expected as species that require shade for thermoregulation were found to inhabit recently burnt habitats. Studies conducted elsewhere in semi-arid southern Australia have returned similar results, reporting that the composition of post-fire lizard assemblages diverged significantly from predictions based on life history and habitat-use traits (Driscoll and Henderson 2008, Nimmo et al. 2012a). In another recent study in a semiarid region in south-eastern Australia, no lizard species were associated with a diversity of vegetation ages within a landscape. Lizard occurrence was instead negatively related with both recently burnt (≤ 10 years post fire) and long unburnt (≥

30 years post fire) vegetation (Nimmo et al. 2012b). This absence of a generalised fire response, or even a response organised by taxon, makes it difficult to predict the effect of a prescribed burn on an animal assemblage and to determine *a priori* that a prescribed burn will benefit community diversity in arid and semi-arid Australia.

In any given community, it can be expected that a fire will promote the existence of fire tolerant species at the expense of other, more fire sensitive species. The make-up of these response types in an ecological community will depend on the habitat use traits of species inhabiting that community. Friend (1993) found that the fire responses of small mammals depend on their shelter, food and breeding requirements. For example, species requiring abundant shelter and with a restricted life history would likely be negatively impacted by fire, compared with more generalist species that had flexible habitat requirements and a generalist diet. For reptiles, species that tolerate open spaces and higher temperatures are predicted to recolonise sooner after fire than species which require a deep litter layer or spinifex cover, although several of these habitat use associations may interact at once to produce the observed responses to fire (Nimmo et al. 2012a). Fire metrics such as fire severity, extent, frequency and season and external factors such as rainfall or drought will also affect the outcome of a fire on species diversity and assemblage composition. The absence of species-level information in the PMBH means that these subtle fire effects, and the potential post-fire decline of fire-sensitive species, may not be identified. The slight increase in alpha diversity evident after prescribed burns in the meta-analysis may well have occurred at the extent of fire-sensitive species,; however, a diversity-based approach as encouraged by the PMBH does not provide resolution on the responses of individual species to fire and does not further our understanding of the mechanisms behind observed responses.

7.2.2 Influence of interacting factors

As discussed throughout this thesis, a range of biotic and abiotic factors can interact with fire to produce unexpected post-fire successional trajectories and animal assemblages. Rainfall variability, grazing, predation and interspecific competition can all influence species responses to fire, either by acting on the regenerating vegetation or via direct effects on the recovering animal communities (James 2003, Driscoll 2004, Kutt and Woinarski 2007, Letnic and Dickman 2010, Legge et al. 2011). The effects of each of these processes and interactions between them typically vary between regions to generate regionally-specific fire responses and patterns of recolonisation. In some situations, the effects of fire are overshadowed by these external factors so that fire is no longer the primary factor shaping animal and plant assemblages (e.g. Trainor and Woinarski 1994, Pausas and Bradstock 2007, Driscoll and Henderson 2008).

As indicated in Chapter 5, the causes of spatial variation in fire responses are not always easy to identify. Where a prominent rainfall or land-use gradient may appear to be the logical cause of differences in species responses to fire, the actual causes may be more subtle. Lizards, for example, can show contemporary assemblages that reflect previous land uses such as grazing ("ghosts of habitat past"; Knick and Rotenberry 2000, Frank 2010) in addition to current processes such as variable predation pressure (Haythornthwaite and Dickman 2006a), changing soil composition and texture (Driscoll 2004), and climate and interspecific interactions (Daly et al. 2008, Driscoll and Henderson 2008, Nimmo et al. 2012a, Pianka and Goodyear 2012, Read et al. 2012). Given this complex interplay, the identity of key factors influencing lizard communities can be difficult to specify. For example, in a semi-arid system in southern Australia, Driscoll and Henderson (2008) concluded that regional processes were more important than fire history in determining post-fire lizard assemblages; however, the identity of these processes remains as yet undiscovered.

I next discuss two interacting factors that have been highlighted by my research as key influencers of fire effects on small mammals and lizards in the Australian arid zone: rainfall and predation.

7.2.2.1 Rainfall

Rainfall is a key driver of productivity in rainfall-limited arid habitats (Noy-Meir 1973). Being highly variable across space and time, heavy rainfall events stimulate widespread germination and growth of ephemeral, annual and perennial plant species, including green plant material, fruits and seeds (Orians and Milewski 2007, Letnic and Dickman 2010, Morton et al. 2011). These rainfall-driven bursts of primary productivity then drive populations of invertebrate and vertebrate species that depend on these increases in food availability.

In the post-fire environment, rainfall can stimulate rapid animal recolonisation via the pulsed germination and growth of vegetation and hence increase in the availability of food resources. In Chapter 4, for example, the observed response of small mammals to prescribed burning was likely influenced by heavy rainfall that fell both before and after the burns were conducted. This rainfall encouraged rapid recovery of vegetation which facilitated re-colonisation of burnt areas by small mammals more quickly than expected. This was in contrast to the wildfire, which was associated with very little post-fire rainfall, and experienced slow small mammal community recovery as a result. Rainfall is similarly a key driver of small mammal community dynamics in the southern mallee semi-arid zone, where it supersedes fire history as a key influencer of assemblage dynamics (Kelly et al. 2012).

It does not follow that the effect of post-fire rainfall (or lack there-of) on small mammal communities in the Australian arid zone is easy to predict, however, as the effect of rainfall differs between species groups. Rodents, for example, usually show strong behavioural and population level responses to rainfall (Predavec 1994, Dickman et al. 1995, Dickman et al. 1999b, Pavey et al. 2008, Greenville et al. 2012). Breeding is initiated within days of large rainfall events, allowing sharp population increases 3-10 months later (Dickman et al. 1999b, Letnic et al. 2011). Other species groups show weaker associations with primary productivity and display varying responses to rainfall (Southgate and Masters 1996, Letnic and Dickman 2005, Kelly et al. 2011). Small insectivorous dasyurid marsupials, for example, have flexible habitat requirements and relatively fixed breeding cycles which in many cases do not relate to various vegetative seral stages. This is shown in the disparate responses of *Ningaui ridei* to the wildfire in Chapter 4. These species may show no response to rainfall or may even decline in numbers following heavy rain events (Bos and Carthew 2001, Dickman et al. 2001, Haythornthwaite and Dickman 2006a, Greenville et al. 2012). The response of small dasyurids to heavy rainfall is likely limited further by life-history constraints (a single breeding event each year) and vegetative cover rather than rainfall (Dickman et al. 2001). In contrast, larger carnivorous marsupials such as the mulgaras (*Dasycercus blythii* and *D. cristicauda*) often undergo dramatic population increases after rainfall as their populations track increases in the numbers of their primary prey; rodents (Chen et al. 1998, Masters 1998, Letnic et al. 2005, Pavey et al. 2011). Thus heavy pre- or post-fire rainfall can have unexpected effects on small mammal assemblage dynamics in post-fire environments, potentially benefitting some species or groups of species at the expense of others.

For lizards, rainfall can alter the expected post-fire assemblage composition by providing conditions to suit late successional species earlier than anticipated. For example, the post-fire assemblage composition and successional trajectory of lizards after prescribed burns in Chapter 4 was not as predicted according to known habitat use traits, as mid –to-late successional species and spinifex associated species such as *Ctenophorus isolepis* and *Ctenotus pantherinus* were present in recently burnt patches. This mostly likely reflected the heavy rainfall that fell before and after these burns, and the additional shelter provided by the rapid regrowth of grasses and herbs. This effect was also described by Lindenmayer et al. (2008) who concluded that the rapid post-fire recovery of some components of vegetation, as stimulated by heavy rainfall, precluded the recovery of any distinct successional groups of lizards. These effects may be further compounded when species are associated with more than one habitat attribute (Nimmo et al. 2012a) and new interspecific interactions may be introduced in the post-fire environment, when species with a range of habitat associations are provided for. This could potentially be to the detriment of traditionally 'early' successional species which may be out-competed before they have had a chance to recolonise, reproduce and establish viable populations. In contrast, the absence of any substantial post-fire rainfall may have the opposite effect. Post-fire recolonisation by habitat specialists and species with fixed life histories may be delayed, with lizard assemblages dominated by early successional species and those with more flexible life histories.

7.2.2.2 Predation

Predation is a key process affecting vertebrate population and assemblage dynamics in arid Australia, particularly with regards to arid zone mammal species (Newsome et al. 1989, Read 1997, Risbey et al. 2000, Kinnear et al. 2002, Letnic et al. 2009a, Letnic et al. 2009b, Moseby et al. 2009a, Read and Cunningham 2010). Native small mammals in the region are affected more negatively by introduced predators such as foxes (*Vulpes vulpes*) and cats (*Felis catus*) than are equivalent prey in other parts of the world (Salo et al. 2007, Salo et al. 2010), and these predators are highly efficient hunters of both small mammals and lizards in arid environments (e.g. Risbey et al. 2000, Read and Bowen 2001, Kinnear et al. 2002, Pavey et al. 2008, Read and Cunningham 2010, Moseby et al. 2011).

The effects of predation may be magnified further in denuded post-fire habitats, providing an imperative to understand the mechanisms behind these interactions (Russell et al. 2003, Körtner et al. 2007, Wilgers and Horne 2007, Morris et al. 2011b). In Australia, a growing body of research indicates that both cats and foxes exploit the increased accessibility of prey that is provided by newly-open and simplified burnt environments (Letnic et al. 2005, Kutt and Woinarski 2007, Legge et al. 2011, Andersen et al. 2012, Fisher et al. 2013). In these situations, the effects of predation may interact with the need for prey to find food in the newly burnt habitat (Letnic et al. 2004, Letnic and Dickman 2010).

Similar processes exist in other ecosystems. For example, survival of *Peromyscus* mice is higher in burnt habitats when predators are excluded (Morris et al. 2011b). Artificial snakes in tallgrass prairie are subject to higher predation in recently burned habitats (Wilgers and Horne 2007), as are mulgaras (*Dasycercus blythi*) in arid Australian grasslands (Körtner et al. 2007). In eastern Australia, predation by lace monitors (*Varanus varius*) and diamond pythons (*Morelia spilota spilota*) can prevent the recovery of ringtail possum (*Pseudocheirus peregrinus*) populations in burnt habitats (Russell et al. 2003).

My research provides the first experimental evidence that cats and foxes purposefully target burnt and ecotonal habitat after wildfires in the Australian arid zone, and that native small mammals are sensitive to the subsequently increased risk of predation. As demonstrated in Chapter 6, both cats and foxes preferentially move on burn ecotones, where their opportunity for predation success is presumably higher due to the camouflage provided by the nearby unburnt habitat and the open foraging ground located nearby in the burnt habitat. Small mammals in the region appear sensitive to this increased risk of predation, venturing further into burnt areas and foraging for longer when additional protection from predators was provided. Given the abundance of reptiles in the study area (Chapters 4 and 5) and propensity of cats and foxes to prey on them (Paltridge 2002, Pavey et al. 2008, Kutt 2011) it is likely that predators residing in burnt and ecotonal habitat also prey on reptiles.

In post-fire habitats that carry high numbers of predators, the usual food-limited, bottom-up trophic pathways can switch to transitory, top-down pathways as prey-switching predators suppress prey populations in the open post-fire environment (Letnic et al. 2005, Letnic et al. 2011). These effects may be more pronounced when fire is followed by heavy rainfall, as rainfall-driven pulses of primary productivity stimulate increases in prey populations, particularly rodents, which are followed by time-lagged increases in predator populations (Meserve et al. 1999, Read and Bowen 2001, Pavey et al. 2008, Letnic and Dickman 2010). Thus, when post-fire prey numbers boom following rainfall, the effects of introduced predators are likely to be more severe. Under these circumstances, introduced predators certainly have the potential not only to suppress small mammal populations but to cause localised extinctions in burnt habitats where mammal populations may otherwise have recovered. The ability of cats and foxes to suppress prey populations was demonstrated recently in semiarid south-eastern Australia, where predation by cats and foxes caused ten reintroduction attempts of native small mammals to fail (Moseby et al. 2011). It follows that the effectiveness of these predators would be even more magnified in denuded, burnt environments.

The role that predation plays in determining post-fire species distribution is not necessarily limited to introduced predators. In Chapter 5, the region with the most rainfall (Kunnamuka Swamp) supported the lowest numbers of lizards and the highest numbers of native dasyurid predators. While more research is required to confirm the mechanisms responsible for these distributions, it is possible that high numbers of dasyurid predators were supported by the high regional primary productivity, and that these abundant predators regulated the number of lizards. Regulation of lizard populations by native predators has been shown to occur in semiarid Australia shrublands, where the native sand goanna (*Varanus gouldii*) controls populations of small skinks (Olsson et al. 2005).

7.3 PREDICTIVE MODELS

7.3.1 Mammals

Small mammal recovery after fire was first modelled using the habitat accommodation model of succession (Fox 1982). This model proposes that species will enter the post-fire succession when the regenerating vegetation reaches the appropriate seral stage and leave when the habitat or species interactions are no longer optimal. Thus although time since the fire is often used as a surrogate for vegetation type, it is actually the temporal change in vegetation structure that determines species responses to fire (Monamy and Fox 2000, Fox et al. 2003).

The model has been applied to arid zone small mammals with limited predictive success, as many small mammals in the region correlate poorly with vegetation structure (Southgate and Masters 1996, Letnic and Dickman 2005, Kelly et al. 2011). Instead, a range of processes such as predation, competition and climatic variation have been identified as critical in determining the distribution and abundance of arid zone small mammals (e.g. Kelly et al. 2012). These factors interact with fire-generated spatial patterns to determine the distribution of species and the composition of assemblages in arid regions.

To address this, Letnic et al. (2004) developed a state-and-transition model (refined further by Letnic and Dickman 2010) to describe arid zone small mammal dynamics. The model incorporated a range of external biotic and abiotic factors such as predation, grazing and rainfall in addition to fire-stimulated changes in vegetation structure. The results of my research support the predictions of the state-and-transition model.

7.3.2 Lizards

The habitat accommodation model of succession was first adapted for arid and semi-arid regions by Caughley (1985) who identified three distinct responses by reptiles to fire based on habitat use associations. They were: i) that burrowing species would be most common in recently burned sites; ii) that species associated with spinifex would be most abundant after six years (when spinifex has regenerated); and iii) that litter-dwelling species would peak in abundance after 25 years, when the leaf litter layer has recovered. To further increase post-fire predictive accuracy, some researchers have matched the habitat accommodation model with species traits related to vegetation (such as thermoregulatory or dietary requirements) to form 'habitat use' models (Driscoll and Henderson 2008, Lindenmayer et al. 2008, Nimmo et al. 2012a). In these models, species that use similar vegetation structural attributes, such as spinifex cover, are grouped together and a discrete set of fire responses is assumed. For example, species with extreme heat tolerance, such as *Ctenophorus nuchalis*, nocturnal burrowing geckos such as *Rhynchoedura ornata* and *Diplodactylus stenodactylus* and subterranean species such as *Ramphotyphlops endoterus* are expected to be early colonisers of open, burnt habitats. These species will be followed by species that require spinifex for foraging, thermoregulation and protection from predators, such as many *Ctenotus* spp. and *Ctenophorus isolepis*. Many of these species also have more varying dietary preferences, such as *C. isolepis*. As the vegetation recovers further, litter dwelling species such as *Menetia greyii* and *Delma* spp*.,* and arboreal species such as *Gehyra purpurascens* and *Strophurus ciliaris,* would be expected to be present (Fyfe 1980, Masters 1996, Letnic et al. 2004, Wilson and Swan 2008).

However, these models have been applied with limited success. A habitat use model correctly predicted the post-fire responses of just three of 16 common reptile species in semi-arid mallee woodlands (Driscoll and Henderson 2008) and accurately predicted three of 34 proposed reptile response curves in a second mallee study (Nimmo et al. 2012a). A study in forest habitat in eastern Australia produced similarly sparse evidence to suggest that reptile responses to fire were predictable from life history attributes alone (Lindenmayer et al. 2008).

My research has highlighted that the responses of lizards to fire depend on a range of biotic and abiotic processes and interactions, in addition to life history attributes. Thus while spinifex is a keystone structure for lizards in arid Australia, other biotic and abiotic factors may additionally influence the observed distributions of lizards. In addition to this, lizards may associate with more than one habitat trait, so that a combination of traits, such as a flexible habitat association with both leaf litter and spinifex, drives observed species responses to fire (Nimmo et al. 2012a). In my research, lizard assemblages were influenced by rainfall in Chapter 4 and were structured according to region in Chapter 5, despite the structural organisation of vegetation according to fire history. Lizard abundances in Chapter 5 correlated with food availability which, for yet unknown reasons, did not correlate with rainfall. Predation may have also played a role as small mammalian predators were highest at the site with least lizards; this is a result that clearly warrants further research.

My results align with a growing body of research that suggests reptiles may show stronger responses to processes other than fire and rainfall in arid and semi-arid Australia, and that introduce a strong spatial variation component into lizard responses. For example, Read et al. (2012) found that rainfall did not affect lizard abundance in arid Australia as expected. Instead, local scale processes such as vegetation conditions and inter-specific interactions were key influencing factors. Driscoll and Henderson (2008) also found that lizard responses to fire in arid Australia were structured by location rather than fire history, possibly also due to differences in vegetation, species ranges, climate and soil. Lindenmayer et al. (2008) found further that lizard assemblages were structured by processes other than fire. Nimmo et al. (2012a) hypothesized that climatic influences affected post-fire succession and were the likely cause for variation in species relationships with fire across their geographical ranges. Detailed information about species responses cannot be transferred readily between different regions.

Rarity may also confound attempts to model post-fire lizard assemblages from habitat associations alone. Lizard species in arid Australia typically survive in extremely low numbers across the landscape and reach peak abundances only when the necessary resources, such as food, allow them to do so (Pianka 1992). Thus detailed pre-fire knowledge of rare species would be required to accurately predict post-fire assemblages, and assemblages may vary both temporally and spatially depending on the patterns of abundance and rarity that exist at the time of a given fire. A given fire could also benefit a previously undetected species, which may emerge after fire as abundant. This may have contributed to the regionally distinct assemblages observed in Chapter 5, where region had a stronger influence than fire, rainfall or food in grouping lizard assemblages.

Differing detection probabilities can add substantial bias to the results of lizard fire experiments and need to be considered as part of any study. Animal responses to fire are typically measured using methods that depend on measures of animal activity (Schlesinger 2007, Yarnell et al. 2007, Ford et al. 2010); however, animal activity may differ between burnt and unburnt sites which potentially biases results (Driscoll et al. 2012). In a study of post-fire lizard assemblages in semiarid south-eastern Australia, for example, a litter specialist did not have the predicted low abundance after fire due to increased post-fire movement and non-linear recovery of a key habitat component (Driscoll et al. 2012). Species that are otherwise hard to detect may also be more easily detected in newly simplified burnt environments, which may further artificially inflate estimates of species numbers in these habitats (Hossack and Corn 2007). Although differing detection probabilities do not affect all studies (Melbourne 1999, Schlesinger 2007) the available evidence suggests that this is a factor that should be incorporated into post-fire lizard studies, including further work based on the results reported in this thesis.

7.3.3 A revised model for lizards

In response to the shortcomings of the habitat accommodation model of succession and habitat use models I propose the following modified state-and-transition model (*sensu* Westoby et al. 1989) to describe post-fire lizard succession in arid Australian environments. As discussed above, species traits play a key role in determining trajectories of change in lizard communities after fire, but several other biotic and abiotic factors are also important. State-and-transition models (STMs) incorporate this interplay of factors by recognising the existence of multiple “states” of assemblage composition that develop in response to a set of “transitions” (Stringham et al. 2003, Bestelmeyer et al. 2004, Davies et al. 2012b). Transitions among alternative states occur due to the singular or interactive effects of climatic events, management actions and autogenic succession. My state-and-transition model incorporates an additional category, “shared processes”, which describes abiotic or biotic processes that affect lizard assemblage composition at all alternative states. By incorporating key factors that influence species assemblages, STMs help land managers to evaluate the susceptibility of current community assemblages to potential transitions and to predict the effects of events such as rainfall, grazing intensity and fire on community assemblage composition. This then helps the formulation of effective and informed management strategies (Stringham et al. 2003, Bestelmeyer et al. 2004, Briske et al. 2008).

STMs were initially formulated to assist rangeland management (Westoby et al. 1989) but have since been applied to a wide range of terrestrial ecosystems (e.g. Archer 1989, Milton et al. 1994, Bestelmeyer et al. 2004, Chartier and Rostagno 2006, Zweig and Kitchens 2009). Although the effects of scale and spatial heterogeneity have not been traditionally incorporated into STMs, recent approaches have begun to consider the effects of these processes on transitions and state processes (e.g. Bestelmeyer et al. 2006, Bestelmeyer et al. 2009). For example, state transitions may be localised to particular areas depending on factors such as variations in historical land use (eg grazing), heterogeneous fire intensities and variations in soils and landforms (Bestelmeyer et al. 2009). Spatial variability due to climate, landforms, soils and other interacting factors is a key aspect of my study area (Chapter 2) and of resident lizard communities (Chapter 5) and thus I have endeavoured to account for this in my STM. Process B (see Table 7.1) reflects the effects of spatial variability in species assemblages, soil types and land use history and thus adds a spatial component to the model. Revealing processes such as these that interact across spatial scales will help to determine the spatial limit at which STMs can be applied and thus improve their utility as management tools.

My proposed state-and-transition model accounts for species functional traits along with key aspects of a disturbance regime including the interacting effects of rainfall, predation, interspecific competition and commercial grazing to affect lizard assemblages at any stage of post-fire succession. Inherent regional specificity in species assemblages, characteristic species rarity and their joint effects on lizard assemblages at each stage, are also accounted for.

A state-and-transition model is typically accompanied by several catalogues that describe the various aspects of the model. These include i) a catalogue of alternative states; ii) a catalogue of potential transitions; and iii) a catalogue of opportunities and hazards, which are climatic circumstances under which favourable or unfavourable transitions are likely to occur. In my modified model I have included iv) a catalogue of shared processes to describe the biotic and abiotic influences that affect lizard assemblages at all alternative states of the model. The catalogues are presented in Table 7.1.

It is important to note that a key characteristic of arid zone lizard assemblages is the prevalence of rare and regionally-specific species. Thus the examples of dominant species that I have provided in Table 7.1 are examples of common species only. Observed species assemblage composition will depend on the factors described in the model. In the spinifex grasslands of central Australia, it may take in excess of twenty-five years to transition through the three stages proposed in the model, and the timing will depend on rainfall.

Table 7.1 Catalogue of states, transitions, shared processes, and opportunities and hazards for a lizard community state-and-transition model in arid spinifex grasslands in central Australia (Fig. 7.1). Knowledge of alternatives states, potential transitions, opportunities and hazards and shared processes is drawn from Fyfe (1980), Eldridge (1996), Masters (1996), Pianka (1996), James (2003), Letnic et al. (2004), Letnic (2007), Wilson and Swan (2008), Letnic and Dickman (2010), Pianka and Goodyear (2012) and this thesis.

Catalogue of States	
State I	Newly-burnt habitat that is devoid of shelter or structural features. Lizard assemblages are dominated by open-area specialists such as *Ctenophorus nuchalis*, nocturnal, burrowing geckos such as *Rhynchoedura ornata* and *Diplodactylus stenodactylus* and subterranean species such as *Ramphotyphlops* spp. Transient: converts to State II or State III within 1 - 3 years.
State II	Herb and forbs present, along with spinifex and shrub seedlings. Lizard assemblages dominated by State I species together with species that require some vegetation structure but retain reasonable flexibility in their thermoregulatory requirements and diet, such as those that are able to burrow for shelter (such as some *Ctenotus* spp.).
State III	Re-establishment of spinifex as the dominant vegetation type. Shrubs largely regenerated and herbs, forbs and other grasses present. Lizard assemblages dominated by species that require spinifex for foraging, thermoregulation and protection from predators, and soil stability for burrowing. Dominant genera and species may include *Ctenophorus isolepis, Ctenotus calurus, Ctenotus ariadnae, Ctenotus pantherinus*, *Egernia inornata*, *Lerista* spp. and *Varanus eremius.*
State IV	Long unburnt vegetation, ≥ 25 years post fire. Vegetation is structurally diverse with open spaces, high spinifex, tree and shrub cover. Low floristic diversity with few herbs, forbs or grasses. Lizard assemblages similar to State III but with arboreal species such as *Strophurus ciliaris*, *Gehyra purpurascens* and litter dwellers such as *Menetia greyii* and *Delma* spp. present.

Catalogue of Transitions

Transition I	Rainfall promotes vegetation regeneration and seeding of annual or perennial plants. Invertebrate abundance increases and lizard recruitment is generally successful.
Transition 2	Drought reduces vegetation cover and food availability. Seed production is low and invertebrate abundance is reduced. The soil seedbank declines. Lizard recruitment is low.
Transition 3	Heavy rainfall stimulates a strong pulse of primary productivity, characterised by widespread germination and growth of ephemeral, annual and perennial plant species, including green plant material, fruits and seeds. Invertebrate abundances increase. High lizard recruitment.
Transition 4	Commercial grazing reduces resource availability and plant cover via impacts on vegetation and refuge habitats, invertebrate food sources, burrows and cryptogamic crusts.
Transition 5	Prescribed burns reduce the cover of spinifex and simulate the germination and recruitment of annual and perennial plants including herbs, shrubs and non-spinifex grasses.
Transition 6	A medium-high intensity wildfire eliminates virtually all above-surface plant matter. Only occasional trees or shrub skeletons remain. This increases predation risk and may cause food shortages.

Catalogue of shared processes

Process A	Predation and/or interspecific competition influence which species are abundant or rare at any point of the succession. The effects of predation from introduced cats and foxes are particularly important in State 1, where high numbers of cats and foxes can suppress lizard populations and bias assemblages towards species that are less susceptible to predation.
Process B	Regional variation in species assemblages, land use history and the effects of soil type will affect the dominant species at each state.

Opportunities and hazards

Heavy rainfall is an important time for management actions, particularly when it occurs as part of the El Niño Southern Oscillation cycle (ENSO) or Indian Ocean Dipole (IOD) climatic systems. Prescribed burns need to be carried out to prevent the occurrence of wildfires. Following wildfire, land managers need to carry out targeted predator control programs, particularly for cats and foxes which are efficient predators in open post-fire habitats. During times of drought, managers need to control commercial stocking rates to prevent over-grazing in already denuded habitats.


