Scaling the benefits of agri-environment schemes for biodiversity conservation in agricultural landscapes.

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Cover images (anti-clockwise from top): A remnant of critically endangered Box Gum Grassy Woodland; a sign on the gate of a site targeted under an Australian agri-environment scheme (the Environmental Stewardship Program); A Blue-tongued lizard (*Tiliqua scincoides*) and Marbled gecko (*Christinus marmoratus*) detected during biodiversity surveys of Box Gum Grassy Woodland. Images © Geoffrey Kay.

DECLARATION

This thesis is my own work except where otherwise acknowledged.

Geoffrey M. Kay

December 2016

PREFACE

This thesis is structured as a compilation of six connected papers that have all been published in peer reviewed journals or books. These papers are listed at the end of this preface and are referred to in the text by their roman numerals. Additionally, a Context Statement has been provided at the beginning of the thesis, which provides a framework for understanding the relationship between all aspects of the research presented. The Context Statement identifies broad themes that should be relevant for practitioners and applicable to other studies further afield. It contains a brief introduction, outlines of experimental design, short summaries of each paper, and finally, a synthesis of the work of the entire thesis. It is not intended to be a comprehensive literature review. As a result, the thesis does not include a separate conclusion chapter after the main body of work; instead, all conclusions are presented in the context statement at the start of the thesis.

The formatting and content of this thesis complies with The Australian National University's College of Medicine, Biology and Environment guidelines. All papers were intended as stand-alone pieces of work. For this reason, there is some unavoidable repetition of content and methodology between chapters. Because of the data-rich nature of the research in the papers, it was necessary to include supplementary materials including extra tables and figures for papers I – VI. These materials are included at the back of the thesis. In addition, an additional 3 papers that derive from this research, but were not core to this thesis, have been included as appendices. In total, that makes 9 papers that I have been involved with over the duration of the thesis.

I completed the majority of the work for the thesis, including: study design and establishment, data collection, data analysis and write-up. For all papers, I received advice from my supervisors: Professor David Lindenmayer, Professor Don Driscoll, Dr. Saul Cunningham, and Dr. Ayesha Tulloch. For paper I, I received statistical support from Wade Blanchard. All co-authors peer-reviewed written content and agreed to the submission of each paper. The addition of different co-authors to each paper reflects contributions from collaborators, which are detailed below. The author contribution statements below have been agreed to in writing by all authors. Other assistance is acknowledged in the Acknowledgments section at the end of each paper.

Paper I. Kay, G.M., 2016. Scaling the benefits of agri-environment schemes for biodiversity, in: Ansell, D., Gibson, F., Salt, D. (Eds.), *Learning from Agri-Environment Schemes in Australia: Investing in Biodiversity and Other Ecosystem Services on Farms*. ANU Press. Canberra.

> Conceptualisation & design: GK; Manuscript drafting: GK; Manuscript revision: GK.

Paper II. Kay, G.M., Michael, D.R., Crane, M., Okada, S., MacGregor, C., Florance, D., Trengove, D., McBurney, L., Blair, D., Lindenmayer, D.B., 2013. A list of reptiles and amphibians from Box Gum Grassy Woodlands in south-eastern Australia. *Check List* 9, 476–481.

> Conceptualisation & design: GK, DL; Data collection: GK, DM, MC, SO, CM, DF, DT, LM, DB; Data analysis: GK; Manuscript drafting: GK, DM; Manuscript revision: GK, DM, DL.

Paper III. Kay, G.M., Barton, P.S., Driscoll, D.A., Cunningham, S.A., Blanchard, W., McIntyre, S., Lindenmayer, D.B., 2016. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. *Animal Conservation.* 19, 515–525. doi:10.1111/acv.12267.

> Conceptualisation & design: GK, DL, DD, PB; Data collection: GK; Data analysis: GK, DD, PB, WB; Manuscript drafting: GK; Manuscript revision: GK, PB, DD, SC, WB, SM, DL.

Paper IV. Kay, G.M., Mortelliti, A., Tulloch, A.I., Barton, P.S., Florance, D., Cunningham, S.A., Lindenmayer, D.B., 2016. Effects of past and present livestock grazing on herpetofauna in a landscape-scale experiment. *Conservation Biology*. 31, 446-458. doi:10.1111/cobi.12779.

> Conceptualisation & design: GK, AM, AT, PB; Data collection: GK, DF; Data analysis: GK, AM, PB; Manuscript drafting: GK; Manuscript revision: GK, AM, AT, PB, DF, SC, DL.

Paper V. Kay, G.M., Tulloch, A., Barton, P., Cunningham, S.A., Driscoll, D.A., Lindenmayer, D.B., 2017. Species co-occurrence networks reveal patterns of community restructure under agricultural intensification. *Ecography*. 40, 1-13. doi:10.1111/ecog.03079.

> Conceptualisation & design: GK, AT, PB; Data collection: GK; Data analysis: GK, AT, PB; Manuscript drafting: GK; Manuscript revision: GK, AT, PB, SC, DD, DL.

Paper VI. Kay, G.M., Driscoll, D.A., Lindenmayer, D.B., Pulsford, S.A., Mortelliti, A., 2016. Pasture height and crop direction influence reptile movement in an agricultural matrix. *Agriculture, Ecosystems & Environment.* 235, 164-171. doi:10.1016/j.agee.2016.10.019.

Conceptualisation & design: GK, AM, DD; Data collection: GK, SP; Data analysis: GK; Manuscript drafting: GK; Manuscript revision: GK, AM, SP, DD, DL.

Appendices

Appendix I. Michael, D.R., Kay, G.M., Crane, M., Florance, D., MacGregor, C., Okada, S., McBurney, L., Blair, D., Lindenmayer, D.B., 2015. Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems. *Austral Ecology*. 40, 651–660. doi:10.1111/aec.12232

Conceptualisation & design: DM, DL; Data collection: GK, DM, MC, SO, CM, DF, DT, LM, DB; Data analysis: DM, GK; Manuscript drafting: DM, GK; Manuscript revision: DM, GK, DL.

Appendix II. Barton, P.S., Sato, C.F., Kay, G.M., Florance, D., Lindenmayer, D.B., 2016. Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodlands. *Insect Conservation and Diversity*. 9, 124–134. doi:10.1111/icad.12151

Conceptualisation & design: PB, GK, DL; Data collection: GK, DF; Data analysis: PB, GK; Manuscript drafting: PB; Manuscript revision: GK, CS, DL.

Appendix III. Tulloch, A.I.T., Mortelliti, A., Kay, G.M., Florance, D., Lindenmayer, D., 2016. Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies. *Conservation Biology*. 00, 1–38. doi:10.1111/cobi.12672

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I am also indebted to several key collaborators who have helped with various aspects of my research, and perhaps more valuably, have been wonderful mentors and friends over the years. In particular, I would like to thank Philip Barton, for stimulating ideas and for many times provided me with support and a clear path forward when none seemed available. Wade Blanchard provided exceptional statistical guidance, friendship and timely Canadian digression (curling, baseball and US politics – in that order). Alessio Mortelliti opened my eyes to a number of exciting research possibilities, and shared his knowledge with an ever-present positivity.

This project would not have been possible without the support, insight, trust, generosity and encouragement of the many hundreds of landholders within the south-eastern Australian woodlands. The relationships developed over the past 7 years have inspired and challenged me deeply. Above all else, I hope this work goes some way to fulfilling the many

discussions we shared over the kitchen table and in the woodlands. Similarly, the staff of a number of NRM agencies provided critical support for which I am grateful, including David Trengove, Gus Arnott and Milton Lewis. Thank you to the Australian Government, Great Eastern Ranges Initiative and the former Lachlan Catchment Management Authority for granting financial support to this project. Thank you also to the ANU College of Medicine, Biology and Environment for providing me with a supplementary scholarship.

There are a great many colleagues from the ANU Fenner School that have helped with various aspects of my research – certainly too many to mention here. I especially would like to thank the ANU Long Term Ecology field team, and particularly Daniel Florance who brought a dedication and boundless energy that made working across this vast study a richly rewarding experience. I also thank my peers for their support and camaraderie over the past few years, including: Ingrid Stirnemann, Dean Ansell, Stephanie Pulsford, David Johnson, Wendy Neilan, Shana Nerenberg, George Olah, Laura Rayner, Chloe Sato, Kathy Eyles, Rick Zentelis, Mishka Talent, Karen Ikin, Clare Foster, Crid Fraser, Ben Scheele and Martin Westgate. Thanks to Ben Broadhurst for the temporary-permanent loan of a $2 UV torch. A legion of Fenner staff also provided support: John Stein for being generaous with his time on so many occasions to assist with assembly of spatial datasets; Sue McIntyre and Emma Burns for providing an understanding of the ecological and policy dimensions of Box Gum Grassy Woodlands; and Claire Shepherd, Amy Chen and Kev Mahoney for helping navigate the University administrative system.

Finally, thank you so much to my amazing family for their love, especially my wife, Maansi Joshi. You are my shining light, my daily inspiration and I could not have done this without you.

ABSTRACT

Agricultural expansion and intensification are major causes of biodiversity loss. To mitigate this, billions of dollars are committed by governments annually to agri-environment conservation schemes aiming to engage landholders, often at large (continental) scales, in sustainable farming practices. While some schemes have been successful in addressing the social and policy elements of farmland conservation, assessments of their effectiveness for conserving biodiversity in farming systems is lacking. Recent studies have demonstrated that the effectiveness of programs is influenced by a number of scale-dependent factors that may influence biodiversity response but remain poorly understood. Specifically, local- and landscape-scale management actions can influence biodiversity response, and hence the effectiveness of programs, but this aspect has been little explored.

My research aimed to identify ways to enhance the effectiveness of agri-environmental schemes through a better understanding of scale-related management effects on herpetofauna (reptiles and amphibians); a critical and declining vertebrate group severely threatened by agricultural development.

First, I summarise current knowledge of local- and landscape-scale factors influencing agri-environment scheme effectiveness for biodiversity, highlighting novel research priorities relevant to practitioners (Paper #1). I then conducted baseline herpetofaunal surveys at 325 treatment/control sites within a critically endangered remnant woodland targeted under a large-scale (>1000 km; 172,000 km^2) agri-environment scheme; the Australian Government Environmental Stewardship Programme (Paper #2). This is the most extensive

herpetofaunal survey conducted to date throughout this woodland ecosystem. I found high levels of spatial variation in species detected across the study area; with large differences in species richness between biogeographic regions but not between treatment and control sites.

Second, I conducted multi-season vegetation, habitat structural and herpetofaunal surveys at each of the 325 sites to identify key habitat variables (Paper #3) and management activities (livestock grazing; Paper #4) at local levels. I found that habitat use varied over biogeographically distinct regions, suggesting schemes that consider regional differences in local habitat preferences may be more effective than schemes that ignore such variation. Furthermore, past and present livestock grazing influenced herpetofaunal populations, but in complex and varied ways that have previously been overlooked.

Finally, I collected data on land-use surrounding the remnant woodland sites and its influence on reptile movement to quantify the impact of landscape modification on community structure (Paper #5) and habitat connectivity (Paper #6). Landscape modification resulted in a change in community composition and a loss of species co-occurrence, but not a loss of species. Importantly, changes in co-occurrence pattern were complex and allowed for a novel classification of species susceptibility to the threat of land modification. Additionally, I found that pasture height and crop-sowing direction influenced reptile movements within the agricultural matrix, and hence must be considered where connectivity is a goal of agri-environment investment (Paper #6).

Collectively, my research identifies several outcomes that strengthen the theoretical and applied opportunities for enhancing effectiveness of agri-environment schemes. These include:

(1) An improved knowledge of the environmental and anthropogenic drivers of the distributions of herpetofauna
(2) Incorporating ecological effects operating at different scales can help agri-environment schemes to become more effective
(3) A range of management actions is required to meet the conservation requirements for herpetofauna
(4) Large occupancy datasets should be collected to extend observations of ecological patterns to identify underlying ecological processes
(5) Management recommendations can be adaptively integrated into existing agri-environment schemes; as well as in new schemes.

Such considerations are of broad relevance for the design of large-scale conservation strategies targeting the conservation of biodiversity across agricultural landscapes.

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CONTEXT STATEMENT

Introduction

"…the oldest task in human history: to live on a piece of land without spoiling it"

~ Aldo Leopold (1991; pg. 254)

Human activities have immense, long lasting impact on the natural environment, resulting in unprecedented and accelerated biodiversity loss (Ceballos et al., 2015; Novacek and Cleland, 2001). So profound is this impact that many scientists consider the Earth to have entered a new Epoch – the Anthropocene (Corlett, 2015; Lewis and Maslin, 2015) – with human-induced biodiversity losses estimated to be 100 to 1,000 times that of pre-human levels (Barnosky et al., 2011; Dirzo et al., 2014). Habitat removal and fragmentation associated with the expansion and intensification of agricultural landscapes remains the single largest driver of terrestrial biodiversity loss (Foley, 2005; Haddad et al., 2015). By 2050, the human population is expected to exceed 9.6 billion (UN, 2013), requiring a 70% increase in world food supply from current levels that could result in a further one billion hectares of habitat being converted for agricultural purposes (Alexandratos and Bruinsma, 2012; Tilman et al., 2011; Tscharntke et al., 2012a). As such, the conservation of Earth's biodiversity has never before depended so much on the management of agricultural landscapes.

A major challenge facing conservation practitioners is the limited empirical knowledge about best-practice management of agricultural landscapes for biodiversity (Brussaard et al., 2010; Miller and Hobbs, 2002). These landscapes have historically attracted considerably less attention from conservation researchers than other more natural environments, preventing the development of progressive and innovative land management approaches (Lindenmayer et al., 2012a). Indeed, much current conservation research remains largely focussed on the small proportion (~15%: UNEP-WCMC and IUCN, 2016) of land earth persisting within reserves and with low levels of human impact rather than on the far greater area of human-modified landscapes (Fazey et al., 2005; Miller and Hobbs, 2002). It is increasingly recognised that nature reserves alone will be insufficient for conserving a majority of species, natural resources, and ecological processes (Chazdon et al., 2009; Cox and Underwood, 2011; Reyers, 2013). Consequently, conservation initiatives that transcend the existing reserve network to integrate with the large areas of production-focussed agricultural landscapes are considered necessary to reverse this biodiversity decline (Franklin and Lindenmayer, 2009; Stoate et al., 2001).

Agri-environment schemes have emerged as an increasingly popular tool to conserve the environmental, ecological and social values of agricultural landscapes (Batáry et al., 2015; Kleijn and Sutherland, 2003; Lindenmayer et al., 2012c). Each year, billions of dollars are committed by governments and conservation agencies for the development of these schemes which, although variable in their structure and application (Ansell et al., 2016), generally employ a market-based approach to pay private land managers for conservation activities such as strategic grazing, habitat restoration and exotic species management (Burrell, 2012; European Commission, 2014a). Some of these schemes are large in scale and operate over long timeframes. For instance, since 2002, funding for schemes in the United States have increased tenfold with over US$28 billion pledged between 2014 to 2018 (USDA, 2014). In Europe, almost €20 billion have been paid to farmers in schemes during the last eight years (European Commission, 2014a). Thus, at a global scale, these schemes represent some of the largest investments into the conservation of biodiversity in private-tenure landscapes.

While some schemes have been successful in addressing the social and policy elements of farmland conservation (e.g. Zammit, 2013), far fewer have demonstrated effective biodiversity outcomes across the scale of program implementation (Whittingham et al., 2007). One broadly acknowledged reason is a scarcity of robust empirical assessment and monitoring available to quantify the effectiveness of current schemes as well as to guide the design of new schemes (Kleijn and Sutherland, 2003; Lindenmayer et al., 2012c; Michael et al., 2014). However, even where empirical monitoring is present, it remains spatially and temporally limited and largely focussed on one, or a few, well-studied taxonomic groups (Lüscher et al., 2014). A second, more complex and less explored reason is that the effectiveness of agri-environment schemes has recently been shown to be influenced by a number of scale-dependent factors. These include the amount of habitat invested in agri-environment schemes (Dallimer et al., 2010; Hiron et al., 2013), the surrounding landscape context (Batáry et al., 2011; Concepción et al., 2012; Gabriel et al., 2010), and the underlying delivery mechanisms used in scheme design (Hajkowicz et al., 2009; Siriwardena, 2010). Therefore, enhancing the effectiveness of these popular, wide-spread (and costly) agri-environment investments requires greater understanding of the role of scale-effects learned from large-scale, long-term empirical datasets.

The objective of this thesis is to address critical gaps in knowledge about scale-effects to enhance the effectiveness of agri-environment conservation programs, using data and insights from one of the largest (>172,000 km^2, 325 sites) multi-season empirical biodiversity monitoring programs conducted in any agri-environmental scheme; the Australian Environmental Stewardship Programme.

Conceptual design

The overarching objective of my research is to identify how knowledge of scale-effects may enhance the effectiveness of private protected areas for the conservation of biodiversity; specifically for agri-environment schemes as a popular and rapidly expanding policy approach. Each of the papers in this thesis uses a varied and modern suite of analytical tools to reveal opportunities for enhancing agri-environment scheme effectiveness. This thesis comprises six first-authored peer-reviewed scientific publications, plus an appendix of three relevant publications, all of which are structured around three main components (Figure 1).

The first component of this thesis comprises two parts. First, an introduction is presented to outline the role of scale for enhancing the effectiveness of agri-environment schemes for biodiversity, highlighting possible areas where research may be useful, recognizing that change can be made both at the local scale (i.e., the target patch) as well as into the broader landscape. This work was published as a book chapter following a workshop aimed at practitioners and farmers (Kay, 2016). The chapter is not intended to be an exhaustive literature review but rather to identify core opportunities to enhance agri-environment scheme effectiveness which are the focus of remaining chapters.

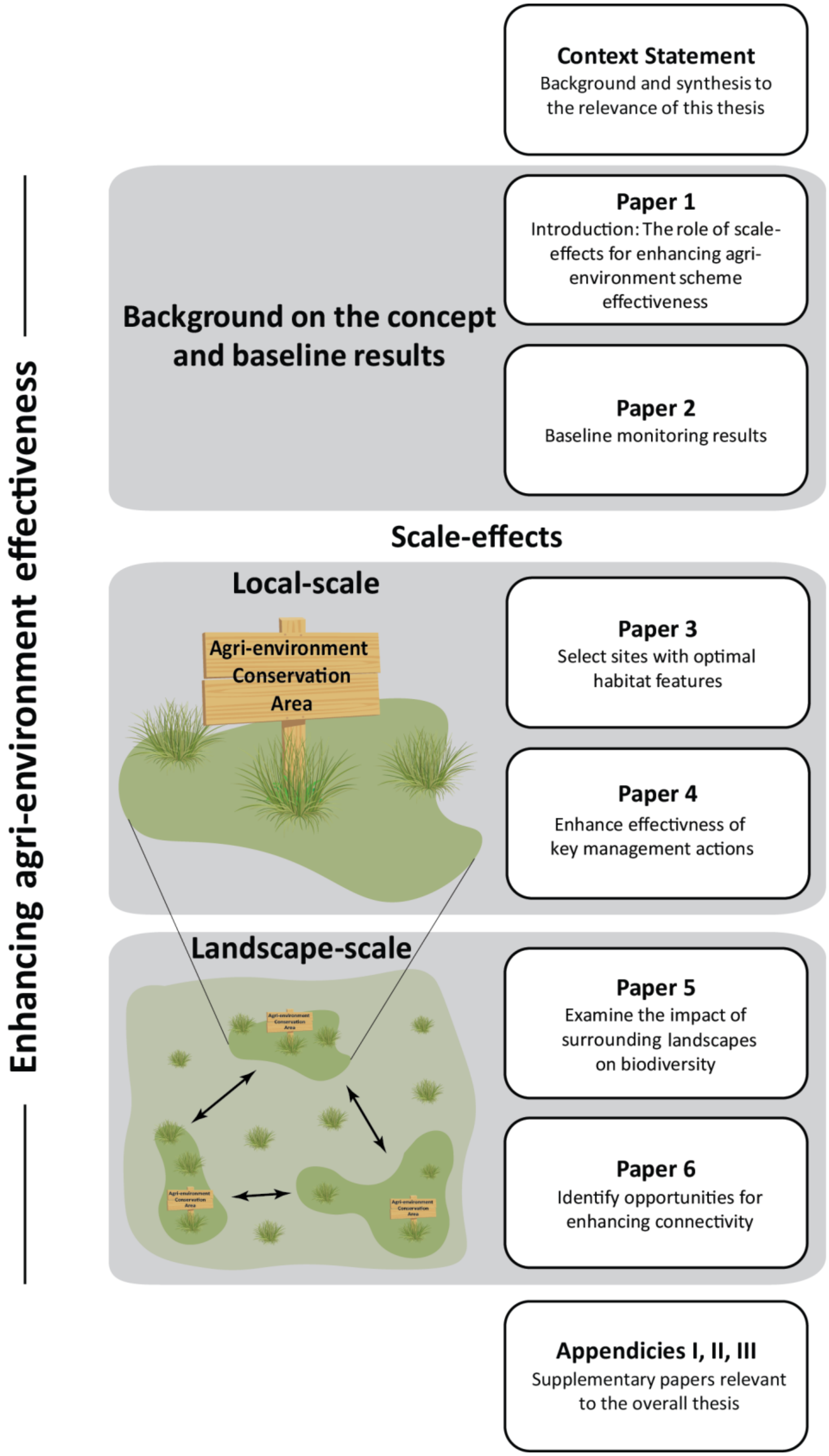

Figure 1. *Outline of the structure of this thesis, showing the three core components (grey) and associated papers.*

One of the critical elements for assessing effectiveness of agri-environment schemes is the establishment of robust empirical biodiversity monitoring programs. Therefore, a second publication in this thesis addresses this by providing results from the baseline monitoring from the focal agri-environment scheme (the Australian Environmental Stewardship Programme) to provide an inventory of species present in the system (Kay et al., 2013).

Components two and three of this thesis employ a suite of modern analytical approaches on a large empirical dataset (>172,000 km^2, 325 sites) to explore opportunities for enhancing scheme effectiveness at both local and landscape scales, respectively. At the local-scale (Component 2 in this thesis), Paper 3 addresses a key challenge for agri-environment scheme design by identifying a method to identify the most important habitat features to include for enhancing biodiversity. The paper goes on to explore whether these features vary geographically, enabling managers to design more refined schemes (Kay et al., 2016a). Paper 4 explores whether local management actions employed as part of agri-environment schemes can be made more effective – such as livestock grazing management (Kay et al., 2016b). Additional publications conceived from this dataset, but peripheral to the main focus of this thesis, are included as appendices. The work published in Michael et al. (2015) revealed that classifying species by ecological niche breadth and microhabitat guild can also help identify key habitat features critical for including within agri-environment schemes, while Barton et al. (2016) and Tulloch et al. (Tulloch et al., 2016b) quantify the impacts of key management actions on invertebrates and birds, respectively.

At landscape scales (Component 3 in this thesis), Paper 5 reveals how modification of the landscapes surrounding target patches can influence resident biotic communities, specifically through the way in which species associate (co-occur) (Kay et al., 2017). Paper

6 examines how the type and structure of surrounding landscapes may influence the ability of species to navigate, and hence connect, between habitat patches (Kay et al., 2016c).

Study area

I conducted my research within remnants (>10ha) of critically endangered Box Gum Grassy Woodland ecosystem targeted as part of a large (325 sites, >172,000 km^2) agri-environment program in south-eastern Australia – termed the Environmental Stewardship Programme (Commonwealth of Australia, 2009, 2013). The Programme spanned multiple biogeographic regions, ranging from Warwick, Queensland (28°1’32”S, 152°12’22”E) in the north to Albury, New South Wales (36°4’47”S, 146°54’59”E) in the south (Figure 2).

This area supports some of the most productive landscapes for cereal cropping and livestock grazing in Australia, and is characterized by moderate rainfall (400 – 1200 mm per annum) and moderate to highly fertile soils (Commonwealth of Australia, 2013). Two broad agro-climatic systems were defined across this study area (Paper 3; Kay et al., 2016a), based on previous classifications of landscapes with similar climate, vegetation and common land-use (Hutchinson et al. 2005). These systems include a winter-rainfall mixed grazing and cropping system (Tablelands; Figure 2), and a low-rainfall cropping system (Western; Figure 2). Within each region, dominant land-uses include cropping, grazing of improved pastures, and grazing of native pastures.

Study groups

Reptiles and amphibians (known collectively as herpetofauna) represent a significant proportion of Earth’s vertebrate biodiversity, occupying most habitats throughout Earth’s

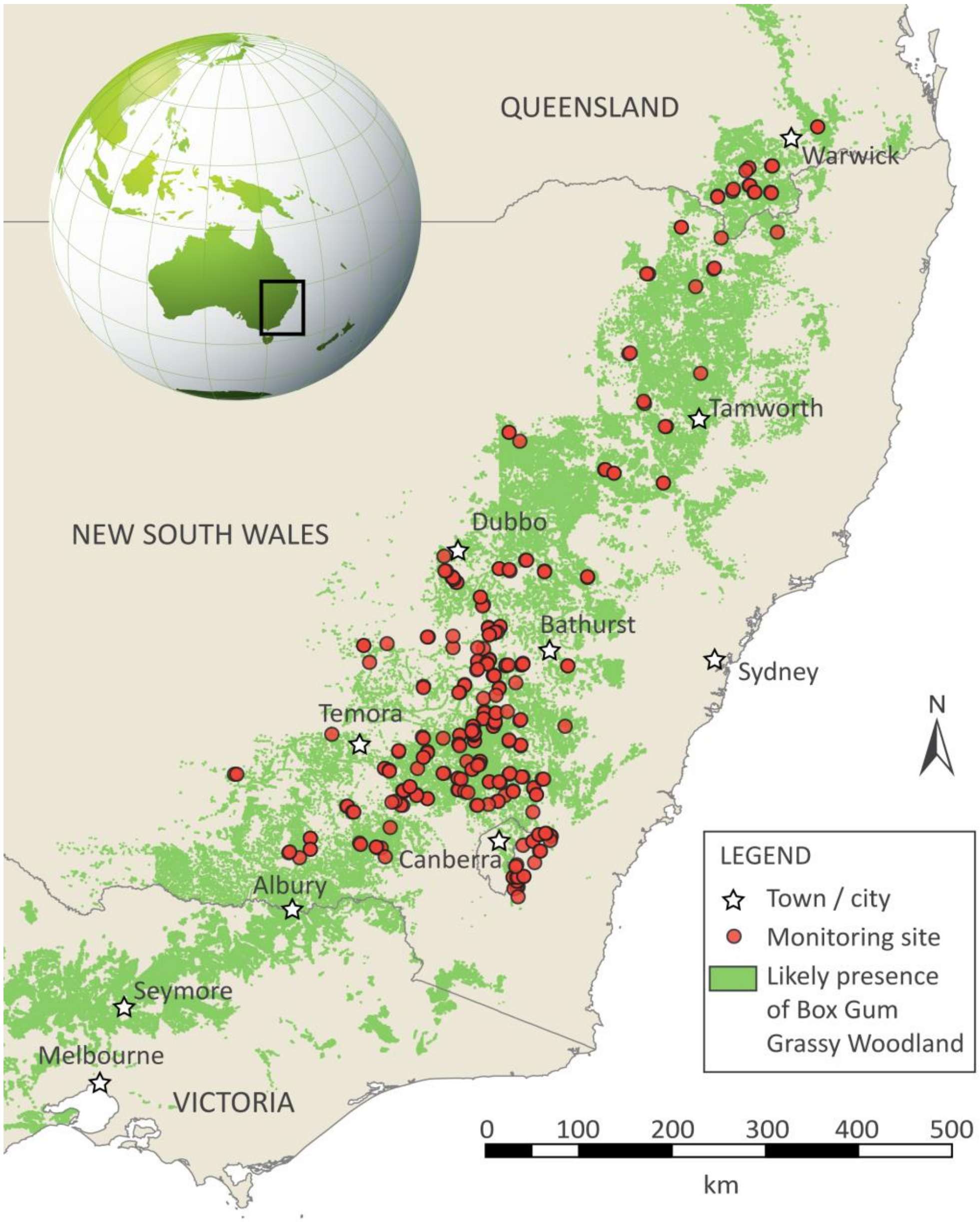

Figure 2. *Location of the study area spanning the New South Wales (NSW) and southern Queensland (QLD) States of south-eastern Australia showing the location of monitoring sites (n=325) and extent of critically endangered Box Gum Grassy Woodland ecosystem. Box Gum Grasy Woodland data source: Environmental Resources Information Network (ERIN), Department of Sustainability, Environment, Water, Population and Communities (SEWPAC).*

terrestrial, freshwater and marine environments (Böhm et al., 2013; Tingley et al., 2016). Herpetofauna also fulfil important functional roles in natural systems, as predators, prey, grazers, seed dispersers and micro-site ecosystem engineers; as well as act as bio indicators of environmental and anthropogenic change. Although significant in terms of diversity and function of Earth’s ecosystems, populations are currently undergoing catastrophic and unprecedented decline world-wide, sparking wide-spread conservation concern (Alford and Richards, 1999; Böhm et al., 2013; Gibbon et al., 2000; Nori et al., 2015).

Habitat loss and landscape fragmentation from agricultural development is considered a primary cause for global decline in herpetofauna (Böhm et al., 2013). This is because these animals are particularly vulnerable to land modification due to their ground-dependency, low mobility, narrow distributional range and high reliance on groundcover habitats (Brown et al., 2011; Fischer et al., 2004; Jellinek et al., 2004; Schutz and Driscoll, 2008). The recognised lack of ecological data for this group (Bland and Böhm, 2016) greatly limit our understanding of the mechanisms causing this decline and hence efforts to conserve them in agricultural landscapes. Herpetofauna therefore represent a particularly relevant group to examine how agri-environment conservation strategies like land stewardship can be made more effective for biodiversity conservation in private protected areas.

Summary of outcomes

Paper I: Scaling the benefits of agri-environment schemes for biodiversity.

In paper I, I introduce the concept of scale and how this might influence the outcomes of agri-environment schemes. I identify how agri-environment scheme effectiveness is heavily reliant on the spatial (and temporal) scale of implementation. I summarise current knowledge (from a workshop and the literature) to identify research priorities that can enhance understanding of local- and landscape-scale factors influencing agri-environment scheme effectiveness for biodiversity. I found that, at local-scales, information about how species respond to environmental features, as well as the impact of management actions, could improve site selection and effectiveness of management prescriptions. At landscape scales, the offsite benefits of agri-environment schemes could be enhanced by better understanding the impact of surrounding landscape context.

Paper II: A list of reptiles and amphibians from Box Gum Grassy Woodlands in south-eastern Australia.

In paper II, I asked: What species occur throughout box gum grassy woodlands? Obtaining this baseline information is a necessary first step towards future examinations of agri-environment effectiveness. I conducted baseline herpetofaunal surveys at 325 treatment and control sites within critically endangered remnant woodland targeted under a large-scale agri-environment scheme; the Australian Governments' Environmental Stewardship Programme. I recorded 69 species from ten families, and found high levels of spatial variation in species detected across the study area; with large differences in species richness between water catchments, but not between treatment and control sites. This is the most extensive survey of reptiles and amphibians conducted to date throughout the critically endangered Box Gum Grassy Woodland ecosystem.

Paper III: Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes.

In paper III, I asked: Do reptile assemblages show different environmental associations across biogeographically distinct regions? No studies have examined the habitat requirements of reptiles across this critically endangered Box Gum Grassy Woodland at this scale. Moreover, incorporating regional-scale differences in habitat associations have rarely been considered in designing large-scale conservation programs like agri-environment schemes. I identified a range of local-scale habitat variables that would enhance the effectiveness of schemes for herpetofaunal diversity, and that importantly, varied over biogeographically distinct regions. I identified four key implications for managers: (1) large-scale conservation schemes can achieve better outcomes for reptiles using regional-scale knowledge of environmental associations; (2) regional-scale knowledge is particularly valuable for conservation of rare reptile taxa; (3) consideration of abiotic environmental features which cannot be directly managed (e.g. aspect and elevation) is important; (4) programmes can be tailored to better support reptile groups at higher conservation risk. This study showed that reptile-environment associations differ among biogeographic regions, and this presents opportunities for tailoring stronger policy and management strategies for conserving large-scale agricultural landscapes globally.

Paper IV: Effects of past and present livestock grazing on herpetofauna in a landscape-scale experiment.

In paper IV, I asked: <u>What are the effects of past and present grazing management on ground-dwelling herpetofauna?</u> Livestock grazing is the most widespread land use on Earth, and a widely-applied management action in agri-environment schemes. Yet, many of the mechanisms by which grazing leads to changes in biodiversity remain unresolved. I conducted a landscape-scale replicated grazing experiment (15,000 km^2, 97 sites) to examine the impact of past grazing management and current grazing regimes (intensity, duration, and frequency) on a community of ground-dwelling herpetofauna (39 species). Past grazing practices did not influence community richness but did affect community composition and patch colonization and extinction for four of seven species. Present grazing parameters did not influence community richness or composition, but six of the seven target species were affected by at least one grazing parameter. Grazing frequency had the most consistent influence, positively affecting three of seven species (increased colonization or decreased extinction). Past grazing practice affected community composition and population dynamics in some species in different ways, which suggests that conservation planners should examine the different grazing histories of an area. Species responded differently to grazing practices. Thus, incentive programs that apply a diversity of approaches rather than focusing on a change such as reduced grazing intensity should be considered. Based on these findings, determining fine-scale grazing attributes is essential for advancing grazing as a conservation strategy.

Paper V: Species co-occurrence networks reveal patterns of community restructure under agricultural intensification.

In paper V, I asked: Does agricultural intensification alter reptile diversity, composition or the ability of species to co-occur? Agricultural intensification is one of the greatest threats to biodiversity. This may reduce the effectiveness of agri-environment programs in a number of ways including reducing the connectivity of landscapes or alter species associations. Yet knowledge of whether and how anthropogenic landscape modification restructures communities of co-existing species remains limited. I contrasted assemblages from sites surrounded with intact and modified landscapes and tested the hypothesis that agricultural intensification leads to declines in species richness and altered composition, which leads to declines in co-occurrence due to reduced landscape occupancy by species. Modified landscapes were also characterized by differences in network structure; with species sharing fewer sites with each other (reduced co-occurrence connectance) and fewer highly-connected species (truncation of the frequency distribution of co-occurrence links).

Critically, other network metrics revealed that overall loss of co-occurrence was underpinned by complex changes to the number and distribution of pair-wise co-occurrence links, with 41-44% of species also gaining associations with other species. Changes to co-occurrence were not well-predicted by changes in occurrence, nor by species taxonomic or functional group membership, allowing a novel classification of species susceptibility to agricultural intensification. Our study reveals the value of using co-occurrence analysis to uncover impacts of agricultural intensification that may be masked in conventional studies of species richness and community composition.

Paper VI: Pasture height and crop direction influence reptile movement in an agricultural matrix.

In paper VI, I asked: <u>How does the quality of the agricultural matrix influence the fine-scale movement of reptiles?</u> Using agri-environment schemes to tackle the threat of habitat fragmentation on biodiversity requires knowledge of how species move within agricultural landscapes. I assessed how matrix type (improved pasture, native pasture or crop) and structure (grass height) influenced fine-scale reptile movement, as well as influences of crop sowing direction and setting-sun position. In an agricultural region of south-eastern Australia, I first released 20 individuals of an arboreal gecko (*Christinus marmoratus*) at set distances from trees to determine the distance at which they could perceive their tree habitat (perceptual range). I then translocated 36 individuals into six matrix environments within their perceptual range of isolated trees to examine how gecko movement was modified by the type and structure of the matrix. I also recorded crop sowing direction and setting-sun position and examined all recorded tracks using angular statistics. I found that geckos exhibited a perceptual range of 40–80m. Short matrix environments promoted direct movements towards trees, irrespective of matrix type. Furthermore, movements were significantly affected by crop sowing direction with individuals following the planted lines. This study has three significant implications: (i) restoring mature tree spacing to 80 m apart will assist gecko movements, (ii) targeted management for low pasture height, such as by maintaining directional narrow strips of low vegetation among taller pastures, might assist movement and facilitate increased connectivity, (iii) directional sowing of crops between habitat patches presents a simple but potentially effective tool for reconnecting fragmented landscapes.

Synthesis

The intensification and expansion of agricultural practices remains a primary threat to terrestrial biodiversity (Alexandratos and Bruinsma, 2012). Global efforts to enhance the effectiveness of large-scale conservation programs are urgently needed within agricultural landscapes (Batáry et al., 2015). Agri-environment schemes represent a popular and heavily funded approach (European Commission, 2014a; USDA, 2014), but empirical assessments of their effectiveness are lacking; often focussed on spatially limited ecological data for one, or a few, well-studied taxonomic groups (Ansell et al., 2016; Gonthier et al., 2014). My research identifies drivers of herpetofaunal diversity in an agricultural landscape, with the goal of seeking opportunities for enhancing effectiveness of agri-environment programs by addressing factors that can influence biodiversity at local- and landscape-scales. Below I synthesise outcomes from my research to strengthen the theoretical and applied opportunities for enhancing effectiveness of agri-environment schemes. I provide three clear outcomes informed directly from my results, with two additional insights that broadly emerged from this study that I believe are highly relevant for conservation scientists, policy, and practitioners for advancing effectiveness of these programs into the future.

1. *An improved knowledge of the environmental and anthropogenic drivers of the distributions of herpetofauna*

My work improves knowledge of the ecology of herpetofauna, a consistently understudied group undergoing rapid decline throughout agricultural landscapes globally (Bland and Böhm, 2016; Tingley et al., 2016). Specifically, the spatial scale of our monitoring program allowed us to complete the most comprehensive assessment of species-environment associations ever conducted for herpetofauna within the critically endangered Box Gum Grassy Woodland ecosystem of south-eastern Australia (Paper 3). The scale of our study also enabled us to investigate the ecological impact of livestock grazing management (Paper 4), which is considered to have widespread impact on biodiversity globally yet mechanistic effects remain poorly resolved (Briske et al., 2011a). Furthermore, we demonstrate empirically how landscape modification has a strong influence on the way reptiles co-occur, and reveal certain species-groups for which the impact can be predicted to be greatest (Paper 5). Finally, we reveal how reptile movement decisions are strongly influenced by the quality of the surrounding landscape matrix (Paper 6). Considering this, our work contributes to a comprehensive understanding of habitat requirements and management actions for a complete assemblage of herpetofauna that have never before been surveyed so extensively throughout this critically endangered woodland ecosystem.

2. *Incorporating ecological effects operating at different scales can allow agri-environment schemes to become more effective*

A key finding from this research is that agri-environment schemes can be made to be more effective for conserving biodiversity when integrating knowledge of ecological processes that act at local- and landscape-scale on biota. At local-scales, I found that the optimal set of environmental attributes to be targeted under agri-investment was not static and responded to spatial differences in species-environment associations (Paper 3). Likewise, understanding how biota respond to key management actions at local-scales, like livestock grazing, can assist in better targeting those beneficial areas to invest, and so prescribe more targeted management (Paper 4). At landscape scales, surrounding land-use directly reduces the capacity of species to co-occur with one another (Paper 5), and influences the navigation ability of dispersing reptiles (Paper 6).

While the importance of considering scale in ecological process remains a fundamental concept in ecology (Barton et al., 2013; Cunningham et al., 2014; Cushman and McGarigal, 2002), opportunity yet exists for it to be widely integrated into agri-environmental policy. For instance, many programs aim to select a consistent set of habitat variables across the extent of a program, failing to account for regional differences in species-environment relationships that my research identifies (Paper 3). Likewise, programs often assume that a management action (e.g. livestock grazing) in one place will be as effective as that same action in another place, yet I found that biotic response is influenced by past and present characteristics of management actions (Paper 4).

Considering this, my research identifies that programs could be made more effective by employing a range of strategies that promote diversity in biotic communities. For the purpose of clearly translating our findings into management-relevant findings, I present the observations from this research in Table 1 along with appropriate recommendations that will be of use to conservation practitioners in agricultural landscapes. This above list demonstrates a range of important opportunities to implement changes that result in beneficial ecological responses.

Table 1. *Summary table of the research observations and identified management implementation opportunities*

Observation	Recommendation for management	Source
• A range of habitat variables is important for enhancing reptile diversity, and these vary depending on the type of diversity targeted	Select key features for enhancing diversity, being aware that a different set of features are needed for conserving rare species richness	Paper 3
• The importance of habitat variables varies geographically	Allow programs to be more flexible and accommodate regional variation	Paper 3
• Past grazing practices affect community composition and population dynamics for some species but effects differ among different species	Consider grazing history of an area before implementing management; application of a single type of grazing will not enhance diversity as some species are benefited while others not.	Paper 4
• Present grazing parameters did not influence community richness or composition, but did affect population dynamics, again in different ways among different species	Incentive programs that apply a diversity of approaches rather than focusing on a single variable (like intensity) are required.	Paper 4
• Land modification causes loss in co-occurrence associations, change in species composition but not reduction in species richness	Where the goal is to increase species co-occurrence, managers could: (i) reduce the areas of modified landscapes surrounding habitats (through restoration), or (ii) target sites with high quality surrounding landscapes.	Paper 5
• Changes in co-occurrence are underlain by complex changes to the number and distribution of links between species, and are not well predicted by occurrence, allowing for a novel classification of species susceptibility.	Establish management goals specific to certain species based on their susceptibility classification derived from co-occurrence networks.	Paper 5
• Some species of reptile have a perceptual range of 40-80m	Maintaining habitat features within matrix at relevant densities (in this case trees ~80m apart) will enhance ability of species to make decisive movements towards habitats.	Paper 6
• Short matrix environment promote direct movements towards trees, irrespective of matrix type	Targeted management for low pasture height, such as by maintaining directional narrow strips of vegetation among taller pastures, might assist movement and facilitate increased connectivity	Paper 6
• Movements significantly affected by crop sowing direction with individuals following planted lines.	Directional sowing of crops between habitat patches presents a simple but potentially effective tool for reconnecting fragmented landscapes	Paper 6

3. *A range of management actions is required to meet the conservation requirements for herpetofauna*

It is clear from our results, as well as Table 1, that complex interactions between management actions and species management exist. For example, our results show that policies encouraging the adoption of fixed grazing management actions across large areas and different agro-climatic systems would benefit some species but not others (Paper 4). This indicates that no single management action is likely to result in universally positive ecological response for all herpetofauna. Therefore, managers of agri-environment programs need to think about multiple management actions, and may need to develop adaptive programs that have multi-pronged approaches. This could include setting flexible bounds on management actions based on certain criteria (e.g. adjusting the time of a management action based on the specific geographic or climatic context of a management region).

Further to the above points, which are directly linked to research results, my experience conducting this research and working with land managers have led me to develop some additional ideas for improving agri-environment schemes, as described below.

4. *Large occupancy datasets should be collected to extend observations of ecological patterns to identify underlying ecological processes*

Occupancy datasets (e.g. species lists) represent one of the most common forms of ecological data that are routinely used in conservation management decision making. These data can be useful for examining changes in patterns of richness and diversity, but less capable of identifying mechanistic ecological processes driving these patterns. My research demonstrates in several cases that occupancy data can extend beyond examinations of richness and composition to identify the impact of ecological processes driving observed patterns in communities. In my thesis, observing processes of species' patch colonization and extinction in addition to occupancy allowed for a detailed assessment of the impacts of livestock grazing management (Paper 4). Similarly, changes in species co-occurrence revealed processes driving patterns of herpetofaunal communities under landscape modification (Paper 5). The identification of these processes was possible only through the collection of highly spatially replicated, multi-year, repeat visit datasets. Consequently, gathering such datasets can provide opportunity to identify key processes impacting biota, and hence may improve effectiveness of conservation programs including agri-environment schemes.

5. *Management recommendations can be adaptively integrated into existing agri-environment schemes; not only new schemes.*

In addition to setting foundations for future agri-environment schemes, many of the management recommendations suggested in this thesis can be adapted to existing programs. For example, in the case study presented in this thesis, future rounds of investment targeting the selection of particular habitat variables relevant across the different biogeographic regions covered under the Environmental Stewardship agri-environment scheme could enhance program outcomes (from Paper 3). Likewise, investments to alter grazing management (Paper 4), or cropping practices outside of patches (Paper 6), as described in this study could be used to further maximise program outcomes. This provides an important opportunity to learn from successes and failures, and to adaptively manage agri-environment programs as we advance our scientific understanding. Adapting programs in such a way has several important advantages for practitioners. These include cost saving measures of implementing new programs, which can be expensive to establish. It also means programs can be made policy-relevant without the expense and time required to establish programs from scratch. It can maintain existing stakeholder networks, which can take a long time to establish, can be easily eroded, but represent a powerful opportunity to embed essential ecological principles.

Concluding remarks

My research has shown that biodiversity responses in agricultural landscapes are influenced by a range of factors operating at different scales. Efforts to conserve biodiversity in agricultural landscapes through the use of agri-environment schemes (and other large-scale conservation programs) could benefit from an understanding of these effects. Given the extent of investment into agri-environment schemes globally, the recommendations presented from this work should be of direct interest to conservation practitioners in many agricultural landscapes globally. Future research that determines how these ecological responses translate into performance of agri-environment schemes should be prioritised to support biodiversity conservation in agricultural landscapes. Ongoing empirical monitoring, for a range of taxa, would help identify the medium to long-term benefits of agri-environment response to the recommendations presented here. Overall, this thesis highlights the value of integrating scale-effects to enhance the effectiveness of agri-environment schemes, providing practical evidence-based solutions to effectively implement conservation within agricultural landscapes.

References

Alexandratos, N., Bruinsma, J., 2012. World agriculture towards 2030/2050: the 2012 revision. Food and Agriculture Organization of the United Nations, Rome.

Alford, R.A., Richards, S.J., 1999. Global Amphibian Declines : A Problem in Applied Ecology. Annu. Rev. Ecol. Syst. 30, 133–165. doi:10.1146/annurev.ecolsys.30.1.133

Ansell, D.H., Gibson, F., Salt, D., 2016. Learning from Agri-Environment Schemes in Australia: investing in biodiversity and other ecosystem services on farms. ANU Press, Canberra.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., Mcguire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? Nature 470, 51–57. doi:10.1038/nature09678

Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B., Didham, R.K., 2013. The spatial scaling of beta diversity. Glob. Ecol. Biogeogr. 22, 639–647. doi:10.1111/geb.12031

Barton, P.S., Sato, C.F., Kay, G.M., Florance, D., Lindenmayer, D.B., 2016. Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodlands. Insect Conserv. Divers. 9, 124–134. doi:10.1111/icad.12151

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B Biol. Sci. 278, 1894–1902. doi:10.1098/rspb.2010.1923

Batáry, P., Dicks, L. V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. doi:10.1111/cobi.12536

Bland, L.M., Böhm, M., 2016. Overcoming data deficiency in reptiles. Biol. Conserv. doi:10.1016/j.biocon.2016.05.018

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., Rhodin, A.G.J., Stuart, S.N., van Dijk, P.P., Young, B.E., Afuang, L.E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L.R. V, Allison, A., Ananjeva, N., Anderson, S., Andrén, C., Ariano-Sánchez, D., Arredondo, J.C., Auliya, M., Austin, C.C., Avci, A., Baker, P.J., Barreto-Lima, A.F., Barrio-Amorós, C.L., Basu, D., Bates, M.F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M.D.R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J.R., Chapple, D.G., Cheylan, M., Cisneros-Heredia, D.F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G.C., Couper, P.J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P.A., Crother, B., Cruz, F., Daltry, J.C., Daniels, R.J.R., Das, I., de Silva, A., Diesmos, A.C., Dirksen, L., Doan, T.M., Dodd, C.K., Doody, J.S., Dorcas, M.E., Duarte de Barros Filho, J., Egan, V.T., El Mouden, E.H., Embert, D., Espinoza, R.E., Fallabrino, A., Feng, X., Feng, Z.J., Fitzgerald, L., Flores-Villela, O., França, F.G.R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S.R., Garcia, M. a., García-Pérez, J.E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J.C.T., Gower, D.J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A.M., Hare, K., Hedges, S.B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F.M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J.S., Köhler, G., Kuchling, G., Kumlutaş, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A.S., López-Luna, M. a., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W.E., Mahler, D.L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O. a V, Márquez, R., Martins, M., Masterson, G., Mateo, J. a., Mathew, R., Mathews, N., Mayer, G., McCranie, J.R., Measey, G.J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D. a., Montgomery, C., Morato, S. a a, Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T.Q., Nilson, G., Nogueira, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, J., Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O.S.G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E.R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G.E., Radder, R., Ramer, J., Rasmussen, A.R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E.L., Riservato, E., Rivas, G., da Rocha, P.L.B., Rödel, M.O., Rodríguez Schettino, L., Roosenburg, W.M., Ross, J.P., Sadek, R., Sanders, K., Santos-Barrera, G., Schleich, H.H., Schmidt, B.R., Schmitz, A., Sharifi, M., Shea, G., Shi, H.T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H.J., Tognelli, M.F., Tolley, K., Tolson, P.J., Tuniyev, B., Tuniyev, S., Üzüm, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Veselý, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R.C., Wearn, O.R., Werner, Y.L., Whiting, M.J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K., Zug, G., 2013. The conservation status of the world's reptiles. Biol. Conserv. 157, 372–385. doi:10.1016/j.biocon.2012.07.015

Briske, D.D., Derner, J.D., Milchunas, D.G., Tate, K.W., 2011. An Evidence-Based Assessment of Prescribed Grazing Practices. Conserv. benefits Rangel. Pract. Assessment, Recomm. Knowl. Gaps 21–74.

Brown, G., Dorrough, J., Ramsey, D., 2011. Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. Landsc. Urban Plan. 103, 277–288. doi:10.1016/j.landurbplan.2011.08.002

Brussaard, L., Caron, P., Campbell, B., Lipper, L., Mainka, S., Rabbinge, R., Babin, D., Pulleman, M., 2010. Reconciling biodiversity conservation and food security: Scientific challenges for a new agriculture. Curr. Opin. Environ. Sustain. doi:10.1016/j.cosust.2010.03.007

Burrell, A., 2012. Evaluating policies for delivering agri-environmental public goods. Eval. Agri-environmental Policies Sel. Methodol. Issues Case Stud. 49–68.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human – induced species losses: entering the sixth mass extinction. Sci. Adv. 1, 1–5. doi:10.1126/sciadv.1400253

Chazdon, R.L., Harvey, C.A., Komar, O., Griffith, D.M., Ferguson, B.G., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Van Breugel, M., Philpott, S.M., 2009.

Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. Biotropica. doi:10.1111/j.1744-7429.2008.00471.x

Commonwealth of Australia, 2013. Environmental Stewardship [WWW Document]. URL http://www.nrm.gov.au/national/continuing-investment/environmental-stewardship

Commonwealth of Australia, 2009. Environmental Stewardship Strategic Framework. Department of the Environment, Water, Heritage and the Arts, Canberra.

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., Diaz, M., Baldi, A., Batary, P., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J. Appl. Ecol. 49, 695–705. doi:10.1111/j.1365-2664.2012.02131.x

Corlett, R.T., 2015. The Anthropocene concept in ecology and conservation. Trends Ecol. Evol. doi:10.1016/j.tree.2014.10.007

Cox, R.L., Underwood, E.C., 2011. The importance of conserving biodiversity outside of protected areas in mediterranean ecosystems. PLoS One 6. doi:10.1371/journal.pone.0014508

Cunningham, R.B., Lindenmayer, D.B., Crane, M., Michael, D.R., Barton, P.S., Gibbons, P., Okada, S., Ikin, K., Stein, J.A.R., 2014. The law of diminishing returns: woodland birds respond to native vegetation cover at multiple spatial scales and over time. Divers. Distrib. 20, 59–71. doi:10.1111/ddi.12145

Cushman, S.A., McGarigal, K., 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landsc. Ecol. 17, 637–646. doi:10.1023/A:1021571603605

Dallimer, M., Gaston, K.J., Skinner, A.M.J., Hanley, N., Acs, S., Armsworth, P.R., 2010. Field-level bird abundances are enhanced by landscape-scale agri-environment scheme uptake. Biol. Lett. 6, 643–6. doi:10.1098/rsbl.2010.0228

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science (80-.). 345, 401–406. doi:10.1126/science.1251817

European Commission, 2014. Agri-environment measures: Agriculture and rural development. [WWW Document]. URL ec.europa.eu/agriculture/ envir/measures/index_en.htm.

Fazey, I., Fischer, J., Lindenmayer, D.B., 2005. What do conservation biologists publish? Biol. Conserv.

Fischer, J., Lindenmayer, D.B., Cowling, A., 2004. The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. J. Appl. Ecol. 41, 32–44. doi:10.1111/j.1365-2664.2004.00869.x

Foley, J.A., 2005. Global Consequences of Land Use. Science (80-.). doi:10.1126/science.1111772

Franklin, J.F., Lindenmayer, D.B., 2009. Importance of matrix habitats in maintaining biological diversity. Proc. Natl. Acad. Sci. 106, 349–350. doi:10.1073/pnas.0812016105

Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E., Benton, T.G., 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. Ecol. Lett. 13, 858–869. doi:10.1111/j.1461-0248.2010.01481.x

Gibbon, J., Scott, D., Ryan, T., Buhlmann, K., Tuberville, T., Metts, B., Greene, J., Mills, T., Leiden, Y., Poppy, S., Winne, C., 2000. The Global Decline of Reptiles, Déjà Vu Amphibians. Bioscience 50, 653–666.

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.-Y., Iverson, A.L., Batáry, P., Rudolphi, J., Tscharntke, T., Cardinale, B.J., Perfecto, I., 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proc. Biol. Sci. 281, 20141358. doi:10.1098/rspb.2014.1358

Haddad, N.M., Brudvig, L. a., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, a. J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B. a., Nicholls, a. O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, 1–9. doi:10.1126/sciadv.1500052

Hajkowicz, S., Collins, K., Cattaneo, A., 2009. Review of agri-environment indexes and stewardship payments. Environ. Manage. 43, 221–236. doi:10.1007/s00267-008-9170-y

Hiron, M., Berg, Å., Eggers, S., Josefsson, J., Pärt, T., Berg, T., Eggers, S., Josefsson, J., Pärt, T., 2013. Bird diversity relates to agri-environment schemes at local and landscape level in intensive farmland. Agric. Ecosyst. Environ. 176, 9–16. doi:10.1016/j.agee.2013.05.013

Jellinek, S., Driscoll, D. a., Kirkpatrick, J.B., 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. Austral Ecol. 29, 294–304. doi:10.1111/j.1442-9993.2004.01366.x

Kay, G.M., 2016. Scaling the benefits of agri-environment schemes for biodiversity, in: Ansell, D., Gibson, F., Salt, D. (Eds.), Learning from Agri-Environment Schemes in Australia: Investing in Biodiversity and Other Ecosystem Services on Farms. ANU Press.

Kay, G.M., Michael, D.R., Crane, M., Okada, S., MacGregor, C., Florance, D., Trengove, D., McBurney, L., Blair, D., Lindenmayer, D.B., 2013. A list of reptiles and amphibians from Box Gum Grassy Woodlands in south-eastern Australia. Check List 9, 476–481.

Kay, G.M., Barton, P.S., Driscoll, D.A., Cunningham, S.A., Blanchard, W., Mcintyre, S., Lindenmayer, D.B., 2016a. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. Anim. Conserv.

19, 515–525. doi:10.1111/acv.12267

Kay, G.M., Mortelliti, A., Tulloch, A., Barton, P., Florance, D., Cunningham, S.A., Lindenmayer, D.B., 2016b. Effects of past and present livestock grazing on herpetofauna in a landscape-scale experiment. Conserv. Biol. 0, 1–35. doi:10.1111/cobi.12779

Kay, G.M., Driscoll, D.A., Lindenmayer, D.B., Pulsford, S.A., Mortelliti, A., 2016c. Pasture height and crop direction influence reptile movement in an agricultural matrix. Agric. Ecosyst. Environ. In Press. doi:10.1016/j.agee.2016.10.019

Kay, G.M., Tulloch, A.I.T., Barton, P.S., Cunningham, S.A., Driscoll, D.A., Lindenmayer, D.B., 2017. Species co-occurrence networks reveal patterns of community restructure under landscape modification. Ecography, 40, 1-13.

Kleijn, D., Sutherland, W.W., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40, 947–969.

Leopold, A.S., 1991. Engineering and conservation, in: Flader, S.L., Callicott, J.B. (Eds.), The River of the Mother of God and Other Essays. University of Wisconsin Press, Madison, USA, pp. 249–254.

Lewis, S.L., Maslin, M. a, 2015. Defining the Anthropocene. Nature 519, 171–180. doi:10.1038/nature14258

Lindenmayer, D.B., Cunningham, S.A., Young, A., 2012a. Land-use intensification: Effects on agriculture, biodiversity and ecological processes. CSIRO Publishing.

Lindenmayer, D.B., Zammit, C., Attwood, S.J., Burns, E., Shepherd, C.L., Kay, G., Wood, J., 2012b. A Novel and Cost-Effective Monitoring Approach for Outcomes in an Australian Biodiversity Conservation Incentive Program. PLoS One 7, (e50872). DOI: 10.1371/journal.pone.0050872. doi:10.1371/journal.pone.0050872

Lüscher, G., Jeanneret, P., Schneider, M.K., Turnbull, L.A., Arndorfer, M., Balázs, K., Báldi, A., Bailey, D., Bernhardt, K.G., Choisis, J.-P., Elek, Z., Frank, T., Friedel, J.K., Kainz, M., Kovács-Hostyánszki, A., Oschatz, M.-L., Paoletti, M.G., Papaja-Hülsbergen, S., Sarthou, J.-P., Siebrecht, N., Wolfrum, S., Herzog, F., 2014. Responses of plants, earthworms, spiders and bees to geographic location, agricultural management and surrounding landscape in European arable fields. Agric. Ecosyst. Environ. 186, 124–134. doi:10.1016/j.agee.2014.01.020

Michael, D.R., Kay, G.M., Crane, M., Florance, D., MacGregor, C., Okada, S., McBurney, L., Blair, D., Lindenmayer, D.B., 2015. Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems. Austral Ecol. 40, 651–660. doi:10.1111/aec.12232

Michael, D.R., Wood, J.T., Crane, M., Montague-Drake, R., Lindenmayer, D.B., 2014. How effective are agri-environment schemes for protecting and improving herpetofaunal diversity in Australian endangered woodland ecosystems? J. Appl. Ecol. 51, 494–504. doi:10.1111/1365-2664.12215

Miller, J.R., Hobbs, R.J., 2002. Conservation where people live and work. Conserv. Biol. doi:10.1046/j.1523-1739.2002.00420.x

Nori, J., Lemes, P., Urbina-Cardona, N., Baldo, D., Lescano, J., Loyola, R., 2015. Amphibian conservation, land-use changes and protected areas: A global overview. Biol. Conserv. 191, 367–374. doi:10.1016/j.biocon.2015.07.028

Novacek, M.J., Cleland, E.E., 2001. The Current Biodiversity Extinction Event: Scenarios for Mitigation and Recovery. Proc. Natl. Acad. Sci. U. S. A. 98, 5466–5470.

Reyers, B., 2013. Conserving Biodiversity Outside Protected Areas, in: Encyclopedia of Biodiversity. pp. 289–305. doi:10.1016/B978-0-12-384719-5.00359-2

Schutz, A.J., Driscoll, D. a., 2008. Common reptiles unaffected by connectivity or condition in a fragmented farming landscape. Austral Ecol. 33, 641–652. doi:10.1111/j.1442-9993.2007.01830.x

Siriwardena, G.M., 2010. The importance of spatial and temporal scale for agri-environment scheme delivery. Ibis (Lond. 1859). 152, 515–529. doi:10.1111/j.1474-919X.2010.01034.x

Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R. De, Eden, P., 2001. Ecological impacts of arable intensification in Europe. J. Environ. Manage. 63, 337–365. doi:10.1006/jema.2001.0473

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl Acad. Sci. 108, 20260. doi:10.1073/pnas.1116437108

Tingley, R., Meiri, S., Chapple, D.G., 2016. Addressing knowledge gaps in reptile conservation. Biol. Conserv. doi:10.1016/j.biocon.2016.07.021

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. doi:10.1016/j.biocon.2012.01.068

Tulloch, A.I.T., Mortelliti, A., Kay, G.M., Florance, D., Lindenmayer, D., 2016. Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies. Conserv. Biol. 0, 1–38. doi:10.1111/cobi.12672

UN, 2013. World population prospects: the 2012 revision, volume I: comprehensive tables. Department of Economic and Social Affairs, Population Division, New York.

UNEP-WCMC, IUCN, 2016. Protected Planet Report 2016. How protected areas contribute to achieving global targets for biodiversity. UNEP-WCMC and IUCN., Cambridge, UK and Gland, Switzerland.

USDA, 2014. 2014 Farm Act Continues Most Previous Trends In Conservation. United States Department of Agriculture, Washington.

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D., Freckleton, R.P., 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. Ecol. Lett. 10, 25–35. doi:10.1111/j.1461-0248.2006.00992.x

Zammit, C.C., 2013. Landowners and conservation markets: Social benefits from two Australian government programs. Land use policy 31, 11–16. doi:10.1016/j.landusepol.2012.01.011

PAPER I: SCALING THE BENEFITS OF AGRI-ENVIRONMENT SCHEMES FOR BIODIVERSITY.

We begin with an introduction to the role of scale for enhancing the effectiveness of agri-environment schemes for biodiversity, highlighting possible areas where research may be useful, recognizing that change can be made both at the local-scale (i.e., the target patch) as well as into the broader landscape. This work was published as a book chapter aimed at practitioners and farmers, and is not intended to be an exhaustive literature review but rather to identify core opportunities to enhance agri-environment scheme effectiveness which are the focus of remaining chapters.

A site targeted under an Australian agri-environment scheme – the Environmental Stewardship Program.

Kay, G.M., 2016. Scaling the benefits of agri-environment schemes for biodiversity, in: Ansell, D., Gibson, F., Salt, D. (Eds.), Learning from Agri-Environment Schemes in Australia: Investing in Biodiversity and Other Ecosystem Services on Farms. ANU Press.

Scaling the benefits of agri-environment schemes for biodiversity.

Key points

- Agri-environment schemes have mixed outcomes for biodiversity, and more monitoring is needed particularly for certain taxonomic groups.
- Agri-environment scheme effectiveness is heavily reliant on the spatial scale of implementation, and addressing this at local and landscape scales is critical for advancing their application for conservation of biodiversity in agricultural landscapes.
- At local scales, information about how species respond to environmental features, as well as the impact of management actions, could improve site selection and effectiveness of management prescriptions.
- At landscape scales, the offsite benefits of agri-environment schemes could be enhanced by better understanding the impact of surrounding landscape context.
- Incorporating information about the patterns of diversity over large areas, as well as the role and sensitivity of habitat metrics to biodiversity, could greatly enhance the biodiversity benefits of agri-environment schemes.

Introduction

Demand for agri-environment schemes to counteract global biodiversity loss has resulted in the development of some large, continental-scale agri-environment schemes. While some schemes have been successful in addressing the social and policy elements of farmland conservation (Zammit, 2013), very few have been able to demonstrate effective biodiversity outcomes across the scale of program implementation (Whittingham et al., 2007). One of the key reasons for this is that, in order to work across large spatial scales, programs have tended to employ rigid management actions, or a one-size-fits-all approach (Batáry et al., 2011; Kleijn and Sutherland, 2003). However, recent studies have demonstrated that the effectiveness of agri-environment schemes is influenced by a number of scale-dependant factors, including the amount invested in agri-environment schemes (Dallimer et al., 2010; Hiron et al., 2013), surrounding landscape context (Batáry et al., 2011; Concepción et al., 2012; Gabriel et al., 2010), and the underlying delivery mechanisms used in scheme design (Hajkowicz et al., 2009; Siriwardena, 2010). Designing better agri-environment schemes requires a greater understanding and incorporation of these scale-effects.

One of the critical aspects of scale relates to management rules applied to achieve agri-environment scheme goals (see Figure 1). Management rules can be applied at one of two scales: locally at the site (i.e. within a single management unit), or across the whole landscape (i.e. at multiple management units). Irrespective of the goal of a particular agri-environment scheme, both the local and landscape- wide management rules are important for achieving conservation outcomes (Gonthier et al., 2014). If we want to conserve targeted species then it is important to not only protect key habitats but also the potential processes aiding their dispersal and other important aspects of their biology (see metapopulation theory). Conversely, if we want to conserve whole communities, we need to understand how they respond to local-scale management. Despite this recognition, our knowledge and integration of these scale-effects into agri-environment schemes remains very limited (Siriwardena, 2010). For example, site- level management actions (such as prescribed or rotational grazing) remain poorly resolved (Briske et al., 2011b), and landscape-scale dispersal information is poorly understood for many taxa (Driscoll et al., 2014). Better knowledge of local- and landscape-scale factors that influence conservation outcomes would therefore address a key knowledge gap and provide an opportunity to enhance biodiversity outcomes of agri-environment schemes.

In this chapter, we address this knowledge gap by revealing opportunities to integrate scale-effects to improve agri-environment scheme effectiveness for biodiversity across both local and landscape scales. First, we address the need for biological monitoring over ecologically relevant time frames for quantifying scale-effects on agri-environment schemes. Summarising current knowledge of how local- and landscape-scale factors influence agri-environment schemes, we then provide novel research priorities at these scales.

Monitoring outcomes of agri-environment schemes

Quantifying scale-effects on agri-environment schemes relies on a thorough understanding of the biodiversity response to management decisions at different scales. However, despite the significant investment and widespread implementation, many agri-environment schemes have not demonstrated effective outcomes for biodiversity (Kleijn and Sutherland, 2003; Lindenmayer et al., 2012c; Michael et al., 2014). Amongst other reasons, this is due to a paucity of rigorous assessment and monitoring (Herzog, 2005; Perkins et al., 2013), especially for certain taxonomic groups, such as reptiles (Michael et al., 2014). Even where monitoring data is available, our understanding of the scale-effects on biodiversity have largely emerged from what we know of agri-environment schemes in a limited set of regions (e.g. American and European landscapes) (Batáry et al., 2015). To properly assess the biodiversity responses to agri-environment schemes we need to develop robust, statistically verified scientific monitoring programs (Lindenmayer et al., 2012c) across a wider set of ecological systems (see Chapter 3). Such programs must be designed around specific agri-environment scheme goals (i.e. single species versus whole communities), and focus on observing population- or community-level changes across multiple taxa at target sites, as well as comparable reference sites.

It is important to consider the time frames necessary for biodiversity response to agri-environment schemes when developing monitoring programs. The inability of many

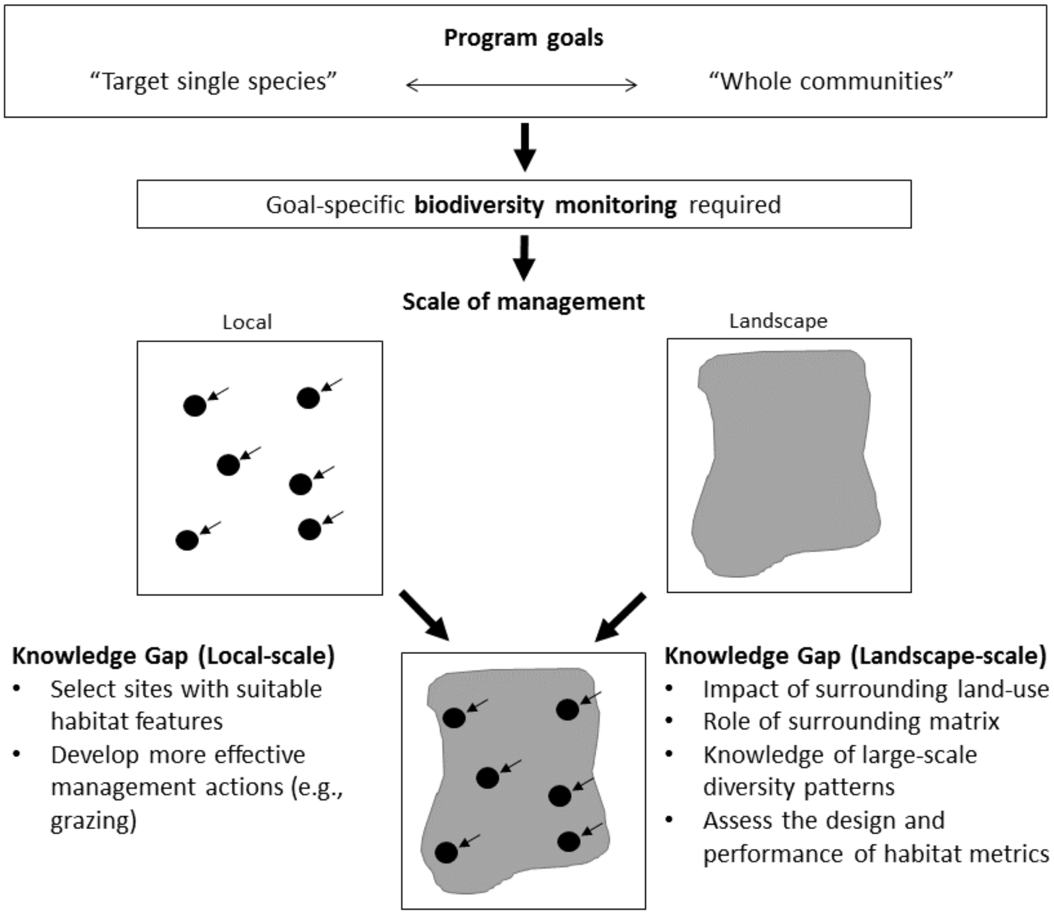

Figure 1: *Conceptual flow for the advancement of agri-environment schemes through incorporation of scale-effects. Regardless of agri-environment scheme program goals, biodiversity monitoring is required to validate program success. Opportunities to enhance performance of agri-environment schemes by addressing key knowledge gaps*

existing monitoring programs to show effective biodiversity response may not reflect failure of the program per se, but that insufficient time has passed for relevant ecological processes to succeed. This emphasizes the need to continue monitoring over long timeframes far exceeding policy cycles. Critically, however, this does not mean we need to wait until we detect positive change to identify the perfect program. Instead, the limited capacity demonstrated in agri-environment scheme for achieving mid-term outcomes could be addressed by identifying opportunities to enhance the current models, and this is the focus of the next section.

Key research priorities:

1. *There is a great need for more rigorous, scientifically designed biodiversity monitoring to quantify effectiveness of agri-environment schemes, particularly outside of American and European landscapes, and for some under-represented species groups (e.g. reptiles)*

2. *Monitoring of such programs must be long lasting to adequately capture their positive ecological effects.*

Advancing agri-environment schemes through understanding scale-effects

Local-scale

Fundamentally, the success of any agri-environment scheme relies on the positive response of biodiversity to investment at the local (i.e., field or investment) scale. This is the smallest management scale within an agri-environment scheme, typically 1-10 kilometres, to which landholders apply the funded conservation management actions.

These actions are generally targeted towards specific groups of organisms or agricultural practices, which often include (but are not limited to) promotion of native vegetation, soil health and habitat components (possibly for target species), and prevention of damaging management practices such as fertilization and overgrazing (Zammit et al., 2010). Positive biodiversity response in agri-environment schemes therefore depend on two fundamental assumptions: suitable habitat is incorporated within the investment sites selected; and the imposed management actions enhance or maintain suitable conditions (e.g. habitat) for biota. Despite the wide application of agri-environment scheme, major knowledge gaps surround both of these assumptions (Figure 1).

The incorporation of suitable habitat (or the provisioning for future habitat) is critical for achieving biodiversity gain in any agri-environment scheme program. This requires careful consideration of the sites being selected. However, one of the major assumptions regarding site selection is that all habitat within a given ecosystem or species range are equal in condition and extent. For example, native vegetation cover is considered important for a wide number of species (McElhinny et al., 2006) and so is included in the site selection of many Australian agri-environment scheme. However in many ecosystems targeted under agri-environment schemes, little is known about which habitat features are most important for species. Moreover, the positive influence of specific environmental features is likely to vary for different species, whole communities and across different biogeographic or climatic zones (Whittingham et al., 2007). It may therefore be important to ask whether targeting certain habitat features (e.g. those important for rare species) can improve the effectiveness of agri-environment scheme for other biota. Indeed, some of the most important drivers of biodiversity may be climatic or landscape features (e.g. elevation), which cannot be influenced by management.

Central to agri-environment schemes policy is the use of carefully prescribed site-level management actions, which counteract the negative influence of agriculture on biodiversity. Management actions addressing the impact on biodiversity from wide-spread agricultural practices (e.g. livestock overgrazing, fertiliser application) are considered most desirable (Dallimer et al., 2010). Despite a focus on these management actions in agri-environment schemes, their role in averting biodiversity loss is poorly known. For example, there is little consensus on the impacts of livestock grazing as a management tool for biodiversity, despite widespread application and decades of research (Briske et al., 2011b). A better understanding of the outcomes of management actions on biodiversity (particularly large-scale ones, such as livestock grazing) would have large implications for enhancing site-level response to agri-environment schemes.

Key research priorities:

3. *A better understanding of the influence of environmental features on biodiversity is important for enhancing local-scale agri-environment scheme effectiveness. This information can then be integrated with the site selection stage as well as developing on-ground strategies to support these features, either by selecting for them or restoring them.*

4. *A better understanding of the influence of conservation management actions – such as livestock grazing – should be developed so that this knowledge can be incorporated into agri-environment scheme policy in a more refined way.*

Landscape scale

An underlying basis for successful agri-environment schemes is that they propagate positive biodiversity benefit from investment sites into the broader landscape. The extent to which this occurs depends heavily on the hostility of the surrounding landscape (Tscharntke et al. 2005). Yet the mechanisms remain poorly understood. This is particularly the case for species with limited dispersal (e.g. terrestrial invertebrates, reptiles), which are most sensitive to the negative impacts of fragmentation in an agricultural matrix.

Recent studies have found that the biodiversity response to agri-environment scheme investment is influenced by the context of the surrounding landscape (Carvell et al. 2011; Concepción et al. 2012), although this response is inconsistent and poorly resolved (Batáry et al. 2011). The greatest positive biodiversity response has been observed in landscapes with an intermediate level of ‘complexity’ — the degree of variation within landscape (Concepción et al. 2012). Despite this, other studies have found inconsistent results for different taxonomic groups for both simple and complex landscapes, and that the effect of complexity depends on the type of surrounding vegetation (Batáry et al. 2011). Landscapes with a greater proportion of area covered by management demonstrate stronger positive biodiversity response (Baker et al. 2012; Dallimer et al. 2010), although whether this is in response to direct agri-environment scheme investment or greater inclusion of suitable landscapes remains unclear. A greater number of studies exploring the influence of surrounding landscape on agri-environment schemes success are clearly required to systematically investigate each of these conflicting elements. Given that our current understanding is nearly exclusively from European (e.g. Concepción et al. 2012) and American landscapes (e.g. Carvell et al., 2011), future investigations of this kind within

Australian landscapes are critical for providing a more rounded understanding of how to enhance agri-environment schemes at landscape scales.

Recent studies have found that the biodiversity response to agri-environment scheme investment is influenced by the context of the surrounding landscape (Carvell et al., 2011; Concepción et al., 2012) although this response is inconsistent and poorly resolved (Batáry et al., 2011). The greatest positive biodiversity response has been observed in landscapes with an intermediate level of "complexity" (where complexity is the degree of variation within landscape) (Concepción et al., 2012). Despite this, other studies have found inconsistent results for different taxonomic groups for both simple and complex landscapes, and further that the effect of complexity depends on the type of surrounding vegetation (Batáry et al., 2011). Additionally, landscapes with a greater proportion of area covered by agri-environment scheme management demonstrate stronger positive biodiversity response (Baker et al., 2012; Dallimer et al., 2010) although whether this is in response to direct agri-environment scheme management or greater inclusion of agri-environment scheme "suitable" landscapes remains unclear. A greater number of studies exploring the influence of surrounding landscape on agri-environment scheme success are clearly required to systematically investigate each of these conflicting elements. Given that our current understanding is nearly exclusively from European (e.g. Concepción et al., 2012) and American landscapes (e.g. Carvell et al., 2011), future investigations of this kind within an Australian landscape are critical for providing a more rounded understanding of how to enhance agri-environment scheme at landscape scales.

In addition to understanding *how* landscape context can affect agri-environment scheme success, it is important to know *why* landscape context may affect agri-environment scheme success. One of the key assumptions in agri-environment scheme policy is that investment will promote propagation of biodiversity into the broader landscape evenly (Whittingham et al., 2007), although it is clear that dispersal into surrounding landscapes for some species (e.g. ground-dependant species such as reptiles) will be more challenging than others (e.g. birds). This is because the type of land-use and style of management employed in surrounding landscapes is likely to greatly influence the capacity of species to disperse, particularly for those with limited dispersal ability most at risk to fragmentation. For agri-environment scheme to better support the conservation of such species in the broader landscape, it is crucial that a greater understanding of how these species disperse in different matrix environments is gained – so that non-hostile matrix environments can be created. We can achieve this by examining the effect of surrounding land-use (e.g. native, improved or cropped landscapes), as well as the impact of certain management actions (e.g. grazed and open pastures vs ungrazed and dense pastures), on the movement of limited-dispersing species.

Key Research Priorities:

5. *A better understanding of the influence of surrounding landscape (including land-use context and landscape complexity) on biodiversity response to agri-environment schemes would; (i) improve site selection processes, and (ii) provide prescription for management incentives in surrounding landscapes.*

6. *A better understanding of the influence of land-use on the movement of low-dispersal taxa could enhance regional effectiveness of agri-environment schemes by targeting specific management actions that reduce the hostility of the matrix for dispersers.*

Conclusions

Enhancing the effectiveness of agri-environment schemes for biodiversity conservation requires management attention at multiple scales, from local to landscape. We have identified key knowledge gaps and priority areas for research that would improve the rigid one-size-fits-all model commonly applied to agri-environment schemes. We contend that the effectiveness of agri-environment schemes must be advanced if we are to counter the effects of agriculture on biodiversity, and that monitoring data across multiple scales, for a much wider range of taxa, is required.

References

Baker, D.J., Freeman, S.N., Grice, P. V., Siriwardena, G.M., David, J., Stephen, N., Phil, V., Gavin, M., Baker, D.J., Freeman, S.N., Grice, P. V., Siriwardena, G.M., 2012. Landscape-scale responses of birds to agri-environment management: A test of the English Environmental Stewardship scheme. J. Appl. Ecol. 49, 871–882. doi:10.1111/j.1365-2664.2012.02161.x

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B Biol. Sci. 278, 1894–1902. doi:10.1098/rspb.2010.1923

Batáry, P., Dicks, L. V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. doi:10.1111/cobi.12536

Briske, D., Sayre, N., Huntsinger, L., Fernandez-Gimenez, M., Budd, B., Derner, J., 2011. Origin, Persistence, and Resolution of the Rotational Grazing Debate: Integrating Human Dimensions Into Rangeland Research. Rangel. Ecol. Manag. 64, 325–334. doi:10.2111/REM-D-10-00084.1

Carvell, C., Osborne, J.L., Bourke, A.F.G., Freeman, S.N., Pywell, R.F., Heard, M.S., 2011. Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. Ecol. Appl. 21, 1760–1771. doi:10.1890/10-0677.1

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., Diaz, M., Baldi, A., Batary, P., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J. Appl. Ecol. 49, 695–705. doi:10.1111/j.1365-2664.2012.02131.x

Dallimer, M., Gaston, K.J., Skinner, A.M.J., Hanley, N., Acs, S., Armsworth, P.R., 2010. Field-level bird abundances are enhanced by landscape-scale agri-environment scheme uptake. Biol. Lett. 6, 643–6. doi:10.1098/rsbl.2010.0228

Driscoll, D. a., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., Lindenmayer, D.B., Smith, A.L., Berry, L.E., Burns, E.L., Edworthy, A., Evans, M.J., Gibson, R., Heinsohn, R., Howland, B., Kay, G., Munro, N., Scheele, B.C., Stirnemann, I., Stojanovic, D., Sweaney, N., Villaseñor, N.R., Westgate, M.J., 2014. The Trajectory of Dispersal Research in Conservation Biology. Systematic Review. PLoS One 9, e95053. doi:10.1371/journal.pone.0095053

Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E., Benton, T.G., 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. Ecol. Lett. 13, 858–869. doi:10.1111/j.1461-0248.2010.01481.x

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.-Y., Iverson, A.L., Batáry, P., Rudolphi, J., Tscharntke, T., Cardinale, B.J., Perfecto, I., 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proc. Biol. Sci. 281, 20141358. doi:10.1098/rspb.2014.1358

Hajkowicz, S., Collins, K., Cattaneo, A., 2009. Review of agri-environment indexes and stewardship payments. Environ. Manage. 43, 221–236. doi:10.1007/s00267-008-9170-y

Herzog, F., 2005. Agri-environment schemes as landscape experiments. Agric. Ecosyst. Environ. 108, 175–177. doi:10.1016/j.agee.2005.02.001

Hiron, M., Berg, Å., Eggers, S., Josefsson, J., Pärt, T., Berg, T., Eggers, S., Josefsson, J., Pärt, T., 2013. Bird diversity relates to agri-environment schemes at local and landscape level in intensive farmland. Agric. Ecosyst. Environ. 176, 9–16. doi:10.1016/j.agee.2013.05.013

Kleijn, D., Sutherland, W.W., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40, 947–969.

Lindenmayer, D.B., Zammit, C., Attwood, S.J., Burns, E., Shepherd, C.L., Kay, G., Wood, J., 2012. A Novel and Cost-Effective Monitoring Approach for Outcomes in an Australian Biodiversity Conservation Incentive Program. PLoS One 7, (e50872). DOI: 10.1371/journal.pone.0050872. doi:10.1371/journal.pone.0050872

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2006. Fauna-habitat relaionships: A basis for identifying key stand structural attributes in temperate Australian eucalypt forests and woodlands. Pacific Conserv. Biol.

Michael, D.R., Wood, J.T., Crane, M., Montague-Drake, R., Lindenmayer, D.B., 2014. How effective are agri-environment schemes for protecting and improving herpetofaunal diversity in Australian endangered woodland ecosystems? J. Appl. Ecol. 51, 494–504. doi:10.1111/1365-2664.12215

Perkins, G., Kutt, A., Vanderduys, E.P., Perry, J., Perryl, J.J., 2013. Evaluating the costs and sampling adequacy of a vertebrate monitoring program. Aust. Zool. 36, 373–380.

Siriwardena, G.M., 2010. The importance of spatial and temporal scale for agri-environment scheme delivery. Ibis (Lond. 1859). 152, 515–529. doi:10.1111/j.1474-919X.2010.01034.x

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D., Freckleton, R.P., 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. Ecol. Lett. 10, 25–35. doi:10.1111/j.1461-0248.2006.00992.x

Zammit, C., Attwood, S., Burns, E., 2010. Using markets for woodland conservation: lessons from the policy-research interface, in: Lindenmayer, D.B., Bennett, A.F., Hobbs, R.J. (Eds.), Temperate Woodland Conservation and Management. CSIRO Publishing, Melbourne, pp. 297–307.

Zammit, C.C., 2013. Landowners and conservation markets: Social benefits from two Australian government programs. Land use policy 31, 11–16. doi:10.1016/j.landusepol.2012.01.011

PAPER II: A LIST OF REPTILES AND AMPHIBIANS FROM BOX GUM GRASSY WOODLANDS IN SOUTH-EASTERN AUSTRALIA.

One of the critical elements of assessing effectiveness of agri-environment schemes is the establishment of robust empirical biodiversity monitoring programs. In this paper, we report the baseline monitoring results from the focal agri-environment scheme (the Australian Environmental Stewardship Programme) to provide an inventory of species present in the system, and to identify the effects of agri-environment schemes on biodiversity.

A Shingleback lizard (Tiliqua rugosa) detected during surveys of the Environmental Stewardship Program.

Kay, G.M., Michael, D.R., Crane, M., Okada, S., MacGregor, C., Florance, D., Trengove, D., McBurney, L., Blair, D., Lindenmayer, D.B., 2013. A list of reptiles and amphibians from Box Gum Grassy Woodlands in south-eastern Australia. Check List 9, 476–481.

A list of reptiles and amphibians from Box Gum Grassy Woodlands in south-eastern Australia.

Abstract

A large-scale biodiversity monitoring program examining the response of herpetofauna to the Australian Government's Environmental Stewardship Program is taking place in south-eastern Australia within the critically endangered Box Gum Grassy Woodland vegetation community. Field surveys involve counting reptiles in areas under Environmental Stewardship management. These "Stewardship" areas have been matched with areas managed for primary production (domestic livestock grazing). We list reptiles recorded during surveys conducted between 2010 and 2012. We recorded sixty-nine species from ten families. The list will be useful for workers interested in the zoogeographical distribution of reptiles and amphibians in fragmented agricultural woodland ecosystems.

Introduction

Reptiles and amphibians have experienced unprecedented levels of population decline and extinction on a global scale (Alford and Richards 1999; Gibbons *et al.* 2000, Houlahan *et al.* 2000, Araujo *et al.* 2006). This trend has sparked widespread concern over the cause and effect of this global decline (Gibbons *et al.* 2000, Blaustein and Kiesecker 2002, Whitfield *et al.* 2007) and has led to the recognition that baseline distribution data are fundamental for resolution of this issue (McDiarmid *et al.* 2012). However, such data are lacking for many taxa (Foster *et al.* 2012), particularly on private-tenure land, and this is of major concern given the impact of agricultural practices on herpetofaunal diversity (Michael and Lindenmayer 2010).

Agricultural expansion, intensification and climate change are considered primary causes of reptile and amphibian declines worldwide (Fabricius *et al.* 2003, Driscoll 2004, Whitfield *et al.* 2007, Brown *et al.* 2008, Ribeiro *et al.* 2009, Sinervo *et al.* 2010). To address this issue, a number of agri-environment schemes (AES) have been developed around the world, whereby billions of dollars are spent annually (Donald and Evans 2006) in an attempt to integrate biodiversity conservation with production in agricultural landscapes (Kleijn and Sutherland 2003, Kleijn *et al.* 2006). However, many of these schemes have been criticised for their lack of rigorous assessment and monitoring to quantify their effectiveness for biodiversity (Kleijn and Sutherland 2003, Kleijn *et al.* 2006, Zammit *et al.* 2010). In recognition of the growing concern about biodiversity conservation issues in production landscapes, the Australian Federal Government established the Environmental Stewardship Program (ESP). This program aims to maintain and/or improve the condition and extent of targeted ecological communities of national environmental significance under the *Environment Protection and Biodiversity Conservation Act 1999*. The first target for the ESP was the Box Gum Grassy Woodland (BGGW) vegetation type, which is an endangered ecological community. This community extends from Queensland through New South Wales to Victoria (a region known as the wheat-sheep belt of south-eastern Australia) and has been reduced to less than four per cent of its original extent and occurs as remnants of varying condition on productive agricultural land (Zammit *et al.* 2010).

The ESP offers private land managers financial incentives to undertake prescriptive management interventions which may include reducing grazing intensity by domestic livestock, reducing fertilizer use, undertaking exotic plant management, and replanting of local provenance native species. Land managers in the ESP receive funds from the

Australian Government once they have entered into a contractual agreement ranging from four to 15 years. To help evaluate the success of this program, The Australian National University was engaged to develop and implement a biodiversity monitoring program across the BGGW ecosystem. In this paper, we provide baseline data for reptiles and frogs recorded between 2010 and 2012 as part of the ESP BGGW project.

Methods

Study area

The study was undertaken within the critically endangered BGGW ecosystem in south-eastern Australia, covering five water catchments in New South Wales and two catchments in southern Queensland. These catchments were the Murrumbidgee (MCMA), Lachlan (LCMA), Central West (CWCMA), Namoi (NCMA), Border Rivers – Gwydir (BRCMA), Maranoa-Balonne (MBCMA) and Condamine (CCMA) (Figure 1). This area extends from Warwick in the north-east (28°1’32” S, 152°12’22” E) to Bredbo in the south (35°56’32” S, 149°9’32” E), and Leeton in the west (34°40’43”S, 146°16’48” E).

The annual average rainfall in the region ranges from 504mm in the south (Bredbo weather station, BOM) to 692mm in the north (Canning Downs weather station, BOM). The study area is characterised by a slightly wetter spring-summer period than autumn-winter period. The average minimum and maximum summer temperature ranges from 9°C – 27°C in the South (Cooma weather station, BOM) and 14.3°C – 29.4°C in the north (Killarney weather station, BOM). Average minimum and maximum winter temperatures range from -2.8°C – 13.4°C in the south (Cooma weather station, BOM) and 2.1°C – 18.7°C in the north (Killarney weather station, BOM).

The BGGW community comprises a diverse vegetation assemblage dominated by the overstorey species white box *Eucalyptus albens* (Benth 1867), yellow box *E. melliodora* (A.Cunn. ex Schauer sensu Chah 2006), and Blakely's red gum *E. blakelyi* (Maiden 1917). Several additional overstorey species also co-occur in BGGW, including grey box *E. microcarpa* (Hook 1842), white cypress pine *Callitris glaucophylla* (Joy Thomps. and L.A.S.Johnson 1986), black cypress pine *C. endlicheri* ((Parl.) F.M.Bailey 1883), red box *E. polyanthemos* (Schauer 1843), red stringybark *E. macrorhyncha* (F.Muell ex Benth 1867), long-leaved box *E. goniocalyx* (F.Muell. ex Miq. 1856), apple box *E. bridgesiana* (Baker 1898), mugga ironbark *E. sideroxylon* (Woolls 1990), and kurrajong *Brachychiton populneus* (Schott and Endl. 1844). Different overstorey plant assemblages define sub-vegetation communities within the broader BGGW community as identified in the NSW Vegetation Classification and Assessment (VCA) scheme (NSW Office of Environment and Heritage, 2012).

The understorey of BGGW is typically dominated by perennial native grasses and forbs with few or no shrubs. Dominant grass species include kangaroo grass *Themeda australis* (R.Br.Stapf 1918), red-leg grass *Bothriochloa macra* (Blake 1969), wallaby grasses *Austrodanthonia* spp., and spear grasses *Austrostipa* spp. Included within the endangered BGGW community is a Derived Native Grasslands sub-community, which contains a largely intact assemblage of BGGW understorey flora but has experienced extensive removal of the dominant overstorey and midstorey species.

Survey design

We established a single monitoring site within discrete areas of remnant vegetation on 153 farms funded under the ESP. These sites, which are subject to management intervention,

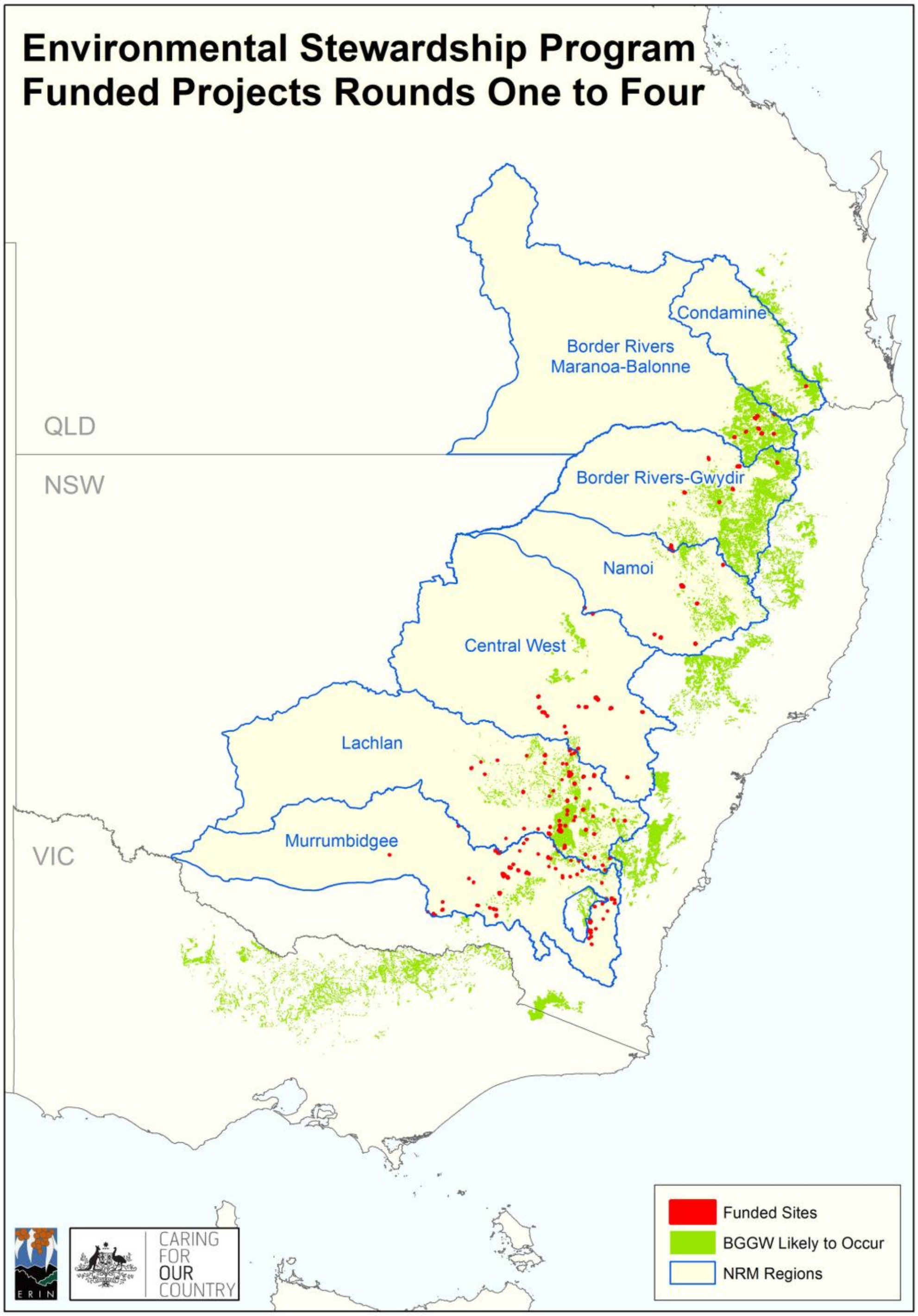

Figure 1: *Box Gum Grassy Woodland Project study area and monitoring site locations (n=262) across seven catchment management zones. Maps produced by the Environmental Resources Information Network (ERIN), Department of Sustainability, Environment, Water, Population and Communities (SEWPAC).*

are termed ‘treatments’. In addition, we established a monitoring site on the same property within an area of remnant vegetation managed for agricultural production (i.e. not funded under ESP). These sites in areas not funded under ESP served as matched external spatial reference areas and are termed ‘controls’. Because it was not possible to find matched controls on 44 farms (either because suitable remnant vegetation did not exist or the same vegetation community was not present) we established 109 control sites in the final design, giving 263 sites in total. The establishment of spatial controls was important to determine if changes in vegetation condition or biodiversity are due to management intervention and not climatic factors or local population fluctuations. Table 1 provides the number of sites in each management class, which span seven regional catchment management areas (CMA’s).

Reptile Surveys

We established a permanent 200 m transect on all stewardship and control sites. Along each transect we placed two arrays of cover objects 100 m apart. Each array consisted of four roof tiles (32 cm x 42 cm), two sheets of corrugated iron (1 m x 1 m) stacked on top of each other and four wooden sleepers (1.2 m long). At each site, we conducted a 20-minute active search for reptiles by inspecting exfoliating bark, fallen timber, surface rocks, leaf litter and arrays of artificial refuges (ARs) within a 1 ha search area (200 m x 50 m). These methods are effective for surveying a broad range of herptofauna in temperate woodland ecosystems (Michael et al. 2012). The same group of experienced field ecologists from

The Australian National University conducted all surveys. We surveyed all sites over the 2-year baseline period (2010-2011) in spring (September-October) using active searches and inspection of ARs. Extensive rain in 2010 prevented all sites in the northern catchments (NCMA, BRGCMA, BRMB CMA and CCMA) from being surveyed. All sites were again surveyed by inspection of ARs only during the summer/autumn (February-April) of 2012. We conducted all surveys between 09:00 h – 16:00 h on clear days with minimal wind. We identified species using keys and descriptions in Cogger (2000), Wilson and Swan (2010) and Tyler and Knight (2011), and individuals were released once recorded. We conducted surveys under the Department of Environment and Climate Change scientific license number 13174 and Queensland Government Environmental Protection Agency scientific licence number WISP08460910. Individual animals were only recorded without any specimens being taken. Where identification was difficult the animal was hand-captured and released to the same location it was caught after approximately a 1 minute handling time.

Statistical analyses

Herpetofaunal species richness recorded in each of the stewardship and control treatments was analysed using a paired t-test using the package GenStat14 (VSN International 2011). Differences in species richness between catchments, between stewardship and control sites within catchments and their interaction were investigated further by fitting generalised linear models with an over dispersed Poisson distribution and a log-link function. Significance of effects was assessed from deviance ratios represented as F statistics.

Results & Discussion

Table 1 contains a list of reptiles and amphibians recorded during field surveys between 2010 and 2012. We recorded 69 species from ten families. This total represents 61.9% of species expected or known to occur in the study area based on the literature and wildlife atlas databases (Atlas of Living Australia 2012, Robinson 1998, Wilson and Swan 2010). Notable absences from our list of recorded species include the Spotted Python *Antaresia* *maculosa* (Kluge 1993), Carpet Python *Morelia spilota* (Barker and Barker 1994), Green Tree Snake *Dendrelaphis punctulata* (Gray 1827) and Common Death Adder *Acanthophis antarcticus* (Shaw and Nodder 1802).

Over the entire region, we found that overall herpetofaunal species richness was significantly different between catchments ($F_{6,241}=10.10$; $P<0.001$). The northern Namoi, Border Rivers-Gwydir and Maranoa-Balonne catchments contained higher average herpetofaunal richness per site than those in the south. The Condamine catchment represented an exception to this trend, however this catchment also had the least number of surveys and greatest error (Table 2). Our results follow a common pattern of higher species richness with decreasing latitude – a well-known result for species richness patterns (Gaston and Spicer 2004). Furthermore, species richness within certain genera appeared to correlate with latitude, with *Ctenotus* and *Lymnodynastes* having greater diversity at higher latitudes and *Amalosia*, *Amphibolurus*, *Carlia*, *Cryptoblepharus* and *Delma* diversity being higher at lower latitudes. This latitudinal gradient of within- genera diversity is of importance for large-scale (State or Federal) conservation managers because the northern and southern catchments exhibit marked differences in the composition of herpetofaunal assemblages despite having similar levels of overall herpetofaunal species richness.

We found high spatial variation in species detected across the study area, with distinct assemblages associated with elevation and sub-vegetation communities. *Hemiergis decresiensis* and *Lampropholis guichenoti* were commonly found in association with *Eucalyptus viminalis* (Labill. 1956) communities at mid-elevations and moist drainage lines. These associations highlight the importance of some kinds of vegetation remnants on agricultural land, which can be relatively species-rich in this highly fragmented and critically endangered BGGW ecosystem. These initial findings from the ESP BGGW project revealed no significant difference in herpetofaunal species richness between stewardship and control sites (t=0.1, P=0.91). This result is expected given the early stage of this study and the rigorous site matching process pairing sites on the basis of vegetation type, vegetation condition and other characteristics such as landform, patch size and patch connectivity. However, ongoing surveys are required to evaluate the effectiveness of ESP management intervention over time.

Table 1. *Reptile and amphibian species detected between 2010 and 2012 in seven catchment areas in south-eastern Australia, classified by management type (C = control, S = stewardship). The seven Catchment Management Areas (CMA) surveyed include Murrumbidgee (MCMA), Lachlan (LCMA), Central West (CWCMA), Namoi (NCMA), Border Rivers – Gwydir (BRGCMA), Border Rivers Maranoa-Balonne (BRMBCMA) and Condamine (CCMA). Codes are absent (-), S = sparse (detected at < 5% sites), R = rare (detected at 5 – 25% of sites), U = uncommon (detected at 26-50% of sites), C = common (detected at > 51 % of sites). Listed vulnerable (*) and threatened (**) taxa listed in bold. Nomenclature follows Wilson and Swan (2010) and AROD (2012).*

	MCMA		**LCMA**		**CWCMA**		**NCMA**		**BRG CMA**		**BRMB CMA**		**CCMA**		**Tot**
	C	**S**	**C**	**S**	**C**	**S**	**C**	**S**	**C**	**S**	**C**	**S**	**C**	**S**	
	Number of sites														
Scientific Name	42	57	36	56	17	16	5	6	4	7	7	8	1	1	*263*
AGAMIDAE															
Amphibolurus burnsi	-	-	-	-	-	-	-	-	R	R	-	-	-	-	*2*
Amphibolurus muricatus	-	S	S	S	-	-	-	-	-	-	R	R	-	-	*8*
Diporiphora nobbi	-	-	-	-	-	-	-	-	-	U	U	-	-	-	*5*
Physignathus lesueurii	-	-	-	-	-	-	-	-	-	R	-	-	-	-	*1*
Pogona barbata	S	R	R	S	R	R	R	R	R	-	-	-	-	-	*12*
CHELIDAE															
Chelodina longicollis	-	-	-	S	-	-	-	-	-	-	-	-	-	-	*1*
ELAPIDAE															
Demansia psammophis	-	-	S	-	-	-	-	R	U	U	U	-	-	-	*9*
Furina diadema	-	-	-	-	-	-	R	-	-	-	-	R	-	-	*2*
Parasuta dwyeri	S	-	R	S	R	R	-	-	-	-	C	-	-	-	*11*
Pseudechis guttatus	-	-	-	S	-	-	-	-	-	-	-	-	-	-	*1*
Pseudechis porphyriacus	-	S	-	-	-	-	-	-	-	-	-	-	-	-	*1*
Pseudonaja textilis	-	R	R	R	R	R	-	-	-	R	-	R	-	-	*20*
Cryptophis nigrescens	-	-	-	-	-	-	-	-	-	-	-	-	-	C	*1*
Suta suta	-	-	-	-	-	-	-	-	-	R	-	-	-	-	*1*
Vermicella annulata	-	-	-	-	-	-	-	-	-	-	R	-	-	-	*1*
GEKKONIDAE															
Amalosia rhombifer	-	-	-	-	-	-	-	-	R	-	-	-	-	-	*1*
Amalosia robusta	-	-	-	-	-	-	-	-	-	-	-	R	C	-	*3*
Amalosia tryoni	-	-	-	-	-	-	-	R	R	-	-	-	-	-	*2*
Christinus marmoratus	R	R	U	R	-	-	-	-	-	-	-	-	-	-	*30*
Diplodactylus vittatus	S	R	R	R	R	-	-	-	-	-	-	R	-	-	*18*
Gehyra variegata	-	S	R	S	R	R	-	-	-	-	-	U	-	-	*9*

	MCMA		**LCMA**		**CWCMA**		**NCMA**		**BRG CMA**		**BRMB CMA**		**CCMA**		**Tot**
	C	**S**	**C**	**S**	**C**	**S**	**C**	**S**	**C**	**S**	**C**	**S**	**C**	**S**	
	Number of sites														
Heteronotia binoei	-	-	-	-	-	-	-	-	-	U	C	C	-	-	*15*
Lucasium steindachneri	-	-	-	-	-	-	-	-	-	-	R	-	-	-	*1*
Strophurus intermedius	-	-	S	-	-	-	-	-	-	-	-	-	-	-	*1*
Underwoodisaurus milii	-	S	-	-	-	-	-	-	-	-	-	-	-	-	*2*
HYLIDAE															
Litoria caerulea	-	R	R	R	-	-	C	-	-	C	U	R	-	C	*24*
Litoria latopalmata	S	-	R	-	-	-	-	R	-	-	U	R	-	-	*10*
Litoria peronii)	S	S	C	R	R	R	-	-	-	R	-	-	-	-	*37*
Litoria rubella	-	-	-	-	-	-	-	-	R	R	R	-	-	-	*3*
MYOBATRACHIDAE															
Crinia parinsignifera	R	-	-	S	-	-	-	-	-	-	-	R	-	-	*6*
Crinia signifera	-	S	R	R	-	-	-	-	C	C	-	-	-	-	*16*
Limnodynastes dumerilii	-	-	-	S	-	-	-	-	-	-	-	-	-	-	*1*
Limnodynastes fletcheri	-	-	S	-	-	-	-	-	-	-	-	-	-	-	*1*
Limnodynastes interioris	-	S	R	-	R	R	-	-	-	-	-	-	-	-	*5*
Limnodynastes peronii	S	S	R	S	-	-	-	-	R	-	-	-	-	-	*7*
Limnodynastes tasmaniensis	C	U	C	C	R	-	-	R	-	U	-	R	C	-	*161*
Notaden bennettii	-	-	-	S	-	-	-	-	-	-	-	-	-	-	*1*
Pseudophryne bibronii	-	-	-	-	-	-	-	R	-	-	-	-	-	-	*1*
Uperoleia laevigata	U	U	R	U	-	-	-	-	R	-	R	R	-	-	*64*
Uperoleia rugosa	-	-	-	-	-	-	-	-	-	-	-	U	-	-	*4*
PYGOPODIDAE															
Aprasia parapulchella	S	R	R	S	-	-	-	-	-	-	-	-	-	-	*14*
Delma inornata	R	S	R	S	-	-	U	-	-	R	-	-	-	-	*12*
Delma plebeia	-	-	-	-	-	-	-	R	-	R	U	R	-	-	*6*
Delma tincta	-	-	-	-	-	-	-	-	-	R	-	-	-	-	*1*
SCINCIDAE															
Acritoscincus platynota	-	R	-	-	-	-	-	-	-	-	-	-	-	-	*3*
Anomalopus leuckartii	-	-	-	-	R	R	-	R	U	U	R	R	-	-	*7*
Carlia tetradactyla	U	U	C	R	R	-	-	R	-	-	U	U	-	-	*83*
Carlia vivax	-	-	-	-	-	-	-	-	-	-	U	R	-	-	*3*
Cryptoblepharus pannosus	R	U	R	R	R	R	R	-	R	R	-	R	-	-	*45*
Cryptoblepharus pulcher	-	-	-	-	-	-	C	U	-	C	R	U	-	-	*14*
Ctenotus orientalis	S	S	S	-	-	-	-	-	-	-	-	-	-	-	*3*
Ctenotus robustus	C	U	C	R	C	U	C	C	C	C	U	R	-	-	*163*
Ctenotus taeniolatus	S	R	R	R	-	-	-	-	-	-	-	-	-	-	*23*
Egernia cunninghami	R	R	R	S	R	-	-	-	-	-	-	R	-	-	*13*
Egernia striolata	R	S	R	S	-	R	R	R	-	U	U	C	-	-	*26*
Eulamprus quoyii	-	-	-	-	-	-	-	-	-	R	-	-	-	-	*1*
Hemiergis decresiensis	R	U	C	U	R	-	U	U	C	C	-	-	-	-	*106*
Lampropholis delicata	R	U	U	R	-	-	-	-	C	C	R	-	-	-	*69*
Lampropholis guichenoti	-	S	S	S	-	-	-	-	C	C	-	-	-	-	*12*
Lerista bougainvillii	-	-	R	R	R	-	-	R	-	-	-	-	-	-	*17*
Lerista timida	-	-	-	S	-	R	-	-	-	-	C	R	-	-	*9*
Lygisaurus foliorum	-	-	-	-	-	-	-	-	R	-	C	C	-	C	*17*
Menetia greyii	-	R	-	-	-	-	-	-	-	C	R	-	-	-	*9*
Morethia boulengeri	C	C	C	C	R	U	R	C	U	C	C	C	-	-	*276*
Tiliqua rugosa	S	-	R	R	-	-	-	-	-	-	-	-	-	-	*17*
Tiliqua scincoides	-	S	R	R	-	-	R	U	-	-	-	-	-	-	*11*
TYPHLOPIDAE															
Ramphotyphlops nigrescens	-	-	R	S	R	-	-	-	-	-	-	R	-	-	*5*
Ramphotyphlops wiedii	-	-	-	-	-	-	-	R	U	R	-	R	C	C	*8*
VARANIDAE															
Varanus varius	-	-	-	S	-	-	-	-	-	-	-	-	-	-	*2*
	23	*31*	*35*	*36*	*17*	*12*	*11*	*17*	*18*	*28*	*23*	*27*	*3*	*4*	*70*

Table 2. *Average reptile species richness for both control (c) and stewardship (S) management treatments in each of the seven Catchment Management Area's surveyed, including (in decreasing latitude) Murrumbidgee (MCMA), Lachlan (LCMA), Central West (CWCMA), Namoi (NCMA), Border Rivers – Gwydir (BRGCMA), Border Rivers Maranoa- Balonne*

Catchment	Number of surveys	Mean richness per site	Standard Error
MCMA	283	1.80	0.12
LCMA	288	1.72	0.12
CWCMA	92	1.19	0.17
NCMA	38	2.22	0.39
BRGCMA	45	2.90	0.44
BRMBCMA	8	3.10	0.42
CCMA	55	1.26	0.60

The detection of threatened species (specifically *Aprasia parapulchella* and *Amalosia rhombifer*) at a number of sites emphasizes the value of conducting baseline surveys on private land for assessing status of species of conservation significance. Detection of *A. parapulchella* at a number of previously unknown sites highlights the limited knowledge about the distribution and habitat of this enigmatic species (Wong et al. 2011). Ongoing surveys are needed to provide a better understanding of the extent of its occurrence on private land. Further, detection of *A. parapulchella* outside of ESP managed areas emphasizes the significant need for sensitive management of remnant vegetation on private land for all woodland taxa. The list we present in Table 1 provides the first quantitative set of baseline data for reptiles and amphibians found throughout the endangered BGGW system. As such it provides an important baseline resource for future BGGW policy and planning. The list should also be of broad interest to many groups, including natural resource managers, workers interested in the zoogeographical distribution of reptiles and frogs in temperate zone woodlands, and those interested in studying biodiversity in fragmented agricultural landscapes. Field surveys of reptiles in BBGW are on-going. Major re-survey of sites will recommence in coming years to monitor and compare changes in vegetation condition between stewardship and control sites.

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References

ALA. 2012. *Atlas of Living Australia*. Electronic Database accessible at http://www.ala.org.au. Captured on 24 July 2012.

Alford, R.A. and S. J. Richards. 1999. Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* 30: 133–165.

Araujo, M.B., Thuiller, W. and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33: 1712-1728.

AROD. 2012. *Australian Reptile Online Database*. Electronic Database accessible at http://www.arod.com.au. Captured on 20 July 2012.

Blaustein, A.R. and J.M. Kiesecker. Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology Letters* 5(4): 597-608.

Brown, G.W., Bennett, A.F., and J.M. Potts. 2008. Regional faunal decline – reptile occurrence in fragmented rural landscapes of south-eastern Australia. *Wildlife Research* 35(1): 8–18.

Donald, P.F. and A.D. Evans. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology* 43: 209-218.

Driscoll, D.A. 2004. Extinction and outbreaks accompany fragmentation of a reptile community. *Ecological Applications* 14: 220-240.

Fabricius, C., Burger, M. and P.A. Hockey. 2003. Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: arthropods and reptiles. *Journal of Applied Ecology* 40: 392–403.

Foster, M.S., McDiarmid, R.W. and N. Chernoff. 2012. Studying reptile diversity; p. 3-5 *In* R.W. McDiarmid, M.S. Foster, C. Guyer, W. Gibbons and N. Chernoff (ed.). *Reptile Biodiversity: Standard Methods for Inventory and Monitoring*. USA: University of California Press.

Gaston, K. and J. Spicer. 2004. *Biodiversity: An introduction.* 2nd edn. Oxford: Wiley-Blackwell Publishing. 191 p.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S. and C. T. Winner. 2000. The global decline of reptiles, de´ja` vu amphibians. *BioScience* 50: 653–661.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, D.R. and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. *Nature* 404: 752-755.

Kleijn, D., Baquero, R. A., Clough, Y., Diaz, M., De Estaban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzchuh, A., Johl, R., Knop, E., Kruess, A., marshall, E. J., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T. M. and J. L. Yela. 2006. Mixed biodiversity benefits of agri- environment schemes in five European countries. *Ecology Letters* 9: 243-254.

Kleijn, D. and W. J. Sutherland. 2003. How effective are European agri- environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40: 947-969.

McDiarmid, R., Foster, M., Guyer, C., Gibbons, J. and N. Chernoff. 2012. *Reptile biodiversity; standard methods for inventory and monitoring.* California: UC Press. 424 p.

Michael, D.R., Cunningham, R.B., Donnelly, C. and D. B. Lindenmayer. 2012. Comparative use of active searches and artificial refuges to survey herpetofauna in temperate eucalypt woodlands. *Wildlife Research* 39: 149-162.

Michael, D. R. and D. B. Lindenmayer. 2010. The conservation of reptiles in the temperate woodlands of southern New South Wales; p. 217- 223 *In* D.B. Lindenmayer, A. Bennett and R. Hobbs (ed.). *Temperate Woodland Conservation and Management*. Melbourne: CSIRO Publishing.

NSW Office of Environment and Heritage. 2012. *New South Wales Vegetation Information System Classification Database 2.0*. Electronic Database accessible at http://www.environment.nsw.gov.au/ research/Vegetationinformationsystem.htm. Captured on 21 July 2012.

Ribeiro, R., Santos, X., Sillero, N., Carretero, M. A. and G. A. Llorente. 2009. Biodiversity and land uses at a regional scale: Is agriculture the biggest threat for reptile assemblages? *Acta Oecologica* 35(2): 327- 334.

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-

Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Duarte Rocha, C. F., Ibargüengoytía,N., Puntriano, C. A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D. G., Bauer, A. M., Branch W. R., Clobert, J. and J. W. Sites. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894–899.

Tyler, M. and F. Knight. 2011. *Field guide to the frogs of Australia.*CSIRO. Melbourne: Publishing. 200 p.

VSN International. 2011. GenStat for Windows 14th Edition. VSN International Ltd, Hemel, Hempstead, United Kingdom.

Whitfield, S.M., K.E. Bell, T. Philippi, M. Sasa, F. Bolaño, G. Chaves, J.M. Savage and M.A. Donnelly. 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences of the United States of America* 102: 8352-8356.

Wong, D., S. Jones, W. Osborne, G. Brown, P. Robertson, D. Michael and G. Kay. 2011. The life history and ecology of the Pink-tailed Worm-lizard *Aprasia parapulchella* Kluge – a review. *Australian Zoologist* 35(4): 927-940.

Zammit, C., S. Attwood and E. Burns. 2010. Using markets for woodland conservation on private land: lessons from the policy-research interface; p. 297-307 *In* D.B. Lindenmayer, A.F. Bennett and R.J. Hobbs (ed.). *Temperate Woodland Conservation and Management.* Melbourne: CSIRO Publishing.

PAPER III. INCORPORATING REGIONAL-SCALE ECOLOGICAL KNOWLEDGE TO IMPROVE THE EFFECTIVENESS OF LARGE-SCALE CONSERVATION PROGRAMMES.

Enhancing the effectiveness of large-scale agri-environment schemes requires that land managers are able to manage for a specific set of habitat features at the local or field scale. However, species may not necessarily use habitat features in a consistent way across entire biomes, preferring certain features across different biogeographic regions. In this paper, we identify that incorporating regional-scale differences in habitat use by species can greatly benefit some taxa, and so provides an opportunity for enhancing large-scale conservation programs. Additionally, we include (as Appendix 1) a study revealing how classifying species by ecological niche breadth and microhabitat guild can further identify key habitat features critical for including within agri-environment schemes. This paper helps to fill basic natural history information that is lacking for many terrestrial species, particularly reptiles in temperate regions of the world.

A blue-tongued lizard (Tiliqua scincoides) basks on fallen timber within Box Gum Grassy Woodland

Kay, G.M., Barton, P.S., Driscoll, D.A., Cunningham, S.A., Blanchard, W., McIntyre, S., Lindenmayer, D.B., 2016. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. Anim. Conserv. 19, 515-525. doi:10.1111/acv.12267

Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes.

Abstract

Land-stewardship programs are a major focus of investment by governments for conserving biodiversity in agricultural landscapes. These programs are generally large-scale (e.g. >1000 km) spanning multiple biogeographic regions but developed using spatially limited (e.g. landscape-scale; <100 km) ecological data interpolated across broad areas for one, or a few, well-studied taxonomic groups. Information about how less-studied taxa respond to regional differences in management and environmental effects has potential to further inform land-stewardship conservation programs, but suitable datasets are rarely available. In this study, we sought to enhance planning of large-scale conservation programs by quantifying relationships between reptile assemblages and key environmental attributes at regional scales within a large-scale (>172,000 km^2) Australian land-stewardship program. Using 234 remnant woodland monitoring sites spanning four distinct biogeographic regions, we asked: Do reptile assemblages show different environmental associations across biogeographically distinct regions? We found that environmental features important to reptile diversity differed over each region. Abundance and rare species richness of reptiles responded at regional-scales to elevation, native groundcover and aspect. We identified four implications from our study: 1) large-scale conservation schemes can achieve better outcomes for reptiles using regional-scale knowledge of environmental associations, 2) regional-scale knowledge is particularly valuable for conservation of rare reptile taxa, 3) consideration of abiotic environmental features which cannot be directly managed (e.g. aspect, elevation) is important, 4) programs can be tailored to better support reptile groups at higher conservation risk. Our study shows that reptile-environment

associations differ among biogeographic regions, and this presents opportunity for tailoring stronger policy and management strategies for conserving large-scale agricultural landscapes globally.

Introduction

Agricultural expansion and intensification are major causes of biodiversity loss (Barnosky et al., 2011). To address this, billions of dollars are committed by governments to large-scale land-stewardship conservation programs targeting private-tenure agricultural landscapes (European Commission, 2014b; USDA, 2014). While increasing the scope of these programs is a global priority (e.g. UN Millennium Development Goals; IUCN, 2010), they remain founded on spatially limited ecological data interpolated across broad areas (Gonthier et al., 2014; Whittingham et al., 2007) and largely focus on one, or a few, well-studied taxonomic groups (Lüscher et al., 2014). An emerging challenge for conservation practitioners is to find ways to refine large-scale land-stewardship programs, by incorporating high-resolution ecological information for an increasing range of taxa.

Species respond to environmental drivers and ecological processes at multiple spatial scales (Cushman and McGarigal, 2002), so an understanding of these issues is likely to improve effectiveness of large-scale conservation programs. However, it can be difficult to implement large-scale programs (i.e. across >1000 km) while accommodating complexity in fine-scale (i.e. 1-10 km) biological patterns. Subsequently, land-stewardship programs have generally focused only on a few management objectives across coarse scales. Exploring regional-scale (i.e. 10-100 km) habitat relationships using regions defined by shared environmental condition (e.g. biogeographic regions) is likely to capture important patterns of response to habitats and management (Báldi et al., 2013; Batáry et al., 2011; Concepción et al., 2012) and provides a possible balance between generality and finer resolution. The benefits of incorporating regional-scale criteria into conservation planning have recently been acknowledged for some beetles (Liu et al., 2014) and birds (Whittingham et al., 2007) but there are only a few studies, limited to European landscapes. Broadening our understanding of biodiversity responses in larger multi-regional contexts, and in other parts of the world, is therefore important.

Another challenge facing conservation managers is to develop conservation programs based on a wide variety of taxa. Data for large-scale land-stewardship programs are generally limited to a few well-studied groups like plants, birds and some invertebrates (Batáry et al., 2015; for review see Whittingham, 2011). Ground-dependent reptiles have received considerably less attention (but see Michael et al., 2014) despite representing one of the most diverse and rapidly declining vertebrate groups in agricultural landscapes globally (Böhm et al., 2013). Further, reptiles have ecological requirements that are distinct from other vertebrate taxa, such as limited dispersal capacity and temperature-dependent activity (Guisan and Hofer, 2003; Schutz and Driscoll, 2008). Consequently, building on known ecological requirements of reptiles by incorporating regional-scale knowledge of environmental associations can enhance effectiveness of large-scale conservation programs.

In this study, we examined habitat requirements for reptiles by studying their associations with a set of biotic and abiotic environmental variables, across multiple biogeographic regions, within the Australian Environmental Stewardship Programme (Commonwealth of Australia, 2009, 2013; Lindenmayer et al., 2012c). This topic is of particular conservation interest given its relevance to the widely adopted and costly agri-environment schemes (sensu Kleijn and Sutherland, 2003). These schemes aim to promote biodiversity in farming landscapes, but despite billions of dollars of investment annually, their benefit remains undemonstrated for declining ground-dwelling vertebrates including reptiles (see Michael et al., 2014). Our study is the first to examine spatial variation in habitat requirements for reptiles across a conservation program of this scale, covering >172,000 km^2 (approximately the size of Uruguay). Using 234 remnant woodland monitoring sites across four distinct biogeographic regions (Commonwealth of Australia, 2014; sensu Thackway and Cresswell, 1995), we asked: Do reptile assemblages show different environmental associations across biogeographically distinct region? To answer this question, we examined different aspects of the reptile assemblages, including total abundance and species richness, as well as richness of rare species and relative abundance (evenness) of the assemblage. Because reptiles exhibit strong associations with climate and geography (Kay et al., 2013; McCain, 2010) we predicted that the relationships between environmental variables and measures of reptile diversity would vary across the regions observed, providing opportunity for improving design of land-stewardship programs. Our results identify four key conservation implications for decision makers, underscoring opportunities to advance conservation programs in the future.

Methods

Study Area

Our study is set within the critically endangered Box Gum Grassy Woodland ecological community targeted under the Environmental Stewardship Programme in south-eastern Australia (Lindenmayer et al., 2012c). This woodland community is characterised by an understorey of native tussock grasses, herbs and scattered shrubs, and an open tree strata that was originally dominated by white box (*Eucalyptus albens*), yellow box (*E.*

melliodora) and Blakely's red gum (*E. blakelyi*) (Commonwealth of Australia, 2013). Spanning >1000 km north-to-south, this community has been reduced to <4% of its original extent due to clearing over the past 150 years (Lindenmayer et al., 2010). The southern extent is particularly threatened by intensive agriculture (Hoekstra et al., 2005) and now occurs as small and isolated remnants of varying condition (Commonwealth of Australia, 2013). The community also supports a rich woodland-dependent reptile fauna (Kay et al., 2013), with over 120 species of reptiles recorded across the extent of the study area (Wilson and Swan, 2013).

Experimental design

We established 234 monitoring sites in remnant woodland on 152 farms (≤ two sites per farm) involved in the Programme (Fig. 1). These sites represent the highest quality woodland remnants remaining (see Fig. S1 for typical site). An implicit assumption from the outset of the Programme was that its effectiveness for biodiversity would be homogenous across its spatial extent despite spanning a range of biogeographic and climatic boundaries known to influence ecological communities (Commonwealth of Australia, 2009). To test this, we grouped sites of similar climate, geology and landform by well-defined biogeographic regions (sensu Thackway and Cresswell, 1995) which have been used to define agro-climatic systems throughout our study area (Hutchinson et al., 2005).

We first separated sites on the basis of broad agro-climatic system from Hutchinson *et al.* (2005): a winter-rainfall improved-pasture system and a low-rainfall native-pasture system. Within each agro-climatic system, we then grouped sites by clearly defined biogeographic regions (Commonwealth of Australia, 2014). Sites within the winter-rainfall system were thus separated into the elevated Southern Highlands region (61 sites) and the fertile Southern Slopes region (82 sites). Sites within the low-rainfall system were similarly separated into a Northern Slopes (53 sites) region and two smaller northern biogeographic regions that, due to limited sampling across both biogeographic regions, were combined to create a single Northern region (38 sites). Additional descriptions for the final set of four regions are provided as supporting information (Table S1).

Reptile surveys

We surveyed each site for reptiles three times (September 2010, February 2012 and September 2012) along a 200 x 40 m transect. We used a time- and area-constrained (20 min x 0.8 ha) survey protocol (following Michael et al., 2012), involving active searches of natural habitat and inspections of two artificial refuge arrays. Both arrays were placed 100 m apart and consisted of four concrete roof tiles (32 x 42 cm), one double-layered stack of corrugated galvanized steel and four wooden railway sleepers (1.2 m long).

We conducted surveys on clear days between 0900 and 1600 hours with the same group of experienced field ecologists. We identified species using Wilson & Swan (2012). Our analyses focussed on whole assemblages at site level, so we pooled observations within sites and across survey times to define a reptile assemblage at every site.

Measurement of environmental features

We measured a suite of environmental features relevant to conservation managers. We included variables commonly considered for management (e.g. vegetation characteristics) plus those likely to be important for reptiles but not influenced by management (e.g. topographic position, climate).

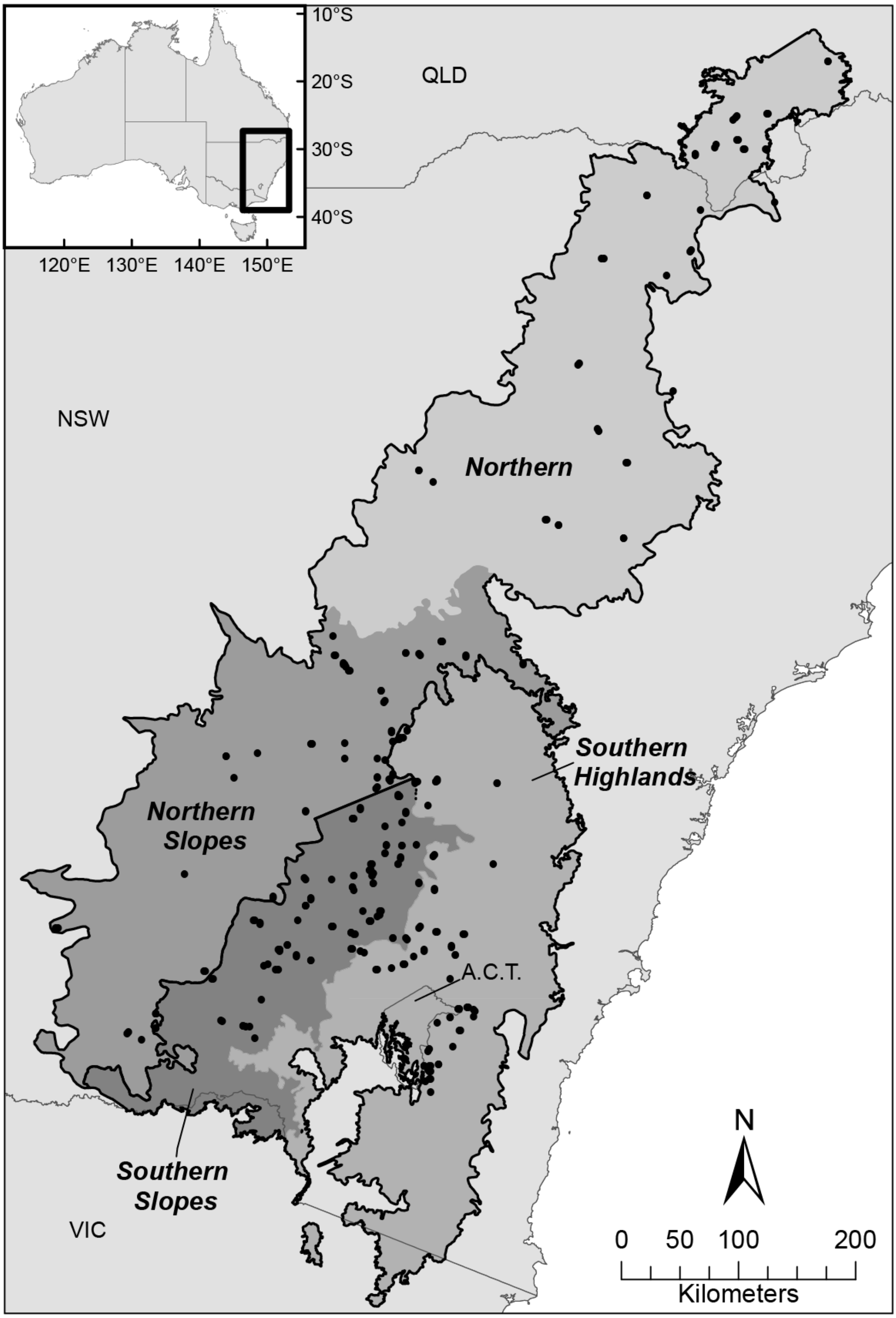

Figure 1. Location of the study area spanning New South Wales (NSW) and southern Queensland (QLD) of south-eastern Australia showing the location of monitoring sites (n=234) surveyed across the four study regions (greyed fill) and two agro-climatic systems (black boundary).

We surveyed vegetation at each site during February 2010 and 2012 and averaged data at the site level. We measured native plant species richness in a 20 x 20 m plot midway along the transect and recorded length of logs in two 50 x 20 m plots at the extreme ends of a transect. We estimated percentage cover of bare ground, organic litter, rock, overstorey and midstorey by recording these attributes every metre along two 50 m transects (for details see Michael et al., 2014).

We obtained elevation and aspect for each site using nine second resolution spatial data (Hutchinson et al., 2011). Large-scale geographic effects on species richness are known to occur for reptiles (Brown et al., 2011; Rodríguez et al., 2005) driven by latitudinal influences on ambient energy (temperature and solar radiation) and moisture-driven habitat gradients. Because our study area encompasses confounding latitudinal and rainfall gradients, we used a 'growth index' derived from ANUCLIM (Xu and Hutchinson, 2013) to combine the effect of temperature, moisture and daylight into one energy related variable (see Appendix S1 for details).

Statistical analysis

We used an information-theoretic approach (Burnham and Anderson, 2002) to test whether large-scale conservation programs could be made more effective by incorporating regional-scale ecological knowledge of reptiles. We fitted generalised linear mixed models (GLMMs) to examine the relationship between environmental variables and reptile diversity. Conservation programs generally measure biodiversity success through change in overall richness or abundance over time (Batáry et al., 2011) despite these being relatively crude measures (Morris et al., 2014). Additionally, biodiversity success may be measured through a positive response in species of conservation concern (Cunningham et al., 2014), as well as the relative abundance (evenness) of species, where greater evenness implies more robust populations (Magurran and McGill, 2011). Therefore, we used four measures of reptile diversity as our response variables, with higher values indicating improved outcome: (i) richness of all reptile species, (ii) richness of rare reptile species (the number that occurred at < 5% of all sites), (iii) abundance of all reptile species, and (iv) assemblage evenness (Shannon Evenness; Magurran and McGill, 2011). We used a Poisson distribution with a log link to model richness, rare species richness and overall abundance. For evenness, we used a Gaussian distribution with an identity link. “Farm” was fitted as a random effect in all models.

We reduced the number of potential explanatory variables for use in models by: (i) using features identified in previous studies of reptile ecological requirements (e.g. Brown et al., 2011 and references within), as well as expert knowledge of experienced wildlife scientists, from within Australian temperate woodlands, and (ii) eliminating highly correlated variables (examining pairwise scatterplots and correlation coefficients with $r > 0.5$ cutoff) (Zuur et al., 2009). This gave a set of eight predictor variables useful for testing regional-scale habitat relationships for reptiles: growth index, aspect (scaled from +1 [northerly] to -1 [southerly]), elevation, richness of native groundcover, log cover (length), rock cover, bare ground cover and native overstorey cover.

To test whether regional-scale information could enhance conservation programs, we fitted region and the interaction of region with each of the eight predictor variables. To explore the correlative influence of region with environment, we repeated our analysis with the environmental variables standardised within region (i.e., the within-region mean subtracted from the values within that region). If region was important in models only with standardised environmental variables, we inferred that regional differences are otherwise accounted for by environmental gradients across the whole study area. Conversely, if environmental variables are important only in models without standardisation, it would imply that broad-scale regional differences drive changes in reptile diversity and within-region variation in these parameters is not important.

We used Akaike information criterion (AIC, Burnham and Anderson, 2002) to select top-ranked models and included all models within 2 units in our inference (Arnold, 2010). We checked for over-dispersion by dividing the Pearson goodness-of-fit statistic by the residual degrees of freedom and found no values greater than one suggesting that our data were not over-dispersed (McCullagh and Nelder, 1989). We inspected the residual vs. fitted plots of each model to confirm that residuals were approximately randomly distributed with respect to fitted values. We assumed sites on different farms were independent, and tested for spatial dependence in the residuals using a Moran's I test (Cliff and Ord, 1981), finding no evidence of spatial autocorrelation. We undertook all analyses using the *MuMIn* package in R (Bartoń, 2009).

Results

We recorded 57 species of reptiles from ten families (Table S2). Species richness ranged from one to 10 species per site, with a decline in richness with increasing latitude (slope= -0.061±0.018, $p<0.001$) corresponding to approximately one less species for every five degrees of latitude (Fig. S2). Species accumulation curves for each study region and the whole study area approached an asymptote (Fig. S3), ranging between 72.4% and 92.9% of the estimated true richness (Table S3).

The top-ranked model for species richness across the study area included a positive effect of growth index, log cover, native groundcover richness and rock cover with lesser negative effects of elevation, native overstorey cover, and northerly (sunlit) aspect (Table 1, Fig. 2). Region was included in the model although its effects were weak with no interaction effect apparent.

Rare species richness was explained across the study area by a positive effect of rock cover and, to a lesser extent, a negative effect of native overstorey cover (Table 1, Fig. 2). Rare species richness was negatively associated with elevation in the Southern Highlands and Northern Slopes regions, and positively in the remaining regions. An interactive effect of region also occurred with native groundcover richness, which was positively associated in all but the Northern region.

Reptile abundance was explained across the study area by a positive effect of rock cover and interactions of region with elevation, northerly (sunlit) aspect and native groundcover richness (Table 1, Fig. 2). Reptile species evenness was explained across the study area by positive effects of growth index and, to a lesser extent, positive effects of rock cover and native groundcover richness and negative effects of elevation (Table 1, Fig. 2). There was no interaction effect of region.

Standardizing predictor variables for all diversity measures revealed the same result, with evenness revealing an additional effect of region (Table S4), indicating environmental terms had similar effects at the within-region and between-region scales.

Discussion

We used an information-theoretic approach to assess how incorporating spatial variation in habitat requirements can assist large-scale conservation planning. Our study revealed that environmental features important in driving reptile diversity differed for each region. Critically, two of the four measures of reptile diversity responded at the regional-scale, in some cases reversing the direction of effect. Our work provides

Table 1. *Summary of the best model for reptile diversity response (species richness, rare species richness, abundance, evenness) as predicted by eight environmental variables: growth index (Gr_id), northerly aspect (Asp_N), elevation (Elev), native groundcover richness (NGR), length of log cover (LogLth), rock cover (Rock), bare ground cover (BG) and native overstorey cover (NOS_cvr) plus interaction with region (Reg). The Northern Region is incorporated in the intercept as the reference category against which all regions, and their interactions, are measured. Unstandardized models are provided (these match the standardized models). Direction of response is given (sign)*

Response	**Model terms**	**Direction**	**Estimate**	**SE**	**F**	**P**
Species richness	Reg + Rock + NGR + Gr_id + Asp_N + Elev + LogLth + NOS_cvr					
	(Intercept)		0.294	0.517	0.567	0.5705
	Reg(NS)	+	0.006	0.218	0.025	0.9798
	Reg(SH)	+	0.347	0.264	1.318	0.1876
	Reg(SS)	+	0.192	0.230	0.836	0.4029
	Rock	+	0.021	0.007	3.072	0.0021
	NGR	+	0.021	0.008	2.722	0.0065
	Gr_id	+	6.815	3.184	2.14	0.0323
	Asp_N	–	-0.106	0.058	-1.82	0.0686
	Elev	–	-0.001	3.17 x 10^{-04}	-2.01	0.0443
	LogLth	+	0.004	0.002	2.038	0.0415
	NOS_cvr	–	-0.003	0.002	-1.56	0.1198
Rare species richness	Reg + Elev + Reg*Elev + Rock + NOS_cvr + Reg*NGR + NGR					
	(Intercept)		-0.161	0.840	-0.191	0.8482
	Reg(NS)	+	0.340	0.991	0.343	0.7315
	Reg(SH)	+	2.169	1.107	1.960	0.0500
	Reg(SS)	–	-0.811	0.936	-0.866	0.3862
	Rock	+	0.025	0.011	2.326	0.0200
	NOS_cvr	–	-0.005	0.003	-1.742	0.0815
	Elev	+	0.002	0.001	1.296	0.1951
	Reg(NS)*Elev	–	-0.003	0.002	-2.019	0.0435
	Reg(SH)*Elev	–	-0.004	0.002	-2.497	0.0125
	Reg(SS)*Elev	+	4.19 x 10^{-04}	0.001	0.280	0.7791
	NGR	–	-0.049	0.055	-0.889	0.3741
	Reg(NS)*NGR	+	0.119	0.061	1.949	0.0513
	Reg(SH)*NGR	+	0.068	0.057	1.190	0.2339
	Reg(SS)*NGR	+	0.085	0.059	1.452	0.1465
Abundance	Reg + Reg*NGR + NGR + Rock + Elev + Reg*Elev + Asp_N + Reg*Asp_N					
	(Intercept)		1.282	0.518	2.475	0.0133
	Reg(NS)	+	1.469	0.685	2.144	0.0320
	Reg(SH)	+	1.734	0.870	1.993	0.0462
	Reg(SS)	+	0.628	0.596	1.054	0.2918
	Rock	+	0.023	0.007	3.149	0.0016
	NGR	–	-0.025	0.027	-0.920	0.3575
	Reg(NS)*NGR	+	0.035	0.034	1.037	0.2998
	Reg(SH)*NGR	+	0.044	0.030	1.445	0.1484
	Reg(SS)*NGR	+	0.101	0.029	3.435	0.0006
	Elev	+	0.002	0.001	1.978	0.0480
	Reg(NS)*Elev	–	-0.005	0.001	-4.029	0.0001
	Reg(SH)*Elev	–	-0.004	0.001	-3.042	0.0023
	Reg(SS)*Elev	–	-0.004	0.001	-3.612	0.0003
	Asp_N	–	-0.347	0.150	-2.312	0.0208
	Reg(NS)*Asp_N	+	0.322	0.211	1.530	0.1260
	Reg(SH)*Asp_N	+	0.096	0.205	0.467	0.6402
	Reg(SS)*Asp_N	+	0.533	0.170	3.138	0.0017
Evenness	Rock + NGR + Elev + Gr_id					
	(Intercept)		0.477	0.116	4.124	0.0000
	Rock	+	0.009	0.005	1.890	0.0588
	NGR	+	0.007	0.004	1.587	0.1141
	Elev	–	-2.25 x 10^{-04}	1.39 x 10^{-04}	-1.624	0.1044
	Gr_id	+	2.620	0.875	2.996	0.0027

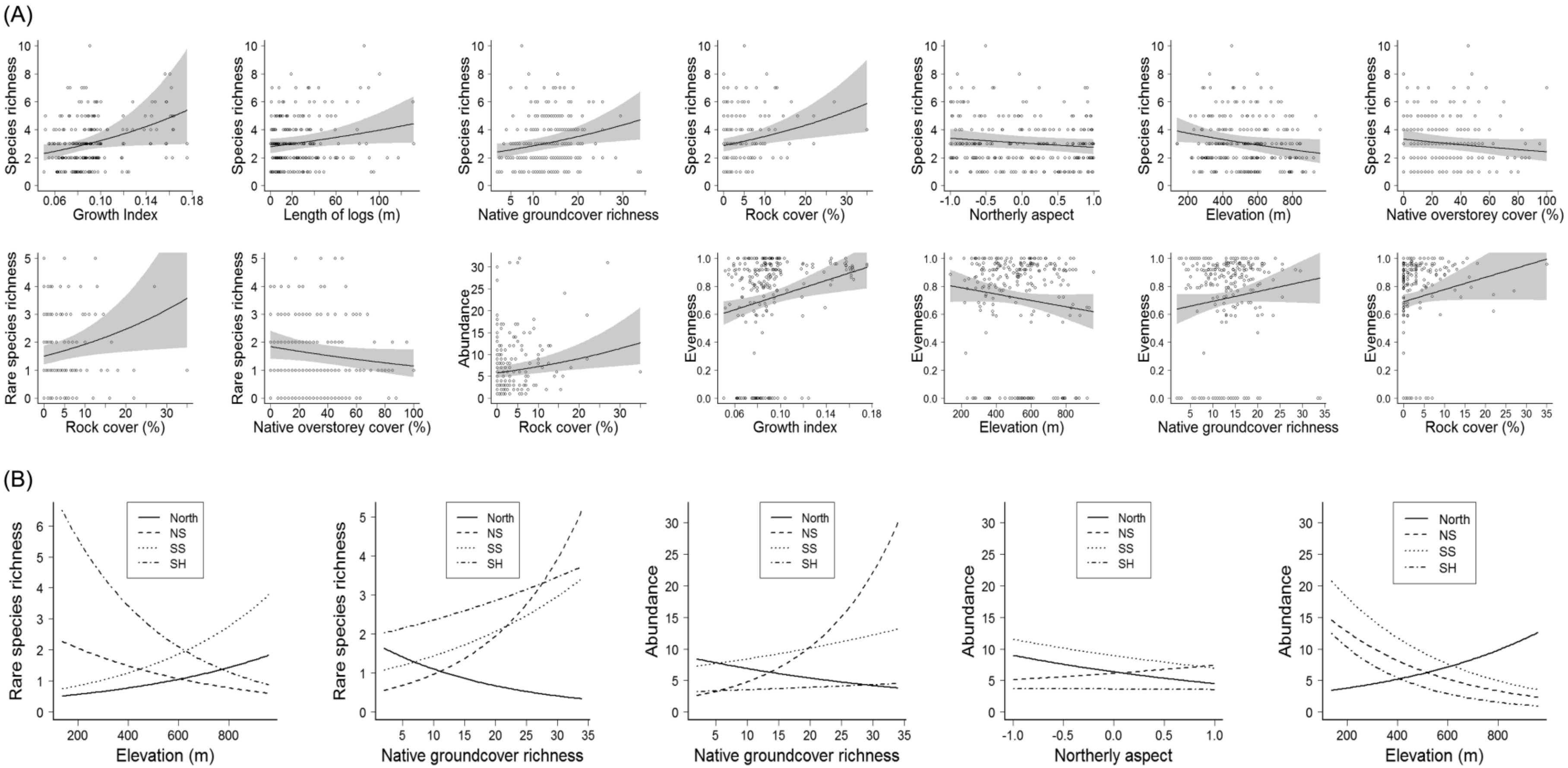

Figure 2. *Relationships of all linear predictors (plus confidence intervals) in the top-ranked models for (A) the different reptile assemblage measures within the whole study area, and (B) important interactions with the four study regions: Northern (North), Northern Slopes (NS), Southern Slopes (SS) and Southern Highlands (SH) regions*

empirical support for incorporating regional-scale criteria into conservation planning, addressing an emerging need in conservation science (Lüscher et al., 2015)

Biological interpretation of the models

To understand the appropriate regional-level conservation planning and management outcomes of this study, it is important to consider the mechanisms behind region-specific responses to environment by reptiles. We found two abiotic variables (elevation, aspect) and one biotic variable (native groundcover richness) were important drivers of abundance and rare species richness that varied in effect at the regional level (Fig. 2b). In two of the southern (colder) regions, lower elevation corresponded with lower numbers of reptiles and rare species, while in the warmer Northern and Northern Slopes regions the pattern was reversed. This is consistent with known thermoregulatory limits which reptiles experience at higher elevations (Fischer and Lindenmayer, 2005; McCain, 2010). In contradiction to this idea was the positive effect of elevation on rare species richness in the Southern Slopes (Fig. 2b). However, this might reflect extensive native vegetation loss in the fertile lower slopes of this region compared with hilltops where native vegetation is often retained (Fischer et al., 2010).

Northerly (sunlit) aspects generally supported higher reptile abundance, although this also differed by region. At cooler (higher) latitudes, higher reptile abundance on northerly (sunlit) aspects within the Northern Slopes and Southern Highlands regions is consistent with reptile thermal requirements (Brown et al., 2011). This effect also could be expected for the cooler Southern Slopes, although similar preference by livestock for these north-facing warmer and more productive pastures may contribute to lower reptile abundance observed here based on the demonstrated impact of grazing on reptiles (Dorrough et al., 2012; Howland et al., 2014). Higher abundance on southerly (shaded) aspects in the warmer Northern region may reflect a preference for species to occupy mesic refugia when thermoregulatory processes are not limiting, a recognised pattern in reptiles (Duckett and Stow, 2013).

Native groundcover richness influenced rare reptile species richness and abundance at the regional-level, with positive effects in all but the Northern region. This regional effect probably reflects differences in climate (Hutchinson et al., 2005) and cultivation histories (Hoekstra et al., 2005) between the regions, with a greater reliance on native groundcover richness by reptiles in the more intensively cultivated southern regions. This is consistent with the well-established negative impact of agricultural land-use recognised for reptiles globally (Fabricius et al., 2003; Ribeiro et al., 2009).

Five of the seven environmental features identified in top models for reptile diversity were linked to reptile thermoregulatory behaviour. Ground-layer structural attributes related to reptile basking, including cover of rocks (Seebacher and Franklin, 2005) and overstorey (Pike et al., 2011), as well as broad thermally-relevant climatic variables of growth index, elevation and aspect were important in driving reptile diversity. This suggests inclusion of features that influence thermoregulatory environments enhances regional effectiveness of conservation programs for reptiles.

Implications for conservation

To facilitate adaptive learning (sensu Perkins et al., 2010) from the Environmental Stewardship Programme that was the focus of this investigation, we present a summary of suggested management actions to inform future programs. We summarise features important for conserving overall reptile diversity, and identify features important at the regional-level for conserving rare species within this Programme (Table 2). To help guide conservation planning more generally, we identify four key management recommendations that emerge from our study.

Table 2. *Recommendations for scheme development, particularly targeting site prioritisation aiming to enhance overall reptile richness and rare species richness for sites included in the four study regions within the study area*

Region	**To conserve overall richness**	**To conserve rare reptiles**
Whole study	• Target high (>3%) rock cover • Target high (>300m/ha) log cover • Target open (<20%) overstorey • Target sites at low (<500m) elevation • Target high (1.0) growth index • Target high (>0.033 species/m^2) native groundcover richness	• Target high (>3%) rock cover • Target open (<20%) overstorey
Northern	• As for whole study	• Target sites at high (<540m) elevation • Target southerly (shaded) aspect • Target low (<0.037 species/m^2) native groundcover richness
Northern Slopes	• As for whole study	• Target sites at low (<430m) elevation • Target high (>0.037 species/m^2) native groundcover richness
Southern Slopes	• As for whole study	• Target sites at high (>430m) elevation • Target southerly (shaded) aspect • Target high (>0.033 species/m^2) native groundcover richness
Southern Highlands	• As for whole study	• Target sites at low (<730m) elevation • Target northerly (sunlit) aspect • Target high (>0.038 species/m^2) native groundcover richness

1) *Incorporating regional-level responses of species diversity to environmental features allows greater sophistication in conservation program design*

The results of our study suggest conservation programs will be more effective if they incorporate regional variation in important environmental features. The identification of regional patterns for reptile abundance and rare species is of specific value for conservation managers. This is because bolstering existing populations and increasing species of conservation concern is fundamental to arresting biodiversity erosion in fragmented agricultural landscapes (Gonthier et al., 2014). Our work addresses the need to shift beyond the ‘one-size-fits-all’ approach commonly applied to large-scale programs (Batáry et al., 2011; Whittingham et al., 2007), underscoring the value of considering the disproportionate benefit some environmental features provide in certain contexts. Managers can apply regional-level biodiversity information either by selecting sites containing certain attributes, or for targeted restoration activities. For example, restoration of native groundcover (e.g. Lindenmayer et al., 2010) would be most effectively applied for restoring rare reptile diversity in southern regions of this study (Fig. 2b). Although similar studies across a suite of taxonomic groups are needed, the habitat recommendations identified in this study are largely consistent with, and unlikely to be detrimental for, many other ground-dependent fauna including mammals and amphibians (McElhinny et al., 2006).

2) *Rare species need special consideration*

Despite the overarching objectives of many conservation programs to conserve targeted ecological communities, it is evident that rare and threatened taxa may continue to decline (Kleijn et al., 2006), or show time-lags in response to conservation programs (Michael et al., 2014). Procedures for ensuring robust protection of rare and threatened species in land-stewardship conservation programs are limited (Batáry et al., 2011; Whittingham, 2011) and have not previously involved recommendations for management at the regional-level (Table 2). An explicit recommendation from our study is to incorporate regional environmental features important for conserving rare species at the site selection stage and focus management actions at this level. Applying this approach for rare species in other taxonomic groups may help identify important features for preventing multi-taxon species decline in agricultural landscapes. Where recommendations for different taxonomic groups clash (e.g. positive for reptiles while negative for birds), other approaches such as multi-criteria decision analyses (Huang et al., 2011) could be used to consider a range of contrasting management options.

3) *There is a need to prioritize variables that cannot be managed*

Some of the most important drivers of diversity at the site level are environmental attributes that cannot be influenced by site management, such as aspect, elevation and growth index. Despite their importance for diversity, these abiotic attributes are rarely considered when designing conservation programs (Kleijn et al., 2006). Because these features cannot be managed, their integration at the initial site selection stages of conservation planning, particularly at the regional-level, would enhance species diversity and therefore effectiveness of conservation programs. Although large programs may inadvertently capture these features, a targeted approach would be more effective. This could be achieved by ensuring sufficient representation of these variables in the preliminary stages of program development, but then tailoring site selection to include key features relevant to particular regions.

4) *Programs can be tailored to better support species groups at higher conservation risk*

Many conservation programs differ in effectiveness among species and fail to support species-groups at higher conservation risk. For example, land-stewardship conservation programs are more effective for plants and some invertebrate groups (Whittingham, 2011) with no demonstrable benefit for other rapidly declining groups such as reptiles (Michael et al., 2014). However, we contend that refining programs by incorporating environmental features can benefit these at-risk groups. Our study shows that reptiles, a group experiencing global decline (Böhm et al., 2013), are positively associated with features important for thermoregulation (e.g. aspect, elevation, rock cover). Maintaining important thermoregulatory features, either through site-selection (by considering elevation and aspect) or proposed management actions (such as maintaining rock cover as a non-renewable resource), would help reptiles and possibly other thermoregulating species-groups (e.g. amphibians, invertebrates; Cossins & Bowler, 1987).

The management recommendations we have identified were developed with the goal of enhancing effectiveness of the large-scale land-stewardship conservation programs. Such programs have become one of the most used tools globally for conserving biodiversity in agricultural landscapes (European Commission, 2014b; USDA, 2014). By examining difference between regions, for an important yet poorly studied taxonomic group, we have identified new opportunities for better conservation management in agricultural landscapes that can improve effectiveness of large-scale conservation programs globally.

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References

Arnold, T.W., 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J. Wildl. Manage. 74, 1175–1178. doi:10.2193/2009-367

Báldi, A., Batáry, P., Kleijn, D., 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary – analysing assemblages of 1200 species. Agric. Ecosyst. Environ. 166, 28–34. doi:10.1016/j.agee.2012.03.005

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., Mcguire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth’s sixth mass extinction already arrived? Nature 470, 51–57. doi:10.1038/nature09678

Bartoń, K., 2009. Multi-Model Inference. In: R Package Version 0.12.0, http://r-forge.r-project.org/projects/mumin/.

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B Biol. Sci. 278, 1894–1902. doi:10.1098/rspb.2010.1923

Batáry, P., Dicks, L. V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. doi:10.1111/cobi.12536

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., Rhodin, A.G.J., Stuart, S.N., van Dijk, P.P., Young, B.E., Afuang, L.E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L.R. V, Allison, A., Ananjeva, N., Anderson, S., Andrén, C., Ariano-Sánchez, D., Arredondo, J.C., Auliya, M., Austin, C.C., Avci, A., Baker, P.J., Barreto-Lima, A.F., Barrio-Amorós, C.L., Basu, D., Bates, M.F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M.D.R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J.R., Chapple, D.G., Cheylan, M., Cisneros-Heredia, D.F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G.C., Couper, P.J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P.A., Crother, B., Cruz, F., Daltry, J.C., Daniels, R.J.R., Das, I., de Silva, A., Diesmos, A.C., Dirksen, L., Doan, T.M., Dodd, C.K., Doody, J.S., Dorcas, M.E., Duarte de Barros Filho, J., Egan, V.T., El Mouden, E.H., Embert, D., Espinoza, R.E., Fallabrino, A., Feng, X., Feng, Z.J., Fitzgerald, L., