Fire and fragmentation interactions: effects on reptiles and small mammals in modified semi-arid landscapes

Moloch horridus **– juvenile Thorny Devil**

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Declaration

This thesis is my own work, except where otherwise acknowledged (see Preface and Acknowledgements).

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PREFACE

This thesis consists of four connected papers that present research I undertook for my doctoral program (Papers I-IV). The papers are framed by a brief Context Statement and Synthesis that explain the relationships between the papers and place my thesis in a broader ecological setting. One paper has been published (Paper II) and the remaining papers (Papers I, III and IV) have been prepared for publication, but not yet submitted. The papers were written to stand alone and for this reason there is some unavoidable repetition between them, for example in the background information and the description of study areas. References have been provided at the end of each paper, and a complete reference list is provided in the Consolidated Thesis References section at the end of this document.

I designed my research agenda in consultation with my supervisor, Don Driscoll, to ensure my project targeted specific fire and fragmentation interaction research within the framework of a broader project on the fire ecology of plants, birds and reptiles. The overarching study was funded predominantly by an Australian Research Council grant to Don Driscoll.

I performed the majority of the work for the papers that form this thesis, including developing research questions and experimental designs, conducting the field work for data collection and organised teams of volunteers to assist me. I also undertook the majority of work on the papers including literature searches, data analysis and writing the manuscripts. However, at each, but different, stage of the design, execution and write up of research, my supervisors (Don Driscoll, Chloe Sato, David Keith and Sam Banks) provided advice on how to conceptualise and interpret the findings, and also assisted with the revision of manuscripts. My statistical advisor (Hwan-Jin Yoon) provided expert advice for data analysis for the fire prediction paper. Where there are co-authors in each papers who are not listed as my supervisor, this reflects contributions from collaborators. All other contributions made to the work in this thesis are presented in the Acknowledgements section of each paper.

Paper I: Lazzari, J., Sato, C. F., Keith, D. A. and Driscoll, D. A. Does fire interact with habitat fragmentation to accelerate biodiversity loss? A systematic review. In Prep. for submission to *Journal of Applied Ecology*.

Paper II: Lazzari, J., Yoon, H. J., Keith, D. A. and Driscoll, D. A. Local environmental covariates are important for predicting fire history from tree stem diameters. International Journal of Wildland Fire, 24(6): 871-882. Available at: https://doi.org/10.1071/WF15069

Paper III: Lazzari, J., Sato, C. F., Driscoll, D. A. Fire and fragmentation interactions affect reptile persistence in an agricultural matrix and conservation reserve. In Prep. for submission to *Landscape Ecology*.

Paper IV: Lazzari, J., Sato, C. F., Banks, S. C., Driscoll, D. A. Does patch isolation affect small mammal occurrence and abundance after experimental fire in a fragmented landscape? In Prep. for submission to *Biological Conservation*.

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The South Australian Department of Environment and Natural Resources (DENR) helped me with access to field sites and research permits. Special thanks to Joe Tilley from the Port Lincoln branch for his support and expertise in undertaking the essential project burns. Funding and in-kind support was provided by: an Australian Postgraduate Award; the Australian National University; Deakin University-Burwood; and personal savings. The study was supported by funds from the Australian Research Council and conducted under DENR scientific permit K25737 and animal ethics permits 26/2009-M1 (Government of South Australia) and S.R.E.09.09 (Australian National University).

At a personal level, I expected to be challenged by undertaking such a large project, but I had not expected life's continuous curve balls that strongly tested the bounds of my sanity! Combining both academic and life challenges during my PhD certainly helped exceed my expectations of what I could achieve and overcome while under significant duress and living below the poverty line particularly for such a long period.

And last but not least, thanks to Thea Lazzari, May Lyons, Des Lyons, Orlando Lazzari and Mark Lazzari – many of you were there at the beginning of my PhD, but all of you are now just strong memories, I thank you for helping me distinguish between the priorities that are truly important in my life. Patting 'tolls' for Cookie, Mickey, Florence, Eddie, Bessie and Shadow provided welcome moments of micro-relaxation relief. Simply put – grazie!

ABSTRACT

Interactions between fire and fragmented landscapes could be a primary factor influencing the distribution and persistence of species. However, historical and recent land use change and land management practices have altered the spread, frequency and intensity of fires globally. This presents a major challenge to biodiversity management because ecosystems are being modified by fire in already fragmented systems.

Within fragmented fire-affected landscapes, the use or suppression of fire can provide successional habitats for a range of biota. However, records of fire history that are essential for managing fire-sensitive species, are often limited for many reserves and for remnant patches on private land. In addition, little is known about how reptiles and mammals use fragmented fire-affected landscapes, nor the role of reserves and remnants in mediating the interacting effects of these two major disturbances on co-occurring species. Due to this gap in understanding biodiversity responses to fire in fragmented landscapes, inappropriate fire regimes in such landscapes could lead to species losses.

My aim was to understand species responses to interactions between experimental fire and habitat fragmentation in an agricultural matrix. To achieve this, I conducted studies that specifically addressed: 1) the current status of research, 2) how to build on current knowledge to predict fire age, 3) reptile trait responses, and 4) how small mammals are affected. For study 1) I undertook a systematic review of the literature that discusses the fire-fragmentation interaction effects on biodiversity. For study 2) I developed a model to predict fire age using environmental covariates and stem diameters. For studies 3) and 4), I undertook a natural and manipulative experiment using fire in remnants and trapped reptiles and small mammals.

The key findings are: for study 1) there is limited peer reviewed research that investigates the effects of fire interactions with habitat fragmentation on biodiversity; for study 2) that local environmental covariates influence stem diameter growth, showing strong modelling potential

to predict fire age; for study 3) that reptile trait responses to fire by fragmentation interactions were not detected, but prescribed fire in remnants close to the reserve, with initially low abundance, may provide colonisation opportunities for insectivorous, nocturnal or burrowing species; and 4) that the occurrence of native mammals was affected more by fragmentation than by fire, including a lower occurrence in remnants than the reserve and in remnants further from the reserve, and conversely for the exotic mammal.

To improve our knowledge of reptiles and mammals in fragmented fire-affected, semi-arid mallee cropping landscapes, I recommend that: i) further testing and refining of the fire age prediction models to improve the reliability of mapping fire ages in remnants and reserves; ii) further research into species specific responses be undertaken, including by using reptile mark-recapture data collected in this study; and iii) future studies be undertaken over a longer period than my three year study. Also, to inform and improve conservation management of these species already persisting in small, long unburnt and isolated patches, I recommend that: iv) the use of prescribed fire in reserves and remnants be minimised while; v) more study is conducted to fill the research gaps into the effects of fire interactions with habitat fragmentation on species responses.

In making these recommendations, I emphasise that management strategies targeting the conservation of reptile and mammal persistence in fragmented and fire-affected mallee landscapes, need to i) take a precautionary approach to using prescribed fire, particularly while many of the cause and effect relationships of multiple environmental threats have not been established scientifically, and ii) urgently be informed by empirical research of reptile and mammal species in these landscapes.

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CONTEXT STATEMENT

Introduction

Disturbance ecology is an increasingly important sub-discipline of ecology that investigates the effects of anthropogenic disturbances on biodiversity (Haddad *et al.*, 2015). Key disturbances that often drive changes to ecological processes and systems include altered fire regimes (Bowman *et al.*, 2009) and fragmentation (Gonzalez *et al.*, 2011), and can result in habitat modification and loss (Bowman *et al.*, 2011; Fahrig, 2003). Depending on the habitat requirements of a species, fire or fragmentation can have positive or negative responses (Bond and Keeley, 2005; Fahrig 2017, 2018; Haddad *et al.*, 2015). These disturbances can also interact resulting in additional effects on ecological systems such as increases or declines in biota (Pastro *et al.*, 2011; Sauvajot, 1995). Fire has a major influence on plant and animal communities that can be beneficial and/or detrimental (Bond and Keeley, 2005). Fragmentation and habitat loss are among the worst threats to biodiversity globally (Haddad *et al.*, 2015), notwithstanding that species can respond positively to fragmentation once habitat loss has been accounted for (Fahrig 2017, 2018). These threats lead to the creation of patches of native vegetation (and habitat) that range from small, uncleared remnants to large patches of conservation reserve that encompass habitat patches (Schwartz and van Mantgem, 1997). In many human disturbed systems, remnant patches are often surrounded by a matrix – the cleared area between patches – that is often degraded and inhospitable to native fauna (Driscoll *et al.*, 2013). However, the dynamic agricultural cropping matrix has been identified as providing dispersal opportunities for some ground fauna (Rotem and Ziv, 2016). As a result of fragmentation, fire regimes are modified in these large and small patches, and the changed successional post-fire habitats to which species have adapted are disrupted affecting species persistence (Prowse *et al.*, 2017).

Fire and fragmentation can interact in a number of ways that affect biodiversity. Habitat loss can result from fragmentation (Fahrig, 2003) and species living in these habitat remnants become isolated (Gibson *et al.*, 2013). These species can be disadvantaged further by the resultant changes in natural fire regimes (Wilson *et al*., 2016). Modified fire regimes in small remnants can lead to local extinctions if species cannot recolonise or recover from *in situ* populations (Banks et al., 2011; Sanz-Aguilar *et al.*, 2011). Movement can become an important component in fire-prone environments (Pereoglou *et al.,* 2013; Pierson *et al.,* 2013;), particularly if recolonisation has to occur from outside the patch (Rotem and Ziv, 2016). Knowledge of fire-fragmentation interactions is important for species management (Auld and Keith, 2009), but there is limited information in this area of research. This is particularly the case for small remnants where deterministic extinctions can be followed by limited recolonisation (Driscoll and Henderson, 2008), and the repercussions of fire-fragmentation effects are often unclear (Bennett *et al.*, 2012; Sauvajot, 1995). This lack of research of fire and fragmentation interactions on species responses is challenged further by fire-history data in reserves and on private land often being incomplete or inaccurate (Gill, 2001; Penman *et al.*, 2011; Richards *et al.*, 1999).

Fire-history data are considered critical for understanding and managing fire dependent and fire specialist species living in fire-prone environments (Bradstock and Cohn, 2002; Hutto *et al.*, 2008). Fire histories are used to interpret and make inferences about abundance of fauna (Catling *et al.*, 2001; Kelly *et al.*, 2011; Smith *et al.*, 2012), vegetation succession and vegetation structure (Bergeron and Dansereau, 1993; Gosper *et al.*, 2012; Walsh *et al.*, 2006). This information can then be used to help make management decisions about when, or when not, to use fire. However, gaps in knowledge of fire history in both reserves and remnant vegetation impedes the implementation of effective conservation management at a species level.

In fragmented and fire-prone landscapes, there is evidence that some species tolerate fire less than the same species occupying non-fragmented habitat (Berkunsky *et al.*, 2015; Schrey *et al.*, 2016). This increased susceptibility may arise because dispersal-limited individuals have a lower capacity to escape fire in isolated patches (Neuwald and Templeton, 2013) leading to elevated direct mortality rates (Driscoll *et al.*, 2012). In addition, if fauna survive fire events they could be more susceptible to predation in structurally simplified post-fire remnant patches (How and Dell, 2000). Together, direct mortality, indirect mortality and emigration from patches during and after fire events may lead to local population extinctions.

Semi-arid mallee woodlands are an example of a fragmented and fire prone ecosystem in Australia that has the capacity to support a diversity of reptiles (Driscoll and Henderson, 2008) and small mammals (albeit less diverse and comprising both native and non-native species; (South Australian Government, 2010)). These co-occurring taxonomic groups have specific niche requirements and habitat preferences, as well as different dispersal abilities that affect their persistence – particularly in response to fire (Chia *et al.*, 2016; Neuwald and Templeton, 2013).

To assist the conservation of species in fire affected mallee remnants, the overarching aims of my research were to determine the number and type of fire and fragmentation interaction studies being undertaken and identify research gaps. I also investigate improved methods for predicting the fire age of mallee habitat which is essential knowledge to be able to map and manage the optimal habitat succession that meet the habitat needs of different species. My research aim was to also understand if large reserves with a combination of long unburnt or recently burnt vegetation can act as source populations for isolated remnant patches that support reptile and small mammal species. Recent research acknowledges that species persistence in fire-prone environments is dependent on understanding the interactions between fire and other processes such as fragmentation (Banks *et al.*, 2017; Griffiths and Brook, 2014; Kelly *et al.*, 2017). Thus, improving understanding of interactions between fire and fragmentation will inform the selection and implementation of effective conservation management actions.

Aims and Objectives

The aim of my research was to explore the effects of fire and fragmentation interactions on biodiversity. I did this by first undertaking a systematic review of the literature. More specifically, I sought to quantify the role of large reserves in supporting populations of native species in nearby remnant patches located in a highly modified cropping matrix. Small patches of habitat contain surviving fauna and are acknowledged as important habitat for conservation (Tulloch *et al.*, 2016) as are large reserves (Margules and Pressey, 2000). However, the fire ages and successional vegetation stages of small habitat patches are mostly unknown, yet many species have habitat preferences relating to time since fire. To examine the effects of fire and fragmentation on use and possible colonisation of remnant patches by reptiles and mammals, I experimentally manipulated fire in mallee woodlands in the northern Eyre Peninsula in South Australia. I undertook four separate studies: 1) a systematic review exploring fire and fragmentation interaction research to date and current knowledge gaps, 2) an empirical study investigating the inclusion of environmental covariates to improve the methods for predicting fire age in long-unburnt remnants using stem tree diameters, 3) a natural and manipulative experiment to explore how reptiles respond to fire and fragmentation interactions, and 4) a natural and manipulative experiment to quantify responses of small mammals to fire and fragmentation interactions. This research will help improve the conservation of biodiversity by enhancing knowledge of species-specific reptile and mammal responses to fire in fragmented environments, and thus help land managers design and implement the most appropriate fire management strategies (Keith, 2012). Furthermore, these results will help guide management using fire because the research was conducted at a spatial scale of relevance to land managers e.g. reserve scale.

In *Paper I*, I investigate fire/fragmentation related research to gauge what has been researched in this field of fire ecology. I did this by undertaking a systematic review. The review highlighted that there is limited research in fire-fragmentation interaction effects on biodiversity. In *Paper II*, I build on research by Clarke *et al.* (2010) who found that stem diameter was a useful predictor of fire age in mallee eucalypt species. I did this by examining the relative importance of environmental factors and fire on stem diameter growth in two species of mallee eucalypts. I developed a fire age prediction model and tested model predictions from four sites where fire history was mapped, and performance in another area using sites from outside the original sampling region. In *Paper III*, I examined responses of different reptile trait groups to fire and fragmentation treatments to determine which traits influence species persistence in isolated remnants, and whether nearby reserve populations are influential in species persistence (i.e. act as source populations for remnants). In *Paper IV*, I examined the combined effects of fire and fragmentation on the abundance of individual small mammal species with respect to habitat loss in an agricultural landscape.

Summary of Findings

Paper I: Does fire interact with habitat fragmentation to accelerate biodiversity loss? A Review

The systematic review I conducted in *Paper I* indicates there are few articles that specifically address how fire and fragmentation interact to affect biodiversity. Of the 33 review articles, there are five fire-fragmentation interaction types identified that affect biodiversity. These are: modifications to patch geometry, patch condition, edge habitat, the matrix, and connectivity. Within each category there were a wide range of interaction mechanisms, challenging the ability to draw robust and widely applicable generalisations about where fire occurrence is likely to decrease or increase in response to fragmentation in the landscape. However, despite the variability in how fire occurrence is influenced by fragmentation, overall there were more negative than positive effects on biodiversity across the five fire-fragmentation interaction categories. Overall, the systematic review identified that there are many gaps in our knowledge regarding the effects of fire-fragmentation interactions on biodiversity. In particular, the limited understanding that we have of fire-fragmentation interactions impedes effective management and may lead to implementing actions that perversely affect biodiversity. In response to this research challenge, I developed a conceptual diagram that integrates the: 1) three key components involved in fire-fragmentation interactions, i.e. fire, patch and matrix, 2) the biodiversity responses to fire-fragmentation interactions, and 3) the mechanisms of interaction responsible for influencing biodiversity. This diagram can be used to determine potential interaction mechanisms where there are few or no studies of a specific interaction type. It also can help to highlight where this a lack of research informing fire-fragmentation interaction types, thus helping to guide future research to maximise understanding of fire-fragmentation interactions.

Paper II: Local environmental covariates are important for predicting fire history from tree stem diameters

Paper II highlighted that, for two mallee woodland species for which I developed fire age prediction models, time since fire accounted for the greatest proportion of the explained variation in stem diameter but variation in mean stem diameters was also influenced by local environmental factors. The simple tool I developed to predict time since fire based on stem diameter and local covariates, performed poorly when tested on mapped fire history from another area. More work to understand what contributed to poor model performance is important for determining the generality of models that can then be applied to predict time since fire. Poor model performance highlights that models developed in one region should be independently verified prior to applying in new regions.

Paper III: Fire and fragmentation interactions affect reptile persistence in an agricultural matrix and conservation reserve

Paper III tested if reptiles responded to fire in a fragmented landscape, i.e. both isolated patches and large reserves, such that species with similar functional traits would be detected in vegetation with similar time since fire ages and condition. I expected that reptiles would be affected by fire in small, isolated patches, in contrast to fire in small patches located closer to large continuous reserves that provide source populations. In addition, reptile species persistence could be affected differently by prescribed fire versus wildfire. This study showed that there was a wide range of variation in reptile trait responses to fire and fragmentation, but I did not detect responses of different trait groups to fire by fragmentation interactions. I found weak evidence that the reserve, with the same recently burnt vegetation as the remnant patches, could mediate the impacts of fire on reptiles in remnant patches. In spite of the temporal and spatial complexity of reptile responses, colonisation opportunities in fire prone and fragmented landscapes may be possible for reptiles that are insectivorous, nocturnal or burrowing. However, it is possible that this pattern in colonisation opportunities for insectivorous, nocturnal or burrowing species, may be driven by *Nephrurus stellatus*, a species that dominated reptile detections in my study.

Paper IV: Does patch isolation affect small mammal occurrence and abundance after experimental fire in a fragmented landscape?

In *Paper IV*, I investigated small mammal responses to interactions between fire and fragmentation, by testing if species occurrence and abundance changed in vegetation with similar time since fire ages. I expected that fire would affect the response of small mammals persisting in small, isolated patches, in contrast to patches nearer to large reserves, because small mammals are known to travel to forage in recently burnt environments. However, I detected a limited response. Fragmentation effects were much stronger than the experimental fire effects for all small mammal species in my study. Both fragmentation factors (i.e. the differences between remnants vs conservation reserves, and remnant distance from the reserve) strongly affected native species with significantly lower occurrence of each species detected in remnants than in the reserve. Conversely, the exotic mammal (*Mus musculus*) was significantly more abundant in remnants. The lack of small mammal response to fire and fragmentation interactions could be due to populations showing limited negative responses to fire thus, there was no requirement for population recovery post-fire. Alternatively, the limited response of small mammals to interactions between fire and fragmentation may be due to *in situ* recovery occurring without the need for immigration from conservation reserves (or other remnant patches). Temporal changes in native species were opposite to the exotic species. Only one native species responded to fire by declining occurrence compared with all unburnt sites. I found no direct evidence that fragmentation constrains population recovery from prescribed fire by small mammal species. However, the impacts of fragmentation were strong and negative for native mammals suggesting that these species may have been relatively rare in remnants to begin with, given the long history of fragmentation in these landscapes.

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Paper I: Does fire interact with habitat fragmentation to accelerate biodiversity loss? A systematic review

Running head: A review of fire-fragmentation interaction effects on biodiversity

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Abstract

Fire and habitat fragmentation are both threatening processes affecting the global loss of biodiversity. There is potential for these two processes to interact to accelerate species loss from fragmented landscapes, but the risk of such loss through the interactive effects of fire and fragmentation has, to date, not been synthesised.

We address this knowledge gap by conducting the first quantitative systematic review of how extensively fire and fragmentation interaction effects on biodiversity appear in the scientific literature. We show there are few articles that specifically address how fire and fragmentation interact to affect biodiversity. We also ascertain trends in geographic regions, focal ecosystems and taxa targeted by the studies.

We present an analysis of 60 articles that identify fire and fragmentation effects on biodiversity. Of these, we found that 33 articles exploring biodiversity effects identified fire-fragmentation interactions as a primary study aim. Our synthesis identified five fire-fragmentation interaction types that affect biodiversity. These are: modifications to patch geometry; patch condition; edge habitat; the matrix; and connectivity. We integrated the classification of the fire-fragmentation types and the three key fire-fragmentation interacting components, i.e. fire, patch and matrix, to develop a table to help identify research gaps. The table can be used to determine where there are few or no studies of an interaction type for each of the key interaction components, thus helping direct future research.

It is critical to understand and categorise the mechanisms responsible in fire-fragmentation interactions influencing species responses. Filling these mechanism knowledge gaps will lead to more effective and targeted practices improving biodiversity in fragmented fire-affected landscapes.

Synthesis and applications. This is the first synthesis of how interactions between fire and fragmentation influence biodiversity. Understanding the mechanisms of fire and fragmentation interactions and their effects on biodiversity improves our ability to direct future research, and to support and incorporate fire as a management tool into policy development and management responses.

Introduction

Investigating interactions between processes that threaten species populations is critical for effectively managing biodiversity (Auerbach *et al.*, 2015; Regan *et al.*, 2010). Together, habitat fragmentation and loss are major threatening processes that can diminish biodiversity (Foley *et al.*, 2005; Haddad *et al.*, 2015; Wilson *et al.*, 2001), notwithstanding that species can respond positively to fragmentation once habitat loss has been accounted for (Fahrig, 2017, 2018). Their impacts may be exacerbated by interactions with other threats including fire (Driscoll *et al.*, 2012; Wilson *et al.*, 2001).

Many plants and animals have evolved life-history and ecophysiological traits to persist in fire-prone ecosystems (Lamont *et al.*, 2004). However, humans have altered patterns of frequency, intensity and season of fire occurrence in ways that threaten biodiversity on a global scale (Barlow *et al.*, 2006; Bowman, 2017; Keith *et al.*, 2002; Sanz-Aguilar *et al.*, 2011; Sauvajot, 1995). Changing fire regimes disrupt above-ground biomass and below-ground biological properties (Neary *et al.*, 1999), biological functioning (Lawson *et al.*, 2010) and evolutionary processes (Templeton *et al.*, 2001). Plants and animals may be particularly vulnerable to inappropriate fire regimes in fragmented landscapes because fragmentation isolates populations in remnants (Ross *et al.*, 2002) and reduces population sizes (Auld and Keith, 2009; Driscoll, 2004). Fragmentation makes small, isolated populations particularly susceptible to climate change (Driscoll *et al.*, 2012; Mantyka-Pringle *et al.*, 2012), predators (Doherty *et al.*, 2015) and invasive species (Gibson *et al.*, 2013; Le Maitre *et al.*, 2004). To better manage fire for biodiversity conservation, a key area of research is interactions between fire and other processes such as fragmentation (Driscoll *et al.*, 2010b).

Much has been learnt about both fire and fragmentation, but they have mostly been studied separately within a single study (Loepfe *et al.*, 2010; Souza and Martins, 2003) or in isolation (Cousins, 2006; Duncan and Schmalzer, 2004). Thus, the interaction of fire and fragmentation is a key knowledge gap (Driscoll *et al.*, 2010b). It is critical that this knowledge gap be addressed as fire and fragmentation can interact in ways that may accelerate species loss and further reduce species persistence in fragmented landscapes (Driscoll and Henderson, 2008; Hobbs and Huenneke, 1992).

Fire and fragmentation can interact in a number of diverse ways to affect biodiversity. Fragmentation can influence fire regimes and their spatial patterns. For example, in fragmented landscapes, early successional, post-fire patch ages are reduced compared to continuous landscapes, and may disadvantage species that depend on those habitats (Wilson *et al.*, 2016). If fire, or lack thereof, in small patches has led to local extinctions, for some species recolonisation must occur from elsewhere. Other species have largely *in situ* population responses to fire and can recover from local survivors (Banks *et al.*, 2011; Sanz-Aguilar *et al.*, 2011), whereas for others, movement is an important component of population dynamics in fire-prone environments (Pereoglou *et al.*, 2013; Pierson *et al.*, 2013). Knowledge of fire-fragmentation interactions is therefore important for improving species management (Auld and Keith, 2009), yet the repercussions of fire-fragmentation effects often remain unclear (Bennett *et al.*, 2012; Sauvajot, 1995). This can impede effective management and conservation of biodiversity in fragments with altered fire regimes.

Fire is a well-studied process with respect to animal habitat generally, but there has not been a specific and targeted focus on fragmented landscapes. In fire-prone fragmented landscapes, little consideration has been given to the impacts and interactions of different fire regimes. Previous reviews have examined landscape modification as a result of threatening processes, such as fire and habitat fragmentation, that are key drivers of species loss (Fischer and Lindenmayer, 2007). However, none have attempted to examine the synergies among fire and fragmentation, and the resulting impacts on plants and animals living in fragmented, fire-prone landscapes.

In this study, we conduct the first, quantitative systematic review (Lortie, 2014) to synthesise available knowledge and improve understanding of the interactive effects of fire and fragmentation on biodiversity. We identified articles that specifically considered fire-fragmentation interactions and sought to quantify: (1) How much research addresses fire-fragmentation interactions? (2) How does fragmentation affect fire occurrence in the landscape and vice versa? and (3) How does the interaction of fire with fragmentation affect biodiversity? Using this literature, we identify knowledge gaps in fire-fragmentation research and priority areas for future research.

Methods

Database searches

We searched four databases – ISI Web of Science (WoS), Scopus, Informit and Google Scholar – using the broad search string 'fire' AND 'fragmentation' on 5 September 2016. Detailed methods for search strings and exclusions based on the peculiarities of each database are provided in Table S1. We identified a total of 840 articles which we then screened to assess their relevance.

Assessing article relevance

To ensure that the articles retained in our final analysis were specifically related to interactive effects of fire and habitat fragmentation on biodiversity, we conducted four levels of screening. In the first level, we excluded duplicate records and records that had not been peer-reviewed. For the books returned by our search, we read and retained relevant chapter articles that were peer-reviewed. In the second level of screening, we read titles and abstracts of journal articles, excluding those without at least one of the terms 'fire', 'fragment', 'burn', or 'remnant' in the title or abstract. In the third level of screening, we first read abstracts only, excluding articles that were not about fire and habitat fragmentation. We then read entire articles, excluding any that did not mention or quantify fire-fragmentation interactions. We subsequently classed these articles as 'direct interaction' if the interaction effect of fire and habitat fragmentation was tested directly, or 'inferred interaction' if we determined that the fire-habitat fragmentation effect was an implied but not studied directly. At each level of screening, we recorded the number of articles identified and the number of studies we included and excluded (Fig. 1).

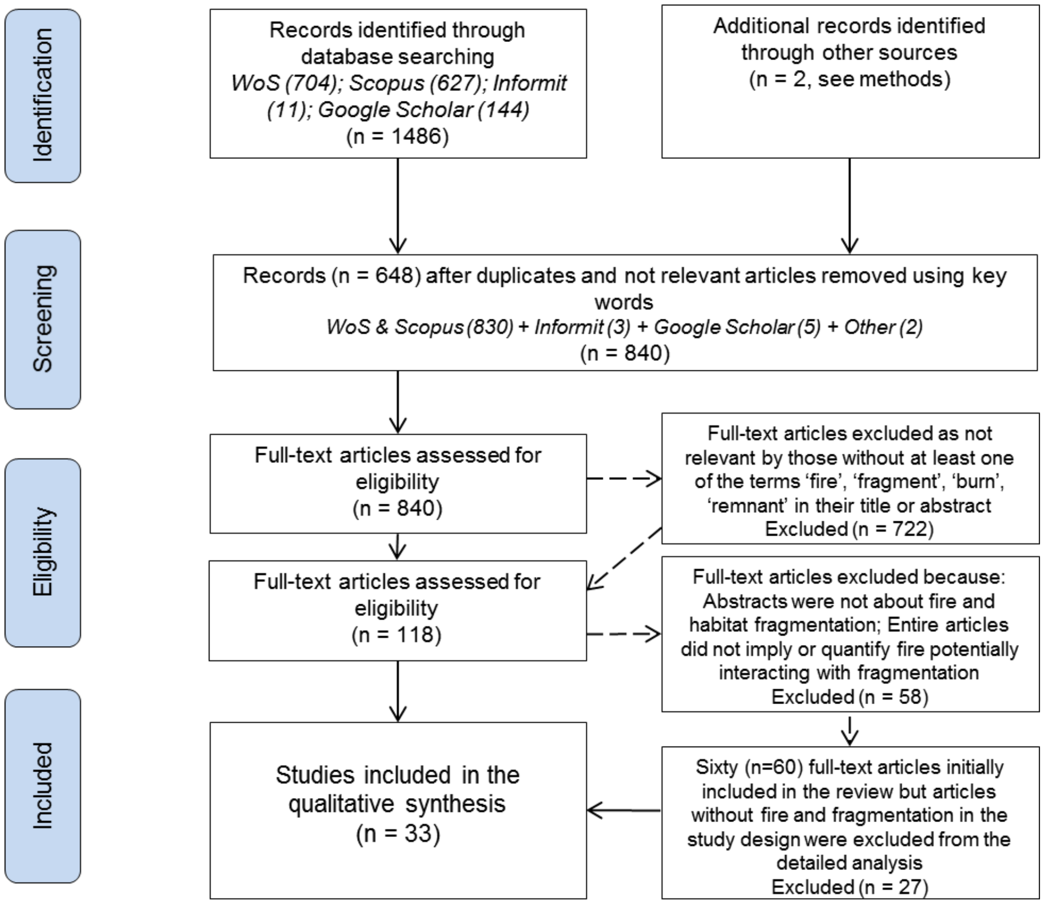


Figure 1. Review methodology. Flow chart based on PRISMA protocols (Moher *et al.*, 2009) outlining how we retained or excluded articles. Of the 840 articles identified originally, an initial 60 were retained as being relevant to the review, before a final 33 articles were retained for the qualitative synthesis.

WoS = Web of Science.

Note: A high level search of WoS and Scopus on 8 December 2018 for the years 2016, 2017 and 2018 show that the number of papers published in this period is comparable to the number published in the preceding period i.e. 2013-2015.

In total, we retained 60 articles from the 840 articles identified in our initial database search.

For the first part of our analysis, we included all 60 articles and used 23 questions (Table S2) to quantify: (1) the current extent of knowledge of the interactive effects of fire and fragmentation for specific ecosystems and habitats; and (2) the importance of the fire-fragmentation interaction in the article (i.e. central or peripheral to the study). To determine the importance of fire-fragmentation interactions in each article, we identified 33 articles where fire-fragmentation interactions were central to the research (i.e. included in the study design or methods). We retained these 33 articles to further quantify: (3) the types of fire-fragmentation interaction mechanisms reported (i.e. general categories for interaction,

Table 1); (4) the effects of fire-fragmentation interactions on biodiversity; (5) the fire types, severity and frequency investigated; and (6) management recommendations arising from the study for applied or theoretical settings.

Table 1. Descriptions of the five types of fire-fragmentation interactions (Groups A to E) identified in retained articles[#], and the number of articles investigating each interaction type*.

Fire-fragmentation interaction groups		
Group name	Group description	Number of articles
A: Patch geometry	Patch shape/size/isolation influences fire risk	9
B: Patch condition	Patch condition change is influenced by fire and fragmentation (irrespective of shape/size)	12
C: Edge	Fragmentation changes edge fire dynamics through changes in edge condition from exposure and extent	6
D: Matrix	Fragmentation changes fire regime in the matrix which in turn alters fire risk in patches	2
E: Connectivity	Fire in the landscape alters patch connectivity (makes the matrix more or less permeable)	4
Total		33

[#] Group descriptions represent the methods used to categorise articles by their mechanisms of interaction.
* Detailed group descriptions and articles are in Table S5.

For our review, fragmentation refers to the landscape-scale process of habitat loss as a result of fragmentation (Fahrig, 2018)(see Table 2 for Glossary of Terms). In addition to articles that directly addressed fire frequency, we also included ones that addressed time since last fire and fire exclusion (suppression) as both have implications for fire frequency. We determined the negative or positive responses of fire-fragmentation interactions in terms of the biodiversity responses (see Table 2 for Glossary of Terms).

Table 2. Glossary of Terms

Terminology	Definition	Reference
Biodiversity	Any ecological response variable that either is or can be related to biological diversity	Fahrig (2003)
Biodiversity response	The effect of a fire-fragmentation interaction on biodiversity where the combination of fire and fragmentation has had a corresponding effect on organisms in each study. For example, 'positive' – increased abundance and genetic diversity, where fire connected fragments and improved reptile habitat (Neuwald and Templeton, 2013); 'negative' – decreased abundance in plant species, increased emigration (Berkunsky *et al.*, 2015); 'not stated – fire alters landscape (Berry *et al.*, 2015a)'; or 'neutral' – no effect on abundance or genetic diversity compared to baseline (Berman *et al.*, 2016)	This article

Condition	Internal suitability and/or quality of a patch or fragment including edges. We define patch condition as an independent component of the fragmentation process because: the condition of patch may be influenced by being long unburnt or recently burnt. This in turn influences species persistence depending on their post-fire successional habitat preferences. Patch geometry could also influence patch condition if edges come close together or overlap, increasing fire interval (see Gill *et al.* 2014). Patch isolation can also influence patch condition.	This article
Connectivity	Both functional (e.g. genetic) and structural (e.g. links between patches such as rocks and grasses)	Cosgrove *et al.* (2018)
Ecosystem	The dynamic complex of plant, animal, and microorganism communities and their nonliving environment interacting as a functional unit	UN (2014)
Fire frequency	Increasing frequency = more fire; decreasing frequency = less fire (Increasing interval = less fire; decreasing interval = more fire, 'interval' is the mathematical inverse of frequency)	Gill *et al.* (2014)
Fire types	Planned and unplanned fires investigated in the review articles (excludes fire severity (intensity) and frequency)	This article
Fragmentation	A landscape-scale process (including as a result from: natural or deliberate fire, absence of fire, agricultural and urban land clearing) that modifies landscape structure (resulting in habitat fragments or patches of various sizes, number, condition, configuration and isolation, within a contrasting matrix)	This article; Fahrig (2018), Sallabanks *et al.* (1999)*
Matrix	The area surrounding fragments of land e.g. a forest (where it encroaches into prairie resulting in prairie grassland fragments), a cropping paddock (where fragments of remnant woodland remain)	This article; Kupfer *et al.* (2006); Jules and Shahani (2003)
Patch	A habitat fragment which is the result of fragmentation	This article; Fahrig (2003)
Systematic review	A type of literature review that employs detailed, rigorous, and explicit methods to answer a specific question	Lortie (2014)
Theoretical study	Studies that use conceptual, mathematical, or simulation methods with real data, to answer ecological questions	Haller (2014)
Type of interactions	The different mechanism types responsible for interactions between fire and fragmentation, that influence biodiversity and ecosystems	This article

* Sallabanks *et al.* (1999) view '…that habitat fragmentation refers to anthropogenic changes (land management issue), and that natural patchiness (of a landscape) is described as such', is captured in our interpretation.

Identifying research gaps

The interaction categories and components of fire in a fragmented landscape are grouped into four parts: (1) fire regime is changed by patch (2) fire regime changes patch (3) matrix is changed by fire regime and (4) matrix changes the fire regime (Table S6a). Table S6a is derived from Table S6b, which is more detailed and presents each review article with its assigned interaction component category i.e. fire, fragmentation and matrix. These categories are aligned to each review article and the biodiversity response for each. We use this method of categorisation and refinement to identify gaps in the fire-fragmentation research literature e.g. there were no articles identified for several research mechanism types in each of the four parts (columns) (see Table S6a).

Results

Our literature search returned 840 articles, of which only 118 addressed fragmentation and fire in a biodiversity context. Of these 118 articles, 60 considered their interaction and were retained for our initial analysis (i.e. summary statistics for temporal, regional and taxonomic extent). Of these 60 articles, fire-fragmentation interactions were central to 33 articles and were the focus of our second analysis (i.e. how fire interacts with fragmentation and affects biodiversity, Table S3). We provide a summary of review questions, methods and results in Table S4 and list all articles (Reference List S1).

We categorise the fire-fragmentation mechanisms of interaction from our 33 articles into five groups (Table S5). We then assign the 33 articles to the interacting components of fire in a fragmented landscape, e.g. fire, patch, matrix (Table S6a and Table S6b). The table we produce from integrating these interaction types and categories that are outlined in the methods, presents an approach to identify research gaps of fire-fragmentation interaction effects on biodiversity (Table 3 and Fig. 2).

Table 3. Identification of research gaps using the 33 review articles. The key interacting components of fire in a fragmented landscape - fire, patch and matrix - are listed in the column at the far left. The mechanisms responsible for the interactions are in columns titled: 'Condition', 'Connectivity', 'Edge', 'Grain and pattern', 'Isolation', 'Shape' and 'Size, extent'. Biodiversity responses are represented by N = negative, P = positive, NS = not stated, Ne = neutral and na = not applicable. (See also Figure 2 and Table S6a).

Mechanisms Interactions	Condition (including structure)	Connectivity	Edge	Grain and pattern	Isolation	Shape	Size, extent
1. Fire regime … is changed by patch (Patch …… changes fire regime)	N	–	N,N	P,N	N,N	NS,P,N*	N
2. Fire regime … changes patch (Patch … is changed by fire regime)	N,*P*,*P*	P,N,NS,Ne,*P*, *Ne*	N,P	–	P,N,N,*N*	–	N
3. Matrix … is changed by fire regime	–	–	–	na	na	na	N
4. Matrix … changes fire regime	–	N	N*,N*,N*	–	na	–	NS**

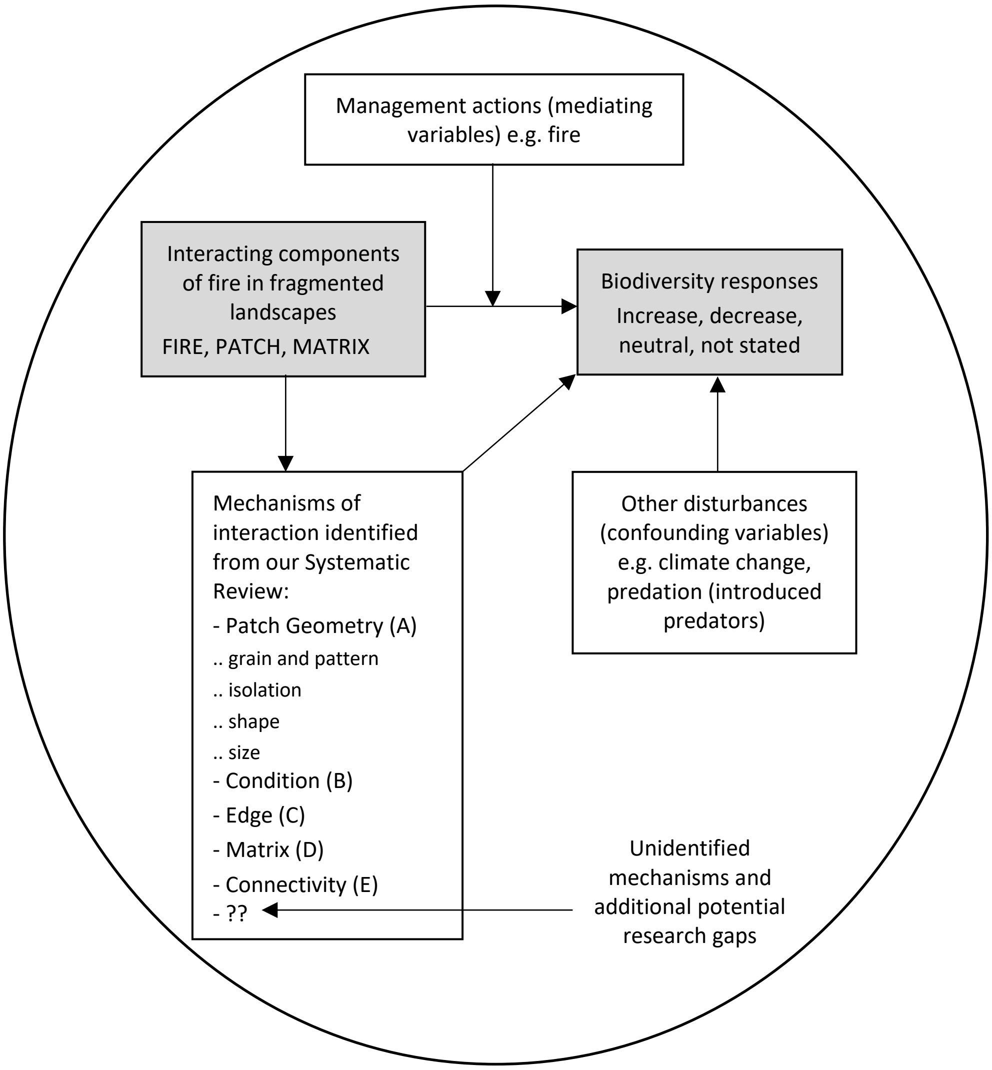
Biodiversity responses: N = negative; P = positive; NS = not stated; Ne = neutral; na = not applicable

Italicised responses are where the articles specify the management fire type (see Table S6a)

*equally applicable to 'shape' and 'size'

**equally applicable to 'size, extent'

Figure 2. Conceptual diagram depicting the relationship between fire interacting with fragmentation (e.g. three interacting components) and the biodiversity responses. Our classification of the fire-fragmentation interaction types, derived from our review articles, identified several mechanisms of interaction (control variables) influencing biodiversity. We list the mechanisms of interaction and highlight that there may be other interactions not yet identified in the empirical literature. See also Table 1 for descriptions of groups A to E and Table 3.



Temporal, regional and taxonomic extent

The 60 articles we analysed spanned 23 years (1994 to 2016). The number of fire-fragmentation interaction articles published per year varied from zero (1995) to five (2007 and 2013) and nine (2015) (Fig. 3 and Table S7).

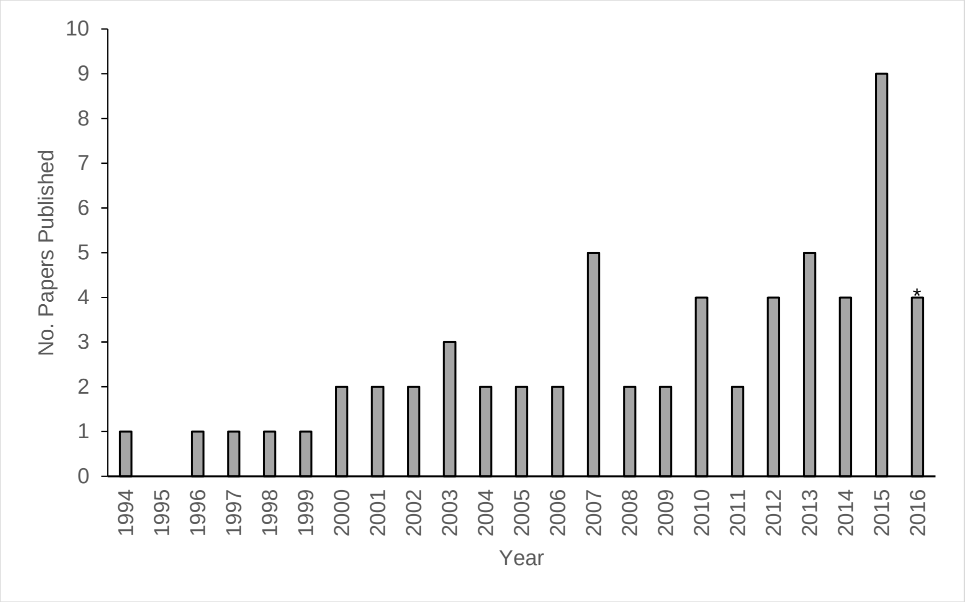


Figure 3. Number of papers investigating fire-fragmentation interactions published each year since 1994 (* indicates 2016 not a full year; search undertaken in September 2016).

Note: A high level search of WoS and Scopus (as per Fig. 1) on 8 December 2018 for the three years 2016-2018 shows that the number of papers published in this period is comparable to the number published in the preceding three year period, i.e. 2013-2015.

Articles focussed almost evenly on the southern hemisphere (31/60) and the northern hemisphere (28/60). Only one article covered more than one country. Studies were conducted most frequently in North America (24/60), South America (17/60) and Oceania (12/60), and least frequently in Europe (3/60), Africa (2/60) and Asia (1/60) (Table S8).

The most studied ecosystem was forest (25/60), and the least studied were grasslands (9/60), woodlands (9/60) and shrublands (7/60). Four articles did not state an ecosystem type (Table S9). Animal taxa were examined in 26/60 studies with invertebrates least studied (4/60). Of the vertebrate studies (22/60), birds (7/22), mammals (6/22) and reptiles (5/22) predominated. However, three of the five reptile articles had common authorship and were on the same species. Plant taxa were examined in 32/60 studies (Table S10).

Mechanisms responsible for fire-fragmentation interactions

Fire-fragmentation interactions were explicitly studied in 33 articles. We categorised these 33 articles into five groups (Table 1). For each group we considered the mechanisms responsible for fire and fragmentation interactions and the effects on biodiversity. Group A articles (9/33) examined the effects of patch geometry (i.e. size, shape, isolation) on fire behaviour. Group B articles (12/33) examined the effects of patch condition on fire behaviour (irrespective of patch shape or size). Group C articles (6/33) investigated fire behaviour in patch edges. Group D articles (2/33) investigated how fragmentation affects fire regimes in the matrix. Group E articles (4/33) investigated fire as a fragmenting process, focusing on how fire alters patch connectivity. We provide detailed descriptions of the fire-fragmentation interaction explored in each article, as well as the group to which we assigned each article in Table S5.

Fire-fragmentation interaction effects on biodiversity

More than half (20/33) the articles we reviewed reported negative effects of fire-fragmentation interactions on biodiversity. Eight reported positive effects on biodiversity, and two found no effect on biodiversity. A further three articles did not explicitly state a biodiversity response to fire-fragmentation interactions (Table 4 and Table S11).

Table 4. Fire-fragmentation interaction categories (Groups A to E) and the corresponding biodiversity responses i.e. 'positive', 'negative', 'not stated' or 'neutral'˜ for each article

Fire-fragmentation interaction groups	Effect of interactions on biodiversity*			
Group name	Positive	Negative	Not stated	Neutral
A: Patch geometry	3	5	1	-
B: Patch condition	3	8	-	1
C: Edge	1	5	-	-
D: Matrix	-	1	1	-
E: Connectivity	1	1	1	1
TOTAL (33)	8	20	3	2

˜ See 'Biodiversity response' under Glossary of Terms

* Detailed group descriptions and articles are in Table S5

Of the 33 articles we reviewed, nine articles (Group A) explored how patch geometry altered fire regimes or how changed fire regimes altered patch geometry – in turn influencing biodiversity. Changes in patch size (n = 2) had variable fire responses with negative effects on biodiversity. Decreased patch size (smaller remnants) decreased fire frequency (i.e. a longer time between fires), which reduced plant species richness in a *Banksia* woodland in Australia (Ramalho *et al.*, 2014). Another study found that small patches of an Australian open woodland experienced increased fire frequency with larger areas burned, leading to an increased extinction risk of a bird (Brooker and Brooker, 1994). Patch shape (n = 2) had variable effects on fire regimes. In eastern Spain, forested corridors fragmented the spatial distribution of fuels (shrubs) and decreased fire spread and intensity (Duguy *et al.*, 2007), with an unstated effect on biodiversity. Grassland corridors within a pine matrix in the USA, increased fire intensity (Brudvig *et al.*, 2012) with positive effects on biodiversity. Patch-isolation (n = 2) articles reported opposing biodiversity responses of patch isolation. In a prairie grassland in the USA, reduced fire incidence in isolated patches led to a decline in patch quality, with negative effects on plant species richness (Alstad and Damschen, 2016). However, in a desert system in the USA, fire resulted in varying levels of patch isolation, with positive effects on arthropod abundance and richness in burned patches with long-lived vegetation (VanTassel *et al.*, 2015) (see Table S6a).

Grain and pattern (n = 2) articles also had opposing biodiversity responses. Coarse-grain fragmentation patterns (i.e. large, aggregated patches) resulted in less frequent fire and fewer changes to vegetation, with positive effects (i.e. reducing the extinction risk) for fire-sensitive species in simulated Mediterranean landscapes (Pausas, 2006). Fine-grain fragmentation patterns (i.e. small, distributed patches) led to uncorrelated fires (changed fire frequency creating spatially separated age classes) across patches, with negative effects on biodiversity in shrubland in the USA (Regan *et al.*, 2010). The patch, shape, size and isolation (n = 1) article reported that patch isolation in Australian mallee decreased fire frequency because fires were uncommon at edges. This led to maximum fire exclusion in narrow patches because edge overlap increases with decreasing patch width (Gill *et al.*, 2014) (see Table S6a).

There were 12 articles (Group B) that explored patch condition change, irrespective of patch shape or size. Fire changed patch condition in 10 articles with negative (n = 6), positive (n = 3) and no effects (n = 1) on biodiversity. Patch condition altered fire frequency in two articles, in rainforest in Brazil and shrubland in southwestern Australia respectively, and both had negative effects on biodiversity (Michalski *et al.*, 2007; Yates and Ladd, 2010). Patch condition was altered by an increase in fire frequency and this had negative effects in seven studies, positive effects in two studies, and a neutral effect in one study (i.e. there was no benefit gained for species from condition change from fire treatment). Patch condition was altered by a decrease in fire frequency in one article and this had a positive effect on biodiversity (Gilfedder and Kirkpatrick, 1998). Driscoll and Henderson (2008) suggested that an increase or decrease in fire frequency could result in a decline in condition and have a negative effect on biodiversity (see Table S6a and Table S12).

Six articles (Group C) explored fragmentation in the context of direct and indirect edge effects. Five articles explored how fragmentation changed, for example by drying, patch edges in South American rainforests, which in turn increased fire frequency and negatively affected biodiversity. Only one 'edge' article in a wetland forest in the USA identified a positive effect on biodiversity in response to fire in patch edges; some burnt patches had cooler and more humid microclimates compared to unburnt patches (Watts and Kobziar, 2015) (see Table 4 and Table 5).

Two articles (Group D) explored how fragmentation changes fire in the matrix. Fragmentation in Mediterranean oak woodlands can alter and increase fire extent and unburnt oak woodland patch vulnerability to fire in the matrix, with negative effects on biodiversity (Guiomar *et al.*, 2015). Conversely, in Canada, fragmentation can influence the fire cycle because land-use change in the matrix can increase fire frequencies in boreal forest patches (Weir *et al.*, 2000). However, effects on biodiversity were not identified in this article (see Table 4 and Table 5).

Four articles (Group E) explored how fire in the landscape alters patch connectivity. Three indicated that increased fire frequency decreased connectivity but with variable effects on biodiversity. Decreased connectivity associated with increased fire frequency had a negative effect on biodiversity in an Australian mallee woodland (Berry *et al.*, 2015b) but a neutral effect on biodiversity in a rainforest in New Caledonia (Berman *et al.*, 2016). One article found that different fire frequencies in montane forests in Australia decreased connectivity and created refuges. However, it did not state a biodiversity response (Berry *et al.*, 2015a). In contrast, one article found that increasing fire frequency in forest glades in the USA, increased patch connectivity, benefiting a reptile species (Neuwald and Templeton, 2013) (see Table 4 and Table 5).

Table 5. Number of fire-fragmentation interaction effects that result from more fire, less fire and both more fire and less fire in the same article*, for each fire-fragmentation category (Groups A to E) of the 33 articles (See Table S11 for a detailed breakdown of the corresponding species responses.)

Fire-fragmentation interaction groups Group name	Interaction effect More fire	 Less fire	 More fire-less fire	 Group totals
A: Patch geometry	4	5	-	9
B: Patch condition	10	1	1	12
C: Edge	5	-	1	6
D: Matrix	1	-	1	2
E: Connectivity	3	-	1	4
TOTAL	23^	6^^	4^^^	33

^ Responses were: 5 positive, 16 negative, and 2 neutral

^^ Responses were: 2 positive, 3 negative, and 1 not stated

^^^ Responses were: 1 positive, 1 negative, and 2 not stated

* An article that investigated both more fire and less fire

Fire types, severity and frequency

Eight articles studied planned fires (of which one was a simulation study), 15 studied unplanned fires (of which two were simulation studies), and 10 studied both fire types (of which three were simulation studies). Fire severity was examined in nine articles and fire frequency was examined in 17 articles (Table S13, Fig. S1 and Fig. S2).

Management recommendations

Of the 33 articles we analysed, 13 offered management recommendations or options in relation to the use of fire (Table S14 and Table S15). No articles recommended fragmentation be reduced (i.e. that connectivity between the patches be increased). However, one article that analysed the roles of fragmentation and edge effects on forest fire occurrence and intensity stated that high connectivity and low forest fragmentation could minimise edge driven fires (Armenteras *et al.*, 2013). Only articles in interaction groups on patch geometry, patch condition and connectivity provided management recommendations. The recommendations were: reduce fire frequency (n = 6); increase fire frequency (n = 3); conduct further research (n = 2); monitor increases in habitat heterogeneity (n = 1); and prepare a fire management strategy (n = 1) (Table S16).

Discussion

Research addressing fire-fragmentation interactions

Our review identified that there is limited research that specifically addresses fire-fragmentation interactions. The studies are spread thinly across different ecosystems and landscape contexts, with biases towards some systems such as forests. This makes it difficult to draw generalisations. The implications of a dearth of knowledge to understand the mechanisms responsible for fire-fragmentation interactions, and the resultant effects on biodiversity, is that actions cannot be appropriately targeted to manage environments effectively. Current management using fire is working on best but limited evidence for directing appropriate management responses and in some instances this could result in perverse outcomes for biodiversity (Driscoll *et al.*, 2010a). For example, applying the same fire regime to different savanna communities coupled with incomplete information on taxa could result in unexpected responses to biodiversity (Bond and Keeley, 2005). Further, in the same savanna ecosystem that is also fragmented, fire adds another level of complexity that, without enough targeted and biome specific research of fire-fragmentation interactions, can make identifying appropriate actions for biodiversity elusive.

It has long been acknowledged that effective management of biodiversity in response to major interacting disturbances such as fire and fragmentation is important (Sauvajot, 1995), but limited progress has been made with regards to this aim. Indeed, both our review and that of Foster *et al.* (2016) found that interacting disturbance mechanisms have direct implications for conservation, yet few management-focused studies identified the different mechanisms underlying disturbance interactions. In this review, we synthesise the literature within and across related ecological disciplines to fire and fragmentation interactions. Our detailed synthesis of the available empirical literature on mechanisms by which fire and fragmentation directly, or indirectly, drives the responses of biodiversity, now make it possible to identify the gaps in the research. It provides the means to recommend the pursuit of research that builds on our categorised interaction mechanisms.

To meet required knowledge of how species respond to fire regimes in fragmented environments for ecologically sustainable management (Driscoll *et al.*, 2010b), we developed a framework from empirical studies that illustrates five categories of fire-fragmentation interaction mechanisms, and demonstrate the variation in biodiversity responses between and within categories. Aside from helping to improve communication of fire-fragmentation interaction ideas, our categories provide a better understanding of the mechanistic processes responsible for affecting biodiversity. By integrating these five categories into a table with the key interaction components of fire and fragmentation (fire, patch and matrix), it provides an extremely useful framework to more easily identify research gaps. This consolidation helps highlight the research gaps that enable planning research into understanding whether fire is interacting with fragmentation to accelerate biodiversity loss.

Categories: fire-fragmentation interaction influences on biodiversity

We found that fire and fragmentation interaction influences on biodiversity were highly variable and context specific. Particular types of fire-fragmentation interaction seem equivocal in generating positive and negative effects on biodiversity responses. The variation within our five categories of biodiversity responses to similar mechanisms highlights the importance of first identifying and understanding the drivers of those responses before considering management applications. By exploring mechanism types and associated biodiversity responses for each fire-fragmentation category separately, we can avoid inappropriate assumptions that may lead to ineffective management actions. For example, fire suppression can degrade a habitat but if introduced it can improve reptile conservation by increasing connectivity (Templeton *et al.*, 2007). However, frequent fire may cause a reptile habitat to degrade (Abom and Schwarzkopf, 2016).

Identifying gaps in the interaction group categories

An important advance in our study is aligning the framework of five fire-fragmentation interaction categories to the interaction components, i.e. fire, patch, matrix. The strength of integrating and presenting these in a table highlights the limited number of articles against each of the mechanisms and thus helps to identify research gaps in the empirical literature. Our table can be used to identify more gaps of ecological research of species- or situation-level mechanisms that will enable generalisations to emerge. For example, reductionist investigations of focal species can, when combined, provide a generalised understanding of the mechanisms between spatial patterns and processes (Wiens *et al.*, 1993) that can inform conservation management. Smith *et al.* (2012) emphasise the value of using conceptual frameworks to guide and target empirical research because it can avoid unexpected and inconsistent biodiversity responses from inappropriate management actions.

In addition, different response variables might have influenced the findings such that biodiversity responses to the same set of interacting processes might appear different if alternative biodiversity metrics are used. For example, measuring a species' response to a fire/fragmentation interaction using presence/absence data or genetic diversity may yield different results. In addition, single species responses might be very idiosyncratic, and might differ from community-level results (Supp and Ernest, 2014).

Management recommendations

Our findings highlight that to avoid implementing the incorrect management approach, management recommendations suggested in fire-fragmentation studies need crossreferencing to the biodiversity response observed, as well as the fire-fragmentation mechanism underpinning the biodiversity response. For example, regarding connectivity, biodiversity responses to fire are contradictory. One article recommends that more fire will increase connectivity (Neuwald and Templeton, 2013), while another article recommends that less fire will retain connectivity (Berry *et al.*, 2015b). This ecosystem complexity leads to variable patterns in biodiversity responses that are difficult to generalise. As such, this limits the formulation of generalised practical recommendations with respect to the use of fire in fragmented landscapes to benefit biodiversity. However, Fahrig (2018) emphasises the relevance of scale and notes that conservation benefits result from both small habitat patches and large contiguous ones and, hence, fragmentation impacts may be lacking at certain spatial scales.

It is evident from both our review and other research (Kelly *et al.*, 2017) that effects from interactions between fire and fragmentation are critical areas of knowledge required for the effective management of fire in modified landscapes. To avoid the risk of perverse outcomes from limited studies and lack of information, there is a need for more empirical case studies to contribute to developing contingent theory (Han, 2016; Smith *et al.*, 2012). Fire can help maintain the integrity and species composition of a range of ecosystems (Syphard *et al.*, 2007), but can also erode it (How and Dell, 2000) particularly where fire regimes modified by anthropogenic activities (such as fragmentation) cause cascading ecological effects (Syphard *et al.*, 2007). In such circumstances, it is important to understand the ecology of the system to determine what the biodiversity response will be (e.g. negative, positive or neutral), in order to apply appropriate management actions that achieve conservation outcomes in fire-affected and fragmented landscapes.

Conclusion

Interactions between processes that affect biodiversity is a critical area of study, in particular from habitat fragmentation and loss which can be exacerbated by threats such as fire. This review shows that there are five fire-fragmentation interaction categories of biodiversity responses (Table 1), based on the empirical research. However, because of the wide range of interaction mechanisms in each category, we were not able to draw generalisations about where fire occurrence is likely to decrease or increase in response to fragmentation in the landscape. Notwithstanding, we found that fire-fragmentation interactions had more negative than positive effects on biodiversity across the five categories. Yet, these identified effects on biodiversity did not translate to generalisable management recommendations. This is because, as shown in Table 3, the same mechanism (e.g. isolation) can be responsible for different biodiversity responses between, and within, interaction components (e.g. fire regime is changed by patch = Negative, and fire regime changes patch = Positive and Negative). Essentially, ecosystem complexity can inhibit generalised management solutions.

Without the knowledge of how fire regimes interact with fragmentation affecting biodiversity, we lack an understanding of how to best manage fire-prone fragmented ecosystems, and this can lead to further declines of biodiversity. Strategic approaches are needed to improve the effectiveness of fire management for conservation purposes in modified landscapes. Critically, this will involve identifying which mechanisms are influencing observed biodiversity patterns. Given that our review shows that fire-fragmentation interactions can have profound and differing effects on biodiversity, targeting the research gaps from the integrated interaction mechanism types and key interaction components is urgently required to improve future management. The limited research into, and understanding of, fire-fragmentation interactions, impedes effective management, and may lead to implementing actions that perversely affect biodiversity.

While there are a number of challenges (and limitations) in this area of research, we consider our table that integrates the fire-fragmentation categories with key fire-fragmentation interaction components can be used to determine potential interaction mechanisms where there are few or no studies of a specific interaction type. It can also help to highlight where this lack of research informing fire-fragmentation interactions types, thus helping to identify and address the knowledge gaps in this important area of study.

Author contributions

JL and DAD conceptualised the study and the study design. JL acquired the data and JL and DAD led analyses; JL led manuscript preparation with substantial critical and editorial input from all authors. JL, CFS and DAK declare no conflicts of interest. DAD is an associate editor of the *Journal of Applied Ecology*. *In prep for the Journal of Applied Ecology*.

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Supporting Information

Table S1. The specific methods taken for each database was a two-stage process used to identify relevant articles for the review. Stage 1 outlines the detailed methods used to interrogate each of the four databases used in the investigation (n = 840); and Stage 2 outlines how the 840 articles were assessed by using key words to examine the eligibility of papers for their relevance (n = 118). A further examination of these 118 articles for references to ‘interactions’ identified the 60 remaining articles for inclusion in the qualitative synthesis. An initial analysis excluded 27 articles for not including fire and fragmentation in their study design resulting in the final analysis of 33 articles.

Database	Search methods	Number of articles
STAGE 1 ISI WoS	• Basic search: fire AND fragmentation - Topic • Timespan: all years • More Settings: selected Web of Science (WoS) Core Collection: Citation Indexes (Science Citation Index Expanded (SCI-EXPANDED)-1900-present; and Conference Proceedings Citation Index-Science (CPCI-S)-1990-present) • Refined search to: 14 WoS Categories (Ecology; Environmental Sciences; Biodiversity Conservation; Forestry; Plant Sciences; Zoology; Multi-disciplinary science; Environmental studies; Ornithology; Entomology; Agriculture Multi-disciplinary; Biology; Genetics heredity; Remote sensing) • Two document types selected: 'Article' and 'Review' • English language texts	823
Scopus	• Search: fire and fragmentation - Article Title, Abstract, Keywords • All years to present • Limited to Life Sciences and Physical Science • Subject Area: Limited to 'Environmental Science', 'Ag and Biol. Sciences', and 'Biochemistry, Genetics and Mol. Biology' • Document Type: Limited to 'Article' and 'Review' • Limit to English	7
Informit	• Search: fire and fragmentation - Social Science database within the 'Humanities & Social Sciences Collection' and 'APAFT (Australian Public Affairs Full Text) databases	3
Google Scholar	• Search for exact phrase 'fire and fragmentation' - anywhere in the article • Exclude patents and citations • Anytime	5
Other	• Articles recommended by ecology expert	2
STAGE 1 TOTAL		840
STAGE 2	• 840 articles then assessed for eligibility and reviewed for inclusion in the qualitative synthesis by: - examining ‘title’ and ‘abstract’ for both ‘fire’ and ‘fragment’ and also ‘burn’ and ‘remnant’; and - examining ‘abstract’, ‘introduction’ and ‘discussion’ for references to ‘interactions’ • 118 articles further reviewed by investigating ‘Is an interaction considered or are fire and fragmentation only discussed as separate processes?’, resulting in 58 documents excluded because these did not identify interactions • The remaining 60 articles were the final database for our review	
STAGE 2 TOTAL		60
	• 60 articles then reviewed against all composite and summary statistic review questions (see Table S2 and Table S4) as part of the initial analysis • 33 articles identified with fire and fragmentation in their study design, e.g. the Methods, and central to the research	27
	TOTAL ARTICLES IN THE FINAL ANALYSIS	33

Table S2. Description of research questions used-to identify papers to be retained in the filtering process from the systematic review (n = 60) (see also Table S4). Relevant data were identified using a 23 question and data collection proforma under categories: Fire and fragmentation (three questions); Fire and fragmentation – central or peripheral (four questions); Fire related (four questions); Fragmentation related (two questions); Publication bias and Management recommendations (two questions); and Summary statistics (eight questions).

Overarching issues	**Research questions**	**Categories**	**Data collected/question asked**	**Possible responses**	**Conditions (if applicable)**
Types of fire-fragmentation interactions Direction of interaction responses	1. What kinds of interactions between fire and fragmentation are reported? 2. Effects of different fire-fragmentation types on biodiversity	Fire and fragmentation	1. Was a fire-fragmentation interaction reported?	Interaction/interaction inferred/NA	-
			2. What was the interaction type?	Types identified	Distilled to five (A to E) different interactions categories (mechanisms) (Table S5)
			3. Was an effect of fire and fragmentation reported?	Yes/no	Species decline/increase (richness or abundance or not stated)
Where the field of fire-fragmentation research is presently Level of priority an interaction is given	3. Where an interaction is considered, is it central to the paper or peripheral?	Fire and fragmentation – central or peripheral?	4. Fire and fragmentation used in <u>introduction</u> only	Yes/no/NA	-
			5. Fire and fragmentation used in <u>discussion</u> only	Yes/no/NA	-
			6. Fire and fragmentation used in <u>introduction and discussion</u>	Yes/no/NA	-
			7. Fire and fragmentation used in <u>methods</u>	Yes/no/NA	-
Identify gaps - identify how studies investigate fire-fragmentation interactions Fire types, severity and frequency Primary aims of research articles	4. For papers with fire and fragmentation in methods, how were these investigated?	Fire related	8. What fire types?	Planned, unplanned, both, none, not applicable	-
			9. Were different levels of severity examined?	Yes/no	-
			10. Were different fire frequencies examined?	Yes/no	-
			11. Was fire management mentioned?	Yes/no	-

Overarching issues	Research questions	Categories	Data collected/question asked	Possible responses	Conditions (if applicable)
Identify gaps – identify how studies investigate fire-fragmentation interactions Fragmentation causes and habitat types Primary aims of research articles	4. For papers with fire and fragmentation in methods, how were these investigated?	Fragmentation related	12. What was habitat fragmentation caused by?	Primary cause; secondary cause	-
			13. What was the habitat type of the fragments? (*see also Q18 and Q21*)	As stated in the journal	-
Future research Research bias Quality and usefulness of knowledge: practical or theoretical application	5. What focus do articles have? 5. Do recommendations arise?	Research bias	14. Organisational level studied	Animal community, animal species, plant community, plant species, fungi, plant and animal communities (ecosystems)	-
		Management recommendations	15. Were recommendations made for animal conservation?	Yes or NA	-
Summary statistics – Extent and type of the research	How representative are articles considering ecosystems, habitat and regional biases? Which habitat types and plant groups were the most or least studied articles?	Summary statistics	16. Author, title, year published	As stated in journal	-
			17. Reference type	Journal article, book	Articles - empirical, reviews or reports
			18. Focus of research (*see also Q13*)	As stated in the journal and interpreted by the author of this systematic review	8 categories^
			19. Hemisphere	Northern/southern	-
			20. Country	As stated in journal	-
			21. Habitat type (*see also Q13*)	Forest, glades, grassland, not mentioned, shrub-land, various (e.g. woodland, forest, grassland)	-
			22. Target group	Amphibian, bat, bird, fish, forest, grassland, mammal, reptiles, shrubs, trees, multiple	-
			23. Target species name	As stated in journal	-

^ fire_behaviour; fire_behaviour and edge; fire_behaviour and fragmentation; fire_behaviour and persistence; fire_behaviour and refuges; fragmentation; fragmentation and edge; fragmentation and fire_behaviour

Table S3. Method used to explore the depth to which fire and fragmentation was central or peripheral to the research. We used filter summaries of the main article headings (Introduction, Methods and Discussion) for the terms ‘fire’ and ‘fragmentation’ and retained 33 review articles from 60 review articles.

	Introduction only	Methods only	Discussion only	Introduction & Discussion	Introduction, Methods & Discussion
'fire' AND 'fragmentation'	0	0	15 (25%)	12 (20%)	33 (55%)

Table S4. Research questions, methods and results used to investigate the main review question. 'Does fire interact with habitat fragmentation to accelerate biodiversity loss?' was investigated in the database articles by using six research questions (response variables). The aim of these questions was to investigate where the field of research is presently, how fire interacts with fragmentation and affects biodiversity, identify gaps, and what research is required. The approaches applied to help investigate these questions are detailed. (Table S2 includes the comprehensive description of the data collected from which questions in **Table S4.** were informed.)

Systematic review question: 'Does fire interact with habitat fragmentation to accelerate biodiversity loss?'		
	Response variables	**Methods and Results**
Number	***Research questions***	
1, 2	***Summary statistics*** ***Where the field of fire-fragmentation is presently***	***60 article database used in research questions 1 and 2***
1.	***Extent and type of research*** How representative are articles considering ecosystems, habitat and regional biases? Which animal and plant groups, and habitat types were the most or least studied? *(Qs 16 to 23 in Table S2*	We summarised empirical, reviews, reports, simulations, and geographical focus and extent. (Tables S7 and S8, Figure 3). Plant and animal representations. (Table S9). Ecosystem (habitat) types (Table S9)
2.	***Fire and fragmentation – are interactions central or peripheral to the research?*** Where an interaction is considered, is it central to the paper or peripheral? What level of priority is the issue given? *(Qs 4 to 7 in Table S2)*	We considered an interaction was central to the paper if it had both fire and fragmentation in the introduction, methods and discussion; and (Table S3) Peripheral if it only mentioned only briefly in introduction or discussion (Table S3). This filtering process of the 60 original articles of the systematic review identified the final 33 articles of the systematic review (Table S3).

Systematic review question: 'Does fire interact with habitat fragmentation to accelerate biodiversity loss?'		
	Response variables	**Methods and Results**
Number	***Research questions***	
3, 4	***Fire and fragmentation*** ***How fire interacts with habitat fragmentation***	***33 article database used in research questions 3 and 4***
3.	***Types of fire-fragmentation interactions*** What kinds of interactions between fire and fragmentation are reported in the literature?	To gauge what kinds of interactions between fire and fragmentation are reported in the filtered articles, we identified five interaction mechanisms in the 33-article database (Tables 2 and S5). These were organised into five groups based on the similarities of the mechanism of the interactions identified in each article. Groups A-Patch geometry (n = 9), Group B-Patch condition (n = 12), Group C-Matrix (n = 2), Group D-Edge (n = 6) and Group E-Connectivity (n = 4) (Table S5).
4.	***Effects of different fire-fragmentation types on biodiversity*** Do the different kinds of interaction have positive, negative, not stated or neutral effects for plant and animal species? *(Qs 1, 2 and 3 in Table S2)*	To determine the biodiversity response from fire-fragmentation interactions we identified whether interaction types were positive, negative, not stated or neutral (Tables 3, 4, S5 and S12).
5	***How studies investigate fire-fragmentation interactions***	***33 article database used in research question 5***
5.1	***Fire related and fragmentation related*** How was fire and fragmentation investigated? *(Qs 8 to 13 in Table S2)*	We investigated the research context of these articles. We analysed fire types, severity and frequency (Table S13).

Systematic review question: 'Does fire interact with habitat fragmentation to accelerate biodiversity loss?'		
	Response variables	**Methods and Results**
Number	***Research questions***	
6 ***(33)***	***Future research and research bias***	***33 article database used in research question 6***
6.1 6.2	***Future research*** What focus do articles have? *(Q 14 in Table S2)* ***Management recommendations*** Do recommendations arise? Is knowledge used in an applied or theoretical sense? *(Q 15 in Table S2)*	In order to determine the focus of the review articles we identified the ecosystem (habitat) type, organisational level, target group, vertebrates/invertebrates, etc., and flora and fauna group (plants / animals) (Table S9). To gauge if knowledge is used in an applied or theoretical sense, e.g. its respective usefulness, we investigated if and what type of management recommendations were made (Tables S15 and S16).

Table S5. Fire-fragmentation interaction groups and assigned article, and effects on biodiversity. The fire-fragmentation interaction mechanisms investigated in 33 review articles, the fire-fragmentation type (Groups A to E) to which each article was assigned, and the corresponding direction of influence and effect on biodiversity. Group A – Patch geometry, shape and/or size and/or isolation (9/33); Group B – Within patch condition, irrespective of shape or size (12/33); Group C – Fragmentation changes edge fire dynamics (6/33); Group D – Fragmentation changes fire in the matrix (2/33); and Group E – Fire in the landscape alters connectivity, increase or decrease (4/33). Articles are cross-referenced with other relevant groups.

	Mechanism of interaction **A – Patch geometry – shape and/or size and/or isolation**	**Mechanism type**	**Mechanism description** **How does patch shape and/or size and/or isolation influence fire or burn risk?**
1	Duguy, B., *et al.* (2007) *International Journal of Wildland Fire*	Shape	**Direction of influence:** Fragment shape affects fire **Effect on fire:** Less fire **Effect on biodiversity:** Not stated (the introduction of wooded patches modifies fire regime) Modifying patch shape by fragmenting shrubland (highly flammable), through the introduction of forest corridors (low flammability), reduces fire spread and temperature in a Mediterranean landscape. (SIMULATION)
2	Brudvig, L. A., *et al.* (2012) *Ecological Applications*	Shape	**Direction of influence:** Fragment shape affects fire **Effect on fire:** More fire **Effect on biodiversity:** Positive (speculate) (corridors modify fire intensity and might promote biodiversity) Grassland corridors increase local fire temperatures by increasing inter-patch connectivity and through within-patch edge effects, from tree litter increasing fuel, promote biodiversity in a longleaf pine woodland matrix.
3	Pausas, J. G. (2006) *Plant Ecology*	Grain and pattern	**Direction of influence:** Fragmentation grain and pattern affects fire **Effect on fire:** Less fire **Effect on biodiversity:** Positive (speculate) (coarse grain landscape structures produce fire dynamics that lead to fire-sensitive species being maintained longer) Coarse-grain (aggregated) patches produced fewer changes from the initial vegetation conditions (slow dynamics) than fine-grain landscape patchiness (greater fragmentation) in which fire-sensitive species turnover faster, increasing extinction risk. (SIMULATION)

4	Regan, H. M., *et al.* (2010) *Ecology*	Grain and pattern	**Direction of influence:** Fragmentation grain and pattern affects fire **Effect on fire:** More fire **Effect on biodiversity:** Negative (beyond a fragmentation threshold, the greater the risk of decline of a plant species) Fine-grain patterns (greater fragmentation) lead to uncorrelated fires (changes in fire frequency) across more patches, creating spatially separated age classes, thus, spreading the risk of decline of an obligate seeder. Beyond a threshold of fragmentation, the population size is reduced because fire is correlated. (SIMULATION)
5	Gill, A. M., *et al.* (2014) *Biological Conservation*	Shape, size and isolation	**Direction of influence:** Fragment shape, size and isolation affects fire **Effect on fire:** Less fire **Effect on biodiversity:** Negative (speculate) (an increase in fire interval (less fire) threatens the ecosystem) Fragmented and isolated remnant edges are fire suppressed and have a reduced fire risk and increased fire interval. At the centre of an isolated fragment away from the edge, fire interval remains the same as prior to fragmentation. Where patch shape is narrow or irregular this can lead to maximum fire suppression from edge overlap.
6	Brooker, L. and M. Brooker (1994). *Pacific Conservation Biology*	Size	**Direction of influence:** Fragment size affects fire **Effect on fire:** More fire **Effect on biodiversity:** Negative (speculate) (a decrease in fire interval (less time between fires - more fire) can lead to a decline in fairy wrens) A decrease in the proportion of area burnt within a fragment creates time since fire mosaics and reduces the vulnerability of a small sedentary bird species to stochastic events, including fire. (SIMULATION)
7	Ramalho, C. E., *et al.* (2014) *Ecology*	Size	**Direction of influence:** Fragment size affects fire **Effect on fire:** Less fire **Effect on biodiversity:** Negative (fragmentation influences fire frequency (low fire frequency (less fire) and can reduce plant species richness)) Fire frequency was lower (fewer fires) in smaller remnants, as well as in more connected, rural remnants. In larger remnants fire frequency was higher (more fire). Reduced patch size and connectivity influenced fire frequency resulting in a decline in woody species richness in remnant *Banksia* woodland plant communities.

8	Alstad, A. O. and E. I. Damschen (2016) *Ecography*	Isolation	**Direction of influence:** Fragment isolation affects fire **Effect on fire:** Less fire **Effect on biodiversity:** Negative (fire suppression in isolated patches can reduce plant species richness in grasslands) Patch quality, represented by time since the last fire, interacts with landscape connectivity (isolation) resulting in a decline in plant species richness in fire-dependent prairie grass communities.
9	VanTassel, H. L. H., *et al.* (2015) *Biological Conservation*	Isolation	**Direction of influence:** Fire affects fragment isolation **Effect on fire:** More fire **Effect on biodiversity:** Positive (this is an inverse patch isolation with the effect increasing abundance and richness in an arthropod community) Rare to non-existent fire in a desert reserve results in varying numbers of remnant vegetation patches and levels of isolation. Arthropod abundance and richness was highest in burned patches with long-lived vegetation, and in both arthropods and small mammals (negative effects of isolation were masked by long-lived perennial vegetation).
	Mechanism of interaction **B – Within patch condition – irrespective of shape or size**	**Mechanism type**	**Mechanism description** **How does fire and/or fragmentation affect patch condition, irrespective of shape or size?**
10	Gilfedder, L. and J. B. Kirkpatrick (1998) *Biological Conservation*	Prescribed fire	**Direction of influence:** Fire affects fragment condition **Effect on fire:** Less fire **Effect on biodiversity:** Positive (greater native plant species richness) Frequency of prescribed fire within a patch influences condition, with increases in exotic plant species if frequency is high (less than seven years), decreases in exotic species and increases in native species richness if frequency is lower (greater than 20 years and up to seven years, respectively), and least invaded by exotic species where fire and grazing pressure was excluded.
11	Michalski, F., *et al.* (2007) *Biotropica*	Time since fragmentation	**Direction of influence:** Fragmentation condition alters fire behaviour **Effect on fire:** More fire **Effect on biodiversity:** Negative (fire severity decreases densities of forest tree species) Time since fragmentation and fire severity changes the taxonomic and functional composition and abundance of tree genera within a patch. High severity fire leads to tree mortality, threatening naturally low densities of tropical forest tree species.

12	Driscoll, D. A. and M. K. Henderson (2008) *Biological Conservation*	Isolation	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire and less fire **Effect on biodiversity:** Negative (speculate) (fire changes habitat that affect the successional spectrum of reptiles) Fire or its suppression in isolated patches changes habitat and influences early and late successional reptiles that without recolonisation leads to step-wise species loss.
13	Van Dyke, F., *et al.* (2004) *Restoration Ecology*	Fire as a restoration tool	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Neutral (fire had no effect on species richness and diversity of plant and bird species) Prescribed fire can homogenise a landscape, reducing habitat heterogeneity that could otherwise counterbalance the effects of fragmentation and declining reserve size to maintain ungulate populations Prescribed fire in small tallgrass prairie patches changed vegetation and habitat structure by retarding shrub encroachment but was ineffective for improving patch condition and thus bird and plant communities.
14	Yates, C. J. and P. G. Ladd (2010) *Plant Ecology*	Fire interval	**Direction of influence:** Fragmentation condition alters fire behaviour **Effect on fire:** More fire **Effect on biodiversity:** Negative (increases extinction risk of an obligate seeder) Increases in fire interval in roadside and reserve remnants can increase the extinction risk of small populations of an obligate seeder plant that could otherwise be moderated by mosaic burns within these small isolated fragments. (SIMULATION)
15	Pires, A. S., *et al.* (2005) *Studies on Neotropical Fauna and Environment*	Edge	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Negative (speculate) (modifies species spatial distribution and abundance) Increasing leaf litter at edge increases fire risk leading to changes in small mammal species spatial distribution – one species could be driven to the core allowing a second species to expand. **(cross-reference with 'edge' group C)**
16	How, R. A. and J. Dell (2000) *Pacific Conservation Biology*	Isolation	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Negative (speculation) (can prevent vertebrate colonisation and lead to extinction) Fragmentation modifies the natural fire frequency in isolated vegetated patches, in an urban matrix, preventing colonisation and leading to extinction (speculation) in ground vertebrates (mammal, amphibian and reptile species).

17	Berkunsky, I., *et al.* (2015) *Avian Conservation and Ecology*	Isolation	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Negative (decline in palm density and hence food and nesting habitat reduces bird occupancy) Fire in a non-fire dependent habitat patch is a threat to habitat quality by modifying and reducing macaw palm density that birds use for food and nesting (cavities), resulting in a decline in the occupancy of naturally fragmented forest patches by some parrot species.
18	Jennings, M. K., *et al.* (2016) *Journal of Wildlife Management*	Fire in an urban matrix	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Negative (speculate) (decline in puma presence) In fire-adapted shrubland patches that have resulted from urbanisation, a trend towards increasing fire frequency and extent from anthropogenic causes is expected to reduce vegetation cover and prey resulting in a decline of puma presence.
19	Schrey, A. W., *et al.* (2016) *Journal of Heredity*	Fire as a restoration tool	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Negative (lowers effective population size in a skink species) Increases in the number of fires and fire frequency in a fire dependent habitat modifies habitat condition resulting in fire mosaics that are unable to support a skink species leading to their decline.
20	Taillie, P. J., *et al.* (2015) *Condor*	Fire as a restoration tool	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Positive (ground cover and structure conducive to sparrow habitat breeding preferences) Frequent, low severity fire in isolated patches of longleaf pine forest maintains open-canopy conditions resulting in vegetation characteristics (groundcover structure and composition) shown to be the most important to the distribution of a sparrow species.
21	Possley, J. E., *et al.* (2014) *Natural Areas Journal*	Fire as a restoration tool	**Direction of influence:** Fire affects fragment condition **Effect on fire:** More fire **Effect on biodiversity:** Positive (increase in fire dependent native herbs and grasses) Prescribed fire influences pine rockland patch condition by increasing native herbs and grass cover and reducing high tree densities that result from fire suppression and that fragment pine rockland preserves.

	Mechanism of interaction **C – Fragmentation changes edge fire dynamics**	**Mechanism type**	**Mechanism description** **When does edge have an effect on fire regime?**
22	Cochrane, M. A. (2001) *Conservation Biology*	Edge drying	**Direction of influence:** Fragment edges affect fire **Effect on fire:** More fire **Effect on biodiversity:** Negative (fragmentation increases vulnerability of forests to fires and threatens ecosystems with rainforest vegetation unable to persist) Increasing forest fragmentation (pasture conversion) and resultant agricultural and settlement matrix, modifies edge dynamics (structural, drying or fuel), increasing fire risk and, thus, decreasing fire intervals.
23	Armenteras, D., *et al.* (2013) *Biological Conservation*	Edge drying, fuel and abiotic	**Direction of influence:** Fragment edges affect fire **Effect on fire:** More fire **Effect on biodiversity:** Negative (fragmentation increases vulnerability of forests to increased fire occurrence and intensity, threatening ecosystems) Forest fragmentation increases edge drying through fuel, light, wind and moisture effects, increasing fire occurrence and intensity at the landscape level, as a result of fire use in the matrix. High forest connectivity and low fragmentation could minimise edge-driven fires. **(cross-reference with 'matrix' group D)**
24	Cochrane, M. A. and W. F. Laurance (2002) *Journal of Tropical Ecology*	Edge drying and fire extent	**Direction of influence:** Fragment edges affect fire **Effect on fire:** More fire **Effect on biodiversity:** Negative (fragmentation increases vulnerability of forests to fires threatening biodiversity) Forest fragmentation increases the vulnerability of fragments to fires that as a result operate as large-scale edge effects (dynamics) by fire in the matrix penetrating forest interiors. **(cross-reference with 'matrix' group D)**
25	Cumming, G. S., *et al.* (2012) *Ecological Complexity*	Edge dynamics	**Direction of influence:** Fragment edges affect fire **Effect on fire:** More fire **Effect on biodiversity:** Negative (fragmentation increases vulnerability of forests to fires threatening forest persistence) Fragmentation increases fire risk in edges compounding the loss of connectivity long before a complete shift from forest to pasture occurs.

26	Benchimol, M. and C. A. Peres (2015) *Journal of Ecology*	Edge drying	**Direction of influence:** Fragment edges affect fire **Effect on fire:** More fire **Effect on biodiversity:** Negative (fragmentation increases vulnerability of forests to fires and threatens ecosystems) Small islands within a water matrix were more susceptible to fire risk (severity and spread) at patch edges because of an increase in drying and dead trees (combustible material). This induced destructive fires and subsequent changes to vegetation composition with lower species diversity and higher dominance.
27	Watts, A. C. and L. N. Kobziar (2015) *Freshwater Science*	Edge drying	**Direction of influence:** Fragment edges affect fire **Effect on fire:** More fire and less fire **Effect on biodiversity:** Positive (fragmentation did not increase vulnerability of forests to fires or threaten ecosystems) Wetland forest patches (cypress domes), in a fire-adapted subtropical ecosystem, that were wildfire burned and unburned interacted with edges but had similar microclimate effects. In some cases burned patches had cooler and more humid microclimates than unburned domes.
	Mechanism of interaction **D – Fragmentation changes fire in the matrix**	**Mechanism type**	**Mechanism description** **When does fragmentation have an effect on fire regime in the matrix?**
28	Weir, J. M. H., *et al.* (2000) *Ecological Applications*	Fire interval	**Direction of influence:** Fragmentation affects fire in the matrix **Effect on fire:** More fire **Effect on biodiversity:** Not stated (changes in fire cycle are expected to have implications) Fragmentation from land-use change in areas surrounding a large reserve, can influence the fire cycle within the reserve. Initial settlement for agriculture result in human-induced, short (15 year) fire cycles extending kilometres into the reserve. Post settlement the fire cycle becomes longer (75 year) because of fewer human-induced fires.
29	Guiomar, N., *et al.* (2015) *Science of the Total Environment*	Fire extent	**Direction of influence:** Fragmentation affects fire in the matrix **Effect on fire:** More fire **Effect on biodiversity:** Negative (oak woodlands transition to shrubland) Large fires modify land cover in Mediterranean oak agroforestry systems (*montados*) creating small and isolated patches of *montados* that makes them more vulnerable to fire in the matrix, which is an early-successional and fire-prone shrub community.

	Mechanism of interaction **E – Fire in the landscape alters connectivity – increase or decrease**	**Mechanism type**	**Mechanism description** **How does fire change the matrix to make it more or less permeable?**
30	Neuwald, J. L. and A. R. Templeton (2013) *Molecular Ecology*	Fire connects habitat	**Direction of influence:** Fire affects landscape changes (connects) **Effect on fire:** More fire **Effect on biodiversity:** Positive (fire connects fragments improving reptile habitat) Fire suppression in the matrix leads to forest encroachment and decreased connectivity between habitat patches (glades) in a reptile species, leading to metapopulation breakdown. Fire reintroduced connectivity. **(cross-reference with 'matrix' group D)**
31	Berry, L. E., *et al.* (2015a) *Journal of Applied Ecology*	Fire fragments habitat	**Direction of influence:** Fire affects landscape changes (fragments) **Effect on fire:** More fire **Effect on biodiversity:** Negative (fire alters landscape producing isolated patches threatening bird species persistence) Fire intensity and spread in a contiguous forest reserve creates a burn matrix that can result in small isolated unburnt patches decreasing connectivity that leads to a decline in bird species persistence, unlike large unburnt habitat patches that increase connectivity and maintain avian diversity.
32	Berry, L. E., *et al.* (2015b) *Ecological Applications*	Fire fragments habitat	**Direction of influence:** Fire affects landscape changes (not stated) **Effect on fire:** More fire and less fire **Effect on biodiversity:** Not stated (fire alters landscape: the distribution of refuges that are dependent on fire condition) Land management practices such as logging may influence fire risk and affect the subsequent distribution of refuges. Different physical landscape properties can mediate fire severity and as a result the establishment and distribution of refuges. For example, more logging and fewer refuges; less logging and more refuges. (SIMULATION)
33	Berman, M., *et al.* (2016) *Conservation Genetics*	Fire fragments habitat	**Direction of influence:** Fire affects landscape changes (neutral) **Effect on fire:** More fire **Effect on biodiversity:** Neutral (fire alters landscape without threatening an ant species) Human induced habitat fragmentation as a result of fire, over 200 years, has had limited impact on levels of gene flow and genetic structure in an ant species living in remnant rainforest patches.

Table S6a. This table identifies the interaction categories and components of fire in a fragmented landscape and presents a method for identifying research gaps in the literature. The interacting components are: fire, patch and matrix. Fragmentation is comprised of both patch and matrix. The columns are in four overarching groups e.g. Fire regime…is changed by patch, their interacting components e.g. condition, that are aligned to Review articles e.g. B14, and the biodiversity response for each. NB: The letter and number for Review articles correspond to Groups (A to E) and numbers (1 to 33), respectively in Table S5 and Table S6b). By assigning our 33 review articles to the relevant interaction we can begin to identify the gaps in the fire-fragmentation research literature – the areas shaded in dark grey show that none of the articles in our review covered the research mechanism type. This table informs Table 3.

Indirect influences on patch changes fire regime:-climate change,-human (reserves, production and urban),-species (natives, exotics, population pressure, resource competition)

1. Fire regime… …is changed by patch (Patch… …changes fire regime)	**Review article OR Gap '–'**	*Biod. Resp.~ N, P, NS, Ne*	**2. Fire regime… …changes patch (Patch… …is changed by fire regime)**	**Review article OR Gap '–'**	*Biod. Resp.~ N, P, NS, Ne*	**3. Matrix… …is changed by fire regime**	**Review article OR Gap '–'**	*Biod. Resp.~ N, P, NS, Ne*	**4. Matrix… …changes fire regime**	**Review article OR Gap '–'**	*Biod. Resp.~ N, P, NS, Ne*
Patch influence specified:			**Fire management NOT specified:**			**Fire influence specified:**			**Fire management NOT specified:**		
-condition (incl. structure)	B14	*N*	-condition (incl. structure)	B11	*N*	-condition (incl. structure)	–	–	-condition (incl. structure)	–	–
-connectivity	–	–	-connectivity	E30,E31,E32,E33	*P,N,NS, Ne*	-connectivity	–	–	-connectivity	B18	*N*
-edge	B15,C24	*N,N*	-edge	C25,C27	*N,P*	-edge	–	–	-edge	C22*,C23*,C26*	*N,N,N*
-grain and pattern	A3,A4	*P,N*	-grain and pattern	–	–	-shape	–	–	-grain and pattern	–	–
-isolation	A8,B16	*N,N*	-isolation	A9,B12,B17	*P,N,N*	-size, extent	D29	*N*	-shape	–	–
-shape	A1,A2,A5*	*NS,P,N*	-shape	–	–				-size, extent	D28	*NS*
-size	A7	*N*	-size	A6	*N*						
			Managed fire type specified:								
			-condition (incl. structure)	B20,B21	*P,P*						
			-connectivity	B10,B13	*P,Ne*						
			-edge	–	–						
			-grain and pattern	–	–						
			-isolation	B19	*N*						
			-shape	–	–						
			-size	–	–						

~Biodiversity response: N=negative; P=positive; NS=not stated; Ne=neutral   *equally applicable to 'shape' and 'size' ** equally applicable to 'size, extent'

Table S6b. This table presents each Review article and its assigned interaction component category e.g. fire, fragmentation and matrix. The brief details for each article were used to assign each to the overarching group (Groups 1 to 4) in Table S6a. Table S6a presents a method to identify research gaps in the fire-fragmentation interactions research literature. These tables inform Table 3.

1. Fire regime **IS CHANGED BY** patch, patch **CHANGES** fire regime										
A1:Patch geometry-**shape** (forest corridors **decrease fire spread and temperature**) not stated Duguy., *et al.* (2007) *International Journal of Wildland Fire*	A2:Patch geometry-**shape** (grassland corridors **increase fire temperature**) +ve Brudvig L.A., *et al.* (2012) *Ecological Applications*	A3:Patch geometry-**grain and pattern** (coarse grain (aggregated **patches**) **slows fire**) +ve Pausas, J.G. (2006) *Plant Ecology*	A4:Patch geometry-**grain and pattern** (fine grain arrangement of **patches** (greater fragmentation) **lead to uncorrelated fire**) -ve Regan, H.M., *et al.* (2012) *Ecology*	A5:Patch geometry-**shape, size and isolation** (isolated, narrow **patches lowers fire frequency**) -ve Gill, A.M., *et al.* (2014) *Biological Conservation*	A7:Patch geometry-**size** (smaller and less connected **patches lowers fire frequency**) -ve Ramalho, C.E., *et al.* (2014) *Ecology*	A8:Patch geometry-**isolation** (isolated **patches lowers fire frequency**) -ve Alstad, A.O. and E.I. Damschen (2016) *Ecography*	B14:Patch condition-**fire interval** (**fragmentation changes fire** regime) -ve Yates, C.J. and P.G. Ladd (2010) *Plant Ecology*	B15:Patch condition-**edge** (**fire risk increased from leaf litter at edge**) -ve Pires, A. S., *et al.* (2005) *Studies on Neotropical Fauna and Environment*	B16:Patch condition-**isolation** (condition of the isolated **patch increases fire risk**) -ve How, R.A. and J. Dell (2000) *Pacific Conservation Biology*	C24:Edge-**edge drying and fire extent** (**more patches** increase edges that **increases** vulnerability of **matrix fires penetrating the patch**) -ve Cochrane, M.A. and W.F. Laurance (2002) *Journal of Tropical Ecology*

2. Fire regime **CHANGES** patch, patch **IS CHANGED BY** fire regime										
A6:Patch geometry-**isolation** (fire **size creates mosaics**) -ve Brooker, L. and M. Brooker (1994). *Pacific Conservation Biology*	A9:Patch geometry-**isolation** (fire **creates different levels of isolation)** +ve VanTassel, H. L. H., *et al.* (2015) *Biological Conservation*	B10:Patch condition-**prescribed fire** (prescribed **fire creates mosaics and increases species richness**) +ve Gilfedder, L. and J. B. Kirkpatrick (1998) *Biological Conservation*	B11:Patch condition-**time since fragmentation** (high severity **fire changes forest composition**) -ve Michalski, F., *et al.* (2007) *Biotropica*	B12:Patch condition-**isolation (fire suppression in patches creates isolated patches that lack successional habitat gradients**) -ve Driscoll, D. A. and M. K. Henderson (2008) *Biological Conservation*	B13:Patch condition-**restoration tool (fire** as a restoration tool **changes structure**) neutral Van Dyke, F., *et al.* (2004) *Restoration Ecology*	B17:Patch condition-**isolation (fire** in a non-fire dependent patch**, changes habitat**) -ve Berkunsky, I., *et al.* (2015) *Avian Conservation and Ecology*	B19:Patch condition-**restoration tool** (increasing **fire** frequency **creates fire mosaics, isolating patches**) -ve Schrey, A.W., *et al.* (2016) *Journal of Heredity*	B20:Patch condition-**restoration tool (fire changes vegetation composition**) +ve Taillie, P.J., *et al.* (2015) *Condor*	B21:Patch condition-**restoration tool** (**changed vegetation composition**) +ve Possley, J.E., *et al.* (2014) *Natural Areas Journal*	C25:Edge-**edge dynamics** (patch is **changed by edge fires decreasing forest connectivity**) -ve Cumming, G.S., *et al.* (2012) *Ecological Complexity*
C27:Edge-**edge drying (changed microclimate**) +ve Watts, A.C. and L.N. Kobziar (2015) *Freshwater Science*	E30:Connectivity-**fire connects habitat (patch connectivity is changed by fire**) +ve Neuwald, J.L. and A.R. Templeton (2013) *Molecular Ecology*	E31:Connectivity-**fire fragments habitat (changes forest connectivity**) -ve Berry, L.E., *et al.* (2015a) *Journal of Applied Ecology*	E32:Connectivity-**fire fragments habitat (creates patches (refuges) in a burn matrix**) not stated Berry, L.E., *et al.* (2015b) *Conservation Genetics*	E33:Connectivity-**fire fragments habitat (changed rainforest connectivity**) neutral Berman, M., *et al.* (2016) Conservation *Genetics*						

3. Matrix **IS CHANGED BY** fire regime
D29:Matrix-**fire extent** (landscape **fire creates** woodland **patches that are** then **vulnerable to the matrix (i.e. a fire-prone shrubland matrix)**) -ve Guiomar, N., *et al.* (2015) *Science of the Total Environment*

4. Matrix **CHANGES** fire regime				
B18:Patch condition-**fire in an urban matrix** (the urban **matrix changes fire** affecting habitat) -ve Jennings, M. K., *et al.* (2016) *Journal of Wildlife Management*	C22:Edge-**edge drying** (increase in agricultural and settlement **matrix** increases **edge fire risk in adjacent forest**) -ve Cochrane, M. A. (2001) *Conservation Biology*	C23:Edge-**edge drying, fuel and abiotic** (**matrix** modifies **edge** dynamics and **increases fire risk**) -ve Armenteras, D., *et al.* (2013) *Biological Conservation*	C26:Edge-**edge drying** (increae in **matrix size** lead to **increases** in patch isolation, **edge drying** and increases **fire risk**) -ve Benchimol, M. and C. A. Peres (2015) *Journal of Ecology*	D28:Matrix-**fire interval** (increasing fragmentation increases the **matrix area and changes fire interval in adjacent reserve (patch)**) not stated Weir, J. M. H., *et al.* (2000) *Ecological Applications*

Table S7. The 35 journal and 1 book title of the 60 review articles that investigated interactions of fire and fragmentation, and the number and percentage of articles published in each.

Publication title	Publication type (Journal or book)	Number of articles (%)
Biological Conservation	J	8 (13.33)
Ecological Applications	J	4 (6.67)
Forest Ecology and Management	J	4 (6.67)
Conservation Biology	J	3 (5.0)
Journal of Wildlife Management	J	3 (5.0)
Animal Conservation	J	2 (3.33)
Ecology	J	2 (3.33)
International Journal of Wildland Fire	J	2 (3.33)
Journal of Tropical Ecology	J	2 (3.33)
Landscape Ecology	J	2 (3.33)
Pacific Conservation Biology	J	2 (3.33)
Plant Ecology	J	2 (3.33)
Various (individual journals x 23 and book x 1)	J* and B**	24 (40.00)
TOTAL		60^

* Journals: *AMBIO*, *Austral Ecology*, *Avian Conservation and Ecology*, *Biotropica*, *Condor*, *Conservation Genetics*, *Diversity and Distributions*, *Ecography*, *Ecological Complexity*, *Freshwater Science*, *Israel Journal of Ecology and Evolution*, *Journal of Applied Ecology*, *Journal of Ecology*, *Journal of Field Ornithology*, *Journal of Heredity*, *Journal of Mammalogy*, *Molecular Ecology*, *Natural Areas Journal*, *PlosOne*, *Restoration Ecology, Science*, *Science of the Total Environment*, *Studies on Neotropical Fauna and Environment* (n=23)

** Book: Brushfires in California Wildlands: Ecology and Resource Management (n=1)

^ Journals x 35 and book x 1

Table S8. Number of articles for each geographic region and the corresponding biodiversity responses~ indicating a predominance of negative responses for the 60 articles.

Geographic region	Number of articles	%	*–ve*	*+ve*	*ns*	*neutral*
North America*	24	40	10	12	1	1
South America**	17	28.3	13	2	2	-
Oceania***	12	20	9	1	1	1
Europe****	3	5	1	1	1	-
Africa*****	2	3.3	2	-	-	-
Asia******	1	1.7	-	-	1	-
Multinational^	1	1.7	1	-	-	-
TOTAL	60	100	36	16	6	2

* USA (21); Canada (2); North America (1) ** Brazil (12); Colombia (1); Bolivia (2); Peru, Bolivia, Brazil (1); Amazon (1) *** Australia (11); New Caledonia (1) **** Portugal (1); Spain (1); Europe-southern (1) ***** South Africa (1); Ethiopia (1) ****** China (1)

^ Metcalf 2007 – Arctic (ground squirrel) and Africa (wildebeest) (1)

~ See Glossary of Terms for 'biodiversity response' as it relates to 'positive', 'negative', 'not stated' and 'neutral'

Table S9. Details of the fauna and flora data results for 60 studies: Ecosystem (habitat) type; Organisational level; Target group; Vertebrates / inverts / fungi; Flora and fauna group (plants / animals)

Author	Ecosystem (habitat) type	Organisational level	Target group	Vertebrates = V Invertebrates = I Fungi = F	Fauna and flora group (plants / animals)
Louzada *et al.* (2010)	savanna and forest	animal community	dung beetles	I	animals
Templeton *et al.* (2007)	grassland (glades)	animal	reptiles	V	animals
*Neuwald and Templeton (2013)	grassland (glades)	animal	reptiles	V	animals
Humple and Holmes (2006)	shrubland	animal	bird	V	animals
Brisson *et al.* (2003)	grassland (glades)	animal	reptiles	V	animals
Metcalf *et al.* (2007)	not_stated	animal community	mammals-various	V	animals
Vogel *et al.* (2007)	grassland	animal community	butterflies	I	animals
Parsons and Gosper (2011)	shrubland	animal	bird	V	animals
Teasdale *et al.* (2013)	woodland	animal community	inverts-various	I	animals
Cromsigt *et al.* (2009)	grassland and woodland	animal community	herbivores	V	animals
*Driscoll and Henderson (2008)	woodland	animal community	reptiles	V	animals
Gavin *et al.* (1999)	grassland	animal	mammal	V	animals
Womack *et al.* (2013)	forest	animal	bat	V	animals
*Pires *et al.* (2005)	forest	animal community	mammals-various	V	animals
Hovick *et al.* (2012)	grassland	animal	bird	V	animals
*How and Dell (2000)	woodland	animal community	amphibians, reptiles, mammals	V	animals
*Brooker and Brooker (1994)	woodland	animal	bird	V	animals
Sauvajot (2005)	not_stated	animal community	wildlife	V	animals
*Berkunsky *et al.* (2015)	forest	animal community	birds	V	animals
*Berry *et al.* (2005a)	mallee	animal community	birds	V	animals
*VanTassel *et al.* (2015)	desert scrub	animal community	verts and inverts	V and I	animals
*Jennings *et al.* (2016)	shrubland	animal	mammal	V	animals
*Schrey *et al.* (2016)	scrubland	animal	reptile	V	animals
*Berman *et al.* (2016)	forest	animal	ants	I	animals
*Taillie *et al.* (2015)	forest	animal	birds	V	animals
Dunham *et al.* (2003)	freshwater (fish)	animal community	fishes	V	fishes
Radies *et al.* (2009)	forest	fungi community	macrolichens	F	fungi
Laurance *et al.* (2002)	forest	plant and animal communities	forest	-	plants
Laurance and Williamson (2001)	forest	plant and animal communities	forest	-	plants
*Weir *et al.* (2000)	forest	plant and animal communities	forest	-	plants
*Gilfedder and Kirkpatrick (1998)	not_stated	plant community	plants-various	-	plants
*Duguy *et al.* (2007)	shrubland and woodland	plant community	shrubs trees GIS	-	plants
Laurance *et al.* (2011)	forest	plant community	forest	-	plants
Pinard and Huffman (1997)	forest	plant community	forest	-	plants
Leach and Givnish (1996)	grassland	plant community	grassland (prairie)	-	plants
Eriksson *et al.* (2003)	woodland and forest	plant community	forest	-	plants

Author	Ecosystem (habitat) type	Organisational level	Target group	Vertebrates = V Invertebrates = I Fungi = F	Fauna and flora group (plants / animals)
Soares-Filho *et al.* (2012)	forest	plant community	forest	-	plants
*Brudvig *et al.* (2012)	woodland	plant community	forest	-	plants
Vasconcelos and Luizao (2004)	forest	plant community	forest	-	plants
Briant *et al.* (2010)	forest	plant community	forest	-	plants
*Cochrane (2001)	forest	plant and animal communities	forest	-	plants
*Michalski *et al.* (2007)	forest	plant and animal communities	forest	-	plants
*Pausas (2006)	shrubland and woodland	plant community	shrubs and trees	-	plants
*Armenteras *et al.* (2013)	forest	plant and animal communities	forest	-	plants
*Cochrane and Laurance (2002)	forest	plant and animal communities	forest	-	plants
*Cumming *et al.* (2012)	forest	plant and animal communities	forest	-	plants
Li *et al.* (2013)	forest	plant and animal communities	forest	-	plants
*Van Dyke *et al.* (2004)	grassland	plant community	grassland (prairie)	-	plants
*Regan *et al.* (2010)	shrubland	plant	shrub	-	plants
*Yates and Ladd (2010)	heath	plant	shrub	-	plants
Cochrane *et al.* (2008)	forest	plant and animal communities	forest	-	plants
*Gill *et al.* (2014)	mallee	plant community	forest	-	plants
*Ramalho *et al.* (2014)	woodland	plant community	woodland	-	plants
*Benchimol and Peres (2015)	forest	plant community	forest	-	plants
*Alstad and Damschen (2016)	grassland	plant community	grassland (prairie)	-	plants
*Watts and Kobziar (2015)	forest	plant community	forest	-	plants
*Berry *et al.* (2015b)	forest	plant community	forest	-	plants
*Possley *et al.* (2014)	forest	plant community	forest	-	plants
*Guiomar *et al.* (2015)	woodland	plant community	woodland	-	plants
Ager *et al.* (2014)	not_stated	plant and animal communities	NA~	-	plants and animals

* indicates the 33 articles included in the final systematic review analysis

~ Reference is about fire transmission risk between remnants/parcels of land

* Habitats – forest=25/60 and 14/33, grassland=9/60 and 3/33, woodland=9/60 and 8/33, shrubland=7/60 and 5/33, multiple=5/60 and 2/33, not_stated=4/60 and 1/33, and freshwater=1/60 and 0/33.

Table S10. Animal and plant categories, target, and species and ecological groups. Sixty review articles and their research focus on animal and plant communities. The animal (26/60) and plant (32/60) articles were dominated by vertebrates (21/60) and forests (22/60). Invertebrates accounted for four articles (4/60). One paper (1/60) investigated both vertebrates and invertebrates. Multiple plant community articles accounted for four (3/60), three grasslands (3/60), two shrubland (2/60) and two woodland (2/60). There was one article on plants and animals and one on fungi.

Group n (%)	n	Target group	n	Species/ecological groups in each article
Animals 26 (43)				
Vertebrates	21	birds	7	Shrikes, sparrows (passerines), Mallee fowl, fairy wrens, parrots
		reptiles^	5	skinks, lizards
		mammals	6	squirrels, ungulates, marsupials, rodents, bats, puma
		fishes	1	salmonids
		multiple	2	wildlife, amphibians, reptiles and mammals
Invertebrates	4	beetles	1	Coleoptera
		butterflies	1	Lepidoptera
		ants	1	Formicidae
		insects	1	morphospecies
Vertebrates and invertebrates	1	multiple	1	small mammals and arthropods
Plants 32 (53)				
forests	22	-	22	tropical, boreal, temperate
woodland	2	-	2	semi-arid, montado
shrubland	2	-	2	Mediterranean
grassland	3	-	3	prairie
multiple	3	-	3	shrubs and trees, plant spp.
Plants and animals 1 (2)~	1	-	1	ecosystem
Fungi 1 (2)	1	-	1	macrolichens
TOTAL 60 (100%)	60		60	

^ Templeton was the common author in three of the articles on the Eastern collared lizard (*Crotaphytus collaris collaris*)

~ Ager *et al.* (2014) reference is about fire transmission risk between remnants/parcels of land

Table S11. The 33 review articles and the interaction effects that result from ‘more fire’, ‘less fire’ and ‘more fire and less fire’, and the corresponding species responses (positive, negative, not stated or neutral) of the interactions for each fire-fragmentation interaction group: A to E.

	Interactions and species responses												Total combined interaction effects and species responses		
	More fire	*+ve*	*spp. –ve*	*ns/neu*	Less fire	*+ve*	*spp. –ve*	*ns/neu*	More fire and Less fire	*+ve*	*spp. –ve*	*ns/neu*	Positive	Negative	Not stated or Neutral
Group A: Patch geometry	4	*2*	*2*	-	5	*1*	*3*	*1*	-	-	-	-	3	5	1
Group B: Patch condition	10	*2*	*7*	*1*	1	*1*	-	-	1	-	1	-	3	8	1
Group C: Edge	5	-	*5*	-	-	-	-	-	1	1	-	-	1	5	-
Group D: Matrix	1	-	*1*	-	-	-	-	-	1	-	-	1	-	1	1
Group E: Connectivity	3	*1*	*1*	*1*	-	-	-	-	1	-	-	1	1	1	2
TOTAL	23	*5*	*16*	*2*	6	*2*	*3*	*1*	4	1	1	2	8	20	5

Table S12. Fire-fragmentation interaction Group B articles on how fire changes patch condition and how patch condition alters fire behaviour, irrespective of patch shape/size. Seventeen (10/33) articles are about how fire changes patch condition and two (2/33) are about how patch condition alters fire behaviour influencing species change. Of the 10 articles where fire changes patch condition there were three (n = 3) positive responses, six (n=6) negative responses and one (n = 1) neutral response influencing species. Patch condition altered fire behaviour and had negative responses.

			Effect of interactions on biodiversity		
Interaction Group B-Patch condition change is influenced by fire and fragmentation (irrespective of shape/size) Author/s	Fire changes patch condition	Patch condition alters fire behaviour	Positive	Negative	Neutral
Gilfedder, L. and J. B. Kirkpatrick (1998) *Biological Conservation*	1	-	*1*	-	-
How, R. A. and J. Dell (2000) *Pacific Conservation Biology*	1	-	-	*1*	-
Van Dyke, F., *et al.* (2004) *Restoration Ecology*	1	-	-	-	*1*
Pires, A. S., *et al.* (2005) *Studies on Neotropical Fauna and Environment**	-	-	-	*1*	-
Michalski, F., *et al.* (2007) *Biotropica~*	-	1	-	*1*	-
Driscoll, D. A. and M. K. Henderson (2008) *Biological Conservation*	1	-	-	*1*	-
Yates, C. J. and P. G. Ladd (2010) *Plant Ecology^*	1	1	-	*1*	-
Possley, J. E., *et al.* (2014) *Natural Areas Journal*	1	-	*1*	-	-
Berkunsky, I., *et al.* (2015) Avian Conservation and Ecology	1	-	-	*1*	-
Taillie, P. J., *et al.* (2015) *Condor*	1	-	*1*	-	-
Jennings, M. K., *et al.* (2016) *Journal of Wildlife Management*	1	-	-	*1*	-
Schrey, A. W., *et al.* (2016) *Journal of Heredity*	1	-	-	*1*	-
TOTAL (12)	10	2	*3*	*8*	*1*

* Cross referenced with Group D – edge

~ Time since fragmentation

^ Simulation

Table S13. Fire types and characteristics. Number of articles studying each type of fire (planned/unplanned/both) and fire characteristic (severity/frequency) where fire-fragmentation was the focus of the research (n = 33).

'fire' AND 'fragmentation'	Total fire types	*Fire types covered*			Fire severity	Fire frequency	Both fire severity and frequency
		Planned	*Unplanned*	*Both*			
A: Patch geometry	9	*3*	*3*	*3*	3	5	1
B: Patch condition	12	*4*	*4*	*4*	1	6	1
C: Edge	6	*0*	*5*	*1*	2	3	2
D: Matrix	2	*0*	*1*	*1*	2	2	2
E: Connectivity	4	*1*	*2*	*1*	1	1	0
TOTAL	33	*8*	*15*	*10*	9	17	6

Table S14. Number of articles (20/33) that did not offer management recommendations or options in relation to the use of fire, even though thirteen of these had negative biodiversity responses as a result of fire interacting with fragmentation.

	Biodiversity response from fire interacting with fragmentation				
Interaction groups	Positive	Negative	Not stated	Neutral	Totals
A: Patch geometry	2	4	1	-	7
B: Patch condition	1	3	-	-	4
C: Edge	1	5	-	-	6
D: Matrix	-	1	1	-	2
E: Connectivity	-	-	-	1	1
TOTAL	4 (20%)	13 (65%)	2 (10%)	1 (5%)	20 (100%)

Table S15. Number of articles (13/33) that did offer management recommendations or options in relation to the use of fire.

	Biodiversity response from fire interacting with fragmentation				
Interaction groups	Positive	Negative	Not stated	Neutral	Totals
A: Patch geometry*	1	1	-	-	2
B: Patch condition*	2	5	-	1	8
C: Edge	-	-	-	-	-
D: Matrix	-	-	-	-	-
E: Connectivity	1	1	1	-	3
TOTAL	4 (31%)	7 (54%)	1 (8%)	1 (8%)	13 (100%)

Table S16. Interaction groups and related management recommendations. The management recommendations or options made in relation to the use of fire for the mechanism of interaction groups.

Interaction groups and authors	What the management recommendations were in relation to the use of fire	
	Fire (increase/decrease); or Other method	Management recommendation and effect on biodversity (+ve, -ve, neutral, not stated)
A: Patch geometry		
Pausas, J. G. (2006) *Plant Ecology*	Further research	Further research into species traits and landscape types and their interaction response to fire in forest restoration for cost-effective planning (+ve)
Brooker, L. and M. Brooker (1994). *Pacific Conservation Biology*	↓	Reduce fire frequency to improve remnant condition to manage decline in fairy wrens (-ve)
B: Patch condition		
Gilfedder, L. and J. B. Kirkpatrick (1998) *Biological Conservation*	↓	Suppress and control fire (-ve)
Driscoll, D. A. and M. K. Henderson (2008) *Biological Conservation*	Further research	Further research into how to implement effective mosaics and application of fire management in reptiles (+ve)
Van Dyke, F., *et al.* (2004) *Restoration Ecology*	↑	Increase fire frequency to increase connectivity and suppress shrub encroachment to prairies to maintain bird numbers (neutral)
How, R. A. and J. Dell (2000) *Pacific Conservation Biology*	↓	Exclude and suppress fire for reptiles (-ve)
Berkunsky, I., *et al.* (2015) *Avian Conservation and Ecology*	Monitor	Monitor habitat heterogeneity for parrots (-ve)
Jennings, M. K., *et al.* (2016) *Journal of Wildlife Management*	↓	Further research, reducing wildfire in fragmented landscape reduces extinction risk of pumas (-ve)
Schrey, A. W., *et al.* (2016) *Journal of Heredity*	Management strategy	Prepare fire management strategy to create fire mosaics (-ve)
Taillie, P. J., *et al.* (2015) *Condor*	↑	Increase fire to prevent woody encroachment (+ve)
E: Connectivity		
Neuwald, J. L. and A. R. Templeton (2013) *Molecular Ecology*	↑	Increase fire frequency to increase connectivity by suppressing woody encroachment (+ve)
Berry, L. E., *et al.* (2015a) *Journal of Applied Ecology*	↓	Reduce prescribed fire spread retaining connectivity (-ve)
Berry, L. E., *et al.* (2015b) *Ecological Applications*	↓	Modify land management practices to reduce escalation of fire risk (not stated)

Figure S1. Number of fire severity and frequency articles and the biodiversity responses

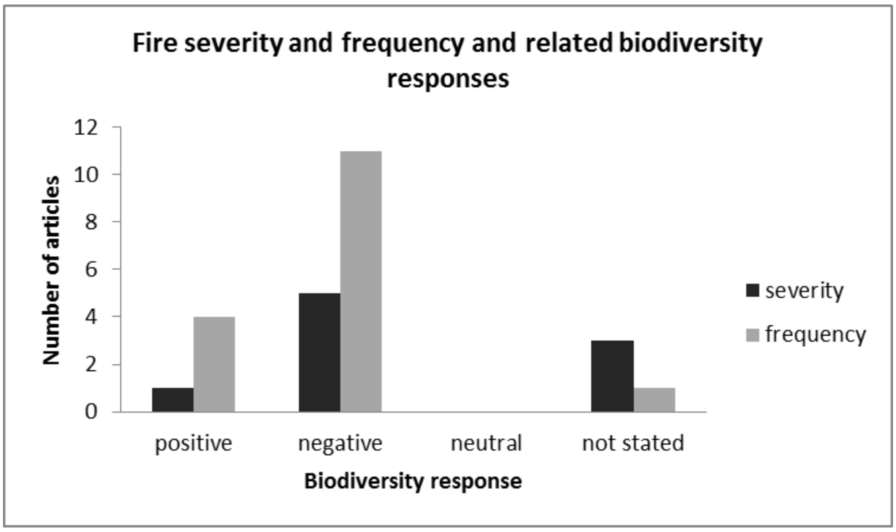
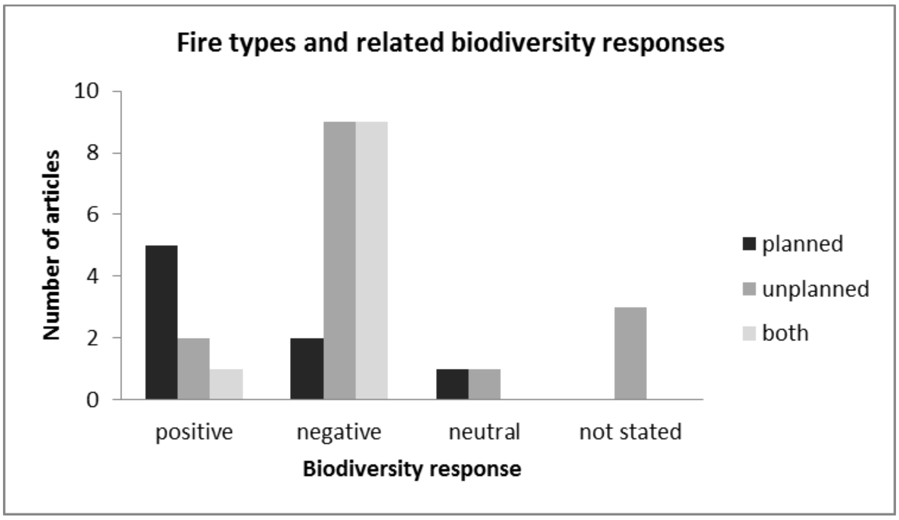


Figure S2. Number of fire type articles and the biodiversity responses



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* indicates the 33 articles included in the final systematic review analysis.

Paper II: Local environmental covariates are important for predicting fire history from tree stem diameters

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Running head: Environmental covariates affect TSF estimates

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Key-words: fragmentation, mallee woodland, plant-stem morphometrics, prediction model, time since fire (TSF)

Lazzari J., Yoon H. J. and Driscoll D. A. (2015). Local environmental covariates are important for predicting fire history from tree stem diameters. *International Journal of Wildland Fire* 24: 871-882.

Abstract

In fire-prone landscapes, knowing when vegetation was last burnt is important for understanding how species respond to fire and to develop effective fire management strategies. Fire history knowledge is paramount for both continuous reserves and modified, fire-prone landscapes with isolated habitat patches. However, fire history is often incomplete or non-existent. We developed a fire age prediction model for two mallee woodland tree species in southern Australia. The models were based on stem diameters from ~1172 individuals surveyed along 87 transects. Time since fire accounted for the greatest proportion of the explained variation in stem diameter for our two mallee tree species but variation in mean stem diameters was also influenced by local environmental factors. We illustrate a simple tool that enables time since fire to be predicted based on stem diameter and local covariates. We tested our model against new data but it performed poorly with respect to the mapped fire history. A combination of different covariate effects, variation in among-tree competition, including above- and below-ground competition, and unreliable fire history may have contributed to poor model performance. Understanding how the influence of covariates on stem diameter growth varies spatially is critical for determining the generality of models that predict time since fire. Models that were developed in one region may need to be independently verified before they can be reliably applied in new regions.

Introduction

Fire influences plant and animal communities globally (Bond *et al.*, 2005; Bowman *et al.*, 2012; Hessl *et al.*, 2012; Keith, 2012). The use of fire as a management tool is important for the persistence of many taxa (Bradstock *et al.*, 2005; Driscoll *et al.*, 2010b; Hanson *et al.*, 2009; Ripley and Archibold, 1999) but inappropriate fire regimes (e.g. fire too frequent or intense) are used with little knowledge and considered a key threatening process in fire-sensitive systems (Australian Government, 2007). Knowledge of fire history is necessary to understand how fire affects plants and animals and to make decisions about when, or when not, to use fire to protect ecological assets (Baker, 2006; Gill, 2001; Penman *et al.*, 2011; Richards *et al.*, 1999). Fire histories can be used to interpret abundance of fauna (Catling *et al.*, 2001; Kelly *et al.*, 2011; Smith *et al.*, 2012) and vegetation succession and structure (Bergeron and Dansereau, 1993; Gosper *et al.*, 2012; Walsh *et al.*, 2006). However, records of fire history in reserves and in remnant habitat on private land are often incomplete or inaccurate, limiting our ability to understand the ecological effects of fire and thus use it effectively as a conservation management tool.

Satellite imagery and aerial photography are used to infer fire history (Li *et al.*, 2010; Roy *et al.*, 2005) but there are limited means of independent ground validation for fire history maps generated from remote sensing data (Armstrong and Phillips, 2012). Moreover, as there are typically few contemporary ground observations that record the extent of burnt areas, retrospective methods are needed to infer the dates of past fires. Tree stem diameters are potentially useful proxies for time since fire (TSF), i.e. the time since the last fire, in species in which aerial stems are killed by fire (Barker, 1988; Burley *et al.*, 2007; Clarke *et al.*, 2010; Rumpff *et al.*, 2009). Other techniques (e.g. dendrochronology of fire scars) are applicable to species in which aerial stems are not fire-killed.

Using stem diameter to estimate TSF may not be straightforward because stem growth rates are influenced by the environment. For example, the influence of soil structure on tree growth rates (Passioura, 1991) is seen in dunes and inter-dune areas (swales) in the Namib Desert, Namibia, because dunes and swales differ in productivity and stability (Seely and Louw, 1980). Stem diameter can also be influenced by environmental variables such as water availability and temperature (Mauseth, 2012), canopy cover (Larcher, 2003), leaf litter (Loydi *et al.*, 2013), weeds(Houehounha *et al.*, 2010), soil type (Noy-Meir, 1974), tree height and crown width (Kalliovirta and Tokola, 2005; Larcher, 2003).

In fragmented landscapes, edge effects are known to have a substantial influence on the rate of tree growth. Trees in remnant native vegetation adjacent to, or surrounded by, cleared land may be affected by changes in light, moisture and air temperature (Gehlhausen *et al.*, 2000) as well as by agricultural inputs such as nitrogen (Rickey and Anderson, 2004), herbicides (Gove *et* *al.*, 2007) and grazing (Kemper *et al.*, 1999). These can increase growth rates or mortality of some native species (Duncan *et al.*, 2008).

Given the range of environmental variables that can influence tree growth rates, it is important that we gain a better understanding of these effects to improve methods to predict TSF. We know that TSF has an effect but we need to know the extent to which environmental variables may influence stem growth.

Mallee woodland communities in southern Australia are extensively fragmented, with reduced fire frequency in agricultural landscapes. Mallee stems in all size classes are typically killed by fire and regenerate from a lignotuber, an underground woody rootstock, meaning that we might expect a relationship between TSF and stem diameter. Indeed, Clarke *et al.* (2010) found stem diameter was a useful predictor of TSF. They found little influence of environmental covariates, with only one of six *Eucalyptus* species influenced by a regional rainfall gradient. However, they did not evaluate local environmental factors that could influence stem growth. To address this knowledge gap, our study examined the relative importance of environmental factors and TSF on stem diameter growth in two mallee eucalypt species *Eucalyptus costata* F. Muell. and Behr ex F. Muell. (yellow mallee) and *E. socialis* F. Muell. ex Miq. subsp. *socialis* (red mallee), from mallee woodlands on the Eyre Peninsula, South Australia. We also tested model predictions by exploring model performance in another area using four sites where the fire history was mapped. We used sites from outside the original sampling region, i.e. the areas used to develop the model, to replicate the future application of the model in remnant vegetation.

Materials and methods

Study area

Our study took place in four conservation reserves on the Eyre Peninsula, South Australia: Hincks, Hambidge, Heggaton and Pinkawillinie: Hincks 33°50′38.76″S, 136°1′6.74″E (67 000 ha);

Hambidge 33°23′6.70″S, 135°55′21.52″E (38 000 ha); Heggaton 33°22′29.20″S, 136°32′35.98″E (6500 ha) and Pinkawillinie 33°05′41.05″S, 135°59′57.75″E (132 000 ha) (Fig. 1a, b). The predominant vegetation consists of mallee *Eucalyptus* species with an understorey of spinifex (*Triodia* spp.) and a mix of shrubs (e.g. *Melaleuca uncinata*) and tussock grass species. Mallee species are multistemmed and generally regenerate by coppicing after fire, and the above-ground parts usually die if burnt (Noble, 2001). Fires in mallee burn with varying intensity and size, influencing landscape structure into a mosaic of patches (Berry *et al.*, 2015; Bradstock and Cohn, 2002; Gill *et al.*, 2003). Variability in understorey composition (e.g. litter quantity and hummock grass sizes), TSF (e.g. tree densities, spatial arrangements and tree height) and wind speeds in mallee resprouters result mostly in crown fires (Bradstock and Gill, 1993; Pausas *et al.*, 2004; Travers and Eldridge, 2012). Soils are primarily aeolian silicious sands of stable NW-SE dunes or of parabolic dune fields (South Australian Government, 2002; 2010; Wasson, 1989). The mean annual rainfall is 353 mm at Hincks, 314 mm at Hambidge and 318 mm at both Heggaton and Pinkawillinie (Bureau of Meteorology, 2013). There is high variability in rainfall between years (Van Etten, 2009). Clarke *et al.* (2010) found no effect of rainfall on stem diameter growth in our study species. Also, given the mallee woodland biogeographic region similarities, in particular climate (South Australian Government, 2010; Victorian Government, 1997), we did not use rainfall as an explanatory variable in our model development.

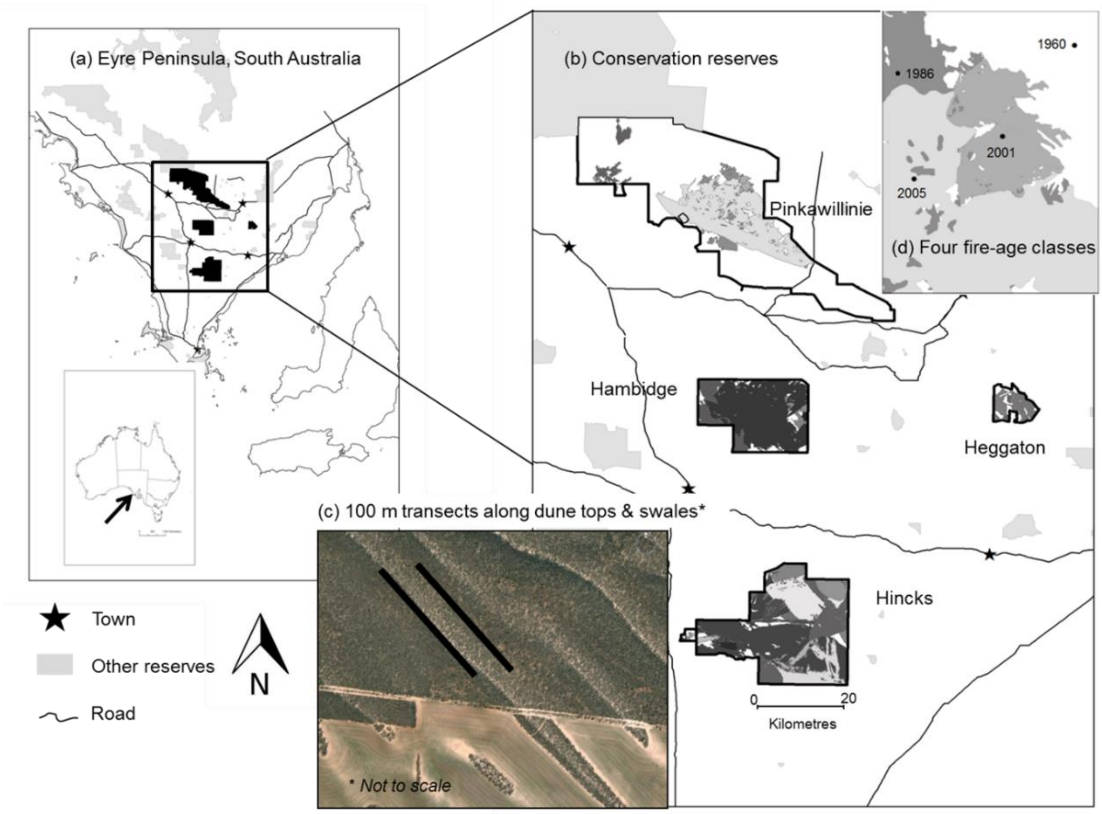
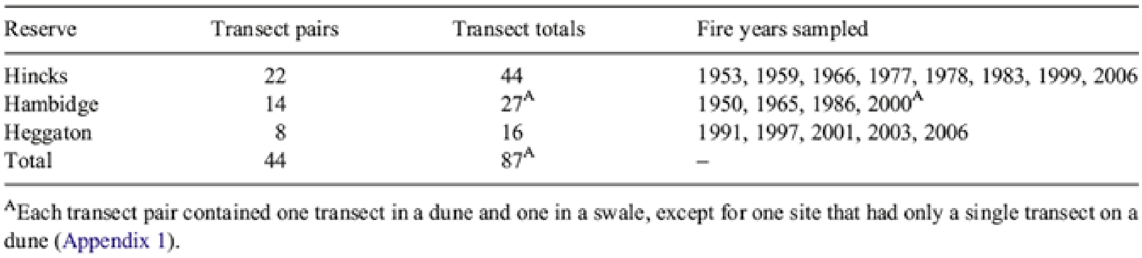


Figure 1. (a) Surveys were undertaken in South Australia in the semiarid Eyre Peninsula. (b) Transects in Hincks, Hambidge and Heggaton were surveyed to develop the time since fire prediction model. Different shading within the reserves indicates time since last fire. (c) Stem diameters were collected along 100 m transects. (d) The model was evaluated using stem diameters and vegetation covariates from four mapped fire histories from transects in (b) Pinkawillinie Reserve.

Study design

Between August and September 2009, data were collected from three reserves from a total of 34 sites (Hincks 20; Hambidge 8; Heggaton 6) encompassing 16 TSF based on fire records (Table 1). TSF is the time since fire burnt at that site in years. TSF sites and years were identified using nature maps (South Australian Government, 2009). We sampled edges within the reserves because we were interested in applying tree-ageing methods in remnant vegetation. Remnant vegetation patches in a mallee agricultural matrix are often narrow and edges are a prominent feature.

Table 1. Study design characteristics
Reserve, transect pairs, transect totals and time since fire (TSF) years from which data were sampled between September and October 2009



Reserve	Transect pairs	Transect totals	Fire years sampled
Hincks	22	44	1953, 1959, 1966, 1977, 1978, 1983, 1999, 2006
Hambidge	14	27^{A}	1950, 1965, 1986, 2000^{A}
Heggaton	8	16	1991, 1997, 2001, 2003, 2006
Total	44	87^{A}	–

[A] Each transect pair contained one transect in a dune and one in a swale, except for one site that had only a single transect on a dune (Appendix 1).

Within each site, we established two transects that extended 100 m into the woodland (one on a dune, one in the adjacent swale) (Fig. 1c; Table 1; Appendix 1). Within each transect, we sampled four plots (10 m radius) – at 0, 20, 50 and 100 m points – and randomly selected six trees within each plot.

Data collection

Stem diameters were measured along transects of dunes and swales. We identified each tree and measured up to 10 of the widest live stems 30 cm above ground level. Most trees had fewer than nine stems (93%, mean number of stems per tree = 4.4, standard deviation = 0.28). Our response variable was stem diameter averaged for each tree species within each plot. Four-hundred-and-thirty stem measurements from rocky transects were removed from the over 10 000-stem dataset because they were not representative of the predominantly sandy soils; there were too few rocky transects to model independently.

Predictor variable data were collected for vegetation variables (canopy, weeds, spinifex, shrubs), site variables (dune and swale (soil type), bare ground, leaf litter) and TSF. These data were collected systematically at the same points along transects (dunes and swales) where tree stems were measured. Visual estimates were taken by one observer for percentage cover of canopy, leaf litter, bare ground, shrubs, spinifex and weeds within each plot. Weeds were a mix of agricultural exotics including wild turnips (*Brassica* spp.), mustard (*Sisymbrium* spp.), pasture grasses (e.g. perennial veldt grass (*Ehrharta calycina*)), wild oats (*Avena* spp.), onion weed (*Asphodelus* spp.), horehound (*Marrubium* spp.) and thistles (*Asteraceae* spp.).

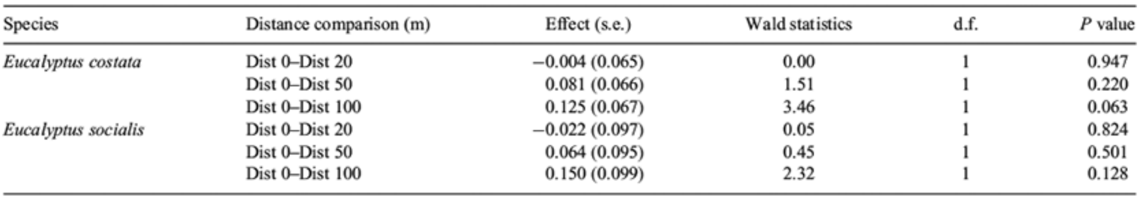
Additional data for testing model predictions

To explore the performance of our model, we tested it in another area by collecting data from four sites with mapped fire histories (TSF in years): 1960 (>53 years), 1986 (26 years), 2001 (11 years) and 2005 (7 years) from within Pinkawillinie Conservation Reserve (Fig. 1b and Fig. 1d). For testing model application, we also collected new data from 18 remnant sites in agricultural land. Stem diameter data were collected in January 2013 from 10 trees at each of the sites. Stem diameter measurements were only taken from *Eucalyptus costata* and *E. socialis* along the top of the dune using transects 10 m in width. This simple method of using two mallee species for data collection was designed for non-expert end-users, such that the data could be used in our exploration of model performance. We did not use swale transects because when this method is applied to the agricultural matrix, the remnants are predominantly dunes. Historically, dunes were considered too sandy and not cleared but swales were cleared and form part of the agricultural matrix, i.e. crop land. Transects varied in length and were dependent on the distance between the first tree and the final tree measured. Vegetation data were collected by one observer using the same methods used for collecting data for the model development – at four plots (10 m radius) evenly spaced along each transect. Percentage cover estimates of leaf litter, canopy cover, spinifex and weeds were recorded.

Statistical analysis

We used the statistical software *Genstat for Windows* 16th Edition (GenStat, 2000-2014). As part of our model simplification process, we first used a linear mixed model to test for tree diameter differences from the edge into the reserve. We did this because, unlike environmental site indicators that could be summarised at transect level, edge-distance would have required an extra nested layer in the analysis, increasing model complexity beyond what the dataset was able to support. Average stem diameter was our response variable and distance from the edge was the explanatory variable. There were no significant edge effects and therefore we did not include edge effects in subsequent analyses. However, there was a trend towards large diameters at the edge in both tree species (Table 2).

Table 2. Comparison of stem diameters at each distance from the edge for *Eucalyptus costata* and *E. socialis*
Mean stem diameters measured at 0 m, 20 m, 50 m, and 100 m from reserve edge for *Eucalyptus costata* and *Eucalyptus socialis* showing no significant edge effects on stem diameter as distance from the edge increased. Edge is significant at *P* < 0.05



Species	Distance comparison (m)	Effect (s.e.)	Wald statistics	d.f.	*P* value
Eucalyptus costata	Dist 0–Dist 20	−0.004 (0.065)	0.00	1	0.947
	Dist 0–Dist 50	0.081 (0.066)	1.51	1	0.220
	Dist 0–Dist 100	0.125 (0.067)	3.46	1	0.063
Eucalyptus socialis	Dist 0–Dist 20	−0.022 (0.097)	0.05	1	0.824
	Dist 0–Dist 50	0.064 (0.095)	0.45	1	0.501
	Dist 0–Dist 100	0.150 (0.099)	2.32	1	0.128

To investigate the relationship of stem diameter (response variable) with TSF and environmental (explanatory) variables for *Eucalyptus costata* and *E. socialis*, we used a generalised linear mixed model (GLMM) with a gamma distribution (log link) (Bolker *et al.*, 2009). The GLMM with gamma is a plausible model as the variance of the stem diameter increases with the mean stem diameter. We used 'burnt area', a variable defining individual fire events as a random effect, to account for pseudoreplication associated with having up to, for example, two or even three transect pairs in the same fire area. The fixed effects were TSF (years), soil type (dunes versus swales), and percentage cover of canopy, leaf litter, bare ground, shrubs, spinifex and weeds. Pairwise correlations of the explanatory variables were < ±0.4. We did not use site in the model because after checking the effect of site as a random effect, it did not account for any variation. We identified the parameters that had substantial effects on stem diameter using a backward elimination method, removing the least significant variable with each iteration of model simplification. We used the Wald test (Bolker *et al.*, 2009) to evaluate the statistical significance of the parameters in the best-fit model and used a threshold significance level of α = 0.05.

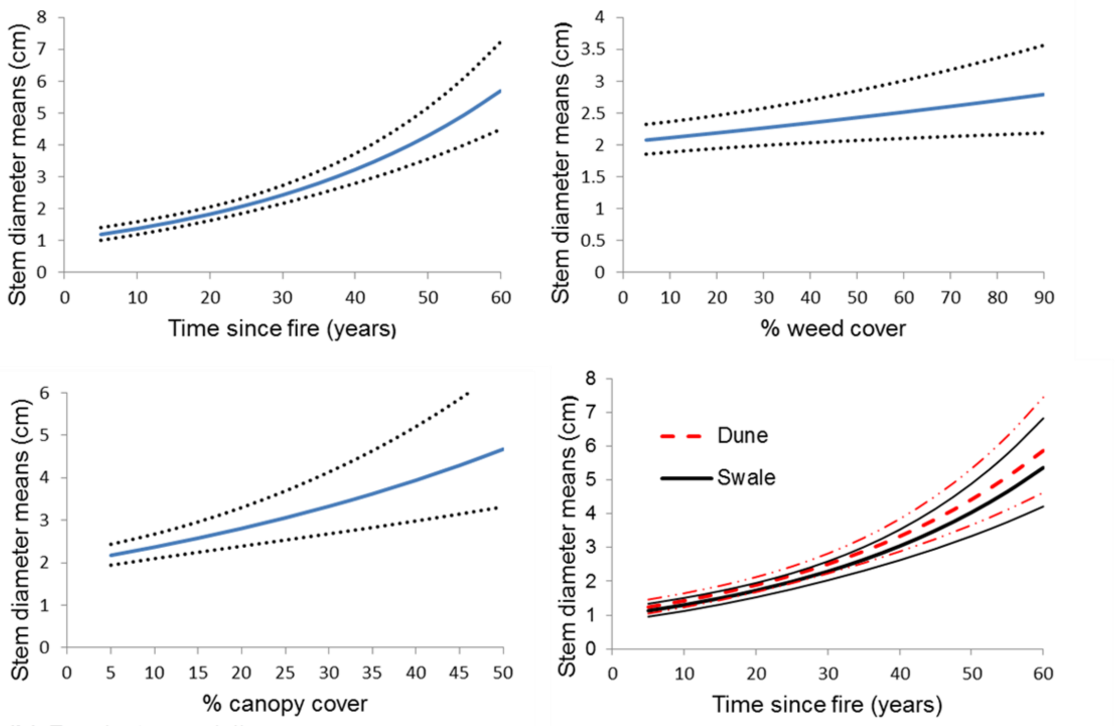
We produced contour plots of stem diameter, for a given TSF, canopy cover and weed cover that were based on the best-fit model, to illustrate how TSF could be estimated using covariate data.

Results

The number of trees used to develop the model was ~804 for *Eucalyptus costata* and 368 for *E. socialis*.

There were significant positive relationships of TSF and canopy cover with stem diameter for both *Eucalyptus* species (Fig. 2 and Table 3). For *E. costata*, weed cover and soil type (where stem diameters were slightly greater on dunes than in swales) had significant positive effects. For *E. socialis*, leaf litter cover had a significant negative effect and spinifex a significant positive effect. Using Wald statistics, the percentage variation in stem diameter explained by TSF was ~65% whereas other explanatory factors accounted for ~35% of the variation (Table 3).

(a) *Eucalyptus costata*



(b) *Eucalyptus socialis*

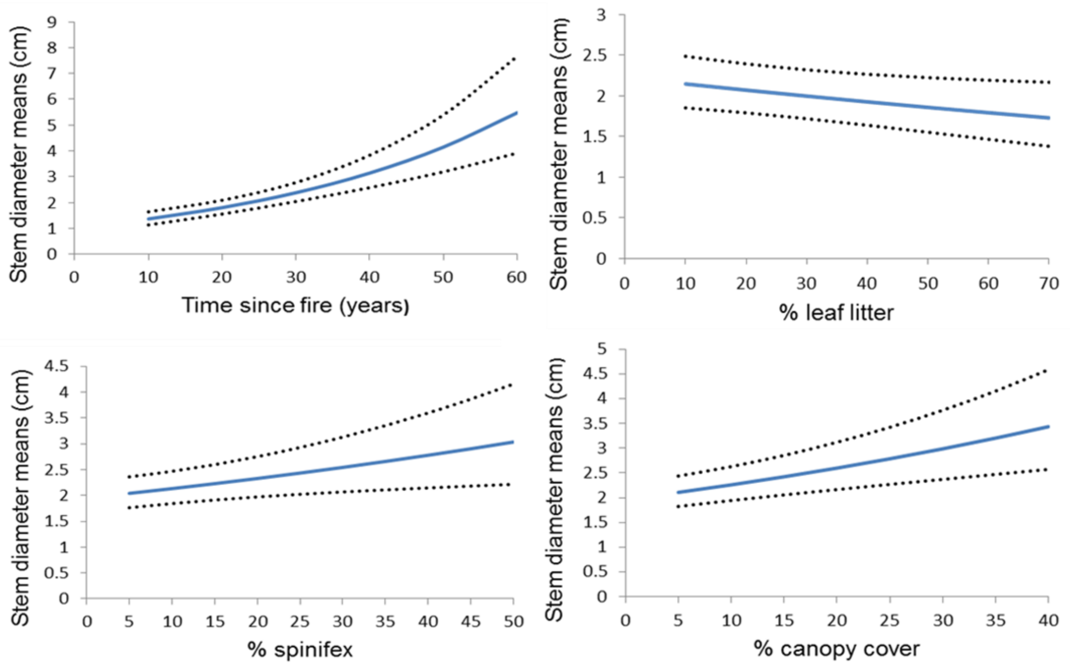


Figure 2. Back-transformed stem diameter means for (a) *Eucalyptus costata*, and (b) *E. socialis* showing responses and 95% confidence intervals to time since fire in years, and to modelled covariables for *E. costata*: weed cover, canopy cover, dunes and swales, and to *E. socialis*: canopy cover, leaf litter cover and spinifex cover.

Table 3. Results of the generalised linear mixed model (GLMM) with gamma distribution
Coefficient estimates, standard errors (s.e.) and *P* values for modelled variables accepted and rejected in the backwards elimination for two species of mallee eucalypts (*Eucalyptus costata* and *E. socialis*) from three conservation reserves: Hincks, Hambidge and Heggaton

Species	Terms	Estimate (s.e.)	Wald statistics	d.f.	*P* value
Eucalytpus costata	Accepted	$^{A}y = \beta 1 \times fage + \beta 2 \times canopy + \beta 3 \times weed + \beta 4 \times dune\ and\ swale$			
	Canopy	0.017 (0.004)	22.98	1	<0.001
	Weeds	0.004 (0.001)	7.01	1	0.008
	Fire-age (fage)	0.030 (0.003)	85.20	1	<0.001
	Dune	−0.090 (0.030)	9.93	1	0.002
	Swale	−0.079 (0.030)			
	Rejected				
	Shrubs	0.000 (0.001)	0.00	1	0.988
	Bare ground	0.000 (0.002)	0.02	1	0.855
	Spinifex	−0.001 (0.002)	0.19	1	0.659
	Leaf litter	0.001 (0.002)	0.30	1	0.587
Eucalyptus socialis	Accepted	$^{B}y = \beta 1 \times fage + \beta 2 \times canopy + \beta 3 \times spinifex + \beta 4 \times leaf\ litter$			
	Canopy	0.014 (0.004)	15.54	1	<0.001
	Spinifex	0.009 (0.003)	6.92	1	0.009
	Fire-age	0.030 (0.004)	42.40	1	<0.001
	Leaf litter	−0.004 (0.002)	4.47	1	0.034
	Rejected				
	Bare ground	0.000 (0.002)	0.00	1	0.989
	Weeds	0.000 (0.002)	0.00	1	0.947
	D_S S (dune and swale)	−0.073 (0.044)	2.74	1	0.098
	Shrubs	−0.003 (0.002)	3.07	1	0.080

[A] Stem diameter = (estimate × fage) + (estimate × canopy) + (estimate × weeds) + (estimate × dune and swale).
[B] Stem diameter = (estimate × fage) + (estimate × canopy) + (estimate × spinifex) + (estimate × leaf litter).

By using contour plots developed from the model data for *Eucalyptus costata* (Fig. 3), we were able to show how TSF may be estimated for a site with unknown fire history, given a mean stem diameter of 4.8 cm, 30% weed cover and 15% canopy cover (Fig. 3b).

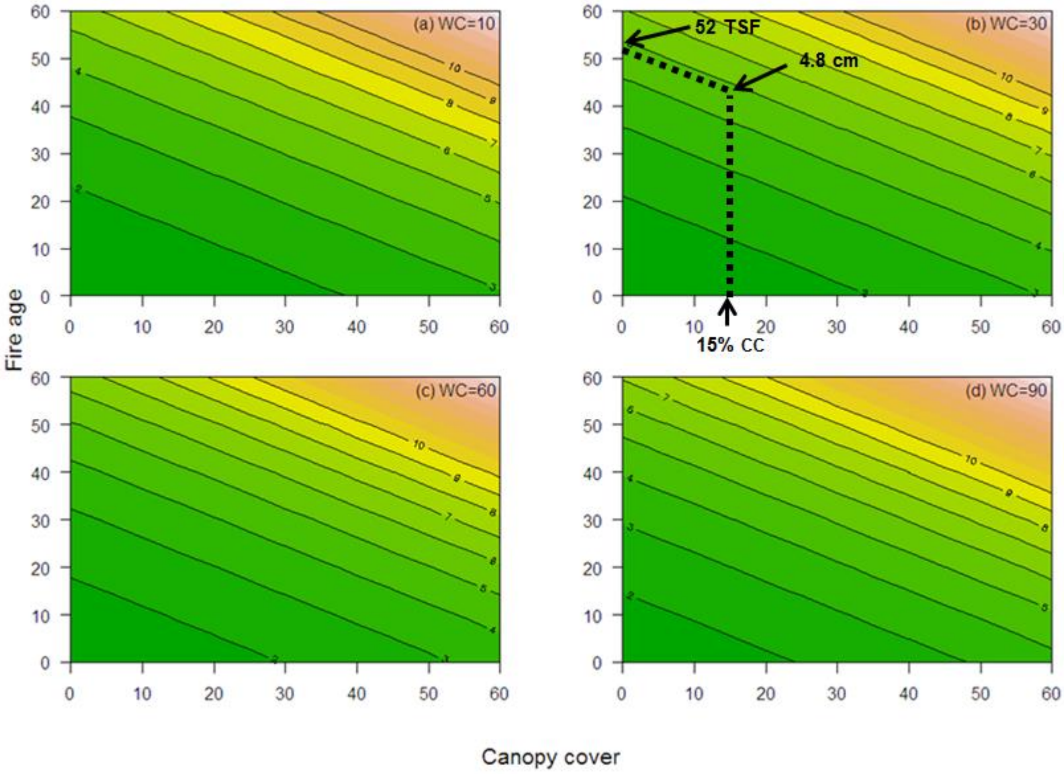


Figure 3. Four contour plots for *Eucalyptus costata* based on the best-fit model time since fire (TSF), canopy cover (CC) and weed cover (WC). Time since fire is on the y axis (years) and

canopy cover (%) on the x axis. The four plots each indicate different weed cover (a) 10%; (b) 30%; (c) 60%; and (d) 90%. Contour lines indicate mean stem diameters. Where additional data are collected, they can be used to predict TSF; for example, a site with weed cover of 30%, 15% canopy cover and a stem diameter (mean) of 4.8 cm would imply a TSF of 52 years. By using the lower and upper confidence intervals for this example site, the estimate is between 48 and 56 years TSF.

Test of model predictions

To show how TSF predictions compared with the model, we used the additional data for *Eucalyptus costata*. These additional data were collected from mapped TSF areas, i.e. 1960 (> 53 years), 1986 (26 years), 2001 (11 years) and 2005 (7 years) within Pinkawillinie Reserve, and were used to predict TSF and then compare these results with the model. Our model substantially underestimated TSF in one site (152%, actual TSF 53 years; Fig. 4a) and overestimated it in three sites (45% (TSF 26 years), 68% (TSF 11 years) and 71% (TSF 7 years); Fig. 4b–d). That is, the additional field data with known TSF years did not compare favourably with the model TSF years.

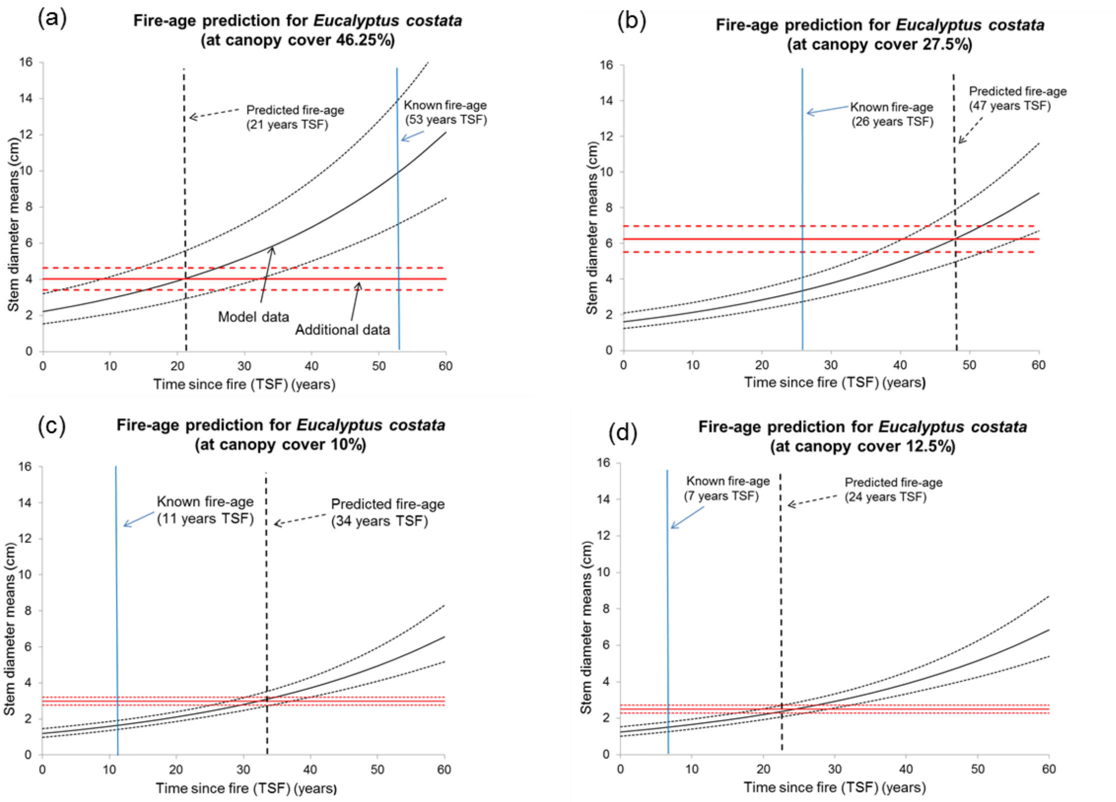


Figure 4. Back-transformed predicted stem diameter means (± 95% confidence intervals) for *Eucalyptus costata* at time since fire (TSF) (a) 53, (b) 26, (c) 11 and (d) 7 years (dashed vertical line) compared with the additional data (solid vertical line). The covariates for *E. costata* are percentage cover for canopy (46.25, 27.5, 10 and 12.5%), weeds (0%) and dunes (soil = 1)

Discussion

Consistent with previous work, there was a strong relationship between mean stem diameter and TSF (i.e. the time since the last mapped fire) for both tree species. However, for both species, TSF accounted for approximately two-thirds of the explained variation in stem diameter, with one-third of variation attributable to local environmental variation. The poor results from testing the models with data collected outside the original domain further indicate that local and regional influences are important considerations in addition to predicting TSF from stem diameter in each species. Our approach extends the work of Clarke *et al.* (2010) by demonstrating that local covariates can be very important influences on plant morphometric variables. Our work highlights the importance of knowing more about the factors that affect stem growth in order to estimate TSF using stem diameter, including in small, fragmented remnants.

Importance of covariates

Weeds were one of four important parameters in our model and had a positive correlation with stem diameter growth, even though weeds are often associated with negative tree growth effects (Houehounha *et al.*, 2010) or no effects on growth (Chapman *et al.*, 2002; Hänninen, 1998; Macmillan Little, 2007). Weeds and tree stems are likely to be responding to the same underlying environmental factors. Weed abundance is most likely indicative of nutrient and moisture enrichment because weeds benefit from nutrient run-on and fertiliser drift at the reserve edge adjacent to agricultural land and pastures (Boutin and Jobin, 1998; Gosper *et al.*, 2011; Hobbs and Atkins, 1988; Rickey and Anderson, 2004). Similarly, eucalypt growth rates can increase with nutrient run-on and application (Birk and Turner, 1992; Smethurst *et al.*, 2003) and increased light or water (Facelli and Ladd, 1996). Weeds could also be responding to environmental cues from tree canopies that increase shade or light and improve water-use efficiency and growth respectively (Argueso *et al.*, 2010; Werner and Schmülling, 2009).

Stem diameters were consistently higher on dunes than in swales for both species. We expected water ponding and nutrient retention in low-relief landscapes (Virginia and Jarrell, 1983) to promote faster growth in swales. The most likely reasons for more limited plant growth in swales than on dunes are that a shallow watertable in winter prevents root development to the same depth that it can occur on dunes (Enright and Lamont, 1989). In addition, although species can adapt to similar environmental niches, subtle distributional differences occur on dunes and swales in *Eucalyptus costata* (more on dunes) and *E. socialis* (more in swales). This could be in response to physiological traits in how they respond to different soil type, e.g. their ability to extract water (Noy-Meir, 1973), and how they access and extract nutrients (Noy-Meir, 1973; Parsons, 1969).

Canopy and spinifex cover were both correlated with stem diameter. Canopy cover had a positive relationship with stem growth for both tree species. This might be attributed to trees with larger crowns (and therefore higher canopy cover) growing faster because greater leaf surface area promotes more efficient light absorption (Binkley *et al.*, 2013). Also, as leaf litter decomposes, released nutrients can leach into the soil (Baker and Attiwill, 1985) and influence stem diameter growth. Spinifex (*Triodia* spp.) is a dominant perennial in mallee woodlands that can cover a high percentage of the ground surface ~15 years after fire, but its cover decreases long after fire (approximately >30 years) (Clarke, 2007; Cohn *et al.*, 2002; Noble, 1989; Wright and Haslem *et al.*, 2011). The positive association of spinifex with *Eucalyptus socialis* probably reflects an indirect relationship, mediated by TSF and soil type, with both taxa performing well on sandy soils (Cohn, 1995).

In our study, edge effects were not significant and we minimised model complexity by excluding distance to edge from our models. However, there was a weak distance effect on stem diameter further from the edge (i.e. stem diameter was largest at the edge). Edge effects will need to be considered when models are developed in new regions because their influence on stem growth has the potential to be important. In some Amazonian forests, increasing fragmentation correlates with significant edge-related desiccation, with deeper edge effects as forest cover declines (Briant *et al.*, 2010).

Generality of models

Model predictions based on the additional data were extremely poor even though data from both locations (i.e. model data and additional data) had similar mallee vegetation. There are at least three factors contributing to the poor predictions. First, no weeds were recorded in any of the four mapped TSF sites at Pinkawillinie, which is beyond the range of weed cover values from most of the transect data used for building the initial model. Closed edges (e.g. tree structure and density) preventing weed penetration (Hamberg *et al.*, 2009) and lack of edge effects, such as increased nutrients and disturbances (Beer and Fox, 1997), can result in fewer weeds. Limiting predictions to sites that are within the range of measured covariates may lead to better predictions. Alternatively, to develop models with broader application, they will need to be developed using sites that cover a wide range of covariate values.

Second, different growth rates relative to tree canopy cover may also have contributed to poor predictive values. Trees with larger canopies are expected to grow faster, explaining the positive relationship between canopy cover and tree diameter in our data (Pacala *et al.*, 1996). However, high canopy cover might also occur in dense tree stands, where competition among trees might slow growth (Berger *et al.*, 2008). In Pinkawillinie at the site of 53-year TSF, the underestimated fire age may have been a result of high among-tree competition, whereas competition among canopies was apparently low in the model dataset. Above- and below-ground competition affects tree growth (within and between species) and is influenced by various biotic and abiotic conditions including, for example, water, nutrients, shade, light, canopy cover and spatial distribution (Canham *et al.*, 2004; Coomes and Allen, 2007; Thorpe *et al.*, 2010). Future research to address the above- and below-ground competition influences on growth in multistemmed mallee trees is necessary for developing a robust fire age prediction model.

A third factor that could have contributed to poor performance of our model in new sites is inaccurately mapped fire histories. Coarse fire history mapping is unable to identify small-scale variations and patchiness that may result from some trees escaping fire, owing to sometimes fires not burning evenly, when stems of neighbouring individuals are killed (Holden *et al.*, 2005). This kind of error would lead to higher estimates of TSF than the mapped time. However, unmapped fires may lead to substantial underestimates of TSF compared with mapped fire history. Maintaining detailed fire maps is critical (Driscoll *et al.*, 2010b), including for developing reliable surrogate measures of TSF.

Further development

Understanding the relationship of environmental covariates with stem diameter growth is essential for predicting TSF (Wang, 1986). Future work will need to understand the environment context in which particular covariates are important and the effects they have on stem diameter growth, and hence identify the most important covariates to consider for predicting fire history using plant morphometrics. It will also be important to better accommodate possible competition effects when there are different tree and canopy densities, and to consider how to minimise effects of mistakes in fire mapping.

Once a reliable model is developed and verified, land managers could use simple tools such as contour plots to estimate TSF (Fig. 3). Using additional data from small fragments, we illustrated that this approach could be applied to new sites. It is a practical approach that could be used by land managers without the need for further development or use of additional complex statistical models.

Until we have a better understanding of the influence of covariates in TSF estimation, we will not know if using models developed in a nature reserve to predict TSF in farmland remnants is appropriate. Remnants differ from the edges of reserves by having livestock grazing pressure that can change the physical structure and hydrology of the soil, affecting ecological processes and therefore plant growth (Greene *et al.*, 1998). These environmental differences between reserve edges and remnants in farmland may mean that different models will be required to estimate TSF depending on landscape context. That is, to estimate TSF from stem diameter, sampling in reserves to predict TSF in reserves and sampling in remnants to predict TSF in remnants. Further work with landholders to reconstruct fire histories for their properties will likely be needed to build and verify TSF models that could be applied with confidence to remnant vegetation in farmland.

Habitat fragmentation, inappropriate fire regimes and grazing are major global threats to many ecosystems, including mallee (Australian Government, 2007). Developing an easily applied method for estimating TSF would be a valuable tool for understanding biodiversity responses to TSF. Our findings emphasise that environmental covariates should be considered to improve methods for predicting TSF. In addition, local variation in environmental covariate values means that models developed in one area may not apply regionally. Our study therefore suggests that a protocol for building models to predict TSF include consideration of local environmental covariates, and how those covariates constrain the geographic extent of prediction.

Author contributions

JL and DAD conceptualised the study and the study design. JL acquired the data and JL and HJY led analyses; JL led manuscript preparation with substantial critical and editorial input from all authors. All authors gave final approval for publication. JL, HJY, DAK and DAD declare no conflicts of interest. Available at: www.publish.csiro.au/WF/WF15069

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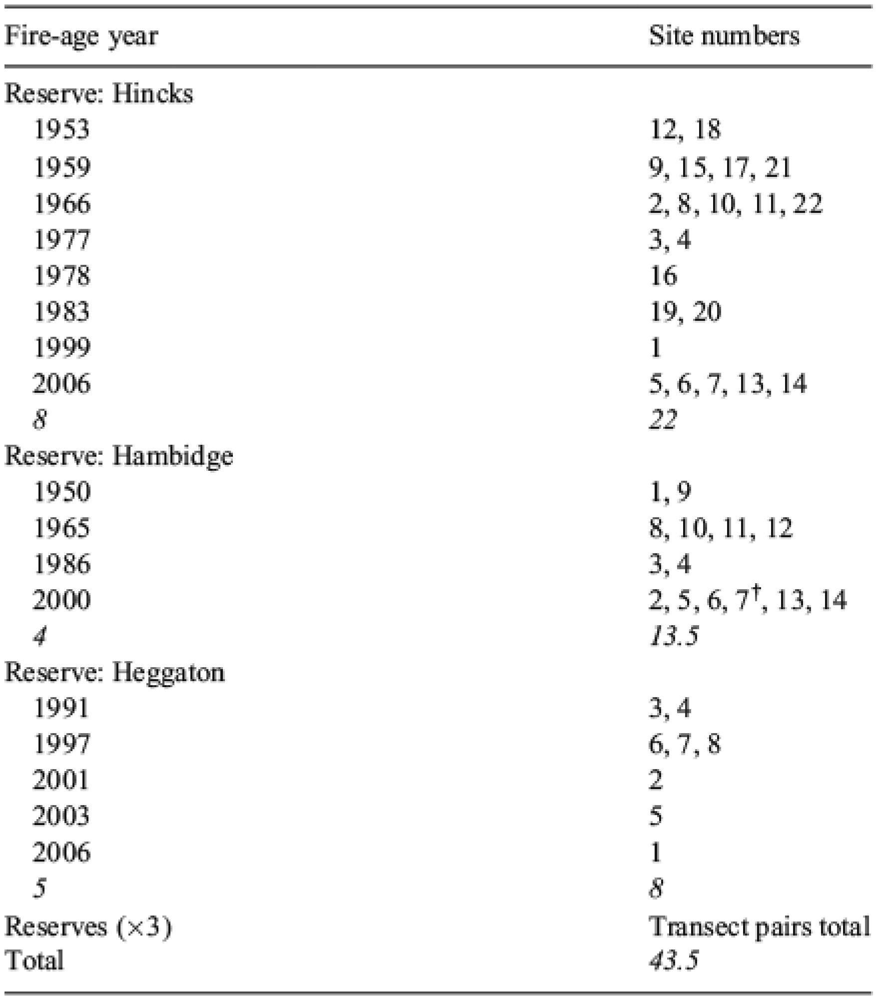
Supporting Information

Appendix 1: Break-down of the data showing fire age years, transects and site number for each transect pair in Table 1. For each reserve, italics in the left hand column denote the sub-total of the number of fire ages and italics in the right hand column denote the sub-total number of sites that contained transect pairs. For the three reserves, the italics at the bottom of the table denote the total number of sites containing transect pairs

The † identifies only one transect: the fire age site was only as wide as the dune and thus it was not feasible to take measurements from swales that may have been in another TSF that we could not identify



Fire-age year	Site numbers
Reserve: Hincks	
1953	12, 18
1959	9, 15, 17, 21
1966	2, 8, 10, 11, 22
1977	3, 4
1978	16
1983	19, 20
1999	1
2006	5, 6, 7, 13, 14
8	*22*
Reserve: Hambidge	
1950	1, 9
1965	8, 10, 11, 12
1986	3, 4
2000	2, 5, 6, 7†, 13, 14
4	*13.5*
Reserve: Heggaton	
1991	3, 4
1997	6, 7, 8
2001	2
2003	5
2006	1
5	*8*
Reserves (×3)	Transect pairs total
Total	*43.5*

Paper III: Fire and fragmentation interactions affect reptile persistence in an agricultural matrix and conservation reserve

Running head: Interactions of fire and fragmentation affect reptile persistence

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Key-words: agricultural matrix, fire, fragmentation, interactions, mallee woodland, reptiles, reserves, semi-arid, traits

Abstract

Individual effects of fire regimes and fragmentation on biodiversity have been extensively investigated. However, an understanding of the interactive effects of fire and fragmentation on biodiversity is lacking due to limited research in this area. This lack of understanding affects our ability to manage environments for the preservation of reptile taxa living in fragmented, fire-affected landscapes. We hypothesised that habitat fragmentation would mediate the impacts of fire on reptile trait responses because isolation would affect population recovery

via recolonisation. As such, we expected reptile species with similar traits would have similar recolonisation responses to fire and isolation.

Reptile pitfall-trap data collected from a combination of natural and manipulative experiments were used to investigate the interactive effects of fire and fragmentation. Data were collected over three years from a conservation reserve and from vegetated dune top remnants in an agricultural matrix adjacent to the reserve. The reserve had two fire categories (recently burnt and long unburnt) and the remnants had one fire category (long unburnt). Paired transects were used in the survey design. The reserve pairs comprised a dune and swale. The agricultural matrix pair comprised two dunes; one as a control while the other was burnt after the first year of trapping was completed. We took this approach to determine if species are persisting in isolated remnants, and whether source populations can influence their persistence.

We found a wide range of variation in the temporal and spatial complexity of reptile trait responses to fire and fragmentation but we did not detect any responses to fire by fragmentation interactions. However, we did find evidence that insectivorous, nocturnal and potentially burrowing reptile species respond to prescribed fire, but only if: (1) the patch is close to a recently burnt large reserve; and (2) reptile numbers in the patch are initially low. Temporal responses in insectivorous and diurnal species are unaffected by prescribed fire in the reserve and remnants in the study area.

Our study highlights the importance of conducting multi-year, robust experiments to inform management in fire-affected and highly fragmented landscapes. Further, there is value in undertaking fire and fragmentation interaction studies on individual species to enhance understanding of different reptile trait group responses, and to expand our knowledge on the mechanisms influencing species responses. Burning some long unburnt remnants near large reserves with the same fire age may provide colonising opportunities for insectivorous, nocturnal and burrowing reptiles but further knowledge is required before this can be a reliable management recommendation. In cases where knowledge is unavailable or not generalisable, as was the case for some reptile trait groups in our study, a precautionary approach to fire management should be practised.

50 word summary for non-specialist reader. Burning long unburnt isolated remnants adjacent to large reserves with similar time since fire ages may provide colonisation opportunities for insectivorous, nocturnal and burrowing reptiles.

Introduction

Fragmentation and altered fire regimes have major impacts on ecological systems globally (Davis and Doherty, 2015; Haddad *et al.*, 2015; Mooney *et al.*, 2012). These impacts are likely to be exacerbated in fragmented and fire-prone landscapes by changing climates (Auld and Keith, 2009). Therefore, it is imperative that we understand how animals are persisting in remnants with modified fire regimes so that effective, on-ground management is implemented to improve biodiversity conservation. However, research targeting the effects of fire-fragmentation interactions on biodiversity is limited (Driscoll and Henderson, 2008; Driscoll *et al.*, 2010b; Lazzari *et al.*, 2018 unpublished manuscript; Sauvajot, 1995). This is despite 70% of remaining forest across the globe within 1 km of forest edges being vulnerable to fragmentation disturbances, including fire, and that habitat fragmentation can reduce biodiversity by between 13 and 75% (Haddad *et al.*, 2015). The limited understanding of fire-fragmentation interactions on biodiversity in an increasingly fragmented and fire-affected environment impedes the implementation of effective conservation management actions.

Research indicates that, in isolation, fauna show diverse responses to fire (Pausas and Parr, 2018) and fragmentation (Phillips *et al.*, 2018). In an unfragmented, fire-dependent landscape, fire can have positive responses for some species (e.g. malleefowl) (Bradstock *et al.*, 2005). However, in fragmented and fire-prone landscapes, there is evidence that some species (e.g. Florida sand skink, and blue-throated macaw) are less tolerant of fire (Berkunsky *et al.*, 2015; Schrey *et al.*, 2016). Increased susceptibility to fire in fragmented landscapes may arise because dispersal-limited individuals have a lower capacity to escape fire in isolated patches (Neuwald and Templeton, 2013) leading to mortality (Driscoll *et al.*, 2012b). An alternative explanation for increased susceptibility of fauna to fire in isolated patches is that individuals survive fire events but then are more susceptible to predation in structurally simplified post-fire remnant patches (How and Dell, 2000). This may particularly be the case for remnant patches with high edge-to-core ratios where predator incursions are likely to be highest (Sato *et al.*, 2014). Further, fire in fragmented landscapes may also prompt individuals to permanently emigrate from fire-affected remnants (Doherty *et al.*, 2015; Sutherland and Dickman, 1999). Together, direct mortality, indirect mortality and emigration from patches during and after fire events (particularly after unintended, intense fires) may lead to local population extinctions.

If localised extinctions occur, it is important to understand if nearby reserves can act as source populations, and if the successional time since fire (henceforth referred to as 'TSF') age of vegetation in nearby reserves alters the ability for those reserves to act as source populations. Previous research shows that post-fire succession of vegetation influences changes in lizard assemblages (Pianka, 1996) but we do not know if species are dispersing to and recolonising similar fire-affected isolated patches. Equally, it is important to understand whether the distance between the reserve and remnant influences the source-population potential of the reserve (Sauvajot, 1995), by either facilitating or impeding movement (Jennings *et al.*, 2016). This understanding will enhance the ability to target and implement effective conservation-focused management.

In our study region, conversion and fragmentation processes of semi-arid mallee woodland for agriculture has occurred extensively since European settlement (South Australian Government, 2010) resulting in habitat modification and loss. What remains are both small remnant patches in an agricultural matrix, and a large nearby reserve. Nevertheless, many species survive and persist (Driscoll and Henderson, 2008; Tulloch *et al.*, 2016; Williams *et al.*, 2012) – including a diverse assemblage of reptiles (Pianka, 1996; Schutz and Driscoll, 2008; South Australian Government, 2010) that occupy both reserves and remnants with different fire histories (Smith *et al.*, 2012a). However, future landscape-scale persistence of these species may be jeopardised due to the competing objectives of conservation and asset protection that lead to different fire regimes in reserves and remnants (Morrison *et al.*, 1996). With limited knowledge of fire history and species responses, reserves are managed with fire in an attempt to replicate natural processes, while fire in remnants is suppressed because of actual and perceived risks to humans, crops, stock and infrastructure (Clarke, 2008).

The variable fire management strategies (and objectives) within our study area results in a landscape-scale mosaic of fire ages and successional habitats that support a diversity of reptiles (Driscoll and Henderson, 2008). This taxon is usually considered to be susceptible to fragmentation because of niche requirements, high habitat specificity and limited distribution (Keinath *et al.*, 2017). Reptiles with early and late successional habitat preferences are found in long unburnt dune top fragments in a cropping land matrix (Driscoll *et al.*, 2012b), and also in dunes and swales in recently burnt reserves (Smith *et al.*, 2013). Despite their apparently versatile responses to fire and fragmentation, the combined (interactive) effects of fire and fragmentation on reptiles – both in our study area and across the globe – is largely unknown (Lazzari *et al.*, 2018 unpublished manuscript).

Given the knowledge gap regarding fire-fragmentation effects on biodiversity generally, and on reptiles more specifically, the aim of our study is to investigate the interacting effects of fire and fragmentation on abundance and richness of different reptile trait groups in an agricultural landscape through time. In this study, we restrict our exploration of fragmentation effects to patch type (i.e. reserve vs remnant) and patch isolation. We focus on whether reptile species richness and abundance are affected by: (1) fire (recently burnt and long unburnt); (2) patch type (remnant and conservation reserve); (3) isolation (distance of remnants from large reserves); and (4) the interaction between fire and isolation and fire and age of nearby source. Specifically, we seek to determine if large reserves with a combination of long unburnt or recently burnt vegetation act as source populations for isolated remnant patches that also contain a combination of long unburnt or recently burnt vegetation.

Based on previous research, we predicted that fire would have contrasting effects on reptile functional groups (Moretti and Legg, 2009; Schlesinger *et al.*, 1997). We expected these responses because reptiles in our study area have successional habitat preferences after fire that are likely to follow several trajectories (Caughley, 1985; Driscoll and Henderson, 2008) that accord to the habitat accommodation model (Fox, 1982). However, as there is also uncertainty around the importance of traits as a predictive tool (Driscoll and Henderson, 2008) it is worth investigating. Indeed, Smith *et al*. (2013) show that a range of post-fire age classes of habitats allow a variety of species to reach their peak abundances between zero and 50 years after fire.

With respect to patch type, we predicted that reserves would have higher reptile species richness and abundance than remnant patches. This is because the reserve in our study area was much larger than the remnant patches and contained two different TSF ages. One TSF age was long unburnt and the other was from a recent wildfire that, although these can burn at a high intensity, in this landscape small unburnt patches can still remain (Bradstock and Cohn, 2002). Thus, these reserves have the potential to accommodate more individuals and niches, and support a greater diversity and abundance of species (Forman and Godron, 1981; Keinath *et al.*, 2017; Simberloff, 1976). As such, reserves can act as sources for new populations in remnant patches containing similar TSF-affected vegetation.

Finally, we predicted that less isolated patches (i.e. those closer to the reserve) would have higher reptile species richness and abundance, given the dispersal limitations of many reptiles (Driscoll, 2004; Driscoll *et al.*, 2014). We further predicted that if fire regimes in reserves and less isolated patches resulted in the same TSF-aged vegetation, reptile richness and abundance would be maximised. This is because where there is suitable TSF habitat to support reptile species persistence (Bradstock *et al.*, 2005), reptile assemblages in the larger conservation reserves could disperse to nearby remnants and, similarly, reptile species in nearby remnants disperse to nearby reserves.

Methods

Study area

Our study was conducted in Pinkawillinie Conservation Park (33°05'41.05"S, 135°59'57.75"E) and adjacent farmland in the northern Eyre Peninsula, South Australia (Fig. 1). The region is a 132,000 ha, semi-arid zone, with a highly variable mean annual rainfall of 318 mm (Bureau of Meteorology, 2018). The low topographic relief comprises shallow and/or nutrient deficient soils that are mainly siliceous and calcareous sands (Blackburn and Wright, 1989; Brandle, 2010). It is a sand dune system (Wasson, 1989) under which lies a calcrete limestone layer (Blackburn and Wright, 1989).

The vegetation in Pinkawillinie reserve and in the linear dune top remnants in farmland is dominated by mallee woodlands. These comprise low, multi-stemmed eucalypts (predominantly *Eucalyptus costata* and *E. socialis*) and are mostly highly flammable. The woodlands are also associated with a shrub layer of predominantly *Melaleuca uncinata* and *Callitris verrucosa* and a ground layer of hummock grass that is characterised by spinifex grasses such as *Triodia irritans* (Robinson and Heard, 1985; Specht, 1972). However, in the remnants, there is a decrease in *T. irritans*, as well as modifications to patch condition and vegetation structure, because of disturbances from cropping (e.g. weeds, pesticides, fertiliser) and livestock grazing (e.g. trampling) (Driscoll *et al.*, 2012b; Moranz *et al.*, 2012; Yates *et al.*, 2000). Also, because of the greater edge to area ratio in small remnants, levels of disturbance can be greater in an agricultural matrix (Saunders *et al.,* 1991). Prior to the declaration of Pinkawillinie reserve in 1970, the area had also been impacted by low levels of livestock use, and is still affected by recreational 4WD use and mineral exploration disturbances such as clearing tracks for access to drilling sites (Scott, 2011).

Pinkawillinie's fire history has been recorded by South Australian government agencies for over 40 years with major fires recorded in 1972, 1986, and 2005 (South Australian Government, 2011). Community concerns have occasionally resulted in prescribed burns in the reserve, but these prescribed burns were not located near to the survey sites.

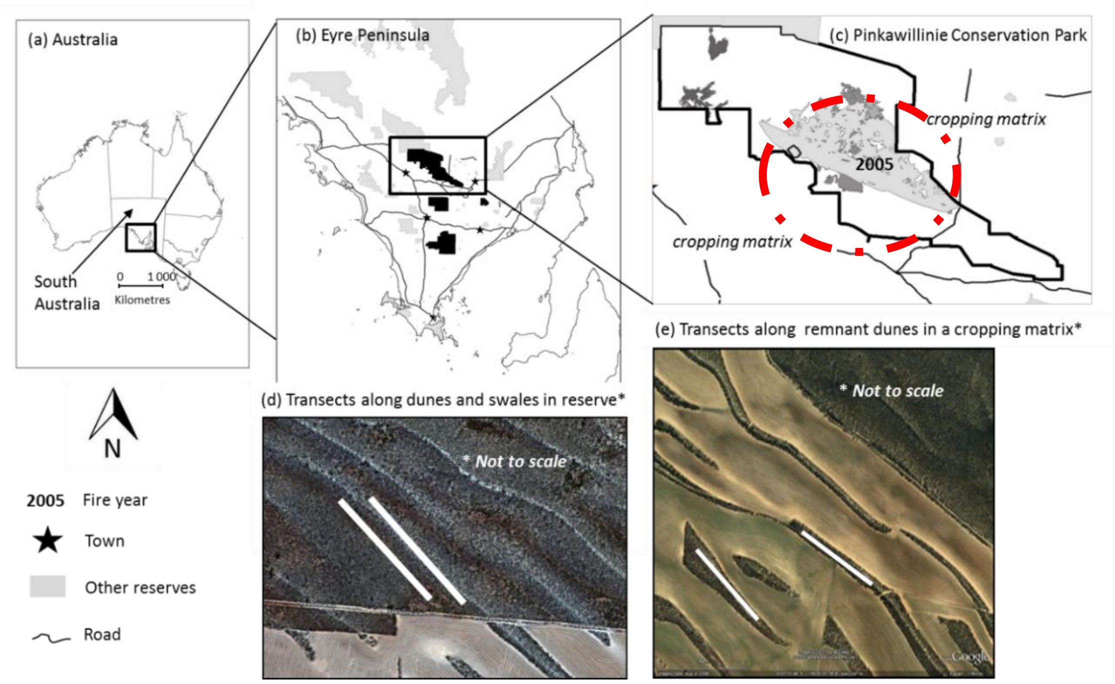


Figure 1. Map of the study area showing (a) South Australia, (b) the semi-arid Eyre Peninsula, and (c) Pinkawillinie Conservation Park reserve, with red dashed lines showing study area. The light grey shading within the black drawn reserve border of Pinkawillinie Conservation Park indicates the recently burnt woodland (i.e. burnt in 2005); the white area within the reserve border is long unburnt woodland. Reptiles were surveyed along a total of 30 single transect sites that were paired and established in (d) dunes and swales in the reserve and in (e) remnant dunes in the cropping matrix.

Wildfire intensity was not able to be replicated in the remnant patches for the experimental burns due to risk of fire escaping. As a result, these prescribed burns were low-to-medium intensity. However, these fires were undertaken in the summer months because, in this vegetation type, too much moisture outside of the hottest period would prevent fire spread.

Site selection

The study (Fig. 1 and Fig. 2) is a replicated natural and manipulative experiment with a paired design to contrast burnt and unburnt areas in a conservation reserve with remnant patches near to and far from the reserve. Sites were located in the burnt and unburnt areas in the conservation reserve and in remnant habitat patches in farmland (i.e. cropping paddocks). The remnant sites were adjacent (near and/or far) to burnt areas of the reserve in the northern part of survey area and adjacent to unburnt areas of the reserve in the southern part of the survey areas. Transects in the reserve were randomly located in areas adjacent to the reserve boundary, and their locations were dictated by where there were both dunes and swales. Transects were placed at the reserve boundary because we were testing whether similar species were found in recently burnt areas of both the reserve and remnants (i.e. persistence versus dispersal to habitat/vegetation with the same post-fire successional stage). Twelve of the 30 survey sites were in dune and swale habitat in the reserve. Six of these survey sites were established in recently burnt areas of the reserve that resulted from a wildfire that occurred four years prior to commencement of this study, and six sites established in long unburnt areas of the reserve. The remaining 18 sites were established in dune-top remnant patches (remnants did not occur in farmland swales). Eight of these remnant sites were experimentally burnt at the end of the first year of surveys, and 10 remained as unburnt controls. Reptiles were surveyed at 12 sites (six paired dunes and swales) within the reserve, and 18 sites (nine paired dunes) in the farmland. In total, 30 sites were surveyed (Fig. 2 and Table S1). Although we were only able to sample swales in the reserve, we did this to understand the pool of nearby species that could potentially use the matrix and colonise dunes in farmland.

Site selection was based on the time since the most recent fires that affected two large areas of the Pinkawillinie reserve. The southern side is long unburnt (> 38 years since the most recent fire) and the northern side is recently burnt (5 years since the most recent fire). We assumed that the two fire age classes of the burnt areas of the study (i.e. 1 and 5 years TSF) supported equivalent reptile assemblages because in this fire-prone ecosystem type, early successional vegetation is considered to be < 10 years TSF, mid-successional between 11-34 years TSF, and late-successional > 35 years TSF. We stratified for fragment type (reserve and remnants), isolation (patches close to and far from the reserve), and TSF (recently burnt and long unburnt). There were six blocks – three in the southern region and three in the northern (Fig. 2). The reserve had three paired transects in the long unburnt southern side and three in the recently burnt northern side (i.e. a total of six paired dune and swale sites). The farmland survey sites in the southern part of the study area had six paired transects (i.e. a total of six paired dune sites) close to and far from the long unburnt area of the reserve (i.e. a total of 12 dunes). The farmland in the northern region had three survey sites (i.e. a total of three paired dune sites) close to the recently burnt area of the reserve (i.e. a total of six dunes). One of the farmland, transect dune pairs was experimentally burnt after the first year of animal surveys, while the other dune transect remained as a control. Dunes close to the reserve were between 0.13 km and 3 km from the reserve edge, and dunes far from the reserve were between 5.6 km to 8.5 km from the reserve edge (Table S2).

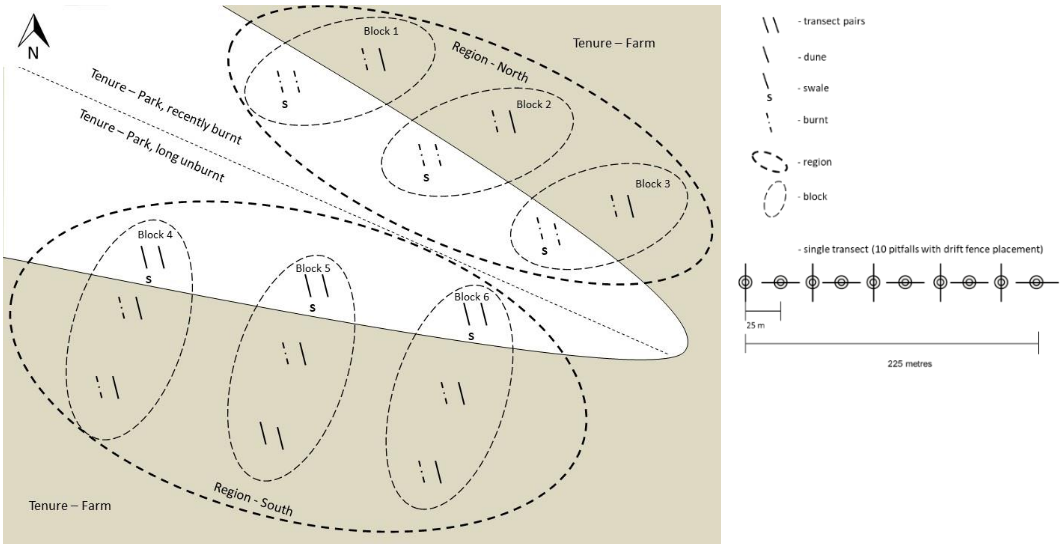


Figure 2. Schematic representation of the survey design of the project, which is a replicated natural and manipulative experiment. The Pinkawillinie Conservation Park is represented as the 'Park' tenure*. It has a recently burnt northern portion and a long unburnt southern portion. The 'Farm' tenure* is the cropping matrix. The Park and Farm tenures occur in both

the northern and southern regions of the study. Each region contains three blocks, with each block containing paired transects: a dune and swale transect in the Park; and in the cropping matrix, either, two dune transects in the northern region, or four dune transects in the southern region. The 'single transect' in the key shows a top view of a transect with 10 m drift fences placed alternately – across and along the dune or swale over each pitfall trap.

*'Tenure' is a simplified term used in our analysis to detect fragmentation responses.

Survey protocol

Reptiles were surveyed at each site using a pitfall trap-line comprised of ten 20 litre plastic buckets, spaced 25 metres apart (30 sites x 10 pitfalls = 300 pitfalls). Buckets were buried so the top was flush with the ground. A 30 cm high x 10 m long, plastic drift fence intersected the pitfall. The fence was placed at alternate right angles for each of the 10 pitfalls (Fig. 2). This method was based on combined pitfall survey design after Hobbs *et al.* (1994) and Morton *et al*. (1988) for reptile surveys. A 15 cm long half PVC pipe was placed in the bottom of each bucket with a 15 x 20 cm wood block leaned against each piece of PVC to act as a shelter and refuge, in case of rain. During each survey period, trapped animals were removed from the site of capture to a base camp for processing. During processing, we recorded the reptile species, trap location and pitfall number, age (i.e. adult or juvenile), and date of capture. Animals were uniquely marked depending on the species by either a temporary paint mark, or toe clipping, and/or fluorescent polymer injections (see Acknowledgements for ethics approval), and this allowed recaptures to be omitted from the analysis. After processing, marked animals were returned and released at the point of capture. Although large pitfalls with drift fences are efficient for reptile trapping (Morton *et al.* 1988; Hobbs *et al.* 1994), some under-sampling can occur in large lizards and snakes, with a bias towards juveniles (Todd *et al.* 2007).

Each site was surveyed for 28 nights over three consecutive summers (2010, 2011 and 2012). We alternated surveys between northern and southern sites, trapping for 14 consecutive nights, four times each summer to manage for temperature gradients across the approximate nine-week field period. In total, we completed c. 25,200 pitfall trap nights.

Testing for effects using traits data

We used published literature to assign traits relevant to reptile fire responses (Blaum *et al.*, 2011; Letnic *et al.*, 2004; Smith *et al.*, 2013) to each species (n = 42) captured in our study. We grouped all species with the same traits. These traits included body size (small, medium, large based on snout-vent length (svl)), reproduction (oviparous, viviparous), habitat-position (above-ground, below-ground), diet (carnivorous, insectivorous, omnivorous), and activity period (diurnal, nocturnal (includes crepuscular), both diurnal and nocturnal) (see Table S3a and Table S3b).

In our study, the likelihood of traits being affected by factors other than fire could be attributed to the body size trait i.e. large bodied animals moving naturally between remnants. Detection of marked individuals needs consideration because large bodied reptiles are given temporary marks or no marks (venomous snakes). Thus, there may be implications for interpreting results in the large body-size trait. Factors influencing species responses might not be due to fire but potentially due to others factors such as scale.

Statistical analysis

Severe fires in mallee vegetation occur on a decadal timescale (Bradstock and Cohn, 2002) with major fires occurring in Pinkawillinie Conservation Reserve in 1972 (23 December), 1986 (20 November), and 2005 (27 December) (South Australian Government, 2019). Although for our survey the 2005 reserve wildfire and the 2010 experimental fires are categorised as early successional, fire intensity differed (high and low intensity, respectively) as did the time of year/season in which the fires occurred, with prescribed burns undertaken on 26 and 27 March. Reptiles are most active during the Australian spring-summer period (November – February). It was not possible to match the fire regime variables (i.e. fire type, intensity and seasonality) among sites and therefore, we were unable to analyse the effects of associated ecological life stages (i.e. food and mate availability, dispersal of young emerging from burrows) that can affect animal abundances (Friend, 1993; Lindenmayer *et al.,* 2008). In addition, the long unburnt vegetation of the reserve and the remnants differed. As such, some of these other factors may have influenced species responses in our study.

We analysed 40 species that had sufficient data to conduct robust analyses, by fitting generalised linear mixed models (GLMMs) (Bolker *et al.*, 2009). We used random effects for 'site' to account for repeated measures, and 'block' to account for the key spatial structure in the data. We also used an observation-level random effect when there was evidence of overdispersion in binomial or Poisson models. Overdispersion was assessed using a Pearson Chi squared test of Pearson residuals divided by residual degrees of freedom (Maindonald and Braun, 2010).

Fixed effects in the models included combinations of variables that delimited our study design (Fig. 1) including certain two and three-way interactions. The analysis used the full data set and each test was applied to the relevant part of the analysis i.e. we fit each variable to test the response to the treatments (fire, fragmentation, and their interactions). Main effects were: 'Region' (Southern, Northern); 'Tenure' (Park, Farm); 'Distance' (Close, Far – relates to fragment isolation from the reserve); 'Burn' (experimentally burnt and unburnt); 'Y1' (2010, 2011-2012 – the survey year before, and the two years after, experimental burns were undertaken); 'Year' (2010, 2011, 2012); and 'Soil' (delimiting swale from dune habitat within the reserve) (see Table S4a for survey site information, and Table S4b variable attributes, categories and descriptions). 'Y1' and 'Year' were examined to explore if the biggest effects were due to being burnt or not, rather than TSF (0 or 1 year for the experimentally burnt sites). The 'Tenure:Region' interaction allowed us to identify any effects attributable to TSF in the reserve. Other interactions were to assess the effects of the experimental burn treatment over time, particularly 'Y1:Burn' (whether burnt patches showed a different response to other sites over time), 'Y1:Region:Burn' (whether burnt patches in the northern region (adjacent to recently burnt habitat) showed a different response over time compared with the southern region (adjacent to long unburnt habitat)), and 'Y1:Far:Burn' (whether burnt sites in the isolated patches showed a different response over time compared with other sites). Appropriate combinations of two-way interactions were included with all three-way interactions. The set of models with 'Y1' were repeated with 'Year'; and 'Y1' and 'Year' were not used in the same models. We ranked the 143 models (Table S5) using Akaike's Information Criterion for small samples (AICc) (Burnham and Anderson, 2002), and a set of best models designated as those with ΔAICc ≤ 2.0. We plotted results for variables with $p \le 0.05$, taking the estimate from the highest ranked model in which that variable occurred.

To avoid over-fitting, we limited the models fitted to each response to those where the number of parameters in the model was less than one third of the number of non-zero response values. We assumed Gaussian distribution of errors for total species richness and total reptile abundance, which were approximately normally distributed. Abundance and richness of the five species trait groups was tested in response to the treatments fire, fragmentation, and their interaction. Species and trait responses with five or fewer values > 2 or with < 10 unique values were converted to presence/absence data and analysed assuming a binomial distribution of errors with a logit link function (Table S6). All other responses were analysed assuming Poisson distribution of errors with a log-link function. Analyses were completed in R (R Core Team, 2012) using libraries *lme4* (glmer) (Bates *et al.*, 2012), *AICcmodavg* (predictSE) (Mazerolle, 2012), *bbmle* (AICctab) (Bolker and R Development Core Team, 2014) and *car* (Anova) (Fox and Weisberg, 2011).

Results

Summary statistics

Overall, we recorded 2200 individual reptiles from 42 species in seven families: geckoes (n = 822, of which 805 individuals were *Nephrurus stellatus*); skinks (n = 637 individuals, n = 21 species); agamids (n = 512 individuals, n = 6 species); typhlopods (n = 111 individuals, n = 2 species); elapid snakes (n = 71 individuals, n = 5 species); varanids (n = 33 individuals, n = 1 species) and pygopods (n = 14 individuals, n = 3 species) (Table S7 and Table S8). In 2010, 2011 and 2012, we recorded 685, 707 and 808 reptiles respectively (Table S9). Within the seven families, we assigned traits to 40 reptile species and used these in our analysis (Table S3a). Of the 40 species analysed, 29 species contained sufficient data for analysis (Table S3a). Of the 29 species results, three groups contained the highest proportion of the same traits (i.e. n = 10, n = 9 and n = 2) with ungrouped (i.e. individual) traits in eight species (see Table S3b).

Reptile trait responses to treatment variables

Seven predictor variables and eight interactions significantly influenced trait group responses (Table 1). Of the seven predictor variables, the sites burnt after the first year of surveys (i.e. 'Y1') influenced the greatest number of trait group responses (n = 8). Of the eight interactions we examined, 'Y1:Region1' and 'Year:Region1' influenced the greatest number of trait group responses (n = 4). We observed no responses to fire, fragmentation or fire-fragmentation interactions for several trait groups including richness of viviparous species, richness of small-bodied reptiles, richness of omnivorous reptiles, and richness and abundance of reptiles active during both the day and night. All plotted results are included in Fig. S1.

Table 1. A summary of the direction of response of five reptile trait groups (for significant relationships p ≤ 0.05) to fire and fragmentation interaction treatments. Traits included reproduction, size, habitat position, diet, and habitat time. To the left of the dashed line are the individual treatments and to the right are the interactions.

			Single predictor variables							Interactions								
	Five species traits	abundance / richness	Fire (burnt=1 or unburnt=0)	Isolation (far=1 or close=0; patch distance from the park)	Tenure (farm=1 or park=0)	Region - north=1 or south=0; farm and park inclusive	Y1 (burnt after 1st year of surveys ^)	year (individual survey years)	soil - dune=0 , swale=1	year:burn	region1:burn	Y1:burn	Y1:region1:burn	Y1:far	tenure1:region1	Y1:region1	year:region1	
1	reproduction - oviparous	richness		−			+											
	reproduction - oviparous	abundance									−						+	
	reproduction - viviparous ~	richness																
	reproduction - viviparous	abundance								▨		−						
2	size - small ~	richness																
	size - small	abundance				−		+										
	size - medium	richness			−													
	size - medium	abundance							−		−					▨		
	size - big	richness					+											
	size - big	abundance			+				+							+		
3	habitat_position - below ground	richness					+											
	habitat_position - below ground	abundance							−		−					▨		
	habitat_position - above ground	richness			−													
	habitat_position - above ground	abundance								▨							+	
4	diet - insectivorous	richness	−	−			+	+										
	diet - insectivorous	abundance				−							▨	▨				
	diet - omnivorous ~	richness																
	diet - omnivorous	abundance													−	+	+	
	diet - carnivorous	richness					+											
	diet - carnivorous	abundance					+	+										
5	habitat_time - day	richness			−		+	+										
	habitat_time - day	abundance	−					+									+	
	habitat_time - night	richness					+											
	habitat_time - night	abundance							−				+					
	habitat_time - day and night ~	richness																
	habitat_time - day and night ~	abundance																
			2	2	4	2	8	5	4	2	3	1	2	1	1	4	4	**45**

~ Five trait categories that recorded no responses to variables and their interactions.

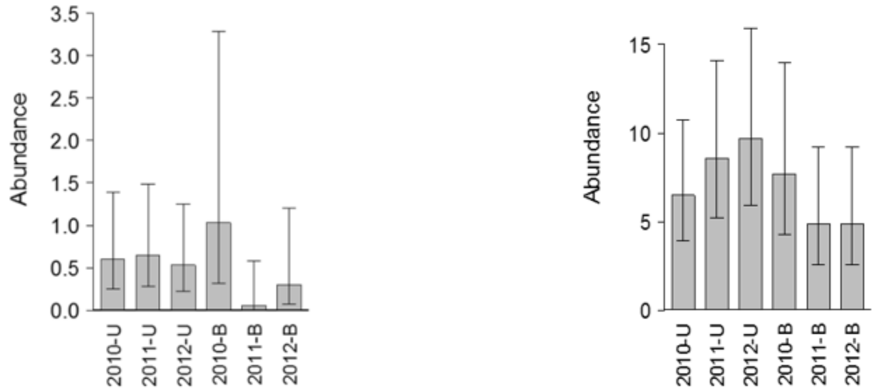
^ Y1 — eight isolated patches were burnt (10 control patches remained unburnt) at the end of the first year of surveys (2010) and then surveyed in each of the following two years (2011-12).

Treatments:
Fire — burn: burnt = 1, unburnt = 0 (eight isolated patches identified for experimental burns)
Isolation / distance — far: far = 1, close = 0 (remnants far and close to the park)
Tenure — ten1: farm = 1, park = 0
2012, 2013 — Y1: 2010 burnt after the first year of surveys, 2011-2012 combined years following burns
Year: 2010, 2011, 2012 (three separate survey years)
Region — reg1: north=1, south = 0 (farm and park inclusive)
Soil: dune = 1, swale = 0 (swales only in the park)

Fire interactions and trait responses

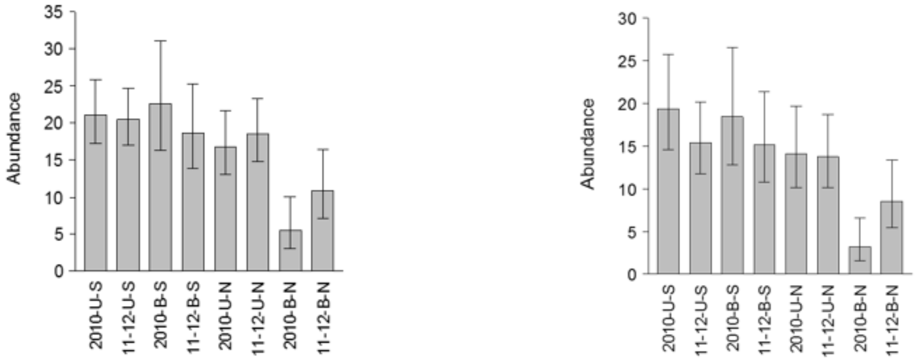
Through time, i.e. over three survey years, burnt remnants exhibited an overall decline in abundance of viviparous species (Fig. 3a), compared with no change in all other sites (i.e. unburnt). In contrast, the abundance of above-ground species showed a decrease in burnt remnants, that then plateaued compared with a consistent increase in all other sites (Fig. 3b).

In the year prior to experimental burning, remnants in the northern region of our study had lower abundance of insectivorous (Fig. 3c) and nocturnal (Fig. 3d) species than either unburnt northern (reserve) sites, or unburnt sites and control patches in the southern region. However, after the northern remnants were burnt, there was an increase in abundance of insectivorous and nocturnal species. In comparison, there was little to no change in either trait group in the northern unburnt remnants. The southern remnants also remained unchanged (Fig. 3c and Fig. 3d).



(a) (year:burn) viviparous p = 0.008

(b) (year:burn) above-ground p = 0.005



(c) (Y1:region1:burn) insectivorous p = 0.024

(d) (Y1:region1:burn) nocturnal p = 0.014

Figure 3. Predicted abundance of (a) viviparous and (b) above-ground reptiles through time in burnt and unburnt remnants ('Year:Burn'). Predicted abundance of (c) insectivorous and (d) nocturnal reptiles in burnt and unburnt remnants, in southern and northern regions, in the first (2010) and subsequent (2011 and 2012 combined) years of survey ('Y1:Region1:Burn'). Error bars indicate 95% confidence intervals.

Oviparous, medium-sized and below-ground species showed similar responses to burning in northern and southern sites (Fig. 4 and Fig. S1). However, we observed contrasting responses in these species in the recently burnt and unburnt sites in the north, compared with the recently burnt and unburnt sites in the south. In the northern sites, we observed a lower abundance of these species, whereas in the southern sites, there was no significant difference (Fig. 4).

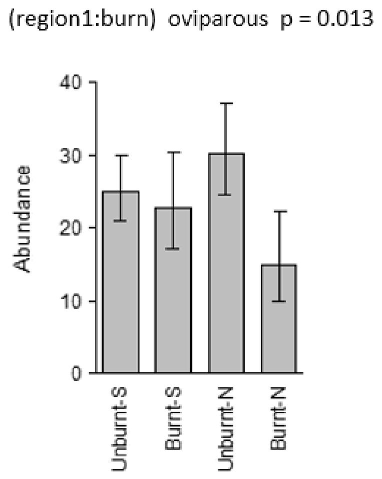


Figure 4. Predicted abundance of oviparous reptiles (medium-sized and below-ground species are in Fig. S1) in burnt and unburnt remnants in northern and southern regions ('Region1:Burn'). Error bars indicate 95% confidence intervals.

For interactions between burnt and unburnt sites, in the first (2010) and subsequent (2011 and 2012 combined) years of survey, viviparous species were less abundant after patches were burnt compared to other sites after the first year of surveys (Fig. 5a).

Through time, reptile abundance in southern (long unburnt) and northern (recently burnt) regions exhibited similar patterns for several traits (Fig. 5b and Fig. S1). In northern sites, diurnal, oviparous, above-ground and omnivorous species' abundances gradually increased each year, but remained mostly unchanged through time in southern sites (albeit with weak positive responses in above-ground (Fig. S1) and diurnal species (Fig. 5b)).

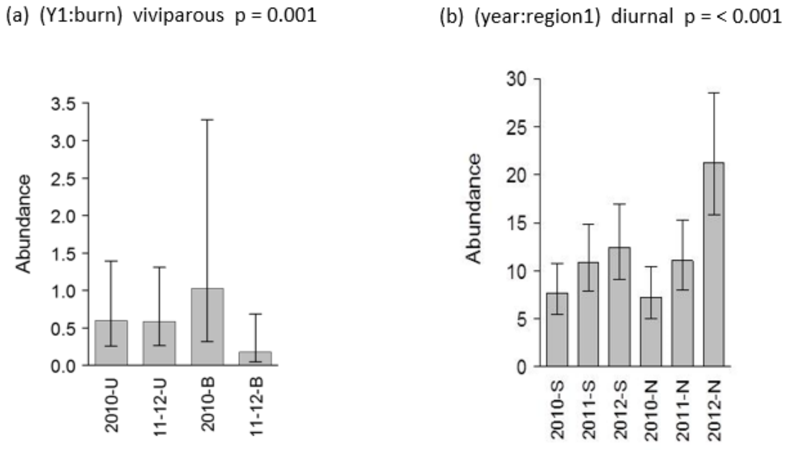


Figure 5. Predicted abundance of (a) viviparous reptiles in burnt and unburnt remnants in the first (2010) and subsequent (2011 and 2012 combined) years of survey ('Y1:Burn'); and abundance of (b) diurnal reptiles (oviparous, above-ground and omnivorous species are in Fig. S1) in northern and southern regions through time ('Year:Region1'). Error bars indicate 95% confidence intervals.

After the first (2010) and subsequent (i.e. 2011 and 2012 combined) years of survey, the northern region had a significant increase in large-bodied reptile abundance (Fig. 6a) but had little to no change in the southern sites. We detected higher abundance of large-bodied reptiles in farm patches than in reserve sites (Fig. 6b).

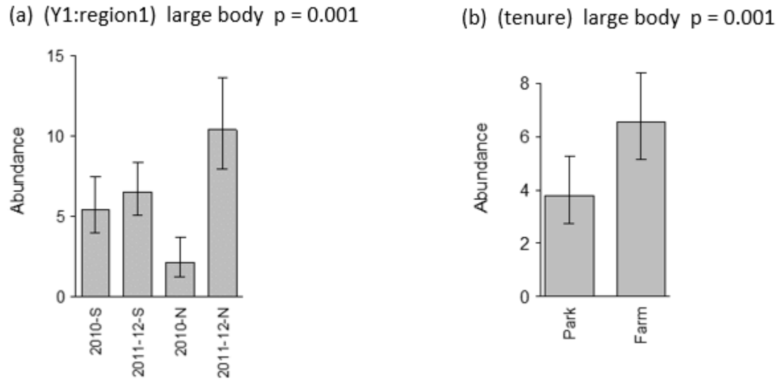


Figure 6. Predicted abundance of (a) large-bodied reptiles to southern and northern regions in the first year, and following two years of surveys ('Y1:Region1'); and predicted abundance of (b) large-bodied reptiles in reserve and farm sites ('Tenure'). Error bars indicate 95% confidence intervals.

Fire over time and trait responses

Through time, species richness of insectivorous (Fig. 7a), and diurnal (Fig. 7b) reptiles, and abundance of carnivorous (Fig. 7c) and small-bodied (Fig. 7d) reptiles increased across the whole study site (includes all recently burnt and long unburnt reserves and remnants).

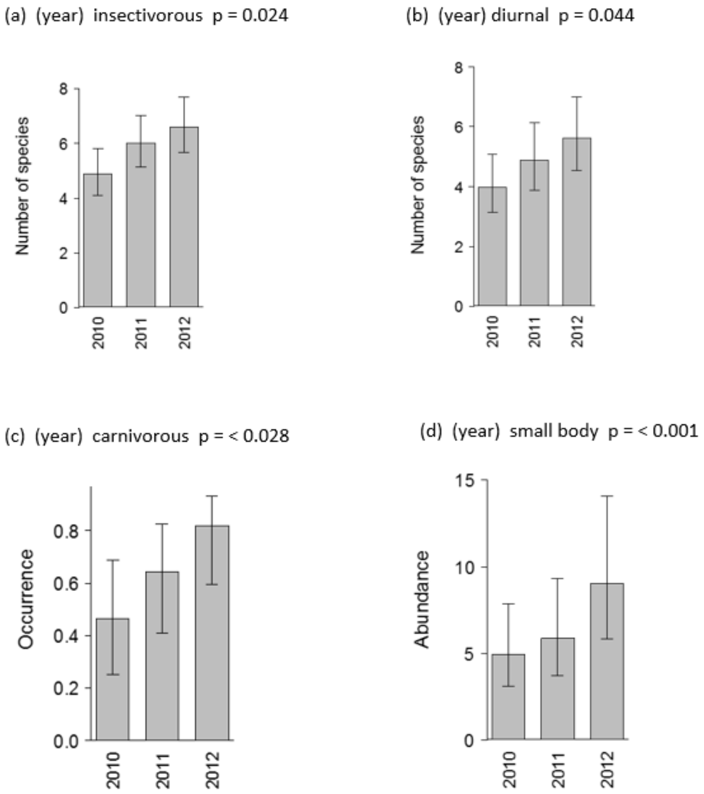


Figure 7. Predicted richness of (a) insectivorous and (b) diurnal reptiles through time; and predicted abundance of (c) carnivorous and (d) small-bodied reptiles through time. Error bars indicate 95% confidence intervals.

However, in experimentally burnt sites, insectivorous species richness (Fig. 8a) and diurnal abundance (Fig. 8b) were both lower than in unburnt remnant sites.

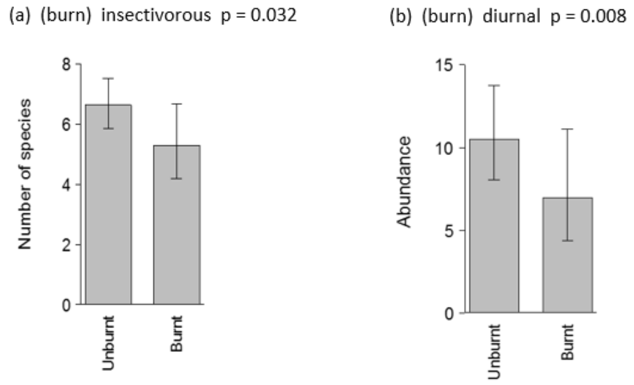
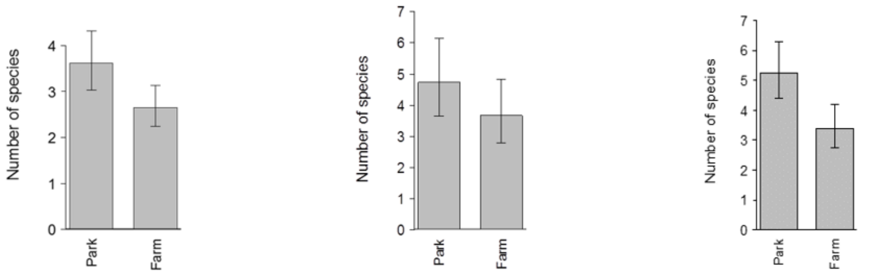


Figure 8. Predicted (a) richness of insectivorous reptiles, and (b) abundance of diurnal reptiles in response to experimental burning ('Burn'). Error bars indicate 95% confidence intervals.

Patch type and fire

We observed lower species richness for medium-sized (Fig. 9a), above-ground (Fig. 9b) and diurnal (Fig. 9c) reptiles in remnants compared with reserves. In addition, in northern sites, we observed a lower abundance of small-bodied (Fig. 9d) and insectivorous (Fig. 9e) reptiles compared with southern sites, where the reserve is long unburnt. Interestingly, only omnivorous species responded to the interaction of these variables, with the northern sites supporting a higher abundance of omnivorous species in the recently burnt reserve than in farm patches. Conversely, in the long unburnt southern sites of the reserve, the abundance of omnivorous species was lower in the reserve than in the farm patches (Fig. 9f).



(a) (tenure) medium body p = 0.01

(b) (tenure) above-ground p = 0.04

(c) (tenure) diurnal p = 0.001

(d) (region) small body p = 0.028

(e) (region) insectivorous p = 0.027

(f) (tenure1:region1) omnivorous p = < 0.001

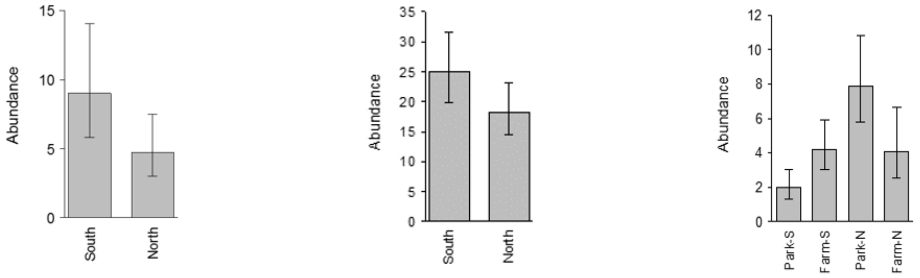
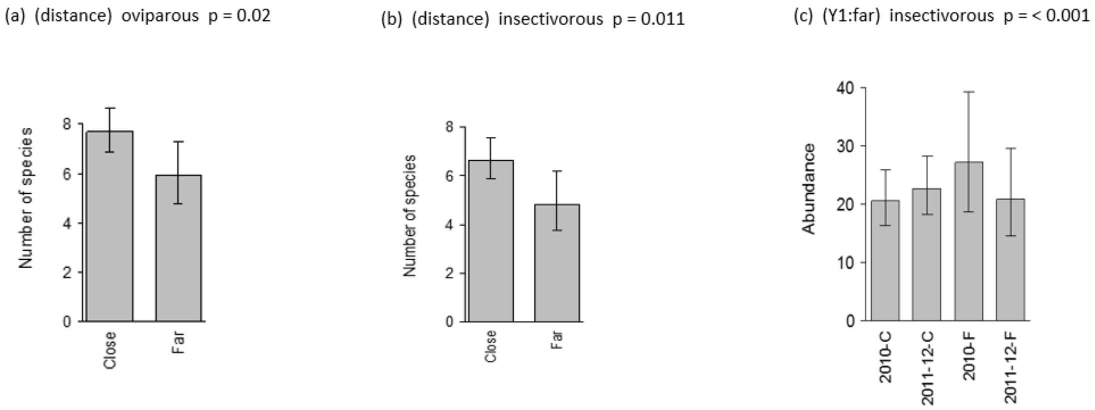


Figure 9. Predicted richness in reserves and remnants for (a) medium-bodied, (b) above-ground and (c) diurnal reptiles ('Tenure'); and predicted abundance for (d) small-bodied and (e) insectivorous reptiles in the northern and southern regions ('Region'). Predicted abundance of (f) omnivorous reptiles in northern and southern reserve sites and farm patches ('Tenure1:Region1'). Error bars indicate 95% confidence intervals.

Patch isolation and fire

We observed lower oviparous (Fig. 10a) and insectivorous (Fig. 10b) species richness in isolated patches (i.e. far from the reserve) than in patches close to the reserve. However, following the first year of surveys, we observed a decline in insectivorous abundance (Fig. 10c) in isolated patches. In contrast, after the first year of surveys, we observed a weak increase in abundance for insectivorous species in patches close to the reserve (Fig. 10c).


(a) (distance) oviparous p = 0.02

(b) (distance) insectivorous p = 0.011

(c) (Y1:far) insectivorous p = < 0.001

Figure 10. Predicted richness for (a) oviparous and (b) insectivorous reptiles in remnants close to and far from the reserve ('Distance'); and the predicted abundance of (c) insectivorous reptiles to remnants close to and far from the reserves in the first (2010) and subsequent (2011 and 2012 combined) years of survey ('Y1:Far'). Error bars indicate 95% confidence intervals.

Discussion

In this study, we sought to determine the effects of fire and fragmentation interactions on reptile functional groups in Australia. Our investigation did not detect a primary interaction between fire and fragmentation in reptile abundance or richness e.g. burn by tenure and/or isolation. However, from our complex analysis examining fire, patch type and patch isolation, we detected significant responses of five functional trait groups to these factors that, to the best of our knowledge, have not been investigated in fire-fragmentation interaction research. Overall, as predicted, our findings highlighted contrasting effects of, and a high degree of variation in, trait responses to individual fire treatments and interactions between treatments, but not between fire and fragmentation (Table 1). In addition, reserves had higher species richness than farm sites and abundance was higher in the southern region that contained a larger proportion of long unburnt vegetation. We argue that this variation in trait responses of reptiles to fire regime changes in highly fragmented landscapes may threaten, instead of promote, the persistence of some species. As such, we recommend that: (1) consideration of how fire may interact with degraded and isolated patches, and how species could respond, must be given to the conservation objectives of ecological burn programs (particularly with respect to potential negative effects on functionally important, or threatened reptiles); and (2) while our research adds to the currently limited knowledge of reptile trait responses in fragmented, fire-affected landscapes, ecological burning should not be undertaken in long unburnt remnants. Fire suppression can also benefit species associated with early post-fire successional habitat, such as a gecko species that Driscoll *et al.* (2012b) detected in long-unburnt and isolated patches where 'niche-related' factors showed gecko abundance and occurrence had a positive relationship with percentage cover of spinifex (*Triodia*). *Triodia* is killed by fire and regenerates slowly (Paltridge and Latz, 2009). Further information regarding faunal responses to fire and fragmentation is necessary, as is the better ability to identify and map fire history of long unburnt remnant habitats to enable us to more accurately ensure that fire regimes meet the spectrum (early, mid, late) of post-fire successional habitat needs of co-occurring species.

This study invokes metapopulation ideas (see Hanski and Gilpin, 1991; MacArthur and Wilson, 1967) and extensions of the ideas that relate to landscape ecology (Hanski and Gilpin, 1991). By investigating how populations may be connected in discrete habitat patches via dispersal, in response to fire, across a cropping matrix, our findings provide a better understanding of the metapopulation structure on reptile populations. Also, given the potential importance of the matrix (Ricketts, 2001), and the role of matrix permeability (Vandermeer and Perfecto, 2006), the degree of matrix resistance to population dispersal (Van Buskirk, 2012) warrants future research.

Fire effect

Fire is an important determinant of the abundance and richness of reptiles in different trait groups occurring in remnant patches and reserves (Smith *et al.*, 2012b). As such, we expected that animals would prefer habitat corresponding to their species-specific, post-fire succession (Driscoll and Henderson, 2008). Our results indicate that insectivorous and nocturnal reptile species respond to prescribed burns, but only if the patch is close to a recently burnt large reserve (i.e. northern region), and where reptile numbers are initially low (Fig. 3c and Fig. 3d). There are several possible explanations for our finding, which may be acting in isolation or in combination.

First, the increase in insectivorous species abundance in experimentally burnt remnants may be because the recently burnt region of the reserve is acting as a population source. This is because invertebrates can persist and increase after fire (Elia *et al.*, 2012; Teasdale *et al.*, 2013) and as such, these increased food resources in burnt remnants could drive reptile dispersal. However, the loss of food resources was untested in my study and it may have been useful to consider because in a post-fire landscape, food resources may also be limiting (Davis and Doherty, 2015). Second, the increase in insectivorous species may have had less to do with improved food resources and more to do with the initial low reptile numbers in the first year of surveys. High canopy cover (Pinto, 2018) and livestock trampling (Haby and Brandle, 2018) can reduce habitat suitability for reptiles (Driscoll *et al.*, 2012b; Yates *et al.*, 2000). However, as livestock grazing occurred across several sites in both the northern and southern regions, grazing and trampling alone cannot be attributed to species low numbers in the north. There may be localised disturbances that species are responding to, such as severe hailstorms that may have only affected sites in the northern region (J. Lazzari, Australian National University, pers. comm.). Finally, our low-to-medium intensity experimental burns removed much of the ground cover leading to more open habitat thus presenting reproductive benefits to some reptile species. For example, in a predominantly insectivorous skink species, longer basking resulted in juveniles being in better condition than offspring born to females with reduced basking opportunities (Wapstra, 2000; Wapstra and Swain, 1996). The simplification of habitat structure after the experimental burns could also make invertebrates more accessible but as shown by Teasdale *et al.* (2013) invertebrate abundance can vary depending on the survey method.

The most abundant reptile captures in our study were of an insectivorous, nocturnal burrower that is also oviparous (the gecko *Nephrurus stellatus*). This species lives in both reserves and remnants (Driscoll *et al.*, 2012b) and is an early successional species after fire (Driscoll and Henderson, 2008). Although survival in recently burnt, early successional areas can be reduced by the higher risk of predation (Fordyce *et al.*, 2016; Hawlena *et al.* 2010), some trait groups may be less susceptible to predation than other trait groups. For example, burrowing could make some reptile species less of a prey risk than reptiles that use above-ground habitats (Sousa, 1984). The reduced predation risk associated with burrowing behaviour may allow burrowing reptiles to be more active dispersers (Bradstock *et al.*, 2005; Keith *et al.*, 2002). As such, our findings suggest that nearby reserves could act as potential sources for recently burnt, isolated remnants for a species such as *N. stellatus* (Fig. 3c and Fig. 3d). However, this is contrary to previous research on *N. stellatus* that suggests other remnants may be acting as sources depending on their spatial arrangement and habitat quality (Driscoll *et al.*, 2012b). These finding suggest that both reserves and remnants are important as source habitat and both may minimise the risk of reptile extinctions in landscapes where fire regimes have been modified.

While some species and trait groups showed an increase in response to fire, we found inconsistent patterns in other reptile trait groups. We observed a significant decline in abundance of oviparous, medium-sized and below-ground species in burnt remnants in the northern region (see Fig. 4 and Fig. S1), and declines in viviparous species in burnt remnants after the first year of surveys (Fig. 5a). Yet, between years, the abundance of diurnal, oviparous and above-ground species increased, as did species richness of diurnal and omnivorous species. This increase occurred across our fragmented study site but strongly in the northern region, i.e. the region with a large, recently burnt area of reserve (Fig. 5b and Fig. S1). These increases in abundance could reflect species preferences for similar post-fire successional vegetation types (Driscoll and Henderson, 2008; Smith *et al.*, 2013) and may be indicative of deliberate dispersal attempts by reptiles. In the southern long-unburnt region of the reserve, there was only a weak positive increase in diurnal and above-ground species (Fig. 5b).

In contrast to this weak positive increase through time, viviparous and above-ground species showed overall declines in burnt compared with unburnt remnants between years (Fig. 3a and Fig. 3b). The variable and contrasting responses of these different trait groups (viviparous, diurnal, oviparous, above-ground and omnivorous) to fire through time makes it difficult to draw robust, generalisable conclusions about reptile responses to fire. That said, our results suggest that long unburnt remnants may offer some refuge to reptiles.

Patch type and fire

As predicted, we found that the reserve had higher species richness compared to patches. This may be accounted for by the reserve in our study being considerably larger, contiguous and a mix of fire ages compared with the isolated, mostly linear patches located in an agricultural matrix (Keinath *et al.*, 2017). However, in the northern region, the area with a large burnt area of reserve, there was a lower abundance of both small-bodied species and insectivorous species (Fig. 9d and Fig. 9e). This may be because omnivorous species are moving to recently burnt areas of the reserve for prey resources (Swan and Wilson, 2015; Teasdale *et al.*, 2013) (Fig. 9 f). The northern area of the reserve may have a greater heterogeneity in vegetation recovering after fire and this could be providing more niches that in turn, may be supporting a greater diversity of plant and animal species (Davis and Doherty, 2015).

Time and fire

Our study found that insectivorous richness and diurnal richness (Fig. 7a and Fig. 7b) and abundance, increased overall over time but insectivorous richness Fig. 8a) and diurnal abundance (Fig. 8b) decreased in burnt sites. Similarly, small-bodied species increased overall (Fig. 7d), yet had a lower abundance in the northern region which contained a large area of recently burnt vegetation. These contrasting responses in the same trait suggest that, overall, reserves and remnants support species richness and abundance over time even though fire-related declines are occurring in both recently burnt remnants and in the reserve. This implies that the current spatial arrangement and extent of reserves and remnants in our study location can counter some reptile species declines after remnants are burnt. As such, some species may be unaffected by burning in remnants if a combination of remnants (unburnt) and reserves (burnt and unburnt) is maintained thus supporting species behaviours, such as movement, by foraging animals that are associated with beneficial fire adaptations (Pausas and Parr, 2018).

Patch isolation

Our finding that remnants close to the reserve had higher species richness and abundance than the remnants further from the reserve supports our prediction. Oviparous and insectivorous richness was higher in less isolated remnants (Fig. 10a and Fig. 10b). This increase in insectivorous richness (Fig. 10b) as well as abundance (Fig. 10c) in remnants near to the reserve after the first year of surveys, could be due to the reserve acting as a population source with species dispersing to remnants with increased resources (Elia *et al.*, 2012; Teasdale *et al.*, 2013).

Management considerations and future research

We found that burning long unburnt remnant patches does not lead to overall declines in some species and may provide colonising opportunities for insectivorous, nocturnal and burrowing reptiles, but only if remnant patches are close to a recently burnt large reserve and reptile numbers are initially low.

We found contrasting responses of reptile functional groups to fire and fragmentation. However, we did find that large reserves had higher reptile species richness and abundance than remnant patches, and that remnants closer to the reserve had higher richness and abundance than more isolated remnants. Previous research indicates that there are many known reptile species successional habitat trajectories in response to fire (Driscoll and Henderson, 2008), and many contrasting responses of reptiles to fire and fragmentation at landscape and micro-habitat scales (Pinto, 2018). This research is supported by our findings. As such, our findings indicate that the range of reptile species requirements and responses can best be met by ensuring that reserves contain different TSF-aged vegetation that provide a range of successional habitats. In our mallee study location, this greater diversity and abundance of species assemblages in large reserves may help to prevent species extinctions in nearby reserves if single wildfires occur in long unburnt vegetation. That is, the reserve may act as a source to remnants close to the reserve.

However, given that the effects of multiple fires and their frequency can influence species occupancy and the composition of animal communities (Morrison *et al.*, 1995), and that limited information is available on reptile responses to fire in remnants a precautionary approach to ecological burning in fragmented, fire-affected landscapes is essential (Connell *et al.*, 2019; Driscoll and Henderson, 2008; Smith *et al.*, 2013).

Further, in some species small sample sizes can preclude adequate statistical testing, but could be addressed by simplifying the study design and using mark-recapture data. For example, Carthew *et al.* (2009) were able to clearly detect movement between adjacent landscape types of small sample sizes using mark-recapture.

Adequate species-related data continues to be important for making fire-related management recommendations that can be adaptive and that can help to avoid perverse outcomes for biodiversity (Lawes *et al.*, 2015; Prowse *et al.*, 2017; Steinitz *et al.*, 2012). This is particularly so with climate change (and increasing climatic variability) potentially exacerbating fire and fragmentation effects (Bussotti *et al.*, 2015) on biodiversity (Driscoll *et al.*, 2012a). To obtain this species-related data, adequate species-level research that is not constrained by time- or sample-limited studies is recommended (Smith *et al.*, 2013), to confirm and clarify the responses to fire and fragmentation in reptiles such that generalisable management recommendations can be made, particularly for remnant patches in modified landscapes.

Author contributions

JL and DAD conceptualised the study and the study design. JL acquired the data and JL and DAD led analyses; JL led manuscript preparation with substantial critical and editorial input from all authors. JL, CFS and DAD declare no conflicts of interest. In prep for the *Journal of Animal Ecology*.

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Supporting Information

Table S1. Study site and location information for data collected from 30 transects. The information includes: location*, region, distance, treatment, dune_swale, block number, latitude and longitude.

Location*	Region	Distance of remnant from the Park (reserve)	Treatment - Park = recent_burn (historical burn) - Remnant = burn OR control	Dune or swale	Block (replicate number)	Latitude	Longitude
CB1	north	close	burn	D	1	-32.95910935	135.9496707
CB2	north	close	burn	D	2	-33.03845244	136.0349894
CB3	north	close	burn	D	3	-33.05690361	136.0359296
CB4	south	close	burn	D	4	-33.08129017	135.707359
CB5	south	close	burn	D	5	-33.1045409	135.8255985
CB6	south	close	burn	D	6	-33.1528811	135.9946178
CU1	north	close	control	D	1	-32.95186797	135.9435893
CU2	north	close	control	D	2	-33.03853878	136.0265788
CU3	north	close	control	D	3	-33.05966277	136.0568958
CU4	south	close	control	D	4	-33.07608065	135.7058498
CU5	south	close	control	D	5	-33.1059839	135.8252969
CU6	south	close	control	D	6	-33.1546337	135.9649633
FB4	south	far	burn	D	4	-33.126037	135.71273
FB5	south	far	control	D	5	-33.17128	135.776916
FB6	south	far	burn	D	6	-33.1875719	135.9584137
FU4	south	far	control	D	4	-33.130628	135.711961
FU5	south	far	control	D	5	-33.166031	135.777068
FU6	south	far	control	D	6	-33.1841212	135.9440336
PD1	north	park	recent_burn	D	1	-32.95908705	135.9332203
PD2	north	park	recent_burn	D	2	-33.0427299	136.0171098
PD3	north	park	recent_burn	D	3	-33.0753982	136.0560399
PD4	south	park	long_unburnt	D	4	-33.049401	135.703465
PD5	south	park	long_unburnt	D	5	-33.107765	135.830549
PD6	south	park	long_unburnt	D	6	-33.129984	135.894447
PS1	north	park	recent_burn	S	1	-32.95770722	135.9332093
PS2	north	park	recent_burn	S	2	-33.04297339	136.0176318
PS3	north	park	recent_burn	S	3	-33.0741653	136.0560673
PS4	south	park	long_unburnt	S	4	-33.047778	135.703106
PS5	south	park	long_unburnt	S	5	-33.10725	135.831099
PS6	south	park	long_unburnt	S	6	-33.129949	135.895748

* Each transect of 10 pitfall traps was allocated a Latitude_Longitude from the first pitfall trap.

Table S2. Distances of isolated dunes from the reserve (km)

Distance (km)	Close-Burnt	Close-Unburnt	Far-Burnt	Far-Unburnt	Close (min. distance)	Far (max. distance)
Min	0.13	0.16	6.09	5.58	0.13	5.58
Max	2.88	2.96	7.69	8.47	2.96	8.47
Range	2.75	2.8	1.6	2.89	2.83	2.89
No. dunes	*6*	*6*	*2*	*4*	*12*	*6*

Table S3a. A list of five species traits (reproduction, size, habitat position, diet, and habitat time) assigned to 40 individual reptile species captured in the study~. The five traits were used to investigate how they might influence species responses to fire and fragmentation interactions in the study. Trait categories were assigned using published literature (Driscoll and Henderson, 2008; Smith *et al.*, 2013). The same shading indicates the same traits. Only species shaded were analysed.

Genus_species~	**Family**	**Reproduction (oviparous, viviparous)**	**svl_cm # (snout-vent length: small, medium, big)**	**Hab_position (above, below ground)**	**Diet (carnivorous, insectivorous, omnivorous)**	**diurnal_nocturnal (diurnal, nocturnal (includes crepuscular), both diurnal and nocturnal**
Lerista_taeniata	Scincidae	oviparous	2.2	below	insectivorous	nocturnal
Menetia_greyii	Scincidae	oviparous	3.4	above	insectivorous	diurnal
Lerista_distinguenda	Scincidae	oviparous	4.3	below	insectivorous	nocturnal
Morethia_boulengeri	Scincidae	oviparous	4.8	above	insectivorous	diurnal
Ctenotus_schomburgkii	Scincidae	oviparous	5.2	above	insectivorous	diurnal
*Hemiergis_decresiensis	Scincidae	viviparous	5.3	below	insectivorous	both
Tympanocryptis_lineata	Agamidae	oviparous	5.3	above	insectivorous	diurnal
Ctenophorus_fordi	Agamidae	oviparous	5.4	above	insectivorous	diurnal
Hemiergis_millewae	Scincidae	viviparous	5.5	above	insectivorous	both
Lucasium_damaeum	Gekkonidae	oviparous	5.5	below	insectivorous	nocturnal
Morethia_butleri	Scincidae	oviparous	5.5	above	insectivorous	diurnal
Ctenotus_leae	Scincidae	oviparous	6	above	insectivorous	diurnal
Lerista_terdigitata	Scincidae	oviparous	6.5	below	insectivorous	nocturnal
Ctenotus_atlas	Scincidae	oviparous	6.9	above	insectivorous	diurnal
*Lerista_dorsalis	Scincidae	oviparous	6.9	below	insectivorous	nocturnal
Ctenophorus_pictus	Agamidae	oviparous	7	below	insectivorous	diurnal
*Ctenotus_regius	Scincidae	oviparous	7.2	above	insectivorous	diurnal
Liopholis_inornata	Scincidae	viviparous	8	below	omnivorous	diurnal
*Delma_australis	Pygopodidae	oviparous	8.4	above	insectivorous	both
Nephrurus_stellatus	Gekkonidae	oviparous	8.5	below	insectivorous	nocturnal
*Delma_butleri	Pygopodidae	oviparous	9.3	above	insectivorous	both
Lerista_edwardsae	Scincidae	oviparous	9.5	below	insectivorous	nocturnal
Ctenophorus_cristatus	Agamidae	oviparous	10.5	above	insectivorous	diurnal
Eremiascincus_richardsonii	Scincidae	oviparous	11	below	insectivorous	nocturnal
Moloch_horridus	Agamidae	oviparous	11	above	insectivorous	diurnal
Aprasia_inaurita	Pygopodidae	oviparous	12.3	below	insectivorous	diurnal
*Cyclodomorphus_melanops	Scincidae	viviparous	13.1	above	omnivorous	nocturnal
Pogona_spp	Agamidae	oviparous	19.5	above	omnivorous	diurnal
*Tiliqua_rugosa	Scincidae	viviparous	25	above	omnivorous	diurnal
*Lialis_burtonis	Pygopodidae	oviparous	29	below	carnivorous	both
Ramphotyphlops_australis	Typhlopidae	oviparous	30	below	insectivorous	nocturnal
Simoselaps_bertholdi	Elapidae	oviparous	30	below	carnivorous	nocturnal
*Tiliqua_scincoides	Scincidae	viviparous	31	above	omnivorous	diurnal
Tiliqua_occipitalis	Scincidae	viviparous	32	above	omnivorous	diurnal
Brachyurophis_semifasciatus	Elapidae	oviparous	35	below	reptile eggs	nocturnal
Parasuta_spectabilis	Elapidae	viviparous	40	above	carnivorous	nocturnal
Ramphotyphlops_bituberculatus	Typhlopidae	oviparous	45	below	insectivorous	nocturnal
*Demansia_psammophis	Elapidae	oviparous	80	above	carnivorous	nocturnal
*Pseudonaja_nuchalis	Elapidae	oviparous	150	above	carnivorous	both
Varanus_gouldii	Varanidae	oviparous	160	below	carnivorous	diurnal

Average svl. Natural break between 13.1 and 19 cm (13 spp > 19 cm). Groups were divided equally to get 13 in small group, 14 in the medium groups and 13 in the big group. Small svl < 6.6 cm; medium svl > 6.5 cm < 14 cm; big svl > 13.9 cm.

~ *Christinus marmoratus* (Gekkonidae) excluded from traits list because the species is common Australia wide in natural and urban environments. A total of three (n = 3) were trapped. *Cryptoblepharus plagiocephalus* (Scincidae) excluded from traits list because trait data not available. A total of two (n = 2) were trapped.

* Species not analysed because catches were ≤ 2.

Trait groups: oviparous, above-ground, insectivorous, diurnal (10 species); oviparous, below-ground, insectivorous, nocturnal (9 species); oviparous, below-ground, insectivorous, diurnal (2 species); plus eight species with ungrouped traits.

Table S3b. Trait group categories and species-specific abundance. Data were extracted from Table S3a and reptile capture data records

n = 9

***Group*: oviparous, below-ground, insectivorous, nocturnal**

Eremiascincus_richardsonii	8	
Lerista_distinguenda	6	
Lerista_edwardsae	118	
Lerista_taeniata	135	
Lerista_terdigitata	27	
Lucasium_damaeum	14	
Nephrurus_stellatus	805	
Ramphotyphlops_australis	18	
Ramphotyphlops_bituberculatus	93	
Total	1224	

Summary

Total analysed for four groups
2180

Total not analysed
20

Total analysed and not analysed
2200

n = 10

***Group:* oviparous, above-ground, insectivorous, diurnal**

Ctenophorus_cristatus	132	
Ctenophorus_fordi	10	
Ctenotus_atlas	74	
Ctenotus_leae	3	
Ctenotus_regius	1	not analysed because ≤ 2
Ctenotus_schomburgkii	44	
Menetia_greyii	110	
Moloch_horridus	4	
Morethia_boulengeri	12	
Morethia_butleri	10	
Tympanocryptis_lineata	30	
Total analysed	429	

n = 2

***Group:* oviparous, below-ground, insectivorous, diurnal**

Aprasia_inaurita	10	
Ctenophorus_pictus	52	
Total	62	

n = 8

***Ungrouped/various combinations* of traits specific to each species**

Brachyurophis_semifasciatus	17	
Christinus_marmoratus	3	not analysed because a common occurring species (including urban environments)
Cryptoblepharus_plagiocephalus	2	not analysed because ≤ 2
Cyclodomorphus_melanops	2	not analysed because ≤ 2
Delma_australis	2	not analysed because ≤ 2
Delma_butleri	1	not analysed because ≤ 2
Demansia_psammophis	1	not analysed because ≤ 2
Liopholis_inornata	48	
Hemiergis_decresiensis	1	not analysed because ≤ 2
Hemiergis_millewae	26	
Lerista_dorsalis	2	not analysed because ≤ 2
Lialis_burtonis	1	not analysed because ≤ 2
Parasuta_spectabilis	18	
Pogona_spp	284	
Pseudonaja_nuchalis	1	not analysed because ≤ 2
Simoselaps_bertholdi	34	
Tiliqua_occipitalis	5	
Tiliqua_rugosa	2	not analysed because ≤ 2
Tiliqua_scincoides	1	not analysed because ≤ 2
Varanus_gouldii	33	
Total analysed	465	

Table S4a. List of the 30 survey sites, the years surveyed and the related site variable and attribute categories used in the analysis

site	year	dist	treat	soil	tenure	region	fire	block
CB1	2010	C	B	dune	farm	n	burnt	1
CB2	2011	C	B	dune	farm	n	burnt	2
CB3	*OR*	C	B	dune	farm	n	burnt	3
CB4	2012	C	B	dune	farm	s	burnt	4
CB5		C	B	dune	farm	s	burnt	5
CB6		C	B	dune	farm	s	burnt	6
CU1		C	U	dune	farm	n	unburnt	1
CU2		C	U	dune	farm	n	unburnt	2
CU3		C	U	dune	farm	n	unburnt	3
CU4		C	U	dune	farm	s	unburnt	4
CU5		C	U	dune	farm	s	unburnt	5
CU6		C	U	dune	farm	s	unburnt	6
FB4		F	B	dune	farm	s	burnt	4
FB5		F	B	dune	farm	s	unburnt	5
FB6		F	B	dune	farm	s	burnt	6
FU4		F	U	dune	farm	s	unburnt	4
FU5		F	U	dune	farm	s	unburnt	5
FU6		F	U	dune	farm	s	unburnt	6
PD1		P	D	dune	park	n	unburnt	1
PD2		P	D	dune	park	n	unburnt	2
PD3		P	D	dune	park	n	unburnt	3
PD4		P	D	dune	park	s	unburnt	4
PD5		P	D	dune	park	s	unburnt	5
PD6		P	D	dune	park	s	unburnt	6
PS1		P	S	swale	park	n	unburnt	1
PS2		P	S	swale	park	n	unburnt	2
PS3		P	S	swale	park	n	unburnt	3
PS4		P	S	swale	park	s	unburnt	4
PS5		P	S	swale	park	s	unburnt	5
PS6		P	S	swale	park	s	unburnt	6

Table S4b. Dummy variable attributes and categories used in the analysis

Dummy variable id	Attribute (matching)	Categories	Description
ten1 (tenure)	farm (park)	reptile$tenure	Sites within farmland; sites within the reserve.
reg1 (region)	n (reg2 – south)	reptile$region	All northern sites in the recently burnt reserve and fragments close to the reserve. All southern sites in the long unburnt reserve and all fragments close and far to the reserve.
far (distance)	F (close)	reptile$dist	Close x 6 sites (av. distance = 0.14 km); Far x 3 sites (av. distance = 5.91 km); Park x 6 sites (in the reserve). These are used to interpret isolation.
burn (fire)	burnt (unburnt)	reptile$fire	Burnt – a patch that was burnt after surveys in 2010; unburnt – a patch that remained unburnt (control) after surveys in 2010. (Excludes all reserve sites.)
burn (year)	2010 (2011 and 2012)	reptile$year1^	Y1 – 2010: survey year before experimental burns; 2011-2012 – two survey years after experimental burns.
year	2010, 2011, 2012	reptile$year	Individual years to assess changes through time.
site – each transect was identified.		Block – 1 to 6 – survey design and groupings of sites with similar environmental variables (see Fig. 2).	

Tenure 0 = park, 1 = farm
Region 0 = south, 1 = north
Distance 0 = close, 1 = far ('Distance' is a subset of 'Tenure')
Burn 0 = unburnt, 1 = burnt
Year^ 0 = 2010, 1 = 2011,2012
Soil 0 = dune, 1 = swale

^This indicates that nothing burnt in 2010, then identifies specific sites burnt after 2010, i.e. 2011 and 2012.

Table S5. 143 ranked models using Akaike's Information Criterion for small samples (AICc). m = model, f = farm, r = region, s = swale, t = tenure, b = burn, Y1 = year 1, x = interactions. Main effects were: Region (South, North), Tenure (Park, Farm), Far (Close, Far), Burn (Unburnt, Burnt), Y1 (2010 before burn treatments, 2011-12 after burns implemented) and Year (2010, 2011, 2012). Interactions (with the exception of Tenure:Region) were to assess the effects of the burn treatment over time. Interactions included: Tenure:Region, Region:Burn, Far:Burn, Y1:Burn, Y1:Far, Y1:Region, Year:Burn, Year:Far, Year:Region, Y1:Region:Burn, Y1:Far:Burn, Year:Region:Burn, Year:Far:Burn. Models that included Burn also included the interaction with Y1 or Year. Appropriate combinations of two-way interactions were included with all three-way interactions. Y1 and Year were not used in the same models.

143 models (listed A to Z)
m0
mf
mr
mrf
ms
msf
msr
msrf
mt
mtf
mtr
mtrf
mtrrxt
mtrrxtf
mts
mtsf
mtsr
mtsrf
mtsrrxt
mtsrrxtf
my
mY1
mY1bY1xb
mY1f
mY1fbbxfY1xbY1xfY1xbxf
mY1fbY1xb
mY1r
mY1rbbxrY1xbY1xrY1xbxr
mY1rbY1xb
mY1rf
mY1rfbbxfY1xbY1xfY1xbxf
mY1rfbbxrY1xbY1xrY1xbxr
mY1rfbY1xb
mY1s
mY1sbY1xb
mY1sf
mY1sfbbxfY1xbY1xfY1xbxf
mY1sfbY1xb
mY1sr
mY1srbbxrY1xbY1xrY1xbxr
mY1srbY1xb
mY1srf
mY1srfbbxfY1xbY1xfY1xbxf
mY1srfbbxrY1xbY1xrY1xbxr
mY1srfbY1xb
mY1t
mY1tbY1xb
mY1tf
mY1tfbbxfY1xbY1xfY1xbxf
mY1tfbY1xb
mY1tr
mY1trbbxrY1xbY1xrY1xbxr
mY1trbY1xb
mY1trf
mY1trfbbxfY1xbY1xfY1xbxf
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Table S6. Presence/absence and abundance results of individual species and trait responses. Both species and trait responses that had five or fewer values > 2 or with < 10 unique values, were converted to presence/absence data (n = 30) and analysed assuming a binomial distribution of errors and using a logit link function. Responses outside of this range specification were unconverted abundance results (n = 26).

Presence/absence *(28 spp., 2 traits)*	**Abundance** *(2 spp., 24 traits)*
Aprasia_inaurita	**Nephrurus_stellatus**
Brachyurophis_semifasciatus	**Pogona_spp**
~Christinus_marmoratus	spovirichness
Ctenophorus_cristatus	spoviabund
Ctenophorus_fordi	spvivirichness
Ctenophorus_pictus	spviviabund
Ctenotus_atlas	spsmallrichness
Ctenotus_leae	spsmallabund
Ctenotus_schomburgkii	spmedrichness
Liopholis_inornata	spmedabund
Eremiascincus_richardsonii	spbigrichness
Hemiergis_millewae	spbigabund
Lerista_distinguenda	spbelowrichness
Lerista_edwardsae	spbelowabund
Lerista_taeniata	spaboverichness
Lerista_terdigitata	spaboveabund
Lucasium_damaeum	spinsectrichness
Menetia_greyii	spinsectabund
Moloch_horridus	spomnivrichness
Morethia_boulengeri	spomnivabund
Morethia_butleri	spcarnivrichness
Parasuta_spectabilis	spdayrichness
Ramphotyphlops_australis	spdayabund
Ramphotyphlops_bituberculatus	spnightrichness
Simoselaps_bertholdi	spnightabund
Tiliqua_occipitalis	spbothdnrichness
Tympanocryptis_lineata	-
Varanus_gouldii	-
spcarnivabund	-
spbothdnabund	-

~ *Christinus marmoratus* was excluded from the final analysis because it is a common species in both natural and urban environments.

Table S7. Reptile species total abundance in Family groups for three survey years: 2010, 2011, 2012

Family (taxa)	Abundance
Agamidae (dragon lizards)	512
Elapidae (venomous land snakes)	71
Gekkonidae (geckos)	822
Pygopodidae (legless lizards)	14
Scincidae (skinks)	637
Typhlopidae (blind snakes)	111
Varanidae (goannas)	33
Total	**2200**

Table S8. Species richness and abundance of families from the 40 reptile species trapped~, and the associated five traits. The table includes species with n ≤ 2 catches (these were not part of the final analysis). Species totals are included under the Abundance column in parentheses.

TRAIT **FAMILY and SPECIES RICHNESS**	***Reproduction***	***Size cm** (svl) **#***	***Habitat position***	***Diet***	***Habitat time***	**ABUNDANCE** * (species totals)
Agamidae (6)	oviparous	5.3-19.5	above (5) below	insectivorous (5) omnivorous	diurnal	512 (284,132,52,30,10,4)
Elapidae (5)	oviparous (4) viviparous	30-150	above (3) below (2)	carnivorous (4) reptile eggs	both nocturnal (4)	71 (34,18,17,1,1)
Gekkonidae (2)	oviparous	5.5-8.5	below	insectivorous	nocturnal	819~ (805,14)
Pygopodidae (3)	oviparous	8.4-12.3	above (2) below (2)	carnivorous insectivorous (3)	both (3) diurnal	14 (10,2,1,1)
Scincidae (21)	oviparous (13) viviparous	2.2-32	above (12) below	insectivorous (15) omnivorous	both (2) diurnal (11) nocturnal	636~~ (135,118,110,74,48,44,27,26,12,10,8,6,5,3,2,2,2,1,1,1,1)
Typhlopidae (2)	oviparous	30-45	below	insectivorous	nocturnal	111 (93,18)
Varanidae	oviparous	160	below	carnivorous	diurnal	33

Minimum and maximum snout vent length (svl) of species trapped within families. Natural break between 13.1 and 19 cm (13 spp > 19 cm). Groups were divided equally to get 13 in the small group, 14 in the medium groups and 13 in the big group. Small svl < 6.6 cm; medium svl > 6.5 cm < 14 cm; big svl > 13.9 cm.

* Species with ≤ 2 catches were not analysed.

~ *Christinus marmoratus* (Gekkonidae) is excluded from traits list because the species is common Australia wide in natural and urban environments. A total of three (n=3) were trapped – South, Y2(PD5), Y3(CB4, PD5).

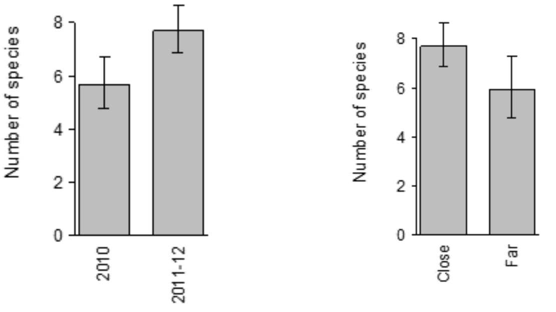
~~*Cryptoblepharus plagiocephalus* (Scincidae) excluded from traits list because trait data not available. A total of two (n=2) were trapped – South, Y1(PS4), North, Y2(PD3).

Table S9. Reptile species abundance in remnants (Farm) and reserves (Park) for each year: 2010, 2011 and 2012

Tenure	Year and abundance			***Park and Farm totals***
	2010	*2011*	*2012*	
Park	253	292	380	*925*
Farm	432	415	4428	*1275*
Year totals	**685**	**707**	**808**	**2200**

Figure S1. Plotted results (n = 45) with variables $p \leq 0.05$, taking the estimate from the highest ranked model in which that variable occurred. Error bars indicate 95% confidence intervals.

Reproduction – oviparous – richness



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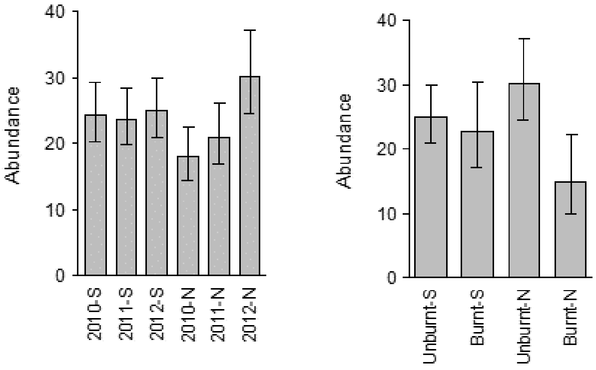
glmm_spovirichnessfar0.02.wmf

Reproduction – oviparous – abundance



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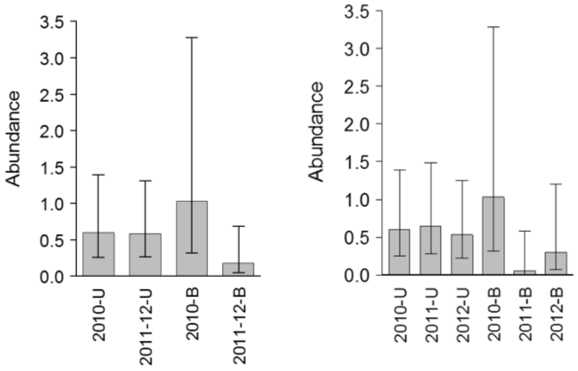
glmm_spoviabundreg1-burn0.013.wmf

Reproduction – viviparous – abundance



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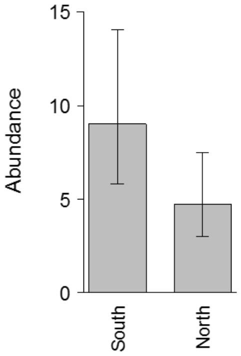
glmm_spviviabundyear-burn0.008.wmf

Size – small – abundance



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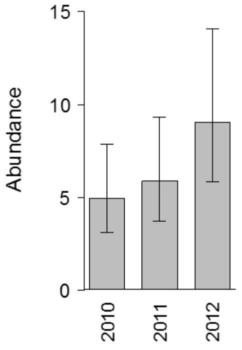

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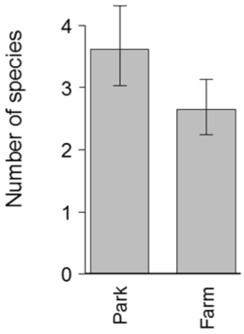
Size – medium – richness



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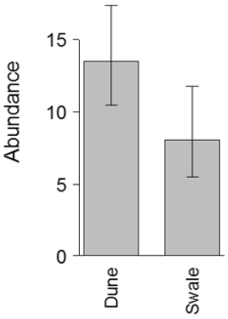
Size – medium – abundance



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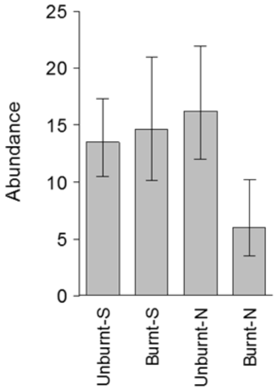

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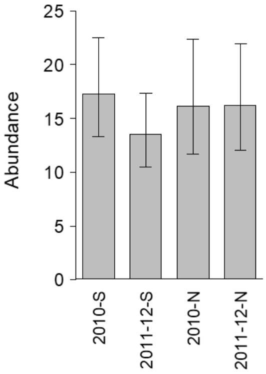

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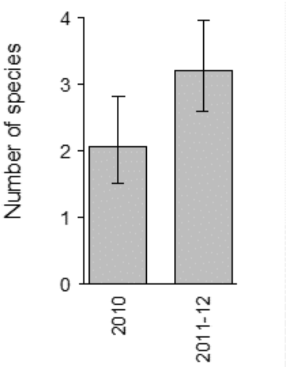
Size – big – richness



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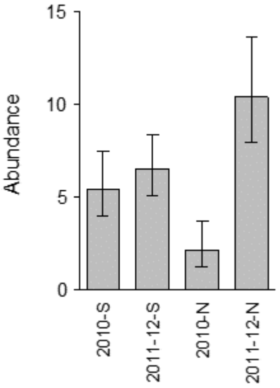
Size – big – abundance



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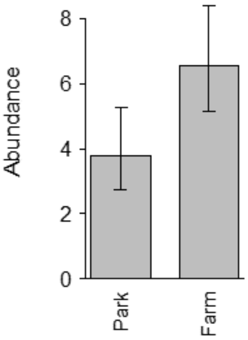

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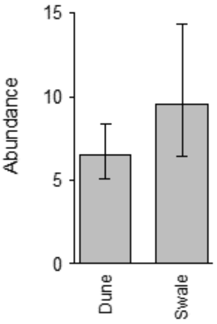

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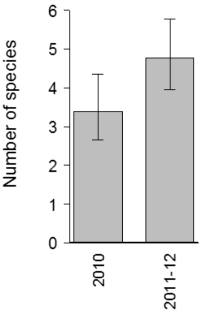
Habitat position – below-ground – richness



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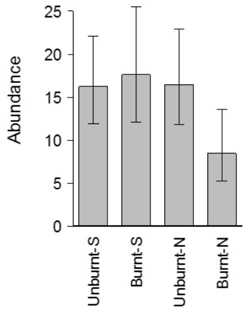
Habitat position – below-ground – abundance



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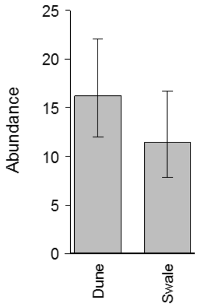

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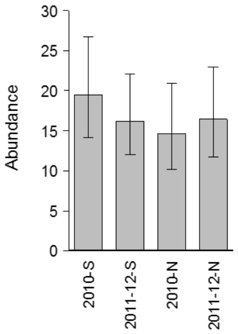

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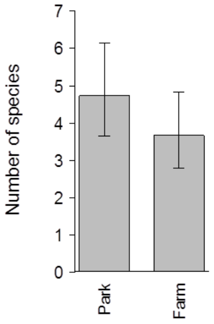
Habitat position – above-ground – richness



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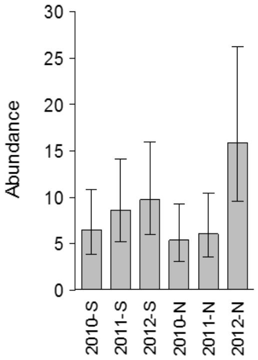
Habitat position – above-ground – abundance



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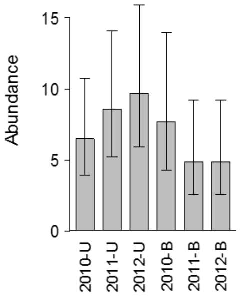

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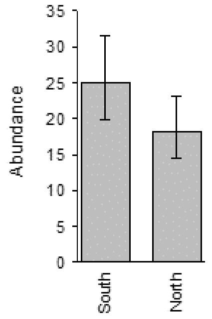
Diet – insectivorous – ABUNDANCE



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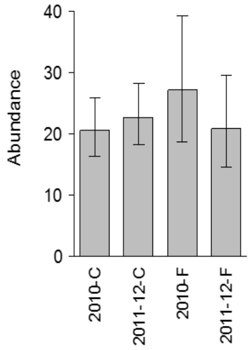

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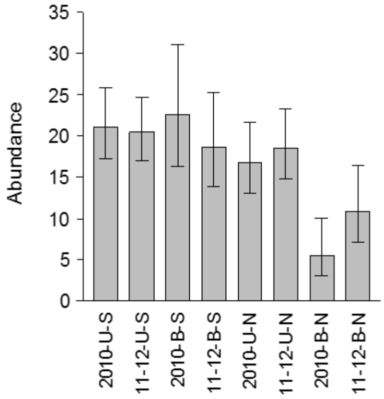

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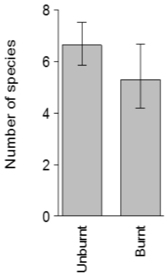
Diet – insectivorous – RICHNESS



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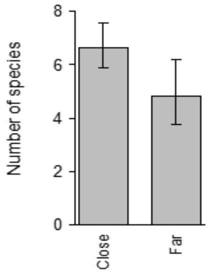

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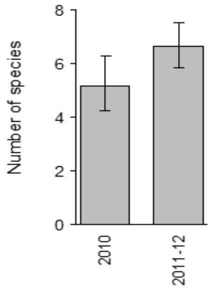

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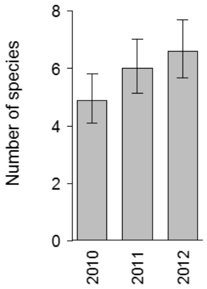

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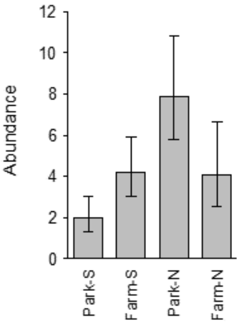
Diet – omnivorous – ABUNDANCE



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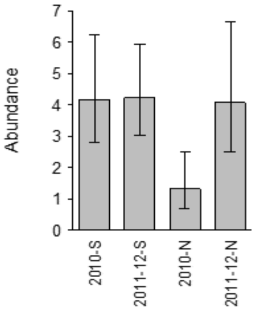

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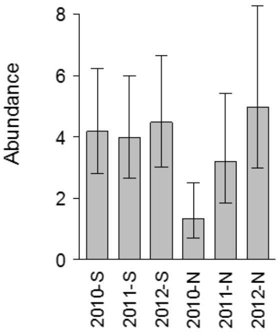

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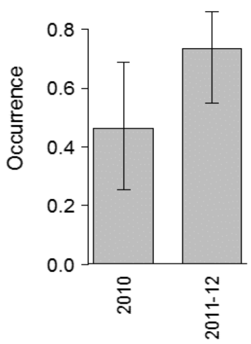
Diet – carnivorous – ABUNDANCE



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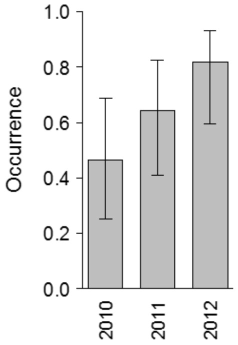

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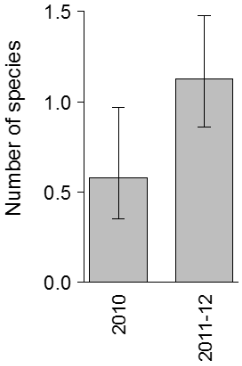
Diet – carnivorous – RICHNESS



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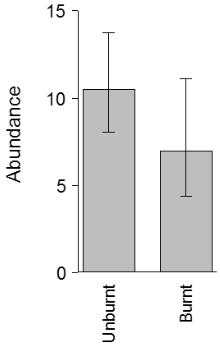
Habitat time – day – ABUNDANCE



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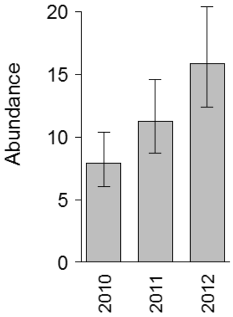

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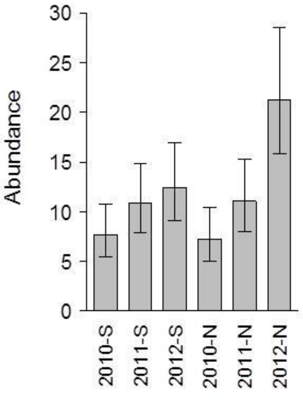

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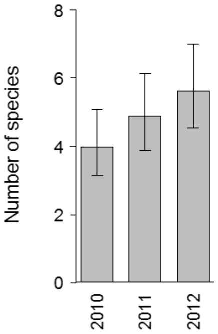
Habitat time – day – RICHNESS



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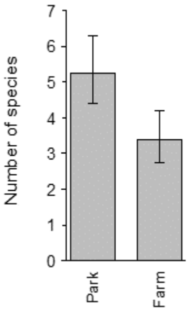

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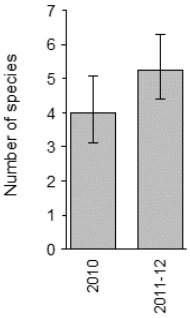

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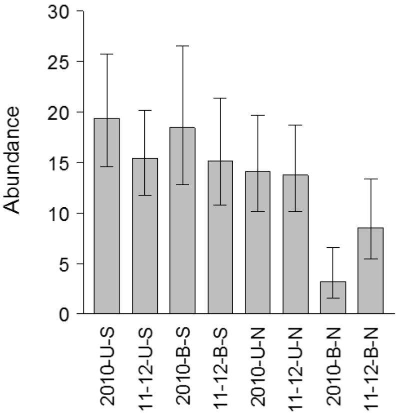
Habitat time – night – ABUNDANCE



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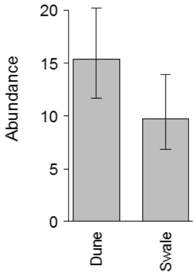

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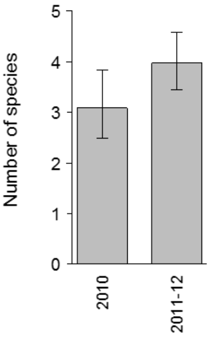
Habitat time – night – RICHNESS



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Paper IV: Does patch isolation affect small mammal occurrence and abundance after experimental fire in a fragmented landscape?

Running head: Do fire and fragmentation interactions affect small mammal abundance and occurrence in semi-arid mallee woodland?

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Abstract

Fire is a common ecological disturbance in vegetated ecosystems and prescribed fire is used as a tool in conservation management. However, knowledge of how to use fire as an effective

conservation management tool is limited in fragmented environments. This is because few researchers have investigated the synergistic effects of fire and fragmentation on species persistence and abundance.

We examined the combined effects of fire and habitat fragmentation in an agricultural landscape on the occurrence and abundance of small mammal species over three years. We hypothesised that patch population recovery after fire would differ between sites in a large habitat reserve and small habitat patches, and that the degree of isolation of habitat patches would influence population recovery after fire. We expected colonisation to be an important process in recovery from fire, and that mammals in remnants distant from large reserves of habitat would recover more slowly than mammals in remnants near large reserves, which would act as sources of recolonising individuals.

We obtained data on four mammal species over three years from 30 sites in mallee eucalypt woodland in South Australia. For this natural and manipulative experiment, we established paired transects in a conservation reserve and in vegetated dune top remnants in cropping land (i.e. an agricultural matrix). The paired transects in the agricultural matrix were established on two dune remnants, with one dune remnant acting as a control and one dune remnant experimentally burnt after the first year of surveys.

Fragmentation effects, including isolation effects, were much stronger than fire effects on mammal occurrence. We did not detect any interactive effects between fire and isolation on small mammals. Fragmentation strongly affected the native species, *Sminthopsis dolichura*, with significantly lower occurrence in more isolated remnants. Two native mammals, *S. dolichura* and *Notomys mitchellii*, had significantly lower occurrence in remnants than in the reserve. However, all three native mammals had significantly higher abundance in the second year of surveys. Conversely, the exotic and most common mammal, *Mus musculus*, was significantly more abundant in remnants compared with the reserve, and had significantly lower abundance in the second year of surveys. *Ningaui yvonneae* declined in abundance in burnt remnants compared with all unburnt sites in the year immediately after fire (i.e. the second year of surveys).

The lack of small mammal response to interactions between fire and fragmentation could be related to the relatively small effect of fire on the abundance of these mammals, such that there was no requirement for population recovery, or there was *in situ* recovery without the requirement for immigration.

These results provide weak evidence that fragmentation constrains population recovery from prescribed fire by these small mammal species. However, the impacts of fragmentation were strong and negative for native mammals to the extent that these species were relatively rare in remnants to begin with.

50 word summary for non-specialist reader. Burning long unburnt isolated remnants adjacent to large reserves with similar time since fire ages did not provide colonising opportunities for three small native mammal species. Fragmentation led to overall native mammal abundance declines in isolated remnants, but conversely, an overall increase in the abundance of a small exotic mammal.

Introduction

Land conversion for agriculture is leading to the fragmentation of remnant habitat around the world and is a recognised threat to biodiversity (Haddad *et al.*, 2015). Fire regimes are changing globally, due to climate (Brando *et al.*, 2014; Campbell *et al.*, 2009; Cochrane and Barber, 2009), land use change (Cochrane and Laurance, 2008; Pausas, 2006; Regan *et al.*, 2010) and direct fire management (Parsons and Gosper, 2011; Smucker *et al.*, 2005). In many landscapes, fire and fragmentation intersect (Sauvajot, 1995; Taillie *et al.*, 2015), resulting in species being subjected to loss and fragmentation of habitat in conjunction with novel fire regimes (Bowman *et al.*, 2012; Bradshaw, 2012; Hantson *et al.*, 2015). Yet many species survive and persist in fragmented and fire-prone ecosystems (Gibson *et al.*, 2013; Swan *et al.*, 2018). However, we know relatively little about how fire interacts with fragmentation and its influence on species persistence over time (Driscoll *et al.*, 2010a; Lazzari *et al.*, 2018 unpublished manuscript; Sauvajot, 1995). Fire history knowledge is important for understanding animal responses to fire and its suppression in order to apply more meaningful management where fire is used as a conservation tool (Chia *et al.,* 2016, Avitabile *et al.,* 2013). However, where fire history is unavailable, tools are needed to predict TSF (Lazzari *et al.,* 2015). This lack of knowledge can lead to poor biodiversity outcomes when fire is used to manage ecosystems and reduce risk to infrastructure by, for example, increasing fire frequency to reduce fuel loads (Driscoll *et al.*, 2010a; Moritz *et al.*, 2014). Improved knowledge of how animal populations respond to fire in highly fragmented landscapes is critical and will enable conservation managers to make informed decisions when they use fire as a management tool (Clarke, 2008).

Both modified fire regimes and fragmentation are identified as key threatening processes to biodiversity (CBD, 2001; Australian Government, 2014). Changes in fire frequency, intensity and spread can have negative consequences in both intact and fragmented landscapes. For example, fire suppression increased vegetation and limited the dispersal of a reptile species that led to a decrease in genetic diversity (Neuwald and Templeton, 2013). In addition, changes in the temporal and spatial scales of fire can threaten the persistence of animal and plant populations (Steinitz *et al.*, 2012). Equally, fragmentation on its own can threaten species by, for example, reducing habitat area and limiting resources (Haddad *et al.*, 2015).

Small mammals are found in fire-prone (VanTassel *et al.*, 2015) and fragmented habitats (Schweiger *et al.*, 2000). However, they are often considered at risk in these ecosystems (Gibson *et al.*, 2013) because of multiple disturbances. For example, changes in fire frequency and intensity can result from climate change (Puig-Gironès *et al.*, 2017), grazing (Schutz and Driscoll, 2008; Radford *et al.*, 2015) and fragmentation (Sandberg *et al.*, 2016). In turn, these changes in fire frequency and intensity can modify vegetation cover and reduce habitat resources (Chia *et al.*, 2016). Similarly, the creation of remnants via fragmentation affects habitat structural complexity. Changes to habitat complexity and cover can then influence predator activity, potentially increasing the risk of predation (Doherty *et al.*, 2015a). Understanding the influence of fire and fragmentation on small mammals is therefore important for planning effective fire management (Driscoll *et al.*, 2010a; Driscoll *et al.*, 2010b).

There is a growing body of knowledge of small mammal responses to fire severity (Chia *et al.*, 2016), fire history (Briani *et al.,* 2004; Swan *et al.*, 2018), fire frequency (Sollmann *et al.*, 2015), and the mechanisms underpinning these response (e.g. *in situ* survival vs recolonising from refuges after fire) (Banks *et al.*, 2017; Stawski *et al.*, 2015). Generally, small mammal abundance has been found to be higher in unburnt than burnt sites (Griffiths and Brook, 2014; Letnic and Dickman, 2005) and small mammals are unlikely to recolonise open habitats after wildfire (Pastro *et al.*, 2011). However, small mammals forage in recently burnt habitat (Doherty *et al.*, 2015a) and they can travel long distances to forage in burnt, heterogeneous environments; from > 400 m in one night (Letnic, 2001; Haythornthwaite and Dickman, 2006; Haythornthwaite, 2005), to > 10 km in a number of weeks (Dickman *et al.*, 1995). This movement may allow small mammals to not only exploit open environments (Spencer *et al.*, 2014) but also disperse to habitats that meet their requirements as a result of low-intensity and patchy prescribed fires (Pastro *et al.*, 2011). Recent research of fire effects in mammals consistently indicates that knowledge of how fire influences persistence and coexistence in species is dependent also on interactions between fire and other processes such as fragmentation (Banks *et al.*, 2017; Griffiths and Brook, 2014; Kelly *et al.*, 2017).

Metapopulation theory asserts that isolated populations or those restricted to their respective patch may be affected by stochastic events (Hanski, 1998; Hanski and Gilpin, 1991) such as fire. These stochastic events can lead to extinctions but can be balanced by recolonisation (van Nouhuys, 2016; Hanski, 1999) including recovery from source populations (Whelan *et al.*, 2002). To avoid regional extinctions in fragmented landscapes, species with reduced levels of dispersal between remnant populations must induce metapopulation dynamics that may counter local extinctions through recolonisation (Driscoll, 2007). The metapopulation concept can help to explain how small mammals respond to fire in patches and how nearby reserves may facilitate their post-fire recovery (Whelan *et al.*, 2002). However, the role that large reserves and small remnants have in mediating interacting fire and fragmentation disturbances is largely unknown because there are few studies exploring these interactions, particularly for small mammals (Lazzari *et al.*, 2018 unpublished manuscript). Investigating how mammals respond to fire in both reserves and remnants with different fire aged vegetation, will help to ascertain whether mammals are recovering and from where they are potentially recolonising.

Our study aims to investigate the interacting effects between fire and fragmentation on the occurrence and abundance of mammals in a semi-arid landscape. In this study location, fragmentation has resulted in habitat remaining in multiple small remnant patches and a large nearby reserve. In this paper we use the term 'fire and fragmentation' to describe our complex analysis that investigates two major study components containing three independent variables and their interactions. We tested the effects of fire and fragmentation by first examining if experimental fire in long-unburnt remnants interacts with isolation, and then if it interacts with source (reserve/park) populations.

Specifically, we quantified the individual and interactive effects of fire and fragmentation on small mammals, focusing on whether occurrence and abundance are affected by: (1) fire; (2) patch type; (3) isolation; and (4) the interaction between fire and isolation. We predicted that as distance of remnants to the reserve increases, the abundance of small mammals would decrease. In experimentally burnt remnants, we predicted that mammal persistence could be mediated by the nearby burnt and unburnt reserve. We focused our investigation on fire (recently burnt and long unburnt), and two fragmentation components – patch type (conservation reserve and remnant in farmland), and patch isolation (distance of remnants from large reserves).

Methods

Study area

Our study was conducted in Pinkawillinie Conservation Park (33°05'41.05"S, 135°59'57.75"E) and adjacent farmland in the northern Eyre Peninsula, South Australia (Fig. 1). The region is a 132,000 ha, semi-arid zone, with a highly variable mean annual rainfall of 318 mm (Bureau of Meteorology, 2018). Soils are shallow and/or nutrient deficient (Blackburn and Wright, 1989; Brandle, 2010). It is a sand dune system (Wasson, 1989) under which lies a calcrete limestone layer (Blackburn and Wright, 1989).

The vegetation in Pinkawillinie reserve and in the linear dune top remnants in farmland is dominated by mallee woodlands. These comprise low, multi-stemmed eucalypts (predominantly *Eucalyptus costata* and *E. socialis*) and are mostly highly flammable. The woodlands are also associated with a shrub layer of predominantly *Melaleuca uncinata* and *Callitris verrucosa* and a ground layer of hummock grass that is characterised by the spinifex grass *Triodia irritans* (Specht, 1972; Robinson and Heard, 1985). However, in the remnants, there is a decrease in *T. irritans*, as well as modifications to patch condition and vegetation structure, because of disturbances from cropping (e.g. weeds, pesticides, fertiliser) and livestock grazing (e.g. trampling) (Driscoll *et al.*, 2012; Moranz *et al.*, 2012; Yates *et al.*, 2000). Also, levels of disturbance in small remnants can be greater in an agricultural matrix because of the greater edge to area ratio (Saunders *et al,.* 1991). Although considerably larger than the small, isolated remnants, Pinkawillinie reserve has also been impacted by livestock, recreational 4WD use and mineral exploration disturbances (Scott, 2011).

Pinkawillinie's fire history has been recorded by South Australian government agencies for over 40 years with major fires recorded in 1972, 1986, and 2005 (South Australian

Government, 2011). Prescribed burns have occasionally been applied in the reserve in response to community concerns. However, these prescribed burns were not within the survey area.

Remnants in this area remain unfenced, and local land managers suppress fire. As such, they are grazed and used for shelter by native animals (e.g. kangaroos and emus) and livestock (e.g. domestic sheep and cattle, and wild goats). Remnants also are subject to the effects of pesticides and fertiliser application in the adjacent cropping paddock matrix. These disturbances can change the vegetation structure and condition of remnants (McIntyre *et al.*, 2003; McIntyre and Hobbs, 1999; Moranz *et al.*, 2012; Yates *et al.*, 2000). However, it is likely that these remnants continue to support the nine native and two non-native species of small mammals known to occur in the northern Eyre Peninsula (South Australian Government, 2010).

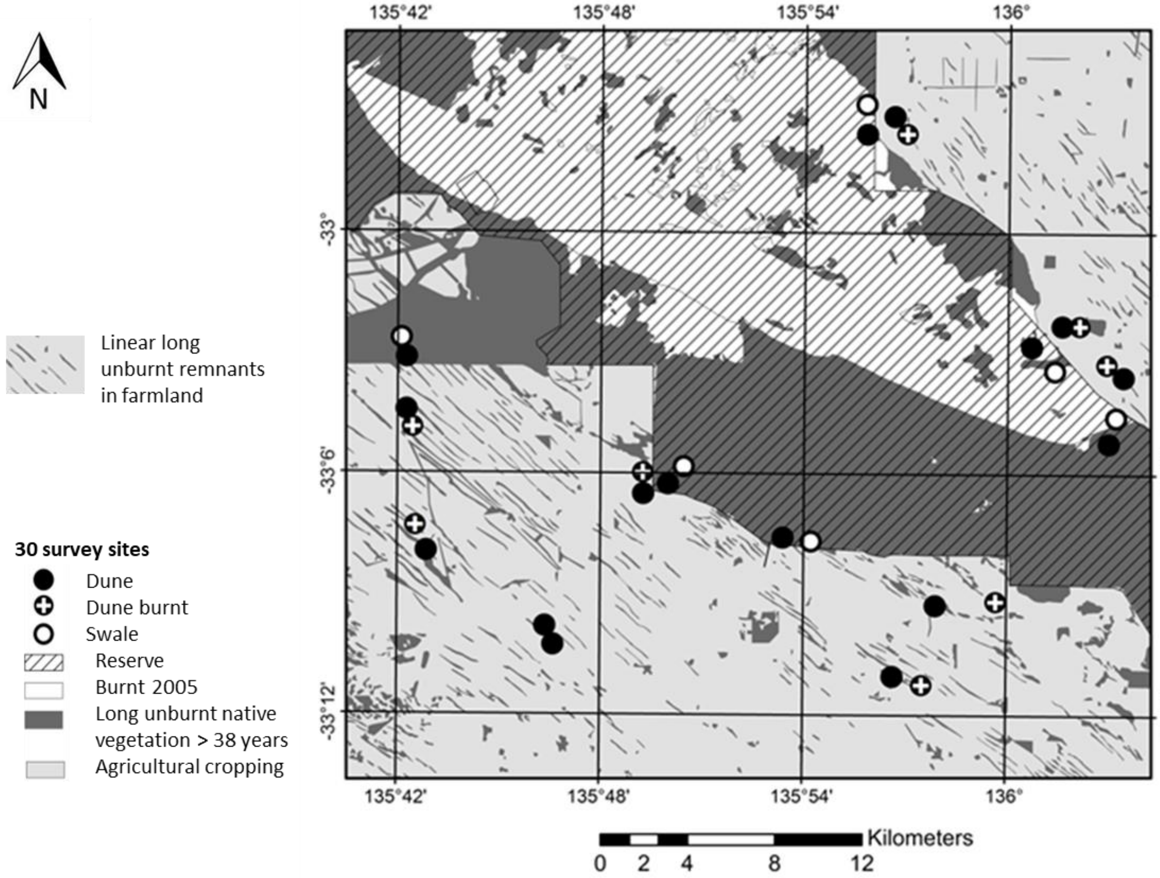


Figure 1. Study area of the Pinkawillinie Conservation Park reserve (diagonal hatching) and linear long unburnt remnants in farmland, Eyre Peninsula, South Australia. The 30 survey sites are shown as: 16 black circles indicating dunes; 6 white circles indicating swales; and 8 black circles with white crosses indicating dunes in farmland that were burnt after the first year of surveys. All dark shading is long unburnt vegetation. The white area in the reserve with diagonal hatching indicates recently burnt woodland (i.e. burnt in 2005). Mammals were surveyed along single transects in the 30 survey sites.

Due to risk of fire escaping, experimental burns were low-to-medium intensity and hence did not replicate wildfire intensity. However, experimental burns were undertaken during the hottest season because too much moisture in the vegetation type within the survey area could prevent fire spread.

Site selection

The study (Fig. 1 and Fig. 2) is a replicated natural and manipulative experiment with a paired design to contrast burnt and unburnt areas in a conservation reserve with remnant patches near to and far from the reserve. Sites were located in the burnt and unburnt areas in the conservation reserve and in remnant habitat patches in farmland (i.e. cropping paddocks). Transects in the reserve were randomly placed at the reserve boundary because we were testing whether similar species were found in recently burnt areas of both the reserve and remnants. Twelve of the 30 survey sites were in dune and swale habitat in the reserve. Six of these survey sites were established in recently burnt areas of the reserve that resulted from a wildfire that occurred four years prior to commencement of this study, and six sites established in long unburnt areas of the reserve. The remaining 18 sites were established in dune-top remnant patches (remnants did not occur in farmland swales). Eight of these remnant sites were experimentally burnt at the end of the first year of surveys, and 10 remained as unburnt controls. In the fire-prone ecosystem type of the study area, early successional vegetation is < 10 years TSF and we therefore assumed that the two fire age classes of the burnt areas of the study (i.e. 1 and 5 years TSF) supported equivalent species assemblages. Mammals were surveyed at 12 sites (six paired dunes and swales) within the reserve, and 18 sites (nine paired dunes) in the farmland. In total, 30 sites were surveyed (Fig. 2 and Table S1). Although we were only able to sample swales in the reserve, we did this to understand the pool of nearby species that could potentially use the matrix and colonise dunes in farmland.

Site selection was based on the time since the most recent fires that affected two large areas of the Pinkawillinie reserve. The southern side is long unburnt (> 38 years since the most recent fire) and the northern side is recently burnt (5 years since the most recent fire). We stratified for fragment type (reserve and remnants), isolation (patches close and far to the reserve), and time since fire (henceforth referred to as 'TSF') (recently burnt and long unburnt). There were six blocks – three in the southern region and three in the northern region (Fig. 2). The reserve had three paired transects in the long unburnt southern side and three in the recently burnt northern side (i.e. a total of six paired dune and swale sites). The farmland survey sites in the southern part of the study area had six paired transects (i.e. a total of six paired dune sites) close to and far from the long unburnt area of the reserve (i.e. a total of 12 dunes). The farmland in the northern region had three survey sites (i.e. a total of three paired dune sites) close to the recently burnt area of the reserve (i.e. a total of six dunes). After the first year of survey trapping, experimental burns were applied to one of the farmland transect pairs, while the other dune transect remained unburnt as the control. Dunes close to the reserve were between 0.13 km and 3 km, and dunes far from the reserve were between 5.6 km and 8.5 km (Table S1 and Table S2).

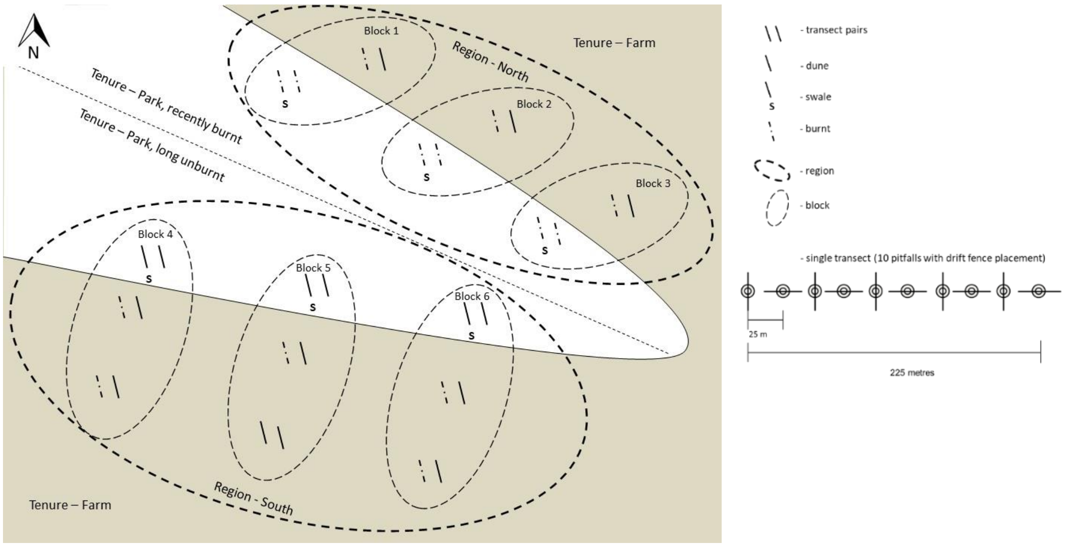


Figure 2. Schematic representation of the survey design of the project, which is a replicated natural and manipulative experiment. The Pinkawillinie Conservation Park is represented as the 'Park' tenure*. It has a recently burnt northern portion and a long unburnt southern portion. The 'Farm' tenure* is the cropping matrix. The Park and Farm tenures occur in both the northern and southern regions of the study. Each region contains three blocks, with each block containing paired transects: a dune and swale transect in the Park; and in the cropping matrix, either, two dune transects in the northern region, or four dune transects in the southern region. The 'single transect' in the key shows a top view of a transect with 10 m drift fences placed alternately – across and along the dune or swale over each pitfall trap.

* 'Tenure' is a simplified term used in our analysis to detect fragmentation responses.

Survey protocol

Mammals were surveyed at each site using a pitfall trap-line comprised of ten 20 litre plastic buckets, spaced 25 metres apart (30 sites x 10 pitfalls = 300 pitfalls). Buckets were buried so the top was flush with the ground. A 30 cm high x 10 m long, plastic drift fence intersected the pitfall. The fence was placed at alternate right angles for each of the 10 pitfalls (Fig. 2). Reptiles were primarily targeted in our surveys, so this method was based on combined pitfall survey design after Hobbs *et al.* (1994) and Morton *et al.* (1988). However, it is also an effective method commonly deployed in small mammal trapping (Chung-MacCoubrey *et al.*, 2009) including rodents (Dickman *et al.* 2011). Still, the use of buckets can lead to survey biases in the types of animals captured. For example, in reptile populations, fewer pygopods and snakes are captured in pitfalls, and some small mammals have higher capture rates using PVC pipes (Thompson *et al.*, 2005). A 15 cm long half PVC pipe was placed in the bottom of each bucket with a 15 x 20 cm wood block leaned against each piece of PVC to act as a shelter and refuge, in case of rain. After identification, animals were immediately released at the point of capture.

Vegetation data to determine habitat condition for unburnt (control) remnants, were collected in 2011 and 2012. Vegetation was surveyed in a 5 x 10 m plot adjacent to each of the 10 pitfall traps, along each 225 metre transect i.e. site. Percentage cover was averaged for each site. For this study we recorded cover for bare ground and weeds (combined), leaf litter, woody debris (including logs, branches and twigs), spinifex, and shrubs (< 0.5 m) (see Table S3).

Climate data

Rainfall and temperature data were extracted from the Australian Bureau of Meteorology (2018) for the Kimba weather station-018040 for the three survey years (2010, 2011 and 2012). We calculated averages for each annual survey period (approximately 56 days i.e. eight weeks). In order to interpret mammal species occurrence and abundance responses to climate data, we recorded and calculated rainfall and temperature in the survey period for each year (Table 1). Average rainfall in the second year was lower than both the first (2010) and the third (2012) year of each survey period. Average maximum and minimum temperatures for the first year were higher (31°C and 16°C) than in the second and third years in which average temperatures were lower (29°C and 15°C) (Table 1).

Table 1. Rainfall and temperature data for the survey period in 2010, 2011 and 2012. Average daily rainfall (mm) and average maximum and minimum temperatures (°C), are calculated by using data for each yearly survey period (approximately 56 days). Major rainfall events are recorded, and the terms 'early', 'mid' or 'late' are used to identify which part of the survey they occurred.

Survey years	**Year 1**	**Year 2**	**Year 3**
Rainfall (average daily mm)*	1.3 mm	1.0 mm	1.4 mm
- rainfall events (survey point)~	32 mm (mid)	43 mm (late)	38 mm (early)
Temperature (°C)*			
Max average	31°C	29°C	29°C
Min average	16°C	15°C	15°C

~ Rainfall events on the last day of the survey period are excluded from our table because rainfall at this point of the survey would not influence our mammal capture rates

* Numbers are rounded

Each site was surveyed for 28 nights over three consecutive summers (2010, 2011 and 2012). We alternated between northern and southern sites, trapping for 14 consecutive nights, four times each summer to manage for temperature gradients across the approximate nine-week field period. In total, we completed c. 25,200 pitfall trap nights. Baits were not used in our pitfall traps and hence we assume a low 'trap happiness' (e.g. recapture probability) because it is usually associated with a baiting response (Umetsu *et al.*, 2006). Recaptured individuals were not identified in the trapping process and have been included in our statistical analysis. We defined capture rate as the number of mammals caught using the same trapping method for the entire study and, as such, our capture rate is an indicator of abundance. It is possible that we captured some individuals multiple times within a survey year. However, previous small mammal studies indicate that recaptures are generally low (Thompson *et al.*, 2005) and this low occurrence of recaptures avoids the risk of bias, from double counting, in analyses (Fuentes-Montemayor *et al.*, 2009).

Statistical analysis

Mallee fires occur on a decadal timescale (Bradstock and Cohn, 2002). The Pinkawillinie Conservation Reserve experienced major fires in 1972 (23 December), 1986 (20 November), and 2005 (27 December) (South Australian Government, 2019). For our survey, the 2005 reserve wildfire and the prescribed fires in 2010 are categorised as early successional habitat types. However, fire intensities differed (high and low, respectively) and the time of year they occurred also differed (December and March, respectively). These differences can affect animal abundances because, for example, season or intensity may affect active breeding individuals, juveniles emerging from burrows, and food availability (Friend, 1993; Lindenmayer *et al.,* 2008). Also, the long unburnt vegetation in the reserve differed to that in the remnants. As such, some of these factors and other niche requirements by small mammals including rainfall and breeding competition may obscure our study findings.

We examined the effects of our study design on the relative abundance of mammals by fitting generalised linear mixed models (GLMMs) (Bolker *et al.*, 2009) for each species. We used random effects for 'site' to account for repeated measures, and 'block' to account for the key spatial structure in the data. We also used an observation-level random effect when there was evidence of overdispersion in binomial or Poisson models. Overdispersion was assessed using a Pearson Chi squared test of Pearson residuals divided by residual degrees of freedom (Maindonald and Braun, 2010).

Fixed effects in the models included combinations of variables that delimited our study design (Fig. 1) including certain two and three-way interactions. The analysis used the full data set and each test was applied to the relevant part of the analysis i.e. we fit each variable to test the response to the treatments (fire, fragmentation, and their interactions). Main effects were: 'Region' (Southern, Northern); 'Tenure' (Park, Farm); 'Distance' (Close, Far – relates to fragment isolation from the reserve); 'Burn' (experimentally burnt and unburnt); 'Y1' (2010, 2011-2012 – the survey year before, and the two years after, experimental burns were undertaken); 'Year' (2010, 2011, 2012); and 'Soil' (delimiting swale from dune habitat within the reserve) (see Table S4a for survey site information, and Table S4b for variable attributes, categories and descriptions). 'Y1' and 'Year' were examined to explore if the biggest effects were due to being burnt or not, rather than TSF (0 or 1 year for the experimentally burnt sites).

The 'Tenure:Region' interaction allowed us to identify any effects attributable to TSF in the reserve. Other interactions were to assess the effects of the experimental burn treatment over time, particularly 'Y1:Burn' (whether burnt patches showed a different response to other sites over time), 'Y1:Region:Burn' (whether burnt patches in the northern region (adjacent to recently burnt habitat) showed a different response over time compared with the southern region (adjacent to long unburnt habitat), and 'Y1:Far:Burn' (whether burnt sites in the isolated patches showed a different response over time compared with other sites). Appropriate combinations of two-way interactions were included with all three-way interactions. The set of models with 'Y1' were repeated with 'Year'; and 'Y1' and 'Year' were not used in the same models. We ranked the 143 models (Table S5) using Akaike's Information Criterion for small samples (AICc) (Burnham and Anderson, 2002), and a set of best models designated as those with ΔAICc ≤ 2.0. We plotted results for variables with $p \leq 0.05$, taking the estimate from the highest ranked model in which that variable occurred.

To avoid over-fitting, we limited the models fitted to each response to those where the number of parameters in the model was less than one third of the number of non-zero response values. We assumed Gaussian distribution of errors for total mammal abundance, which were approximately normally distributed. Species responses with five or fewer values > 2 or with < 10 unique values were converted to presence/absence data and analysed assuming a binomial distribution of errors with a logit link function. All other responses were analysed assuming Poisson distribution of errors with a log-link function. Analyses were completed in R (R Core Team, 2012) using libraries *lme4* (glmer) (Bates *et al.*, 2012), *AICcmodavg* (predictSE) (Mazerolle, 2012), *bbmle* (AICctab) (Bolker and R Development Core Team, 2014) and *car* (Anova) (Fox and Weisberg, 2011).

Results

Summary statistics

A total mammal abundance of 2951 individuals was recorded for four species in two families. These were: the Dasyuridae family, mallee ningaui, (*Ningaui yvonneae*, n = 59) and the little long-tailed dunnart (*Sminthopsis dolichura*, n = 123); and the Muridae family, Mitchell's hopping mouse (*Notomys mitchellii*, n = 41) and the house mouse (*Mus musculus*, n = 2728) (a non-native species) (Table S6). Only two (n = 2) western pygmy possums (*Cercartetus concinnus*) were recorded in the reserve (one in the second year in the long-burnt area and the other in the third year in the recently burnt area) and were excluded from our analysis. In 2010, 2011 and 2012 we captured, respectively, 1325, 396 and 1230 mammals (Table S7).

Small mammals did not exhibit a significant response to interactions between fire and fragmentation. However, three species showed a strong response to fragmentation. Mammals did not show a strong response to fire (Table 3). 'Year' significantly influenced responses of the three native species (Table 3), but only influenced the exotic species, *Mus musculus*, when it interacted with 'Region' (southern and northern) (Table 3). See Table S8 for a summary of fire and fragmentation interaction treatments.

Table 3. Best models testing the effects of fire and fragmentation on four small mammal species: three native, *Sminthopsis dolichura*, *Notomys mitchellii* and *Ningaui yvonneae*, and one exotic species, *Mus musculus*. Models are ranked by AICc (models with ΔAICc ≤ 2.0 are shown), and coefficients are provided for each explanatory variable in each model. Asterisks indicate significance level of predictors. Best models are shaded. Results for predictions are above the broken horizontal line, while results for their interactions are below the line.

Species	*Sminthopsis_dolichura*							*Notomys_mitchellii*			*Mus_musculus*	*Ningaui_yvonneae*					
Model code	mysf	mytf	myf	mysrf	mytrf	mytsf	myrf	mytr	myr	myt	mytrbbxryxbyxryxbxr	mybyxb	my	myf	myfbyxb	myrbyxb	myr
AICc	97.5	97.6	98.2	98.5	98.6	99.1	99.2	79.8	81.5	81.6	718.2	100.1	100.2	101.4	101.5	101.9	101.9
deltaaicc	0	0.05	0.71	1.02	1.07	1.58	1.74	0	1.72	1.73	0	0	0.16	1.36	1.39	1.78	1.83
Intercept (± s.e)	0.97 (± 0.49)*	1.79 (± 0.63)*	1.21 (± 0.47)*	0.64 (± 0.55)	1.49 (± 0.66)*	1.41 (± 0.72)*	0.91 (± 0.53)**	-1.75 (± 0.01)*	-2.77 (± 0.95)*	-1.04 (± 0.69)	3.09 (± 0.14)*	-3.10 (± 1.12)*	-2.30 (± 0.75)*	-2.15 (± 0.77)*	-2.96 (± 1.13)*	-2.79 (± 1.11)*	-2.03 (± 0.80)*
2012	1.070 (0.769)*	1.075 (0.771)	1.050 (0.761)	1.082 (0.772)	1.088 (0.774)	1.079 (0.772)	1.061 (0.765)	1.342 (0.010)*	1.363 (0.757)**	1.333 (0.740)**	-1.012 (0.192)*	3.348 (0.1.194)*	1.942 (0.777)*	1.962 (0.784)*	3.388 (1.209)*	3.394 (1.217)*	1.947 (0.779)*
2013	-0.957 (0.636)*	-0.961 (0.638)	-0.911 (0.616)	-0.982 (0.642)	-0.984 (0.644)	-0.974 (0.646)	-0.932 (0.624)	-1.972 (0.010)*	-1.977 (1.201)**	-1.959 (1.196)	-0.298 (0.178)**	0.984 (1.037)	0.299 (0.777)*	0.302 (0.780)	0.993 (1.042)	0.998 (1.045)	0.300 (0.778)
Tenure (farm=1)	na	-1.021 (0.607)**	na	na	-1.044 (0.612)**	-0.633 (0.711)	na	-1.401 (0.010)*	na	-1.605 (0.780)*	0.457 (0.121)*	na	na	na	na	na	na
Region (N=1)	na	na	na	0.700 (0.602)	0.701 (0.602)	na	0.667 (0.587)	1.404 (0.010)*	1.706 (0.847)*	na	0.583 (0.196)*	na	na	na	na	-0.815 (0.978)	-0.634 (0.803)
Isolation (far=1)	-3.339 (0.887)*	-3.467 (0.907)*	-3.577 (0.878)*	-3.022 (0.923)*	-2.824 (0.945)*	-3.151 (0.909)*	-3.278 (0.910)*	na	na	na	na	na	na	-0.967 (0.957)	-1.141 (1.151)	na	na
Fire (burnt=1)	na	na	na	na	na	na	na	na	na	na	0.005 (0.243)	1.552 (1.396)	na	na	1.623 (1.400)	1.597 (1.407)	na
Soil (dune=1)	1.328 (0.840)	na	na	1.355 (0.846)	na	0.896 (0.978)	na	na	na	na	na	na	na	na	na	na	na
burn:region	na	na	na	na	na	na	na	na	na	na	0.0138 (0.377)	na	na	na	na	na	na
yearY2:burn	na	na	na	na	na	na	na	na	na	na	na	-4.400 (1.974)**	na	na	-4.467 (2.004)*	-4.432 (1.976)*	na
yearY3:burn	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
yearY2:reg1	na	na	na	na	na	na	na	na	na	na	-1.432 (0.323)*	na	na	na	na	na	na
yearY3:reg1	na	na	na	na	na	na	na	na	na	na	-0.737 (0.277)*	na	na	na	na	na	na
yearY2:reg1:burn	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
yearY3:reg1:burn	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na

* p ≤ 0.05 ** p > 0.05 ≤ 0.1

Fire - burn = burnt=1, unburnt=0

Isolation / distance - far = far=1, close=0

Tenure - ten1 = farm=1, park=0

2012, 2013 - Y1 = 2010 burn after the first year of surveys, 2011-2012 combined

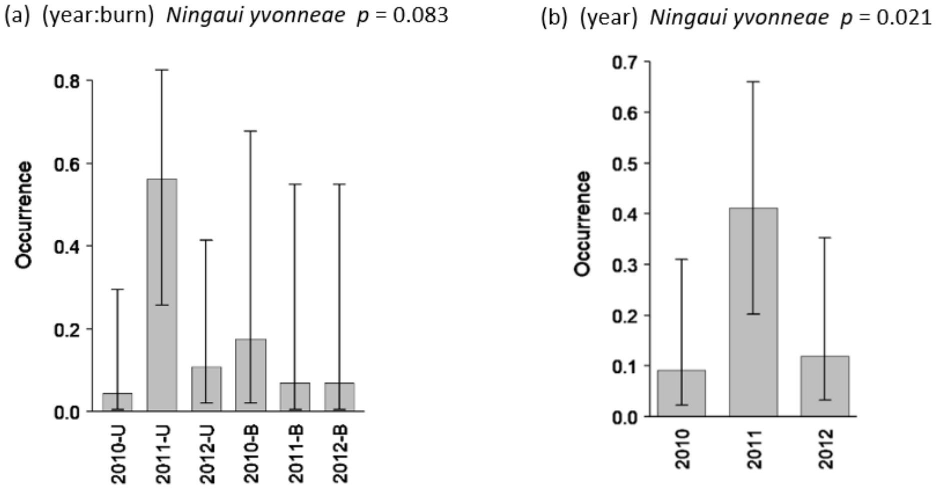
Year - 2010, 2011, 2012

Region - reg1 = north=1, south=0

Soil - dune=1, swale=0

Ningaui yvonneae

Ningaui yvonneae exhibited no response to the main effects of fire or fragmentation ('Tenure' or 'Isolation') but a negative non-significant response to interactions between year and experimentally burnt patches compared with all other sites i.e. unburnt (Fig. 3a). In unburnt remnants, occurrence increased in the second year but in the burnt remnants, this peak occurrence was not observed. Ignoring the interaction, occurrence of *N. yvonneae* was highest in the second year of surveys (Fig. 3b).


(a) (year:burn) *Ningaui yvonneae* $p = 0.083$

(b) (year) *Ningaui yvonneae* $p = 0.021$

Figure 3. Predicted occurrence of *Ningaui yvonneae* (a) through time in burnt and unburnt remnants, and (b) through time across all sites. (Models *mybyxb* and *my* in Table 3.) Error bars indicate 95% confidence intervals.

Sminthopsis dolichura

We observed lower occurrence of *Sminthopsis dolichura* (Fig. 4a) in farm remnants than in the reserve, and significantly lower occurrence in isolated patches (i.e. far from the reserve) than in patches close to the reserve (Fig. 4b). Occurrence of *S. dolichura* was highest in the second year of surveys (Fig. 4c). We detected no significant responses to experimental fire, either as a main effect or through interactions.

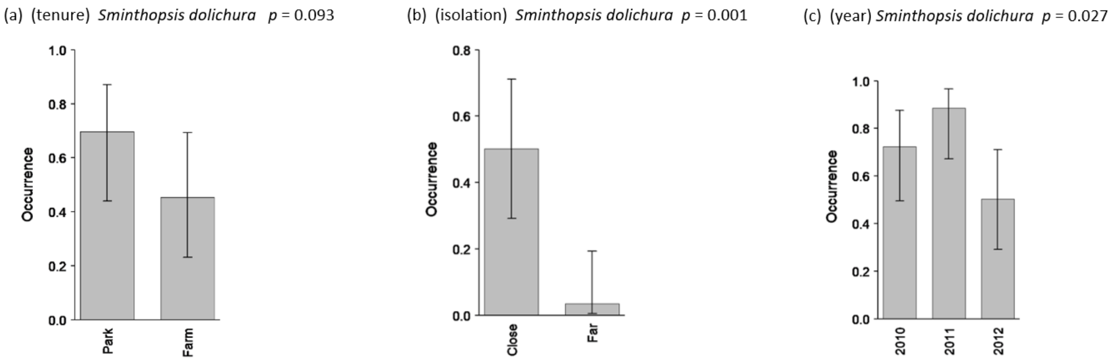


Figure 4. Predicted occurrence of *Sminthopsis dolichura* in (a) reserve and remnants (b) close to and far from the reserve, and (c) through time. (Models *mytf* and *mysf* in Table 3.) Error bars indicate 95% confidence intervals.

Notomys mitchellii

We observed lower abundance for *Notomys mitchellii* in farm remnants than were recorded in the reserve (Fig. 5a) and significantly higher abundance in the northern region compared to the southern region that contains a large long unburnt area of reserve (Fig. 5b). Abundance of *N. mitchellii* was highest in the second year of surveys (Fig. 5c). We detected no significant responses to experimental fire, either as a main effect or through interactions.

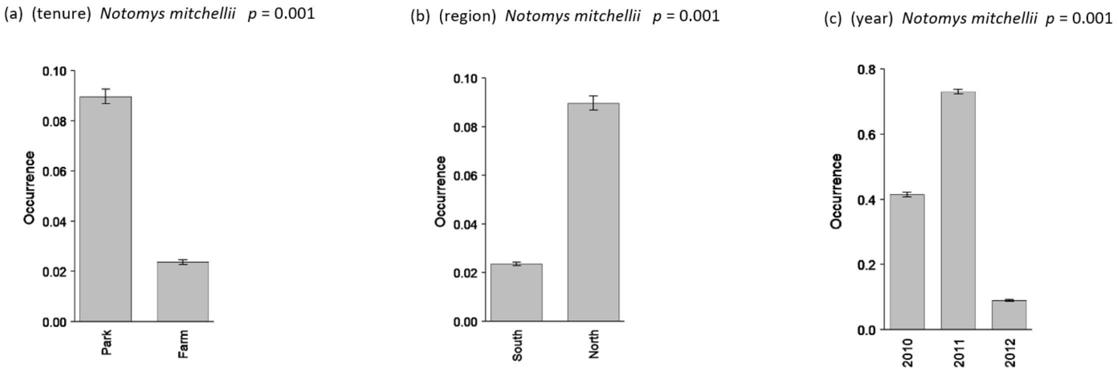


Figure 5. Predicted occurrence of *Notomys mitchellii* in (a) reserves and remnants, (b) in the southern and northern regions of our study, and (c) through time. (Model *mytr* in Table 3.) Error bars indicate 95% confidence intervals.

Mus musculus

In comparison to two native species, abundance of *Mus musculus* was highest in farm remnants compared with the reserve (Fig. 6a). We also observed, in contrast to the three native species, lower abundance of *M. musculus* in the second year of surveys in both northern and southern regions (Fig. 6b). In the southern region, abundance recovered to exceed abundance in the first year of surveys, and in the northern region abundance remained lower than the first year of surveys. The best model contained a non-significant but positive effect of fire.

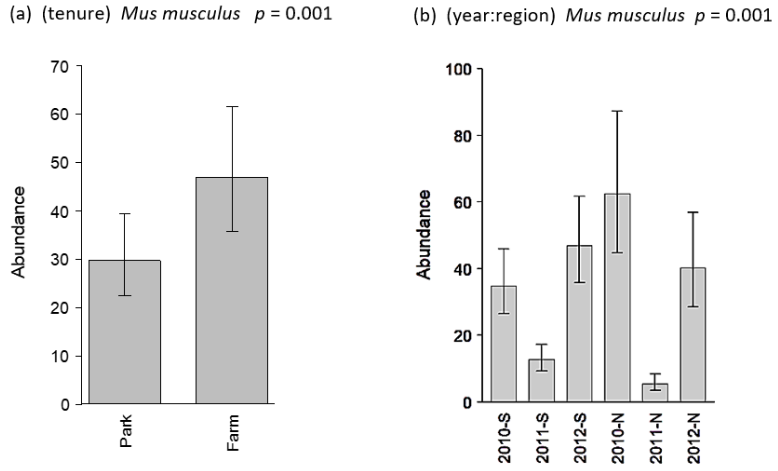


Figure 6. Predicted abundance of *Mus musculus* in (a) reserves and remnants and (b) northern and southern regions through time. (Model *mytrbbxryxbyxryxbxr* in Table 3.) Error bars indicate 95% confidence intervals.

Vegetation data

For our investigation into whether vegetation condition and structure had an influence on small mammal responses, our vegetation data shows that habitat condition for unburnt (control) remnants, that were both 'far' and 'close' to the reserve, had similar vegetation condition (Table 2). Hummock grasses (*Triodia* spp.) are important to small native mammals and therefore we calculated the proportion of percentage cover of spinifex in each of the 'far' and 'close' sites. The highest proportion of spinifex was recorded in the 'far' site in Block 4.

Table 2. Similar vegetation condition in 'far' and 'close' sites. Unburnt vegetation data (mean percentage cover) in the southern region for each block, in each study year (2011 and 2012) in 'far' and 'close' sites. Mean percentage cover for bare ground and weeds, leaf litter, woody debris (including logs, branches and twigs), spinifex, and shrubs (< 0.5 m). (See Table S3 for context and detail.)

Year	Isolation	Block 4 unburnt (spinifex ~) (mean % cover*)	Block 5 unburnt (spinifex ~) (mean % cover*)	Block 6 unburnt (spinifex ~) (mean % cover*)
2011	Far	20 (5)	20 (1)	18 (1)
	Close	22 (1)	21 (2)	15 (2)
2012	Far	19 (4)	21 (1)	21 (1)
	Close	19 (1)	20 (2)	21 (2)

~ Proportion of spinifex that is included in the total

* Numbers were rounded

Discussion

We investigated whether interactions between fire and fragmentation influenced the occurrence and abundance of small mammals in a semi-arid agricultural landscape. There are four key findings: (i) we detected a fire effect on one native mammal (*Ningaui yvonneae*), where occurrence did not increase in burnt fragments, compared to unburnt where occurrence increased in the second year after nearby fragments were burnt; (ii) we observed temporal effects on all native species with an inverse response in the single exotic species (*Mus musculus*), and had temporal effects with a burn interaction (near significant) on one native mammal (*N. yvonneae*); (iii) fragmentation affected occurrence in two native mammals (*Sminthopsis dolichura* and *Notomys mitchellii*), with these two species less common in remnants, while the exotic mammal (*M. musculus*) was more common in remnants; and (iv) patch isolation influenced the occurrence of one native mammal (*S. dolichura*) with occurrence lower in more isolated sites compared to reserve sites.

Fire did not cause a decline in *N. yvonneae* but was associated with a lower degree of increase in abundance in the second year of the surveys compared to all the unburnt sites. Fire may have led to lower occurrence of *N. yvonneae* in burnt remnants relative to unburnt sites in this year because it is spinifex-dependent (Bos *et al.*, 2002) and much of these hummock grasses, and the associated mallee habitat structure, were burnt in the prescribed experimental fire. Previous research has shown that mammals move out of less hospitable burnt sites into areas that are unburnt and have increased structural complexity such as habitat refugia (Berry *et al.*, 2016; Pereoglou *et al.*, 2011). This could also be the case for *N. yvonneae* potentially because burnt remnants do not provide sufficient habitat or structural complexity, in turn increasing predation risk (Doherty *et al.*, 2015a).

Notomys mitchellii had a preference for recently burnt areas of the reserve and a preference for the reserve rather than farm remnants. However, *N. mitchellii* has not shown a significant response to TSF (Doherty *et al.*, 2015b) and has been associated with early successional vegetation after rainfall (Avitabile, 2014). The absence of an interaction between fire and fragmentation in our findings could suggest that *N. mitchellii* has its habitat needs met within both the burnt and unburnt areas of the reserve. This is supported by Doherty *et al.* (2015a) who found that *N. mitchellii* had equal foraging preferences in both long unburnt and in recently burnt vegetation, but would also modify its foraging location – a lower abundance in open areas – with a perceived greater predation risk.

We observed that two native species, *S. dolichura* and *N. mitchellii*, had overall preferences for reserve sites, even though native mammal species can cover significant distances in modified agricultural land searching for resources (e.g. food, shelter) (Letnic, 2001). However, *S. dolichura* had a significantly higher occurrence in remnant patches close to the reserve suggesting that they may be moving between the reserve and remnants. The significantly higher occurrence of *N. mitchellii* in the northern region, where there is a greater proportion of recently burnt vegetation, seems to support a preference for reserve sites. This aligns with findings that foraging behaviour by *N. mitchellii* in fire-affected, more open habitat was unaffected by a perceived predation risk (Doherty *et al.*, 2015a).

In contrast to *S. dolichura* and *N. mitchellii*, the single exotic mammal we recorded, *M. musculus*, preferred farm sites. Introduced species are habitat and diet generalists and can be less territorial than native species (Marvier *et al.*, 2004). Dispersal in *M. musculus* mostly arises from social interactions, such as juveniles being made to disperse through adult aggression (Pocock *et al.*, 2005). This may encourage dispersal of introduced mammals into remnants from the cropping matrix. Alternatively, the preference for farm remnants by *M. musculus* may be driven by resource pulses, or as a consequence of location or proximity to food sources in cropping paddocks (Fitzgibbon, 1997).

Differences between species occurrence in remnants and the reserve may also be responding to predator numbers because baiting occurs regularly in the reserve but only in the cropping matrix when individual landholders determine a need. Baiting and culling for fox, dingo and cat control occurs in the reserve throughout the year (Lindsay Brown, Ranger in Charge, Pinkawillinie Conservation Park, pers. comm.). As far as we are aware, no studies have been undertaken to investigate the role of predators on mammal species in fire-affected fragmented landscapes.

The native species *S. dolichura*, showed a strong response to isolation with significantly lower abundance in remnant patches that are far from the nearby reserve. The species is known to occur in hummock grassland (*Triodia* spp.) as well as other arid and semi-arid vegetation complexes (Friend *et al.*, 1997). Larger taller hummocks are preferred for nesting (Moseby *et al.*, 2016) while smaller, denser and more intact hummocks provide a cooler micro-habitat (Churchill, 2001) and greater protection (McLean, 2015). The vegetation data collected during our study (Table 2) indicates that the remnant sites that were far from and close to the reserve had similar vegetation condition (Table 2 and Table S3). However, while condition was broadly similar, the proportion of spinifex was higher in the sites far from the reserve suggesting that isolation was a stronger driver of *S. dolichura* abundance than spinifex cover (i.e. habitat condition). This suggests spillover could be occurring between the remnants and the reserve

(Blitzer *et al.*, 2012), as well as between remnants. This encompasses both mainland-island metapopulation and source-sink dynamics where small populations depend on immigration from larger and higher quality habitat (Harrison, 1991; Pulliam, 1988). This is especially the case for *S. dolichura* that is a good disperser, having a home range of up to 7.5 ha (Woinarski and Burbidge, 2016) and can move up to two kilometres in two hours (Pearson and Churchill, 2008). Therefore, it would not be constrained by distance in our study (see Table S2) except that the cropping matrix provides a barrier that might only be crossed when annual crops are maturing and provide protective cover from predators.

The agricultural matrix in our semi-arid study area is characterised by the intermittent pulses in resources following crop harvests (e.g. residual grain) and rain (e.g. increased primary productivity) (Dickman *et al.*, 1999) that are related to mammal irruptions. Further, mammalian (cat and fox) and avian (owl) predation of small mammals is common and can lead to booms in predator populations (Krebs *et al.*, 2018; Paltridge and Southgate, 2001). The sharp increases in native mammal abundance in the second year of surveys, followed by declines, could be in response to climatic events. Small mammals are known to respond to climate e.g. rainfall events (Southgate and Masters, 1996), and some species also respond to particular fire regimes (e.g. combination of season, frequency and intensity) rather than fire *per se* (Gill, 1979). However, the exceptional rain events during each annual study survey period did not correlate with any changes, either immediate or delayed, in mammal species occurrence. That said, the average rainfall during the study survey period in the second year of trapping was much lower than in either the first or the third year. Small native mammals in semi-arid and arid habitats, can survive low rainfall conditions that can be less favourable to exotic rodents (Greenville *et al.*, 2012). Notwithstanding adaptations of native species to low rainfall, declines in abundance can still occur if rainfall falls below a threshold limiting their survival, irrespective of fire (Pastro *et al.*, 2011).

Conversely, *M. musculus* had sharp declines in abundance in the second year of surveys in both the recently burnt northern region and long unburnt southern region. Similar to the native species, *M. musculus* also responds to climatic events (Tann *et al.*, 1991) and fire (Seebeck and Menkhorst, 2000). As such, their decline in abundance in the second year may have been in response to lower average daily rainfall while native species remained unaffected (Lock and Wilson, 2017). Also, exceptional rainfall events occurred at the end of the trapping period in 2012. Native mammals could therefore be responding to less direct competition with *M. musculus* in the second year.

Management considerations and future research

To understand how small mammals respond to fire-fragmentation interactions, it is important to recognise that there were limited responses of mammals to fire in our fragmented study landscape. Although our analysis is complex, it highlights that small native mammals were mostly unaffected by an experimental fire event in fragments, but this may be because there were fewer mammals in remnants than the reserve. However, as one native mammal did not show an increase after fire, unlike increases in unburnt sites, and the two other native mammals preferred the reserve and declined with increasing isolation, this suggests that the use of fire should be avoided in remnant patches until further research indicates clear conservation benefits. However, consideration of whether long-term fire exclusion has ecological impacts is also warranted. From the temporal results, we inferred that native mammal occurrence may be affected by lower rainfall because occurrence peaked when rainfall was at its lowest, and conversely the exotic mammal abundance was suppressed. This relationship between low average rainfall and the inverse responses in native and exotic species leads us to recommend that if land managers are considering prescribed fire in the reserve, then burning should only occur when average rainfall is low which is when native mammal occurrence is likely to be higher than the exotic mammal. However, it would be useful to know what is driving these small native mammal responses during low rainfall to be able to make better management decisions to help maximise small mammal persistence in reserves and if this is influencing persistence in remnants.

In our study area, clearing for agriculture ceased several decades ago and consequently the fire regime modified, but it is clear from our findings that small mammals are persisting in isolated remnants. However, fragmented landscapes may have already suffered extinctions of species unable to contend with modified fire regimes and thus, for species with rapid generation times, the remaining species are now adapted to the fire and fragmentation interactions that presently characterise these landscapes (Cardillo, 2003; Jablonski, 2004). This could explain why some species in remnants do not apparently respond to the effects of either fire or fragmentation. It could also be that surviving populations in long unburnt areas might continue to persist until a habitat is burnt or senesces to a point that mimics a burnt landscape, notwithstanding any demographic or inbreeding effects (Cote *et al.*, 2017) or increased extinction sensitivity of specialist species (Henle *et al.*, 2004).

Nevertheless, fire in long-unburnt remnants affected the persistence of one small native mammal (*N. yvonneae*), and fragmentation affected the other native mammals (*S. dolichura* and *N. mitchellii*) showing that they had a preference for reserve sites compared with farm sites, and native mammals having an inverse response to fragmentation with the exotic mammal. These responses raise several questions with respect to understanding the role of reserves and specifically the role of post-fire successional stages as potential source populations for colonising nearby remnants. As such, there is a gap in knowledge for how species are using remnants and genetic research between species in reserve and off-reserve (nearby remnants and agricultural matrix) in burnt and unburnt sites would be useful to determine whether fire management may be encouraging species spillover from reserves to remnants.

Our study has increased understanding of synergistic fire and fragmentation relationships that is important for managing landscapes effectively to maximise conservation outcomes. However, the degree of these effects, either positive or negative, on small native mammals or other terrestrial animal species, living in small and long unburnt patches, is still unknown. Therefore, to avoid affecting the species persisting in these patches, our results indicate that prescribed fire in small habitat remnants should be avoided or used with caution (UN, 1992), especially because remnants contain a diversity of co-occurring taxa (Driscoll *et al.*, 2012) and information of species responses in fire and fragmentation research is limited (Lazzari *et al.*, 2018 unpublished manuscript). Our results also highlight that large reserves remain important for the persistence of small native mammal assemblages and may support or influence source-sink processes in remnants (Villemey *et al.*, 2015). That said, we also acknowledge that future fire-fragmentation research should consider the influence of other disturbances (e.g. grazing) on small mammal occurrence and persistence, as well as other important drivers (e.g. predators), to maximise the effectiveness of conservation actions in semi-arid agricultural landscapes.

Author contributions

JL and DAD conceptualised the study and the study design. JL acquired the data and JL and DAD led analyses; JL led manuscript preparation with substantial critical and editorial input from all authors. JL, CFS, SCB and DAD declare no conflicts of interest. In prep for *Biological Conservation*.

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Supporting Information

Table S1. Study site and location information for data collected from 30 transects. The information includes: location*, region, distance, treatment, dune_swale, block number, latitude and longitude.

Location*	Region	Distance of remnant from the Park (reserve)	Treatment - Park = recent_burn (historical burn) - Remnant = burn OR control	Dune or swale	Block (replicate number)	Latitude	Longitude
CB1	north	close	burn	D	1	-32.95910935	135.9496707
CB2	north	close	burn	D	2	-33.03845244	136.0349894
CB3	north	close	burn	D	3	-33.05690361	136.0359296
CB4	south	close	burn	D	4	-33.08129017	135.707359
CB5	south	close	burn	D	5	-33.1045409	135.8255985
CB6	south	close	burn	D	6	-33.1528811	135.9946178
CU1	north	close	control	D	1	-32.95186797	135.9435893
CU2	north	close	control	D	2	-33.03853878	136.0265788
CU3	north	close	control	D	3	-33.05966277	136.0568958
CU4	south	close	control	D	4	-33.07608065	135.7058498
CU5	south	close	control	D	5	-33.1059839	135.8252969
CU6	south	close	control	D	6	-33.1546337	135.9649633
FB4	south	far	burn	D	4	-33.126037	135.71273
FB5	south	far	control	D	5	-33.17128	135.776916
FB6	south	far	burn	D	6	-33.1875719	135.9584137
FU4	south	far	control	D	4	-33.130628	135.711961
FU5	south	far	control	D	5	-33.166031	135.777068
FU6	south	far	control	D	6	-33.1841212	135.9440336
PD1	north	park	recent_burn	D	1	-32.95908705	135.9332203
PD2	north	park	recent_burn	D	2	-33.0427299	136.0171098
PD3	north	park	recent_burn	D	3	-33.0753982	136.0560399
PD4	south	park	long_unburnt	D	4	-33.049401	135.703465
PD5	south	park	long_unburnt	D	5	-33.107765	135.830549
PD6	south	park	long_unburnt	D	6	-33.129984	135.894447
PS1	north	park	recent_burn	S	1	-32.95770722	135.9332093
PS2	north	park	recent_burn	S	2	-33.04297339	136.0176318
PS3	north	park	recent_burn	S	3	-33.0741653	136.0560673
PS4	south	park	long_unburnt	S	4	-33.047778	135.703106
PS5	south	park	long_unburnt	S	5	-33.10725	135.831099
PS6	south	park	long_unburnt	S	6	-33.129949	135.895748

* Each transect of 10 pitfall traps was allocated a Latitude_Longitude from the first pitfall trap.

Table S2. Distances of isolated dunes from the reserve (km)

Distance (km)	Close-Burnt	Close-Unburnt	Far-Burnt	Far-Unburnt	Close (min. distance)	Far (max. distance)
Min	0.13	0.16	6.09	5.58	0.13	5.58
Max	2.88	2.96	7.69	8.47	2.96	8.47
Range	2.75	2.8	1.6	2.89	2.83	2.89
No. dunes	*6*	*6*	*2*	*4*	*12*	*6*

Table S3. Vegetation data in unburnt remnants for years two, 2011 and three, 2012 in the southern region for each block (4, 5 and 6) in 'far' and 'close' sites to the reserve. Mean percentage cover for bare ground and weeds, leaf litter, woody debris (including logs, branches and twigs), spinifex, and shrubs (< 0.5 m). This data were used to produce Table 2 that shows the similar habitat condition of both the 'far' and 'close' sites.

site_year *	**otherM**	**leaflittM**	**wdM**	**spinM**	**shrubM**	**totals**
CU4_2011	16.8	0.94	1.58	1.22	1.06	21.6
CU4_2012	14	1.32	1.12	1.02	1.16	18.62
CU5_2011	15.3	0.9	0.78	2.36	0.88	20.22
CU5_2012	15.3	1.84	0.42	1.82	0.64	20.02
CU6_2011	9.4	0.84	0.82	2.42	1.62	15.1
CU6_2012	15.5	1.06	0.68	2.48	1	20.72
FB5_2011~	18.7	0.64	0.48	0	0.8	20.62
FB5_2012~	17.7	0.46	0.4	0	1.6	20.16
FU4_2011	10.3	2.12	1.26	5.36	0.44	19.48
FU4_2012	12.7	1.6	0.7	3.56	0.12	18.68
FU5_2011	14.2	3.14	1.42	1.2	0.24	20.2
FU5_2012	16.1	2.68	1	1.08	0.12	20.98
FU6_2011	15.5	0.86	0.7	0.58	0.16	17.8
FU6_2012	15	3.5	0.96	1.02	0.1	20.58

* Site id 'U' denotes unburnt.

Site averages for:

otherM = bare ground and weeds

leaflittM = leaf litter

wdM = woody debris (including logs, branches and twigs)

spinM = spinifex

shrubM = shrubs (< 0.5 m)

Table S4a. A list of the 30 survey sites, the years surveyed and the related site variable and attribute categories used in the analysis.

site	year	dist	treat	soil	tenure	region	fire	block
CB1	2010	C	B	dune	farm	n	burnt	1
CB2	2011	C	B	dune	farm	n	burnt	2
CB3	*OR*	C	B	dune	farm	n	burnt	3
CB4	2012	C	B	dune	farm	s	burnt	4
CB5		C	B	dune	farm	s	burnt	5
CB6		C	B	dune	farm	s	burnt	6
CU1		C	U	dune	farm	n	unburnt	1
CU2		C	U	dune	farm	n	unburnt	2
CU3		C	U	dune	farm	n	unburnt	3
CU4		C	U	dune	farm	s	unburnt	4
CU5		C	U	dune	farm	s	unburnt	5
CU6		C	U	dune	farm	s	unburnt	6
FB4		F	B	dune	farm	s	burnt	4
FB5		F	B	dune	farm	s	unburnt	5
FB6		F	B	dune	farm	s	burnt	6
FU4		F	U	dune	farm	s	unburnt	4
FU5		F	U	dune	farm	s	unburnt	5
FU6		F	U	dune	farm	s	unburnt	6
PD1		P	D	dune	park	n	unburnt	1
PD2		P	D	dune	park	n	unburnt	2
PD3		P	D	dune	park	n	unburnt	3
PD4		P	D	dune	park	s	unburnt	4
PD5		P	D	dune	park	s	unburnt	5
PD6		P	D	dune	park	s	unburnt	6
PS1		P	S	swale	park	n	unburnt	1
PS2		P	S	swale	park	n	unburnt	2
PS3		P	S	swale	park	n	unburnt	3
PS4		P	S	swale	park	s	unburnt	4
PS5		P	S	swale	park	s	unburnt	5
PS6		P	S	swale	park	s	unburnt	6

Table S4b. A list of the dummy variable attributes and categories used in the analysis.

Dummy variable id	Attribute (matching)	Categories	Description
burn (fire)	burnt (unburnt)	mammal$fire	Burnt – a patch that was burnt after surveys in 2010; unburnt – a patch that remained unburnt (control) after surveys in 2010. (Excludes all reserve sites.)
far (distance)	F (close)	mammal$dist	Close x 6 sites (av. distance = 0.14 km); Far x3 sites (av. distance = 5.91 km); Park x 6 sites (in the reserve). These are used to interpret isolation.
ten1 (tenure)	farm (park)	mammal$tenure	Sites within farmland; sites within the reserve.
reg1 (region)	n (south)	mammal$region	All northern sites in the recently burnt reserve and fragments close to the reserve. All southern sites in the long unburnt reserve and all fragments close and far to the reserve.
burn (year)	2010 (2011 and 2012)	mammal$year1^	Y1 – 2010: survey year before experimental burns; 2011-2012 – two survey years after experimental burns.
year	2010, 2011, 2012	mammal$year	Individual years to assess changes through time.
site – each transect was identified.		Block – 1 to 6 – survey design and groupings of sites with similar environmental variables (see Fig. 2).	

^This indicates that nothing burnt in 2010, then identifies specific sites burnt after 2010, i.e. 2011 and 2012.

Table S5. 143 ranked models using Akaike's Information Criterion for small samples (AICc). m = model, f = far, r = region, t = tenure, b = burn, s = soil, y = year, Y1 = 2010, 2011-2012, x = interactions. Main effects were: 'Region' (Southern, Northern), 'Tenure' (Park, Farm), 'Far' (Close, Far), 'Burn' (Unburnt, Burnt), 'Y1' (2010 before burn treatments, 2011-12 after burns implemented) and 'Year' (2010, 2011, 2012). Interactions (with the exception of 'Tenure:Region') were to assess the effects of the burn treatment over time. Interactions included: 'Tenure:Region', 'Region:Burn', 'Far:Burn', 'Y1:Burn', 'Y1:Far', 'Y1:Region', 'Year:Burn', 'Year:Far', 'Year:Region', 'Y1:Region:Burn', 'Y1:Far:Burn', 'Year:Region:Burn', 'Year:Far:Burn'. Models that included 'Burn' also included the interaction with 'Y1' or 'Year'. Appropriate combinations of two-way interactions were included with all three-way interactions. 'Y1' and 'Year' were not used in the same models.

143 models (in alphabetical order)

m0
mf
mr
mrf
ms
msf
msr
msrf
mt
mtf
mtr
mtrf
mtrrxt
mtrrxtf
mts
mtsf
mtsr
mtsrf
mtsrrxt
mtsrrxtf
my
mY1
mY1bY1xb
mY1f
mY1fbbxfY1xbY1xfY1xbxf
mY1fbY1xb
mY1r
mY1rbbxrY1xbY1xrY1xbxr
mY1rbY1xb
mY1rf
mY1rfbbxfY1xbY1xfY1xbxf
mY1rfbbxrY1xbY1xrY1xbxr
mY1rfbY1xb
mY1s
mY1sbY1xb
mY1sf
mY1sfbbxfY1xbY1xfY1xbxf
mY1sfbY1xb
mY1sr
mY1srbbxrY1xbY1xrY1xbxr
mY1srbY1xb
mY1srf
mY1srfbbxfY1xbY1xfY1xbxf
mY1srfbbxrY1xbY1xrY1xbxr
mY1srfbY1xb
mY1t
mY1tbY1xb
mY1tf
mY1tfbbxfY1xbY1xfY1xbxf
mY1tfbY1xb
mY1tr
mY1trbbxrY1xbY1xrY1xbxr
mY1trbY1xb
mY1trf
mY1trfbbxfY1xbY1xfY1xbxf
mY1trfbbxrY1xbY1xrY1xbxr
mY1trfbY1xb
mY1trrxt
mY1trrxtbbxrY1xbY1xrY1xbxr
mY1trrxtbY1xb
mY1trrxtf
mY1trrxtfbbxfY1xbY1xfY1xbxf
mY1trrxtfbbxrY1xbY1xrY1xbxr
mY1trrxtfbY1xb
mY1ts
mY1tsbY1xb
mY1tsf
mY1tsfbbxfY1xbY1xfY1xbxf
mY1tsfbY1xb
mY1tsr
mY1tsrbbxrY1xbY1xrY1xbxr
mY1tsrbY1xb
mY1tsrf
mY1tsrfbbxfY1xbY1xfY1xbxf
mY1tsrfbbxrY1xbY1xrY1xbxr
mY1tsrfbY1xb
mY1tsrrxt
mY1tsrrxtbbxrY1xbY1xrY1xbxr
mY1tsrrxtbY1xb
mY1tsrrxtf
mY1tsrrxtfbbxfY1xbY1xfY1xbxf
mY1tsrrxtfbbxrY1xbY1xrY1xbxr
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mytsrfbbxryxbyxryxbxr
mytsrfbyxb
mytsrrxt
mytsrrxtbbxryxbyxryxbxr
mytsrrxtbyxb
mytsrrxtf
mytsrrxtfbbxfyxbyxfyxbxf
mytsrrxtfbbxryxbyxryxbxr
mytsrrxtfbyxb

m = model
y = year (individual years)
Y1 = 2010, 2011-2012
t = tenure
r = region
f = far
b = burn
s = soil

e.g.
m Y1 t r rxt f b bxf Y1xb Y1xf Y1xbxf
Y1, ten1 ,reg1, reg1:ten1, far , burn , burn:far, Y1:burn, Y1:far, Y1:burn:far

Table S6. Mammal species total abundance for three survey years: 2010, 2011, 2012

Genus_species	Abundance
Mus musculus (House mouse – exotic)	2728
Ningaui yvonneae (Southern ningaui)	59
Notomys mitchelli (Mitchell's hopping mouse)	41
Sminthopsis dolichura (Little long-tailed dunnart)	123
Total	**2951**

Table S7. Mammal species abundance in remnants (Farm) and reserves (Park) for each year: 2010, 2011 and 2012.

Tenure	Year and abundance			***Park and Farm totals***
	2010	*2011*	*2012*	
Park	404	146	454	*1004*
Farm	921	250	776	*1947*
Year totals	**1325**	**396**	**1230**	**2951**

Table S8. A summary of fire and fragmentation interaction treatments. There were eight (n = 8) significant effects (p ≤ 0.05) on mammal abundance and occurrence, and two (n = 2) weak effects (p > 0.05). To the left of the dashed line are the individual treatments and to the right are the interactions. The main study questions relate to the effects of fire ('Burn'), fragmentation ('Isolation') and fire-fragmentation interactions ('Burn:Isolation'). The remaining predictor variables are covariate effects that relate to 'Time', 'Tenure', and 'Region'.

		Predictor variables				***Interactions***		
Mammal species	**abundance / occurrence**	isolation - patch distance from the park	year - 2010, 2011 and 2012 survey years	tenure - park or farm	region - southern or northern	year:burn remnants	year:region	
Mus musculus (exotic)	abundance			*p* = 0.001 +			*p* = 0.001	
Ningaui yvonneae	occurrence		*p* = 0.021			*p* = 0.083		
Notomys mitchellii	occurrence		*p* = 0.001	*p* = 0.001	*p* = 0.001			
Sminthopsis dolichura	occurrence	*p* = 0.001	*p* = 0.027	*p* = 0.093				
		1	3	3	1	1	1	10

Treatments: tenure=park=0, farm=1; region=south=0, north=1; isolation=patches close=0, and far=1 to/from the park; burn=burnt (eight (n = 8) isolated patches identified for burning), unburnt (ten (n = 10) isolated controls); year=three (n = 3) separate survey years (2010, 2011 and 2012).

▒ p >0.05≤0.1

SYNTHESIS

Overview

There have been no previous studies investigating the interaction of fire and habitat fragmentation effects of Australian biodiversity, specifically reptiles and small mammals, in a semi-arid mallee landscape in South Australia. Globally, few studies investigate the interaction of fire and habitat fragmentation and the effects on biodiversity (Paper 1). In fragmented fire-affected mallee landscape in southern Australia, reptile and mammal species are found in large reserves and remnant patches (Carthew *et al.*, 2013; Driscoll, 2004; Williams *et al.*, 2012) and in the agricultural matrix (Driscoll, 2004; Schutz and Driscoll, 2008). Remnant patches contain the original vegetation and are located in a cropping matrix but the fire age of patches and thus the successional stages of the vegetation is unknown. As a result of fragmentation, fire regimes are modified and many remnants are long unburnt because fire is suppressed by land managers. Yet, in large reserves, fire is used as a management tool predominantly to prevent wildfires escaping to surrounding farmland and prevent potential damage to life and property (South Australian Government, 2013). Ecological burning is also undertaken in reserves but with little knowledge of the effects on many animal species.

This thesis builds on our current knowledge of the persistence of reptiles and small mammals in fire-prone, semi-arid mallee by focussing on the effects that fire has in long-unburnt remnant patches and the role of large reserves as a potential colonising source. Counter to the central objective of my research, I did not detect responses of reptiles or small mammals to the interacting effects of fire and fragmentation. Possible reasons could be that extant species have adapted to post-fragmentation and modified fire regimes, or the study survey period of three years might not allow detection of any effects, or the difficulty of separating the potential role of functional responses in species from the influence of other disturbances. However, my research has shown that fire in remnants may provide colonisation opportunities for insectivorous, nocturnal and burrowing reptiles, but that this response may be driven by one species, *Nephrurus stellatus* (Starred knob-tailed gecko), that dominated detections in the reptile study. Mammal responses were limited. One native mammal (*Ningaui yvonneae*), did not increase in experimentally burnt remnants when compared to unburnt sites, and other small mammals remained unaffected. Fragmentation affected all small mammal species, with converse responses in the exotic mammal compared to the three native species. However, native mammals were relatively rare in remnants to begin with. This research found that there are varying responses to fire and fragmentation within and between co-occurring taxa populations persisting in conservation reserves and remnant patches in my study landscape. This highlights the need for management compromises and trade-offs to be considered in order to best achieve the desired conservation outcomes (Driscoll *et al.* 2010a). Essentially, both conservation reserves and nearby remnant patches are providing important habitat to reptiles and small mammals. As such, further research is warranted in fire-prone landscapes to understand the relationships between patches and reserves in response to fire, to improve the management of biodiversity.

Management recommendations

From my systematic review findings, I suggest that future studies present management recommendations that consider and closely align with biodiversity responses observed in the five mechanism of interaction groups in this study: the direction of influence (i.e. fragment affects fire or fire affects fragment), the effect on fire (i.e. more fire or less fire), and the effect on biodiversity (i.e. positive, negative, neutral, not stated). This will help avoid applying management actions that could threaten instead of benefit biodiversity, such as where findings suggest that more fire can increase connectivity (Neuwald and Templeton, 2013), or reduce connectivity (Berry *et al.*, 2015). In addition, this closely aligned approach of management recommendations to biodiversity responses will help to populate, and obtain a better understanding of the gaps in, the five fire-fragmentation interaction categories of biodiversity responses identified from the systematic literature review I undertook.

In the absence of improvements to predict fire age and of better fire mapping records of recent and multiple fires, particularly where there have been other disturbances to habitat, such as grazing, a cautionary use of fire in fragmented fire-prone mallee environments can limit biodiversity losses. For reptile and small mammal populations living in these environments, their persistence can be improved by minimising disturbances to long-unburnt (e.g. ≥ 40 – 50 years) habitat in remnants and reserves as this retains habitat successional stages that are uncommon in the broader mallee landscape (Smith *et al.*, 2013). Although ecosystem complexity leads to variable and difficult to generalise patterns in co-occurring species responses and associated management applications that can result in perverse outcomes (Driscoll *et al.* 2010a), I found there were some specific management actions that could be implemented to facilitate the conservation of reptiles and small mammals in fragmented fire-prone mallee environments. For reptiles, burning long-unburnt remnants adjacent to large reserves with similar TSF-aged vegetation may provide colonisation opportunities for insectivorous, nocturnal and burrowing species. However, if ecological burn programs are being undertaken, they should be underpinned by a robust experimental framework in order to maximise the knowledge obtained from such programs on functionally important or threatened reptiles. For small native mammals, the limited responses to fire in fragments, their preference for the reserve, and their preference for remnants nearer to the reserve, suggested that a precautionary approach to avoid fire in remnant patches is warranted. Although, it is important to note that only one native mammal species was disadvantaged by fire and that the study only considered the short-term effects overall. However, if ecological burns are considered, then burning should only occur when average rainfall is low and when native mammal occurrence is higher than exotic small mammal occurrence.

Future research

In suggesting these management approaches, I recognise that further research is necessary to improve the effectiveness of conservation actions for semi-arid mallee reptiles and small mammals, principally because of the limited ecological research in fragmented fire affected landscapes for these assemblages. My thesis focused on several potential factors that are important for land managers and that can influence the persistence of reptiles and mammals in fragmented fire-affected mallee landscapes – fire history, remnant patches and the role of large nearby reserves as potential source populations, reptile functional traits, and remnant isolation. The determinants of species persistence in fire affected and modified landscapes globally is to have adequate species-related data because it is critical for making fire-related management recommendations. Particularly with climate change potentially compounding species responses to fire in remnants. To better understand reptile responses observed in my study, species-related research should be less constrained by time- and sample-limited studies. This information would improve the ability to make generalisable management recommendations particularly for remnant patches. While for mammals, we do not know how species are using remnants and what role large reserves have in colonising remnants. Genetic research would enable an understanding of how small mammals are using reserves and off-reserve habitats and whether fire encourages spillover from reserves to remnants, or even between remnant patches.

In addition, other important determinants of reptile and small mammal persistence in remnants is the interaction of fire and influence of predators, and fire frequency (fire suppression) in mammals, and potentially if and how grazing in remnants mimics fire disturbance and affects animal persistence, none of which were investigated. Further research should aim to investigate predation effects of reptiles in long-unburnt remnants and establish whether these small habitats provide predator refuges from the large reserve. Another avenue of research from this thesis would be to investigate the role of the cropping matrix and its potential influence of the movement of animals between long-unburnt remnants and the nearby reserve with vegetation of different TSF ages.

Interactions between processes that affect biodiversity is a critical area of study, particularly with regards to the key drivers of biodiversity loss - habitat fragmentation and loss - which can be exacerbated by threats such as fire. Where fire regimes have been modified by fragmentation and potentially cause cascading ecological effects (Syphard *et al.*, 2007), it is important to understand the ecology of the system to determine what the biodiversity response will be. It is evident from my study and other research (Kelly *et al.*, 2017; Sauvajot, 1995) that species responses from interactions between fire and fragmentation are critical areas of knowledge required for the effective management of fire in modified landscapes.

International applicability

The general findings of this study are applicable to other fire-prone ecosystems such that globally there is limited research of fire-fragmentation interactions and thus knowledge gaps of the mechanisms influencing species responses to fire in patches. Also, the continued use of fire as a management tool, even when fire-age is unknown, highlights that it is critical to improve our ability to predict and map fire history by building on the findings of this study. The limited responses to fire and fragmentation interactions by species persisting in small, isolated patches that are long unburnt, indicates that improved knowledge is needed on the effective use of prescribed fire for conservation management. In fire-prone ecosystems, time since fire, e.g. successional stages of habitat, can then be integrated with species responses to fire in continuous and isolated habitat patches.

Summary

In summary, this thesis is building on the limited knowledge we have of interaction processes between fire and fragmentation of semi-arid mallee reptiles and mammals, using South Australian semi-arid, agricultural landscapes as a case study. The study findings represent an in-depth investigation into the responses of reptiles and small mammals to fire in highly modified landscapes and highlights the importance of both remnants and reserves in the persistence of co-occurring species. The findings highlight the importance of fire history information for managing biodiversity, and with the further refinement of my method for predicting fire age, can offer land managers a simple method to assess fire history, and contribute to the fire mapping records. Importantly, this thesis provides precautionary recommendations of fire use that will minimise and potentially mitigate impacts on species persisting in long-unburnt mallee remnants. Looking ahead, this research highlights the need to continue building on our knowledge of how fire regimes interact with fragmentation. In particular, to identify the mechanisms responsible that influence observed biodiversity patterns as this will improve our ability to direct future research, as well as effectively and appropriately incorporate fire use into policy development and on-ground management.

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