State IV. Long-unburnt vegetation dominated by spinifex, shrubs and trees. Lizards characterised by State III species in addition to arboreal and litter dwelling species.
1. Low-medium rainfall
2. Drought
4. Grazing
State III. Spinifex is the dominant vegetation type. Herbs, forbs and shrubs also present. Lizard assemblages dominated by species that require spinifex for foraging, thermoregulation and predator protection.
A. Predation and/or interspecific competition influences which species are abundant or rare
1. Low-medium rainfall
5. Prescribed burns
B. Regional variation in species assemblages, land use history and soil type affect overall assemblage composition
3. Heavy rainfall
6. Wildfire
State II. Vegetation dominated by herbs and forb. Spinifex and shrub seedlings are also present. Lizards characterised by State I species in addition to species that require some vegetative structure.
1. Low-medium rainfall
State I. Newly burnt habitat. Lizard assemblage dominated by open area specialists, nocturnal geckos and subterranean species

Fig. 7.1 (opposite page). State-and-transition model describing the post-fire assemblage composition of lizards in the arid spinifex grasslands of central Australia. Transitions towards a higher state are represented by solid lines; transitions towards a lower state are represented by dashed lines; and shared processes are indicated by irregularly dotted and dashed lines. Refer to Table 7.1 for catalogues of alternative states, possible transitions, key influences and management opportunities and hazards

7.4 CONSERVATION AND MANAGEMENT IMPLICATIONS

Arid and semi-arid grasslands and shrublands cover over one third of the Australian continent and are key habitats affected by both prescribed and wildland fire. Effective and responsible fire management is essential for the region, not only for the conservation of affected fauna and flora, but also because the extremely low levels of productivity that normally prevail mean that fire management outcomes will potentially affect ecological systems there for decades.

A primary implication of my research is that generalised prescribed burning may be an ineffective method of conserving biodiversity and in some cases it may cause more harm than good. My results in Chapters 3 and 4 both highlight that prescribed burning does not benefit patch- and landscape-scale diversity across all taxa, and that in some cases patch diversity may increase at the expense of diversity at the landscape scale. Land managers should aim to design fire management programs that are tailored towards conserving species and habitats of management concern. Prescribed burns should, where possible, be investigative in nature and be carried out in systems in which information about species assemblages, life history traits, dispersal capacity and other influencing processes is known. Detailed post-fire monitoring should also be an essential part of any fire management strategy to assess and confirm species responses.

It remains uncertain whether the majority of reptile species show a strong fire response or whether their responses to fire are determined by other ecological processes such as rainfall and predation. In addition to this, a key factor affecting the extinction risk of arid zone lizards is the elimination of critical habitat via incorrect burning practices (sensu Driscoll and Henderson 2008, Lindenmayer et al. 2008, Nimmo et al. 2012a). Thus it is critical that fire management activities targeting reptiles be based on high quality information, including detailed data on habitat associations and other factors that potentially influence these. To minimise the risk associated with the unintended effects of management activities, data should be species-specific and lizard management models should be developed and tested on an ongoing basis.

Another implication of my research is that species responses to fire are spatially explicit. This should be incorporated into management activities where possible, with land managers placing a limit on the spatial extent over which habitat-use models are applied (Driscoll et al. 2010). Fire management activities should be, where possible, site- or region- specific, and the suitability of existing fire and management models for new regions should be experimentally confirmed.

Prescribed burn programs should also be used to conserve tracts of long-unburnt habitat (e.g. >50 years post fire). Once destroyed, long-unburnt habitat and associated attributes can take decades to develop (Haslem et al. 2011) and relatively small patches of long-unburnt habitat are often susceptible to burning by a single large wildfire. In addition to supporting a range of late-successional small mammals and lizards, habitat remnants may also support source populations which recolonise habitat disturbed by fire (Woinarski et al. 2004, Bradstock et al. 2005, Kelly et al. 2010, Kelly et al. 2011). This further highlights the need to protect these remnants. Similar prescribed burn programs may also be necessary to protect infrastructure and buildings from the effects of wildfires (Gill and Stephens 2009).

My research has also highlighted the need for the urgent control of terrestrial predators in newly burnt environments, particularly of feral cats and foxes. As indicated in Chapter 6, these predators preferentially target newly burnt habitats, and they are very effective hunters under these conditions. They can shift existing trophic pathways to exert temporary but strong top-down control in traditionally bottom-up systems (Letnic et al. 2011) and prevent the recolonisation of pre-fire animal assemblages (Moseby et al. 2011). These effects are heightened after rainfall providing an even greater need for predator control during these times. My research suggests that an essential part of any fire management program should be post-fire predator control and that this should be undertaken after both prescribed burns and wildfires.

However, the control of introduced predators should not be undertaken without concurrent sampling of small mammal and lizard communities, as the cascading effects of keystone predators may have unintended effects. For example, although research reported in this thesis and in supporting literature has indicated that feral cats and foxes can have devastating effects on small mammal communities, under some circumstances they can facilitate native scincid lizard communities by controlling the primary predator of scincid lizards; the sand goanna (*Varanus gouldii*; Olsson et al. 2005). It is likely that, as with small mammals, these effects will be more pronounced in recently burnt habitats; however, this has yet to be experimentally confirmed.

Lastly, to prioritise prescribed burn programs, land managers should first aim to conserve species of management concern whose habitat requirements are known. For example, the death adder (*Acanthophis pyrrhus*) resides in the Simpson Desert, is already predisposed to endangerment through a suite of life-history characteristics, and may be at increased risk through accidental and deliberate burning and fragmentation of old-growth hummock grasslands (McDonald et al. 2012). Targeted prescribed burns to preserve this known habitat would be an effective way to assist in its conservation.

7.5 OPPORTUNITIES FOR FURTHER RESEARCH

Detailed, species-level information on species responses to fire is needed to implement the tailored fire management programs recommended in Section 7.4, particularly for arid zone lizard communities. This includes information about species assemblages, life history traits, abundance, dispersal capacity and behaviour. These data will contribute towards a deeper understanding of the mechanisms that underlie observed species fire responses, including the role of rare species, which will in turn help managers to design and implement effective, predictive fire models. Pre-fire research should also identify any species of management concern to ensure that their habitat requirements are provided for in the proposed management programs.

There is also a need for fire studies that cover broad spatial scales. As indicated in this thesis, species responses to fire may change over broad spatial scales and a deeper understanding of this geographic variation will inform the scale at which fire management programs are developed and implemented (Parr and Chown 2003, Kelly et al. 2011, Kelly et al. 2012). These studies would benefit from considering the interaction of species-level processes with other influencing factors such as climate, substrate, predation and interspecific interactions, to further understand species responses to fire. It is also important that fire research is undertaken at a range of temporal scales to account for differences in season and other temporal variables (Clarke et al. 2010). This is particularly important with regards to lizards. More data are required to identify the key processes affecting lizard succession in different geographical regions and to determine how the various processes interact with one another and with habitat-mediated post-fire lizard succession. Only then will land managers be able to meet management goals aimed all maintaining all species within a region (Dellasala et al. 2004, Clarke 2008, Driscoll et al. 2010)

Further research into the effects of predators in newly burnt environments is also essential for the effective management of small mammals and lizards in burnt habitat. The time taken for predators to arrive in burnt areas, the speed with which introduced predators affect population dynamics in burnt habitats and the prey species most at risk have all yet to be quantified. In addition, the potential for unintended cascading effects of keystone predator control also needs to be investigated further, such as the aforementioned effect of fox control on scincid lizard populations.

Empirical testing of my proposed state-and-transition model for lizard succession after fire in spinifex grasslands is required to generalise the model and include a more complete range of potential transitions. A paucity of empirical testing of STMs, including alternative states, transitions and thresholds, has been identified as a key factor impeding their effective implementation in many ecological systems (Walker and Wilson 2002, Briske et al. 2003, Bagchi et al. 2012). Empirical testing will not only improve the accuracy of the model but will help to define metrics such as transition frequency, magnitude of accompanying compositional change and the presence of unidirectional trajectories (Bagchi et al. 2012). The model should be developed and tested over a range of habitats in the spinifex grasslands of central Australia, under varying conditions of rainfall, previous land use and soil types. Introducing this spatial component will help to maximise the accuracy of the model and its effectiveness as a management tool (Bestelmeyer et al. 2009).

Lester and Fairweather (2011) propose a staged process to develop a multivariate, data-derived STM. Although developed for a wetland ecosystem, their methodology is general and thus likely to have merit in developing and testing STMS in many terrestrial ecosystems, including the spinifex grasslands of central Australia. I summarise their proposed methodology below and propose it to be a suitable approach for future testing of the lizard STM above. In recognition of the importance of spatial hierarchies in STMs (*sensu* Bestelmeyer et al. 2009) model development and testing should be conducted at two scale domains: the site scale and the landscape scale. The methodology is as follows:

1. Divide cases between model calibration and evaluation.
2. Identify preliminary states - use cluster analysis to identify sets of co-occurring biota.
3. Identify associated environmental conditions – identify differences in the physico-chemical data associated with each state using classification trees, with the biotic distinctness of the resultant statistical model tested using analysis of similarities.
4. Confirm distinctness of states.
5. Evaluate new cases to test the predictive capacity of the model.
6. Characterise ecosystem states.

Lastly, more research is needed into the effects of differing detection probabilities between burnt and unburnt habitats in my study area. Recent studies suggest that the easier detection of species in newly simplified burnt environments or increased post-fire movements of some species may artificially inflate estimates of species numbers in these habitats (e.g. Hossack and Corn 2007, Driscoll et al. 2012). This has not yet been quantified across broad spatial scales, however, and the importance of this potentially confounding factor in arid zone small mammal and lizard communities is not yet known. Addressing this in future studies would greatly benefit the robustness of future arid zone fire studies.

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APPENDICES: CHAPTER 3

Appendix 3.1 Fire studies and data used in the meta-analysis

Appendix 3.2 Funnel plot of sample size and alpha diversity effect size

Appendix 3.3 The effect of fire on alpha diversity

Appendix 3.1 Fire studies and data used in the meta - analysis

Table A3.1 Fire studies and data used in the meta-analysis. Explanation of codes: Fire Type: W (wildfire) or PB (prescribed burn). Species list provided: Y (yes) or N (no). Ecoregion: ASG (arid and semi-arid grasslands), MCF (Mediterranean coniferous forests), MGS (montane grassland and shrublands), MOF (Mediterranean oak forests), BT (boreal forests/taiga), FGS (flooded grasslands and savannas), M (mangroves), SW (subalpine woodlands), TBF (temperate broadleaf and mixed forests), TCF (temperate coniferous forests), TGS (temperate grasslands, savannas and shrublands), TS (tropical and subtropical grasslands, savannas and shrublands), TSC (tropical and subtropical coniferous forests), TSD (tropical and subtropical dry broadleaf forests), TSR (tropical and subtropical moist broadleaf forests), T (tundra), XS (xeric shrublands). Continent: Nth Am (North America), Sth Am (South America). Replication: R (replicated) or U (unreplicated). Experimental method: T-C (treatment-control) or B-A (before-after). Fire severity: H (High), L (Low), - (not reported) or N/A (not applicable). Fire severity has only been reported for wildfires. X_e and X_c represent the mean species richness in post-fire burnt and unburnt habitat (treatment - control studies) or in habitat before and after a fire. Effect size: $\ln(X_e/X_c)$, where X_e and X_c are the species richness in treatment and control habitats respectively.

Ref	Author	Fire Type	Taxon	Spp list	Eco-region	Continent	Rep.	Exp. Method	Fire Severity	Spatial scale (ha)	Time since fire (months)	Lati-tude	SSI	Spp. in unburnt habitat	Spp. in burnt habitat	Effect Size $\ln(X_e/X_c)$
1.	(Adeney et al. 2006)	W	Birds	N	TSR	Asia	R	T-C	-	900	120	-0.83	-	31	44	0.350
2.	(Allen et al. 2006)	PB	Birds	Y	TCF	Nth Am	R	T-C	N/A	51	49	35.12	0.99	33	34	0.030
3.	(Allen et al. 2006)	PB	Birds	Y	TCF	Nth Am	R	T-C	N/A	123	13	35.12	0.99	34	33	-0.030
4.	(Apfelbaum and Haney 1981)	W	Birds	Y	TCF	Nth Am	U	B-A	-	6	24	48.25	0.46	12	14	0.154
5.	(Aquilani et al. 2003)	PB	Birds	Y	TBF	Nth Am	R	T-C	N/A	320	48	48.25	0.74	32	30	-0.065
6.	(Barlow and Peres 2004)	W	Birds	Y	TSR	Sth Am	R	T-c	N/A	7	46	-2.73	0.68	-	-	-
7.	(Barlow and Peres 2006)	W	Birds	Y	TSR	Sth Am	R	T-C	L	300	63	-2.73	0.94	22	18	-0.043
8.	(Barlow and Peres 2006)	W	Mammals	Y	TSR	Sth Am	R	T-C	L	300	63	-2.73	0.70	62	63	-0.201
9.	(Barlow et al. 2002)	W	Birds	Y	TSR	Sth Am	R	T-C	L	4	15	-2.73	0.80	24	23	0.016
10.	(Beck and Vogl 1972)	PB	Mammals	Y	TGS	Nth Am	R	T-C	N/A	20	4.25	45.81	0.67	5	7	0.336
11.	(Blake 1982)	W	Birds	Y	TCF	Nth Am	U	T-C	H	6	24	34.58	0.27	21	23	0.091
12.	(Blake 2005)	PB	Birds	Y	TBF	Nth Am	R	T-C	N/A	340	42	39.03	0.96	-	-	-
13.	(Bock and Bock 1983)	PB	Birds	Y	TCF	Nth Am	R	T-C	N/A	17	13	43.58	0.95	21	19	-0.100
14.	(Bock and Lynch 1970)	W	Birds	Y	TCF	Nth Am	U	T-C	H	2	120	39.36	0.65	35	45	0.251
15.	(Brennan et al. 2005)	PB	Birds	Y	FGS	Nth Am	R	T-C	N/A	-	1	40.81	0.82	27	29	0.071
16.	(Cano and Leynaud 2010)	PB	Reptiles	Y	TGS	Sth Am	U	T-C	N/A	800	6.5	-28.00	0.75	4	4	0.000
17.	(Cano and Leynaud 2010)	PB	Amphibians	Y	TGS	Sth Am	U	T-C	N/A	800	6.5	-28.00	0.63	10	9	-0.105
18.	(Christian 1977)	W	Mammals	N	TGS	Africa	U	T-C	-	3	3.5	-25.30	0.75	5	3	-0.511

19.	(Cook 1959)	W	Mammals	Y	TGS	Nth Am	U	T-C	H	2	31	37.90	0.86	7	7	0.000
20.	(Crowner and Barrett 1979)	PB	Mammals	Y	TGS	Nth Am	U	T-C	N/A	1	7	39.51	0.50	3	1	-1.099
21.	(Cunningham et al. 2002)	W	Reptiles	Y	TGS	Nth Am	R	T-C	H	24500	42	33.71	0.78	12	15	0.223
22.	(Cunningham et al. 2002)	W	Reptiles	Y	TBF	Nth Am	R	T-C	H	24500	42	33.71	0.50	7	10	0.357
23.	(Dieni and Anderson 1999)	W	Birds	N	TBF	Nth Am	R	T-C	-	2670	72	45.42	-	34	38	0.111
24.	(Emlen 1970)	PB	Birds	Y	TCF	Nth Am	U	T-C	N/A	800	6	25.29	0.88	26	26	0.000
25.	(Fa and Sanchez-Cordero 1993)	PB	Mammals	Y	MGS	Sth Am	U	T-C	N/A	2	11	-19.15	0.75	5	3	-0.511
26.	(Fitzgerald et al. 2001)	PB	Mammals	Y	ASG	Nth Am	U	T-C	N/A	2	1	31.35	0.67	4	5	0.223
27.	(Fitzgerald and Tanner 1992)	PB	Birds	Y	TGS	Nth Am	R	T-C	N/A	37	12	27.19	0.36	20	31	0.438
28.	(Fontaine et al. 2009)	W	Birds	Y	TBF	Nth Am	R	T-C	H	840	38	42.00	0.84	33	36	0.087
29.	(Ford et al. 1999)	PB	Mammals	Y	TBF	Nth Am	R	T-C	N/A	400	16.5	35.21	1.00	10	10	0.000
30.	(Ford et al. 1999)	PB	Amphibians	Y	TBF	Nth Am	R	T-C	N/A	400	16	35.21	0.86	3	4	0.288
31.	(Fox 1982)	W	Mammals	Y	ASG	Aust	U	T-C	H	11	67	-32.47	0.92	6	7	0.154
32.	(Fyfe 1980)	W	Reptiles	Y	ASG	Aust	U	T-C	H	1	39	-28.25	0.65	21	16	-0.272
33.	(Gabrey and Afton 2004)	PB	Birds	Y	FGS	Nth Am	R	T-C	N/A	50	18	29.68	0.82	9	8	-0.118
34.	(Gabrey et al. 1999)	PB	Birds	Y	FGS	Nth Am	R	T-C	N/A	600	13	29.68	0.50	4	8	0.693
35.	(Gaines et al. 2010)	PB	Birds	Y	TCF	Nth Am	R	T-C	N/A	60	13	47.99	0.93	44	42	-0.047
36.	(Green and Sanecki 2006)	W	Birds	N	SW	Aust	U	B-A	H	45	3	36.39	-	22	11	-0.693
37.	(Gregory et al. 2010)	PB	Birds	N	XS	Africa	R	T-C	N/A	72	36	0.28	-	17	14	-0.194
38.	(Groves and Steenhof 1988)	W	Mammals	Y	ASG	Nth Am	R	T-C	-	4	11.25	42.85	0.33	4	2	-0.693

39.	(Haney et al. 2008)	W	Birds	Y	TCF	Nth Am	U	B-A	H	9	24	47.92	0.54	14	23	0.496
40.	(Haugaasen et al. 2003)	W	Birds	Y	TSR	Sth Am	R	T-C	L	4	16	-2.57	0.88	23	20	-0.140
41.	(Henriques et al. 2006)	W	Mammals	Y	TS	Sth Am	U	T-C	-	2	12.25	-15.95	0.22	7	2	-1.253
42.	(Herrando et al. 2003)	W	Birds	Y	MCF	Europe	R	T-C	H	47	40	41.25	0.36	25	19	-0.274
43.	(Horton and Mannan 1988)	PB	Birds	Y	BT	Nth Am	R	T-C	-	64	5	31.74	1.00	14	14	0.000
44.	(Isacch et al. 2004)	PB	Birds	Y	FGS	Sth Am	R	T-C	N/A	24	13	-37.67	0.76	25	30	0.182
45.	(Isacch et al. 2004)	PB	Birds	Y	FGS	Sth Am	R	T-C	N/A	24	13	-37.67	0.38	16	16	0.000
46.	(Jacquet and Prodon 2009)	W	Birds	Y	MOF	Europe	R	T-C	H	-	49	42.55	0.39	17	14	-0.194
47.	(Kelly et al. 2010)	W	Mammals	Y	XS	Aust	R	T-C	-	1	15	-33.85	0.86	4	3	-0.288
48.	(Killgore et al. 2009)	PB	Mammals	Y	ASG	Nth Am	R	T-C	N/A	2	3.25	33.14	0.67	5	4	-0.223
49.	(Kirkland et al. 1996)	W	Mammals	Y	TBF	Nth Am	R	T-C	L	20	11.5	40.04	0.86	8	6	-0.288
50.	(Kirkland et al. 1996)	W	Amphibians	Y	TBF	Nth Am	R	T-C	L	20	11.5	40.04	0.73	5	6	0.182
51.	(Klaus et al. 2010)	PB	Birds	Y	TBF	Nth Am	R	T-C	N/A	1200	25	34.77	0.71	31	37	0.177
52.	(Kreisel and Stein 1999)	W	Birds	Y	TCF	Nth Am	R	T-C	H	240	51	48.66	0.48	14	15	0.069
53.	(Leavesley et al. 2010)	W	Birds	Y	XS	Aust	R	T-C	-	1998	58	-25.26	-	32	41	0.248
54.	(Legge et al. 2008)	W	Mammals	Y	TS	Aust	R	T-C	H	3	1.5	-17.03	0.89	4	5	0.223
55.	(Legge et al. 2008)	W	Reptiles	Y	TS	Aust	R	T-C	H	3	1.5	-17.03	0.42	12	7	-0.539
56.	(Legge et al. 2008)	W	Birds	Y	TS	Aust	R	T-C	H	3	1.5	-17.03	0.72	52	40	-0.262
57.	(Letnic et al. 2004)	W	Reptiles	Y	ASG	Aust	R	T-C	-	360000	24	-23.50	0.60	11	9	-0.201
58.	(Madden et al. 1999)	PB	Birds	Y	TGS	Nth Am	R	T-C	N/A	1616	37.5	48.62	0.62	5	8	0.470

59.	(Masters 1996)	PB	Reptiles	Y	ASG	Aust	R	T-C	N/A	2	41	-25.28	0.87	36	35	-0.028
60.	(Monasmith et al. 2010)	PB	Mammals	Y	XS	Nth Am	R	T-C	N/A	500	13	32.69	0.78	10	13	0.262
61.	(Moseley et al. 2003)	PB	Reptiles	Y	TBF	Nth Am	R	T-C	N/A	348	6.5	33.09	0.60	3	7	0.847
62.	(Moseley et al. 2003)	PB	Amphibians	Y	TBF	Nth Am	R	T-C	N/A	348	6.5	33.09	0.83	12	12	0.000
63.	(Mott et al. 2010)	PB	Reptiles	Y	TSD	Aust	U	T-C	N/A	200	23.66	-18.47	0.87	15	15	0.000
64.	(Mushinsky 1985)	PB	Reptiles	Y	XS	Nth Am	U	T-C	N/A	2	10	28.08	0.69	15	20	0.288
65.	(Ojeda 1989)	PB	Mammals	Y	ASG	Sth Am	R	T-C	N/A	120	12.25	-34.03	1.00	5	5	0.000
66.	(O'Reilly et al. 2006)	PB	Birds	Y	TS	Africa	R	T-C	N/A	8	23	0.28	0.79	-	-	-
67.	(Pelegrin and Bucher 2010)	W	Reptiles	Y	XS	Sth Am	R	T-C	H	60	99	-30.37	0.93	7	8	0.134
68.	(Peres et al. 2003)	W	Birds	N	TSR	Sth Am	R	T-C	L	4	30	-3.00	-	90	87	-0.034
69.	(Petersen and Best 1987)	PB	Birds	Y	TGS	Nth Am	R	T-C	N/A	13	44	43.78	0.77	6	7	0.154
70.	(Pons et al. 2003)	W	Birds	Y	TS	Africa	U	T-C	L	50	0.2	-16.17	0.55	3	8	0.981
71.	(Pons and Wendenburg 2005)	W	Birds	Y	TSD	Africa	R	T-C	H	-	61	-16.32	0.81	31	38	0.204
72.	(Pope and Block 2010)	PB	Birds	Y	TCF	Nth Am	R	T-C	N/A	856	30	36.58	0.85	31	34	0.092
73.	(Pylypec 1991)	PB	Birds	Y	TGS	Nth Am	U	T-C	N/A	19	32	52.17	0.90	10	10	0.000
74.	(Rana 1985)	W	Mammals	Y	ASG	India	U	T-C	-	3	11	25.12	1.00	5	5	0.000
75.	(Reilly 2000)	W	Birds	Y	TBF	Aust	U	B-A	H	10	51	-38.46	0.79	38	43	0.124
76.	(Reynolds and Krausman 1998)	PB	Birds	Y	TGS	Nth Am	R	T-C	N/A	240	6	28.10	-	20	24	0.182
77.	(Reynolds and Krausman 1998)	PB	Birds	Y	TGS	Nth Am	R	T-C	N/A	240	6	28.10	-	28	34	0.194
78.	(Robel et al. 1998)	PB	Birds	Y	TGS	Nth Am	R	T-C	N/A	619	3	38.79	-	21	26	0.214

79.	(Ruthven et al. 2008)	PB	Amphibians	Y	TGS	Nth Am	R	T-C	N/A	12	4	28.33	0.80	2	3	0.405
80.	(Ruthven et al. 2008)	PB	Reptiles	Y	TGS	Nth Am	R	T-C	N/A	12	4	28.33	0.86	11	10	-0.095
81.	(Ruthven et al. 2008)	PB	Reptiles	Y	TGS	Nth Am	R	T-C	N/A	20	24	28.33	0.87	11	12	0.087
82.	(Santos and Poquet 2010)	W	Reptiles	Y	MOF	Europe	R	T-C	-	295	48	41.65	0.91	11	11	0.000
83.	(Sass and Wilson 2006)	W	Reptiles	Y	XS	Aust	R	T-C	H	1	27	-32.57	0.00	5	7	0.336
84.	(Simons 1991)	PB	Mammals	Y	XS	Nth Am	U	T-C	N/A	2	13	33.57	0.92	-	-	-
85.	(Sgardelis and Margaris 1992)	W	Birds	N	MOF	Europe	U	T-C	N/A	50	24	37.74	0.63	-	-	-
86.	(Sgardelis and Margaris 1992)	W	Mammals	N	MOF	Europe	U	T-C	N/A	50	31	37.74	0.67	-	-	-
87.	(Smith 1989b)	W	Birds	Y	TBF	Aust	U	B-A	L	13	32	-36.67	1.00	51	51	0.000
88.	(Smucker et al. 2005)	W	Birds	y	TCF	Nth Am	R	T-C	H	1040	36	46.05	0.82	57	60	0.051
89.	(Stanton 1986)	W	Birds	Y	XS	Nth Am	U	T-C	L	4	33	34.06	0.95	22	20	-0.095
90.	(Thompson et al. 1989)	PB	Mammals	Y	TBF	Aust	U	B-A	N/A	4	34	-35.27	0.89	4	5	0.223
91.	(Torre and Diaz 2004)	W	Mammals	Y	MOF	Europe	R	T-C	-	1	61	41.28	0.80	2	3	0.405
92.	(Turner 1992)	W	Birds	N	TBF	Aust	U	T-C	-	972	8.25	-34.00	0.66	59	50	-0.166
93.	(Ukmar et al. 2007)	W	Birds	Y	MCF	Europe	U	T-C	H	6	45	41.73	0.78	26	28	0.074
94.	(Vamstad and Rotenberry 2010)	W	Mammals	Y	XS	Nth Am	U	T-C	-	1	27	33.87	0.67	2	4	0.693
95.	(Vieira 1999)	PB	Mammals	Y	TS	Sth Am	U	B-A	N/A	1	24	-15.93	0.93	-	-	-
96.	(Wilgers and Horne 2006)	PB	Reptiles	Y	TGS	Nth Am	R	T-C	N/A	1	24	39.08	-	14	15	0.069
97.	(Willis 2003)	W	Birds	N	TSD	Sth Am	U	B-A	N/A	177	37	-22.13	0.85	-	-	-

98.	(Woinarski 1990)	PB	Birds	Y	TSD	Aust	R	T-C	N/A	3	0.75	-12.47	0.83	43	40	-0.072
99.	(Woinarski 1990)	PB	Birds	Y	TSD	Aust	R	T-C	N/A	3	1.25	-12.47	0.76	43	36	-0.178
100.	(Woinarski et al. 2004)	PB	Reptiles	Y	TSD	Aust	R	T-C	N/A	3	10.5	-12.62	0.89	5	4	-0.223
101.	(Woinarski et al. 2004)	PB	Birds	Y	TSD	Aust	R	T-C	N/A	3	10.5	-12.62	0.88	25	23	-0.083
102.	(Woinarski et al. 2004)	PB	Mammals	Y	TSD	Aust	R	T-C	N/A	3	10.5	-12.62	0.83	5	7	0.336
103.	(Wooller and Calver 1988)	PB	Birds	Y	TBF	Aust	U	B-A	N/A	1	38	-34.43	-	23	15	-0.427
104.	(Zwolak and Foresman 2007)	W	Mammals	Y	BT	Nth Am	R	T-C	H	3	33	47.98	0.81	12	15	0.223

Appendix 3.1 References

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Appendix 3.2 Funnel plot of sample size and alpha diversity effect size

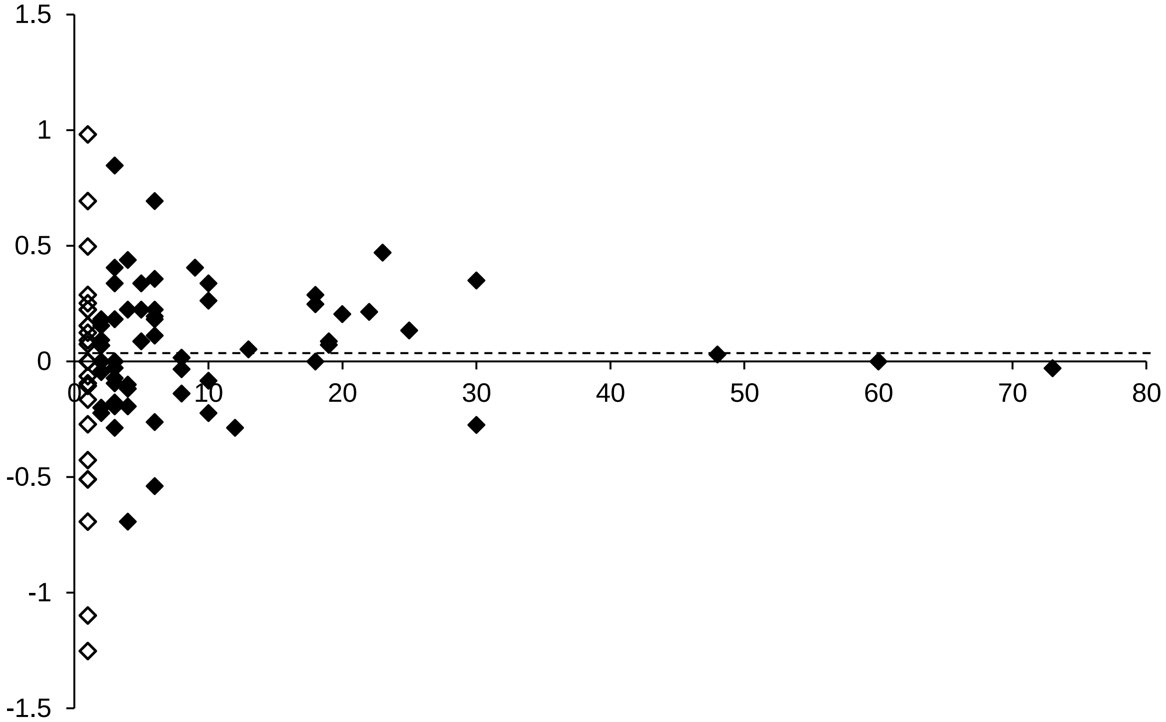

Figure A3.2 A funnel plot of sample size and alpha diversity effect size ln(Xe/Xc) for replicated (shaded diamonds) and unreplicated (open diamonds) studies (n = 96). The dashed horizontal line indicates the combined mean effect size of 0.0287. There is no evidence of publication bias as the variation around the mean decreases with increasing sample size. X_e and X_c represent the mean species richness in post-fire burnt and unburnt habitat (treatment - control studies) or in habitat before and after a fire.

Appendix 3.3 The effect of fire on alpha diversity

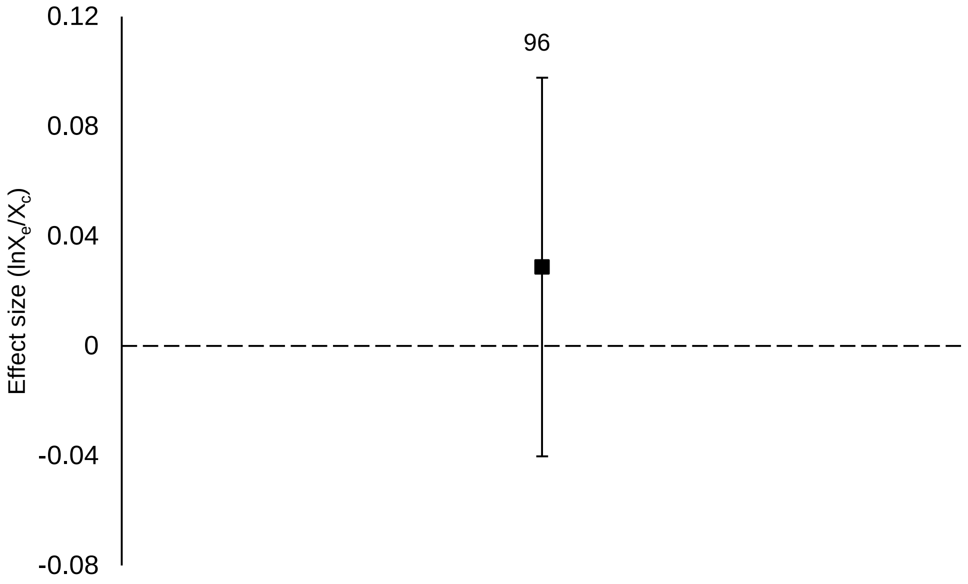

Figure A3.3 Effect size ln(Xe/Xc) ± 95% confidence interval (CI) of fire on the alpha diversity of birds, reptiles, mammals and amphibians. X_e and X_c represent the mean species richness in post-fire burnt and unburnt habitat (treatment - control studies) or in habitat before and after a fire. The number of studies in this analysis is indicated above the bar. A significant effect is obtained if $\ln(X_e/X_c) \pm 95\%$ CI > 0 or $\ln(X_e/X_c) \pm 95\%$ CI < 0.

APPENDICES: CHAPTER 4

Appendix 4.1	Summary of repeated-measures ANOVAs
Appendix 4.2	Results of contrast analyses for the interaction term Time*Fire
Appendix 4.3	Summary of Analysis of Similarity (ANOSIM) of species abundances
Appendix 4.4	Summary of the SIMPER output for all statistically significant MDS ordinations

Appendix 4.1 Summary of repeated-measures ANOVAs

Table A4.1 Summary of repeated-measures ANOVAs investigating the effects of a wildfire and a prescribed burn on plant, mammal and lizard alpha diversity in the Simpson Desert, central Australia.

	Time		Fire		Time*Fire	
	F	*P*	*F*	*P*	*F*	*P*
Prescribed-burn						
Plants	16.261	**0.0001**	10.102	**0.0098**	5.658	**0.0113**
Mammals	4.631	**0.022**	25.311	**0.001**	1.086	0.357
Lizards	4.462	**0.025**	0.317	0.586	4.489	**0.025**
Wildfire						
Plants	1.827	0.1868	3.017	0.113	9.194	**0.0015**
Mammals	49.121	**0.0001**	6.402	**0.0299**	10.703	**0.0007**
Lizards	3.995	**0.0350**	1.522	0.245	0.011	0.989

Note: The table shows the main effects for Time and Fire (degrees of freedom = 2 and 1), and the interaction term Time*Fire (degrees of freedom = 2). A statistically significant fire*time interaction indicates that the alpha diversity of the relevant taxon was affected by the fire. Statistical significance is taken at $P \leq 0.05$ and significant *P* values are indicated in boldface type. Time was treated as the repeated measure.

Appendix 4.2 Results of contrast analyses for the interaction term Time*Fire

Table A4.2 Results of contrast analyses for the interaction term Time*Fire

	Pre-burn		Post-burn I		Post-burn II	
	F	*P*	*F*	*P*	*F*	*P*
Prescribed-burn						
Plants	1.875	0.186	9.020	**0.007**	36.674	**0.000**
Mammals	15.243	**0.001**	3.392	0.080	6.838	**0.017**
Lizards	1.703	0.207	0.135	0.717	7.469	**0.013**
Wildfire						
Plants	1.611	0.219	9.006	**0.007**	21.116	**0.000**
Mammals	3.649	0.0705	8.187	**0.010**	18.946	**0.000**
Lizards	0.0634	0.435	0.916	0.350	0.568	0.460

Note: These analyses compare the alpha diversity of plants, mammals and lizards between burnt and control sites after the prescribed burn and the wildfire in three time periods: Pre-burn, Post-burn I and Post-burn II in the Simpson Desert, central Australia. Statistical significance has been taken at $P \leq 0.05$ and significant *P* values are indicated in boldface type. Degrees of Freedom = 1 for all analyses.

Appendix 4.3 Summary of Analysis of Similarity (ANOSIM) of species abundances

Table A4.3 Global *R* and *P*-values from Analysis of Similarity (ANOSIM) of Bray-Curtis Similarity matrices of species abundances (square-root transformed) present on burnt and unburnt trapping grids across three time periods for a prescribed-burn and a wildfire in the Simpson Desert, central Australia.

	Pre-burn		Post-burn I		Post-burn II	
	R	*P*	*R*	*P*	*R*	*P*
Prescribed-burn						
Plants	0.094	0.193	0.619	**0.002**	0.824	**0.002**
Mammals	0.076	0.245	0.012	0.403	0.017	0.065
Lizards	0.032	0.335	0.319	**0.002**	0.224	**0.009**
Wildfire						
Plants	0.228	0.063	0.556	**0.002**	0.559	**0.002**
Mammals	0.017	0.455	0.328	**0.004**	0.49	**0.009**
Lizards	0.009	0.413	0.081	0.238	0.152	0.074

Note: Significance has been taken at $P \leq 0.05$. Significant *P* values are indicated in boldface type.

Appendix 4.4 Summary of the SIMPER output for all statistically significant MDS ordinations

For plants, mean cover refers to the mean of the coverage values for each species within a 2.5 m radius around six randomly-chosen pitfall trap stations on each sampling plot. For animals, mean abundance refers to the mean capture rate of each species per grid night. Mean dissimilarity (dissim.) values indicate the mean contribution of that species to the overall Bray-Curtis dissimilarity between samples. Dissimilarity/SD indicates the ratio of the mean contribution of the overall dissimilarity among samples to the standard deviation of the mean contribution of the overall dissimilarity among samples. % Contribution (% Cont.) provides the percentage contribution that each species makes to the overall dissimilarity between burnt and unburnt sites in a given time period.

Table A4.4.1 Prescribed-burn Plants, Post-burn I

Species	Mean Cover: Burnt Sites	Mean Cover: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Triodia basedowii	6.72	37.08	20.80	2.08	29.63
Eucalyptus pachyphylla	0.00	1.25	3.79	0.64	5.39
Dodonaea viscosa	1.39	0.00	3.70	0.65	5.27
Aristida contorta	0.50	0.44	3.44	1.91	4.91
Acacia ligulata	0.58	0.00	2.57	0.87	3.67
Trachymene glaucifolia	0.03	0.75	2.46	0.55	3.50
Eriachne aristidea	0.47	0.19	2.33	1.07	3.32
Grevillea juncifolia	0.33	0.28	2.17	0.80	3.09
Sida fibulifera	0.28	0.17	1.96	0.91	2.79
Scaveola parvibarbata	0.00	0.47	1.88	0.73	2.68
Acacia coriaceae	0.00	0.83	1.83	0.44	2.60
Eucalyptus gamophylla	0.00	0.69	1.67	0.44	2.37
Scaevola depauperata	0.22	0.03	1.56	0.83	2.22
Crotalaria cunninghamii	0.03	0.28	1.46	0.58	2.08
Halgania cyanea	0.00	0.25	1.36	0.61	1.94
Newcastelia spodiotricha	0.00	0.56	1.36	0.44	1.93
Tephrosia rosea	0.00	0.56	1.36	0.44	1.93
Grevillea striata	0.00	0.28	1.17	0.44	1.66
Crotalaria eremaea	0.00	0.17	1.13	0.63	1.61
Eragrostis eriopoda	0.19	0.00	1.11	0.64	1.58
Euphorbia drummondii	0.06	0.08	1.07	0.96	1.53
Yakirra australiensis	0.11	0.03	1.00	0.78	1.43

Table A4.4.2 Prescribed-burn Plants, Post-burn II

Species	Mean Cover: Burnt Sites	Mean Cover: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Triodia basedowii	9.08	40.05	11.51	2.22	16.52
Aristida contorta	9.22	0.64	7.39	1.86	10.61
Yakirra australiensis	3.47	0.14	4.71	1.95	6.76
Acacia ligulata	3.08	0.00	4.04	1.08	5.80
Eriachne aristidea	2.00	0.17	3.51	1.80	5.03
Eucalyptus pachyphylla	0.00	1.81	2.80	0.68	4.02
Eragrostis eriopoda	1.22	0.19	2.58	1.45	3.70
Dodonaea viscosa	2.25	0.00	2.39	0.69	3.43
Crotalaria eremaea	0.47	0.86	2.12	1.03	3.04
Oldenlandia pterospora	0.50	0.00	1.84	1.24	2.64
Sida fibulifera	0.39	0.31	1.63	1.36	2.33
Euphorbia drummondii	0.31	0.58	1.53	1.54	2.19
Trichodesma zeylanicum	0.39	0.19	1.43	0.80	2.05
Scaveola parvibarbata	0.18	0.28	1.34	1.28	1.92
Grevillea juncifolia	0.28	0.31	1.26	0.72	1.81
Tephrosia rosea	0.03	0.72	1.24	0.60	1.79
Acacia coriaceae	0.00	0.69	1.19	0.44	1.71
Newcastelia spodiotricha	0.03	0.56	1.02	0.54	1.46
Halgania cyanea	0.00	0.22	0.99	0.82	1.42
Triumfetta winneckeana	0.00	0.69	0.96	0.44	1.38
Calotis erinacea	0.00	0.44	0.95	0.57	1.37
Crotalaria cunninghamii	0.03	0.42	0.94	0.53	1.35
Senna pleurocarpa	0.14	0.00	0.80	0.89	1.15
Goodenia cycloptera	0.08	0.06	0.79	1.08	1.13

Indigofera sp.	0.17	0.00	0.70	0.61	1.01
Dicrastylis costelloi	0.03	0.17	0.67	0.56	0.96
Grevillea striata	0.00	0.28	0.66	0.44	0.94
Calandrinia balonensis	0.00	0.17	0.66	0.62	0.94
Trachymene glaucifolia	0.03	0.17	0.63	0.57	0.91

Table A4.4.3 Prescribed-burn Mammals, Post-burn I

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Sminthopsis youngsoni	0.47	0.33	12.28	1.61	28.60
Notomys alexis	0.36	0.47	8.01	1.20	18.66
Dasycercus blythi	0.00	0.11	6.54	0.92	15.24
Pseudomys desertor	0.06	0.11	5.74	1.01	13.37
Pseudomys hermannsburgensis	0.25	0.36	4.08	1.09	9.50
Sminthopsis hirtipes	0.00	0.11	3.15	0.44	7.33

Table A4.4.4 Prescribed-burn Mammals, Post-burn II

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Pseudomys desertor	1.11	1.81	6.94	1.46	20.92
Dasycercus blythi	0.19	1.06	6.69	1.56	20.16
Notomys alexis	3.36	3.06	4.85	1.59	14.63
Pseudomys hermannsburgensis	2.22	2.33	4.82	1.31	14.53
Sminthopsis hirtipes	0.00	0.19	2.73	1.10	8.24
Ningaui ridei	0.08	0.19	2.73	1.10	8.24
Sminthopsis youngsoni	0.08	0.14	2.47	1.20	7.11

Table A4.4.5 Prescribed-burn Lizards, Post-burn I

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Lerista labialis	1.75	0.61	6.23	1.67	9.20
Ctenotus ariadnae	0.14	0.25	4.93	1.24	7.28
Ctenophorus nuchalis	0.28	0.00	4.55	1.30	6.72
Varanus brevicauda	0.22	0.17	3.81	1.06	5.63
Ctenophorus isolepis	0.08	0.25	3.73	0.99	5.51
Varanus gouldii	0.17	0.06	3.46	1.17	5.11
Ctenotus dux	0.11	0.19	3.41	1.05	5.03
Diplodactylus stenodactylus	0.11	0.00	3.09	1.21	4.57
Egernia inornata	0.14	0.03	3.06	0.96	4.51
Menetia greyii	0.08	0.08	2.95	0.99	4.35
Eremiascincus fasciolatus	0.08	0.06	2.68	0.69	3.96
Rhynchoedura ornata	0.08	0.03	2.45	0.90	3.62
Diporiphora winneckei	0.00	0.08	2.42	0.88	3.58
Morethia ruficauda	0.00	0.11	2.20	0.66	3.25
Ctenotus piankai	0.08	0.03	2.12	0.74	3.13
Ctenotus calurus	0.00	0.08	2.02	0.62	2.98
Ctenotus leae	0.08	0.00	1.94	0.94	2.86
Ctenotus pantherinus	0.06	0.06	1.89	0.72	2.79
Heteronotia binoei	0.03	0.03	1.61	0.58	2.37
Strophurus ciliaris	0.06	0.03	1.6	0.59	2.37
Ctenophorus clayi	0.06	0.00	1.48	0.67	2.19

Table A4.4.6 Prescribed-burn Lizards, Post-burn II

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Ctenophorus isolepis	0.25	0.22	9.03	1.62	12
Ctenotus pantherinus	0.33	0.25	7.78	1.00	10.35
Ctenotus dux	0.17	0.28	6.48	0.93	8.62
Ctenophorus nuchalis	0.00	0.11	6.12	0.99	8.14
Ctenotus helenae	0.00	0.22	5.97	1.24	7.93
Varanus eremius	0.00	0.22	5.95	1.19	7.91
Lerista labialis	0.17	0.17	5.62	1.01	7.48
Ctenotus piankai	0.00	0.08	3.24	0.90	4.31
Morethia ruficauda	0.06	0.03	2.99	0.66	3.98
Ctenotus calurus	0.03	0.06	2.47	0.58	3.28
Varanus gouldii	0.03	0.03	1.76	0.57	2.34
Varanus brevicauda	0.03	0.03	1.76	0.57	2.33
Ctenotus ariadnae	0.03	0.03	1.67	0.59	2.22
Diporiphora winneckei	0.03	0.03	1.56	0.60	2.07
Egernia inornata	0.03	0.03	1.44	0.60	1.92
Delma nasuta	0.00	0.03	1.38	0.42	1.83
Lerista xanthura	0.06	0.00	1.33	0.43	1.77
Ctenotus leonhardii	0.00	0.03	1.21	0.42	1.61

Table A4.4.7 Wildfire Plants, Post-burn I

Species	Mean Cover: Burnt Sites	Mean Cover: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Triodia basedowii	4.24	26.42	17.46	2.34	24.2
Aristida contorta	0.69	4.83	7.18	1.26	9.95
Grevillea stenobotrya	0.00	1.11	3.18	0.58	4.41
Eriachne aristidea	0.86	0.03	2.71	0.84	3.76
Acacia ligulata	0.06	1.39	2.63	0.72	3.65
Eragrostis eriopoda	0.08	0.75	2.60	1.06	3.61
Sida fibulifera	0.31	0.50	2.55	1.16	3.54
Grevillea juncifolia	0.56	0.56	2.32	0.60	3.22
Triumfetta winneckeana	0.28	0.00	2.11	1.16	2.93
Dodonaea viscosa	0.00	0.42	2.08	0.64	2.88
Goodenia cycloptera	0.31	0.22	2.00	1.32	2.77
Crotalaria eremaea	0.11	0.33	1.89	0.83	2.61
Scaveola depauperata	0.14	0.17	0.61	0.72	2.24
Acacia dictyophleba	0.00	0.42	1.59	0.44	2.20
Euphorbia drummondii	0.19	0.03	1.49	1.04	2.07
Halgania cyanea	0.03	0.56	1.44	0.59	2.00
Yakirra australiensis	0.28	0.00	1.37	0.66	1.91
Grevillea striata	0.00	0.83	1.37	0.44	1.90
Senna pleurocarpa	0.17	0.00	1.29	0.89	1.79
Eucalyptus pachyphylla	0.03	0.28	1.21	0.55	1.68
Trichodesma zeylanicum	0.06	0.14	1.06	0.82	1.47
Eremophila obovata	0.00	0.28	1.01	0.44	1.41
Adriana tormentosa	0.31	0.00	0.98	0.44	1.35
Dicrastylis costelloi	0.06	0.06	0.93	0.83	1.29
Newcastelia spodiotricha	0.06	0.03	0.83	0.76	1.14

Table A4.4.8 Wildfire Plants, Post-burn II

Species	Mean Cover: Burnt Sites	Mean Cover: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Triodia basedowii	6.50	35.69	19.41	2.16	26.16
Grevillea stenobotrya	0.28	2.92	4.97	0.88	6.70
Aristida contorta	0.92	2.11	4.22	1.11	5.68
Senna pleurocarpa	0.97	0.00	3.48	1.07	4.69
Dicrastylis costelloi	0.64	0.00	2.80	1.19	3.78
Crotalaria eremaea	0.14	0.78	2.68	0.84	3.62
Eragrostis eriopoda	0.03	0.56	2.47	1.03	3.33
Dodonaea viscosa	0.00	0.69	2.35	0.61	3.16
Acacia dictyophleba	0.17	0.69	2.19	0.68	2.95
Halgania cyanea	0.17	0.42	2.17	1.00	2.92
Acacia ligulata	0.06	0.56	2.14	0.82	2.89
Eucalyptus pachyphylla	0.56	0.00	1.96	0.67	2.64
Sida fibulifera	0.17	0.36	1.89	0.74	2.55
Paractaenum refractum	0.47	0.00	1.87	0.69	2.53
Petalostylis cassioides	0.47	0.00	1.85	0.67	2.49
Eremophila obovata	0.00	0.42	1.69	0.68	2.28
Yakirra australiensis	0.19	0.00	1.57	1.31	2.12
Newcastelia spodiotricha	0.44	0.00	1.32	0.44	1.78
Eremophila longifolia	0.06	0.17	1.23	0.83	1.65
Tephrosia rosea	0.22	0.00	1.16	0.62	1.56
Euphoria drummondii	0.11	0.00	1.11	0.96	1.49
Rulingia loxophylla	0.42	0.00	1.07	0.44	1.44
Triumfetta winneckeana	0.14	0.00	0.81	0.44	1.10
Adriana hookeri	0.14	0.00	0.71	0.44	0.96

Table A4.4.9 Wildfire Mammals, Post-burn I

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Pseudomys hermannsburgensis	0.29	1.87	13.31	1.59	27.11
Pseudomys desertor	0.03	1.12	12.25	2.33	24.95
Notomys alexis	0.79	1.29	6.71	1.29	13.66
Ningaui ridei	0.14	0.09	4.33	1.06	8.83
Dasycercus blythi	0.24	0.44	4.32	1.03	8.80
Sminthopsis youngsoni	0.08	0.13	4.21	0.99	8.58

Table A4.4.10 Wildfire Mammals Post-burn II

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Ningaui ridei	0.03	0.61	21.40	1.75	37.89
Pseudomys hermannsburgensis	0.06	0.17	10.06	1.12	17.81
Pseudomys desertor	0.00	0.14	9.76	0.91	17.27
Dasycercus blythi	0.08	0.08	8.51	0.81	15.06
Sminthopsis youngsoni	0.03	0.03	4.20	0.60	7.44

Table A4.4.11 Wildfire Lizards Post-burn I

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Lerista labialis	0.40	0.41	10.78	1.50	13.52
Varanus gouldii	0.17	0.07	5.83	1.01	7.31
Ctenophorus isolepis	0.14	0.14	5.61	1.01	7.03
Egernia inornata	0.13	0.03	5.33	0.94	6.69
Ctenotus pantherinus	0.03	0.10	5.12	0.91	6.42
Ctenophorus nuchalis	0.16	0.00	4.74	0.67	5.95
Ctenotus ariadnae	0.06	0.14	4.70	1.00	5.90
Ctenotus dux	0.00	0.14	4.67	0.93	5.83
Menetia greyii	0.13	0.03	4.33	0.73	5.43
Ctenotus leae	0.07	0.06	3.55	0.86	4.45
Varanus brevicauda	0.07	0.03	3.54	0.72	4.44
Diplodactylus stenodactylus	0.07	0.00	2.82	0.67	3.54
Eremiascincus fasciolatus	0.00	0.06	1.97	0.69	2.47
Ctenotus calurus	0.00	0.03	1.88	1.42	2.36
Ctenotus regius	0.00	0.03	1.88	0.42	2.36
Lophognathus longirostris	0.04	0.00	1.65	0.43	2.07
Ctenotus helenae	0.04	0.00	1.65	0.43	2.07

T able A4.4.12 Wildfire Lizards Post-burn II

Species	Mean Abundance: Burnt Sites	Mean Abundance: Unburnt Sites	Mean Dissim.	Dissim./ SD	% Cont.
Lerista labialis	1.22	0.42	12.23	1.25	17.08
Ctenotus pantherinus	0.06	0.31	7.60	1.23	10.62
Nephrurus levis	0.17	0.06	5.94	0.87	8.30
Ctenophorus isolepis	0.19	0.08	5.61	0.92	7.84
Varanus brevicauda	0.06	0.08	4.02	0.88	5.61
Menetia greyii	0.00	0.06	3.55	0.60	4.96
Egernia inornata	0.08	0.03	3.28	0.74	4.59
Ctenophorus nuchalis	0.06	0.00	3.18	0.57	4.45
Lerista aericeps	0.06	0.00	3.04	0.65	4.25
Ctenotus calurus	0.06	0.03	2.88	0.75	4.02
Lucasium damaeum	0.08	0.00	2.76	0.64	3.86
Ctenotus dux	0.06	0.06	2.58	0.60	3.61
Ctenotus ariadnae	0.00	0.06	2.26	0.67	3.15
Rhynchoedura ornata	0.06	0.00	2.24	0.67	3.13
Ctenotus brooksi	0.00	0.03	1.42	0.42	1.98
Diporiphora winneckei	0.00	0.03	1.42	0.42	1.98
Varanus gouldii	0.03	0.00	1.37	0.43	1.92

APPENDICES: CHAPTER 5

Appendix 5.1 Species List

Appendix 5.2 Analysis of Variance Results

Appendix 5.3 Canonical analysis of principal coordinates (CAP) summary

Appendix 5.4 Pearson correlations of species/habitat variables with CAP Axes

Appendix 5.1 Species List

Table A5.1 Lizard captures in burnt (B), ecotone (E) and unburnt (U) habitat in the three study regions.

	Field River			Ethabuka East			Kunnamuka Swamp		
	B	**E**	**U**	**B**	**E**	**U**	**B**	**E**	**U**
Ctenophorus clayi	4	2	1	0	0	0	0	0	0
Ctenophorus isolepis	2	1	0	0	0	0	1	3	5
Ctenophorus nuchalis	22	11	8	17	25	10	2	1	0
Ctenotus ariadnae	2	0	4	1	0	0	0	0	1
Ctenotus calurus	0	1	0	0	0	1	0	0	0
Ctenotus dux	0	0	0	0	1	1	1	0	0
Ctenotus helenae	0	0	0	0	0	0	0	1	0
Ctenotus leae	1	0	0	0	0	1	0	0	0
Ctenotus pantherinus	0	0	2	0	2	0	0	0	1
Diplodactylus conspicillatus	0	0	0	0	0	0	0	1	0
Diporiphora winneckei	2	2	0	0	0	0	0	0	0
Egernia inornata	3	1	3	0	0	1	0	0	1
Eremiascincus fasciolatus	5	2	1	0	0	0	0	0	0
Heteronotia binoei	0	2	0	0	1	0	0	0	0
Lerista labialis	13	24	12	16	29	13	10	8	0
Menetia greyii	0	1	4	0	4	5	2	0	0
Nephrurus levis	0	0	1	0	1	0	0	0	0
Rhynchoedura ornata	1	1	0	0	2	2	0	1	0
Strophurus ciliaris	1	0	0	0	0	0	0	0	0
Varanus brevicauda	0	0	2	0	2	1	1	1	1
Varanus gouldii	1	1	0	0	0	0	0	1	0
Total	**57**	**49**	**38**	**34**	**67**	**35**	**17**	**17**	**9**

Appendix 5.2 Analysis of Variance Results

Results of Analyses of Variance investigating the effects of a wildfire on lizard abundance and diversity in three spatially-independent regions of the Simpson Desert, central Australia.

Table A5.2.1 Lizard abundance

	SS	df	MS	F	*P*
Fire	1.130	2	0.565	1.688	0.294
Region	5.442	2	2.721	8.126	**0.039**
Fire * Region	1.339	4	0.335	1.750	0.223

Table A5.2.2 Lizard diversity

	SS	df	MS	F	*P*
Fire	0.153	2	0.077	0.331	0.736
Region	1.408	2	0.704	3.040	0.157
Fire * Region	0.926	4	0.232	2.922	0.084

Note: The effect of the fire was tested in burnt, ecotone and unburnt habitats. A statistically significant fire × region interaction indicates the effect of the fire on lizard abundance or diversity differed according to region. Statistical significance is taken at $P \leq 0.05$ and significant *P* values are indicated in boldface type.

Appendix 5.3 Canonical Analysis of Principal Coordinates (CAP) Summary

Table A5.3 Results from the canonical analysis of principal coordinates (CAP), summarising the chosen number of principle coordinate axes (m), the percent variation explained by each ordination (% variation), Pillai's trace statistic (Q0m'HQ0m) and statistical significance (P). Statistical significance is taken at P ≤ 0.05 and significant P values are indicated in boldface type. The chosen number of principle coordinate axes (m) and the percent variation explained by these is the same for the three lizard analyses and the two habitat variable analyses. This is because these three canonical (CAP) analyses were based on the same principle coordinates anlaysis (PCO). The PCO was then followed by a unique canonical analysis of these principle coordinates (CAP) which tested the relationship of the ordination to fire, region, or the external habitat variable matrix.

	m	**% variation**	**$Q^0_m{}'HQ^0_m$**	***P***
Lizards and fire	3	73.01	0.40215	0.3484
Lizards and region	3	73.01	1.22831	**0.0001**
Lizards against habitat	3	73.01	1.98874	**0.0176**
Habitat variables and fire	2	93.29	0.90659	**0.0005**
Habitat variables and region	2	93.29	0.93669	**0.0004**

Appendix 5.4 Pearson Correlations of Species / Habitat Variables with CAP Axes.

Table A5.4.1 Pearson correlations of the lizard species with each of the CAP axes when the ordination was analysed by region (refer to Figure 5.5).

	CAP Axis 1	CAP Axis 2
C. clayi	0.738379	-0.43876
C. isolepis	-0.42133	-0.72904
C. nuchalis	0.822705	0.26268
C. ariadnae	0.322526	-0.33073
C. calurus	0.230233	0.288664
C. dux	-0.05858	0.42094
C. helenae	-0.46314	-0.10655
C. leae	0.258295	-0.05351
C. pantherinus	0.055702	0.084271
D. conspicillatus	-0.14927	-0.05549
D. winneckei	0.508282	-0.41896
E. inornata	0.397461	-0.57298
E. fasciolatus	0.580545	-0.41784
H. binoei	0.354945	0.117094
L. labialis	0.501562	0.620442
M. greyii	0.027356	0.542954
N. levis	0.074888	0.144746
R. ornata	0.295433	0.313143
S. ciliaris	0.405189	-0.15834
V. brevicauda	-0.44659	0.10708
V. gouldii	0.320369	-0.09813

Table A5.4.2 Pearson correlations of the habitat variables with each of the CAP axes when the lizard matrix was analysed against the external matrix of habitat and resource variables (refer to Figure 5.6a).

	CAP Axis 1	CAP Axis 2
Forbs	0.558685	0.02555
Grasses	-0.5908	0.517906
Lying wood	-0.58147	-0.18686
Shrubs	0.226249	0.171614
Rainfall 0-9 mth	-0.71563	-0.39891
Invertebrate abundance	0.658255	-0.08554
Spinifex	-0.24951	-0.23836
Total plant cover	-0.16792	-0.19343

Table A5.4.3 Pearson correlations of the lizard species with each of the CAP axes when the lizard matrix was analysed against the external matrix of habitat and resource variables (refer to Figure 5.6b).

	CAP Axis 1	CAP Axis 2
C. clayi	0.630619	0.601796
C. isolepis	-0.57458	0.69886
C. nuchalis	0.792448	0.135707
C. ariadnae	0.40042	-0.13854
C. calurus	0.227434	-0.0443
C. dux	-0.04099	-0.19138
C. helenae	-0.50629	0.124347
C. leae	0.211336	0.214335
C. pantherinus	0.204924	-0.54466
D. conspicillatus	-0.21191	0.218453
D. winneckei	0.400658	0.566288
E. inornata	0.322875	0.479967
E. fasciolatus	0.49363	0.501974
H. binoei	0.300987	0.202024
L. labialis	0.484951	-0.05691
M. greyii	0.116816	-0.46975
N. levis	0.129525	-0.22543
R. ornata	0.256818	0.083507
S. ciliaris	0.344898	0.310482
V. brevicauda	-0.40181	-0.24612
V. gouldii	0.225437	0.404692

Table A5.4.4 Pearson correlations of the habitat and resource variables with each of the CAP axes when the ordination was analysed by fire history (refer to Figure 5.7).

	CAP Axis 1	CAP Axis 2
Forbs	-0.13586	0.439241
Grasses	-0.04611	-0.38353
Lying wood	0.5572	-0.51419
Shrubs	0.435239	0.552318
Rainfall 0-9 month prior	0.018839	-0.94164
Invertebrate abundance	0.241391	0.778989
Spinifex	0.952185	-0.11756
Total plant cover	0.972721	0.003911

Table A5.4.5: Pearson correlations of the habitat and resource variables with each of the CAP axes when the ordination was analysed by region (refer to Figure 5.8).

	CAP Axis 1	CAP Axis 2
Forbs	-0.44358	0.120937
Grasses	0.381758	0.059042
Lying wood	0.532721	-0.53951
Shrubs	-0.5373	-0.45365
Rainfall 0-9 months prior	0.941735	0.01299
Invertebrate abundance	-0.77039	-0.26757
Spinifex	0.149668	-0.94767
Total plant cover	0.028959	-0.9723

APPENDICES: CHAPTER 6

Appendix 6.1	Analysis of variance results for cats and fox activity at varying distances from a fire ecotone
Appendix 6.2	Significant Tukey's HSD tests for cat activity
Appendix 6.3	Significant Tukey's HSD test for fox activity
Appendix 6.4	Two-factor ANOVA for cage experiment GUDs
Appendix 6.5	Two-factor nested ANOVA for tunnel experiment GUDs
Appendix 6.6	Significant Tukey's HSD test for *Pseudomys hermannsburgensis* GUDs in the tunnel experiment

Appendix 6.1

Table A6.1.1 One-factor ANOVA for the presence of cats as detected by sandplots at various distances from a wildfire burn ecotone over four years in the Simpson Desert, central Australia. The factor is distance from the burn ecotone (Distance). Significant results are in bold. Due to heterogeneous variances significance has been taken at $P \leq 0.01$ for the 2006 analysis. Significance for all other analyses has been taken at $P \leq 0.05$.

Sampling Year	**Factor**	**d.f.**	**SS**	***F***	***P***
2005	Distance	8	10.280	11.152	**<0.001**
	Error	18	2.074		
2006	Distance	8	8.444	1.733	**0.158**
	Error	18	10.963		
2007	Distance	8	20.977	9.936	**<0.001**
	Error	18	4.750		
2008	Distance	8	14.854	12.340	**<0.001**
	Error	18	2.708		

Table A6.1.2 One-factor ANOVA for the presence of foxes as detected by sandplots at various distances from a wildfire burn ecotone over four years in the Simpson Desert, central Australia. The factor is distance from the burn ecotone (Distance). Significant results are in bold. Due to heterogeneous variances significance has been taken at *P* ≤ 0.01 for the 2005, 2006 and 2008 analyses. Significance for all other analyses has been taken at *P* ≤ 0.05.

Sampling Year	**Factor**	**d.f.**	**SS**	***F***	***P***
2005	Distance	8	12.148	8.386	**<0.001**
	Error	18	3.259		
2006	Distance	8	0.565	0.704	0.685
	Error	18	0.802		
2007	Distance	8	17.796	14.785	**<0.001**
	Error	18	2.708		
2008	Distance	8	13.977	3.692	**0.01**
	Error	18	8.519		

Appendix 6.2

Table A6.2.1 Significant Tukey's HSD test for cat activity as sampled in 2005 by sandplots at nine distances from a wildfire burn ecotone in the Simpson Desert, central Australia. Significance has been taken at $P \leq 0.05$ and P values have been Bonferroni-adjusted. Significant results are in bold.

Transect Position*		**Mean Difference**	**95% Confidence Interval**		***P***
			Lower Bound	**Upper Bound**	
B1000	E	-1.6667	-2.6378	-0.6955	**<0.001**
B750	E	-1.6667	-2.6378	-0.6955	**<0.001**
B500	B10	-1.3333	-2.3045	-0.3622	**0.024**
B500	E	-2.0000	-2.9711	-1.0289	**<0.001**
B250	E	-1.7778	-2.7489	-0.8066	**<0.001**
B10	B500	1.3333	0.3622	2.3045	**0.024**
E	B1000	1.6667	0.6955	2.6378	**<0.001**
E	B250	1.7778	0.8066	2.7489	**<0.001**
E	B500	2.0000	1.0289	2.9711	**<0.001**
E	B750	1.6667	0.6955	2.6378	**<0.001**
E	UB10	1.4444	0.4733	2.4156	**0.016**
E	UB250	1.7778	0.8066	2.7489	**<0.001**
E	UB500	1.7778	0.8066	2.7489	**<0.001**
UB10	E	-1.4444	-2.4156	-0.4733	**0.016**
UB250	E	-1.7778	-2.7489	-0.8066	**<0.001**
UB500	E	-1.7778	-2.7489	-0.8066	**<0.001**

*Explanation of codes: UB = Unburnt, E = Ecotone, B = Burnt. The numerals 10, 250, 500, 750 and 1000 refer to the distance (in metres) from the Ecotone into the Burnt or Unburnt habitat where that transect was located. For example, UB10 indicates a transect that was located 10m into the unburnt habitat.

Table A6.2.2 Significant Tukey's HSD test for cat activity as sampled in 2007 by sandplots at nine distances from a wildfire burn ecotone in the Simpson Desert, central Australia. Significance has been taken at $P \leq 0.05$ and P values have been Bonferroni-adjusted. Significant results are in bold.

Transect Position*		**Mean Difference**	**95% Confidence Interval**		***P***
			Lower Bound	**Upper Bound**	
B10	B1000	2.1667	0.697	3.6363	**0.016**
B10	B750	1.9167	0.447	3.3863	**0.048**
B10	UB500	2.0000	0.5304	3.4696	**0.032**
B1000	B10	-2.1667	-3.6363	-0.697	**0.016**
B1000	E	-2.5833	-4.053	-1.1137	**<0.001**
B250	E	-2.0833	-3.553	-0.6137	**0.024**
B500	E	-2.2500	-3.7196	-0.7804	**0.008**
B750	B10	-1.9167	-3.3863	-0.447	**0.048**
B750	E	-2.3333	-3.803	-0.8637	**0.008**
E	B1000	2.5833	1.1137	4.053	**<0.001**
E	B250	2.0833	0.6137	3.553	**0.024**
E	B500	2.2500	0.7804	3.7196	**0.008**
E	B750	2.3333	0.8637	3.803	**0.008**
E	UB10	2.0833	0.6137	3.553	**0.024**
E	UB250	2.2500	0.7804	3.7196	**0.008**
E	UB500	2.4167	0.947	3.8863	**<0.001**
UB10	E	-2.0833	-3.553	-0.6137	**0.024**
UB250	E	-2.2500	-3.7196	-0.7804	**0.008**
UB500	B10	-2.0000	-3.4696	-0.5304	**0.032**
UB500	E	-2.4167	-3.8863	-0.947	**<0.001**

*Explanation of codes: UB = Unburnt, E = Ecotone, B = Burnt. The numerals 10, 250, 500, 750 and 1000 refer to the distance (in metres) from the Ecotone into the Burnt or Unburnt habitat where that transect was located. For example, UB10 indicates a transect that was located 10m into the unburnt habitat.

Table A6.2.3 Significant Tukey's HSD test for cat activity as sampled in 2008 by sandplots at nine distances from a wildfire burn ecotone in the Simpson Desert, central Australia. Significance has been taken at $P \leq 0.05$ and P values have been Bonferroni-adjusted. Significant results are in bold.

Transect Position*		**Mean Difference**	**95% Confidence Interval**		***P***
			Lower Bound	**Upper Bound**	
B10	B1000	1.6667	0.5569	2.7764	**0.008**
B10	B500	1.6667	0.5569	2.7764	**0.008**
B10	B750	1.4722	0.3625	2.5819	**0.04**
B1000	B10	-1.6667	-2.7764	-0.5569	**0.008**
B1000	E	-2.2778	-3.3875	-1.1681	**<0.001**
B250	E	-1.7222	-2.8319	-0.6125	**0.008**
B500	B10	-1.6667	-2.7764	-0.5569	**0.008**
B500	E	-2.2778	-3.3875	-1.1681	**<0.001**
B750	B10	-1.4722	-2.5819	-0.3625	**0.04**
B750	E	-2.0833	-3.1931	-0.9736	**<0.001**
E	B1000	2.2778	1.1681	3.3875	**<0.001**
E	B250	1.7222	0.6125	2.8319	**0.008**
E	B500	2.2778	1.1681	3.3875	**<0.001**
E	B750	2.0833	0.9736	3.1931	**<0.001**
E	UB250	1.8056	0.6958	2.9153	**0.008**
E	UB500	1.8056	0.6958	2.9153	**0.008**
UB250	E	-1.8056	-2.9153	-0.6958	**0.008**
UB500	E	-1.8056	-2.9153	-0.6958	**0.008**

*Explanation of codes: UB = Unburnt, E = Ecotone, B = Burnt. The numerals 10, 250, 500, 750 and 1000 refer to the distance (in metres) from the Ecotone into the Burnt or Unburnt habitat where that transect was located. For example, UB10 indicates a transect that was located 10m into the unburnt habitat.

Appendix 6.3

Table A6.3.1 Significant Tukey's HSD test for fox activity as sampled in 2005 by sandplots at nine distances from a wildfire burn ecotone in the Simpson Desert, central Australia. Significance has been taken at *P* ≤ 0.05 and *P* values have been Bonferroni-adjusted. Significant results are in bold.

Transect Position*		**Mean Difference**	**95% Confidence Interval**		***P***
			Lower Bound	**Upper Bound**	
B1000	E	-1.8889	-3.1063	-0.6715	**0.008**
B250	E	-1.6667	-2.884	-0.4493	**0.032**
B500	E	-2.0000	-3.2174	-0.7826	**<0.001**
B750	E	-1.8889	-3.1063	-0.6715	**0.008**
E	B1000	1.8889	0.6715	3.1063	**0.008**
E	B250	1.6667	0.4493	2.884	**0.032**
E	B500	2.0000	0.7826	3.2174	**<0.001**
E	B750	1.8889	0.6715	3.1063	**0.008**
E	UB250	2.0000	0.7826	3.2174	**<0.001**
E	UB500	1.7778	0.5604	2.9952	**0.016**
UB250	E	-2.0000	-3.2174	-0.7826	**<0.001**
UB500	E	-1.7778	-2.9952	-0.5604	**0.016**

*Explanation of codes: UB = Unburnt, E = Ecotone, B = Burnt. The numerals 10, 250, 500, 750 and 1000 refer to the distance (in metres) from the Ecotone into the Burnt or Unburnt habitat where that transect was located. For example, UB10 indicates a transect that was located 10m into the unburnt habitat.

Table A6.3.2 Significant Tukey's HSD test for fox activity as sampled in 2007 by sandplots at nine distances from a wildfire burn ecotone in the Simpson Desert, central Australia. Significance has been taken at $P \leq 0.05$ and P values have been Bonferroni-adjusted. Significant results are in bold.

Transect Position*		**Mean Difference**	**95% Confidence Interval**		***P***
			Lower Bound	**Upper Bound**	
B10	B750	1.5000	0.3903	2.6097	**0.032**
B10	UB250	1.5000	0.3903	2.6097	**0.032**
B1000	E	-2.3333	-3.4431	-1.2236	**<0.001**
B250	E	-2.1667	-3.2764	-1.0569	**<0.001**
B500	E	-2.3333	-3.4431	-1.2236	**<0.0010**
B750	B10	-1.5000	-2.6097	-0.3903	**0.032**
B750	E	-2.6667	-3.7764	-1.5569	**<0.001**
E	B1000	2.3333	1.2236	3.4431	**<0.001**
E	B250	2.1667	1.0569	3.2764	**<0.001**
E	B500	2.3333	1.2236	3.4431	**<0.001**
E	B750	2.6667	1.5569	3.7764	**<0.001**
E	UB10	1.9167	0.8069	3.0264	**<0.001**
E	UB250	2.6667	1.5569	3.7764	**<0.001**
E	UB500	2.3333	1.2236	3.4431	**<0.001**
UB10	E	-1.9167	-3.0264	-0.8069	**<0.001**
UB250	B10	-1.5000	-2.6097	-0.3903	**0.032**
UB250	E	-2.6667	-3.7764	-1.5569	**<0.001**
UB500	E	-2.3333	-3.4431	-1.2236	**<0.001**

*Explanation of codes: UB = Unburnt, E = Ecotone, B = Burnt. The numerals 10, 250, 500, 750 and 1000 refer to the distance (in metres) from the Ecotone into the Burnt or Unburnt habitat where that transect was located. For example, UB10 indicates a transect that was located 10m into the unburnt habitat.

Appendix 6.4

Table A6.4.1 Two-factor ANOVA for the giving-up density (GUD) of Pseudomys hermannsburgensis across three exclusion cage treatments and three independent sampling sessions in burnt and unburnt habitat in the Simpson Desert, central Australia. Factors are Fire (burnt, unburnt) and Cage (predator exclusion cage, cage control and open control). Significance has been taken at $P \leq 0.05$ and significant results are in bold.

Sampling Month	**Factor**	**d.f.**	**SS**	***F***	***P***
February 2008	Fire	1	941.296	47.186	**<0.001**
	Cage	2	294.836	7.390	**0.001**
	Fire*Cage	2	644.146	16.145	**<0.001**
	Error	85	1695.633		
April 2008	Fire	1	307.973	17.629	**<0.001**
	Cage	2	342.922	9.815	**<0.001**
	Fire*Cage	2	233.558	6.685	**0.003**
	Error	47	821.056		
June 2008	Fire	1	594.377	43.527	**<0.001**
	Cage	2	268.860	9.844	**<0.001**
	Fire*Cage	2	29.039	10.766	**<0.001**
	Error	38	518.906		

Table A6.4.2 Two-factor ANOVA for the giving-up density (GUD) of Notomys alexis across three exclusion cage treatments and three independent sampling sessions in burnt and unburnt habitat in the Simpson Desert, central Australia. Factors are Fire (burnt, unburnt) and Cage (predator exclusion cage, cage control and open control). Significance has been taken at *P* ≤ 0.05 and significant results are in bold.

Sampling Month	**Factor**	**d.f.**	**SS**	***F***	***P***
February 2008	Fire	1	228.773	16.512	**<0.001**
	Cage	2	81.049	2.925	**0.007**
	Fire*Cage	2	271.810	9.809	**0.001**
	Error	28	387.931		
April 2008	Fire	1	160.164	10.719	**0.002**
	Cage	2	39.877	1.334	0.276
	Fire*Cage	2	44.901	1.503	0.237
	Error	35	522.957		
June 2008	Fire	1	224.271	16.141	**<0.001**
	Cage	2	68.236	2.456	0.100
	Fire*Cage	2	97.177	3.497	**0.041**
	Error	37	514.082		

Table A6.4.3 Two-factor ANOVA for the giving-up density (GUD) of Sminthopsis hirtipes across three exclusion cage treatments and three independent sampling sessions in burnt and unburnt habitat in the Simpson Desert, central Australia. Factors are Fire (burnt, unburnt) and Cage (predator exclusion cage, cage control and open control). Due to heterogeneous variances, significance has been taken at *P* ≤ 0.01 for the June 2008 analysis. Significance has been taken at *P* ≤ 0.05 for all other analyses. Significant results are in bold.

Sampling Month	**Factor**	**d.f.**	**SS**	***F***	***P***
February 2008	Fire	1	132.543	34.817	<0.001
	Cage	2	122.395	16.076	<0.001
	Fire*Cage	2	71.430	9.382	<0.001
	Error	60	228.408		
April 2008	Fire	1	51.566	25.394	**<0.001**
	Cage	2	5.637	14.684	**<0.001**
	Fire*Cage	2	12.296	3.028	0.081
	Error	14	28.429		
June 2008	Fire	1	55.652	12.981	0.002
	Cage	2	12.898	1.504	0.244
	Fire*Cage	2	27.623	3.222	0.059
	Error	22	94.314		

Appendix 6.5

Table A6.5 Two-factor nested ANOVA for the giving-up density (GUD) of two species of small mammal under three predator manipulation tunnel treatments and at varying distances from a wildfire ecotone in the Simpson Desert, central Australia. Factors are Tunnel (predator exclusion tunnel, tunnel control and open control) and Distance from the fire ecotone. The tunnels were positioned in 225 m transects running perpendicular to a wildfire burn ecotone and the food patches were located at 25 m intervals along each tunnel. Apart from the Unburnt and Ecotone patches, all food patches were located in the burnt habitat. Distance is nested within Tunnel. Significant results are in bold. Due to heterogeneous variances significance has been taken at $P \leq 0.01$ for the *N. alexis* analyses. Significance has been taken at $P \leq 0.05$ for all other analyses.

Species	**Factor**	**d.f.**	**SS**	***F***	***P***
Pseudomys hermannsburgensis	Tunnel	2	232.804	8.084	**0.002**
	Distance	27	413.902	2.808	**0.001**
	Error	44	240.208		
Notomys alexis	Tunnel	2	50.868	2.308	0.118
	Distance	27	302.160	1.455	0.133
	Error	43	330.836		

Appendix 6.6

Table A6.6 Significant Tukey's HSD test for Pseudomys hermannsburgensis foraging activity under three predator manipulation tunnel treatments in the Simpson Desert, central Australia, as sampled by giving-up densities (GUDs). The three treatments were a predator exclusion tunnel, tunnel control and open control. Significance has been taken at *P* ≤ 0.05 and *P* values have been Bonferroni-adjusted. Significant results are in bold.

Tunnel Treatment		**Mean Difference**	**95% Confidence Interval**		***P***
			Lower Bound	**Upper Bound**	
Exclosure	Open	-3.2671	-4.8619	-1.6723	**<0.001**
	Tunnel control	-3.5859	-5.1807	-1.9911	**<0.001**
Open	Exclosure	3.2671	1.6723	4.8619	**<0.001**
Tunnel control	Exclosure	3.5859	1.9911	5.1807	**<0.001**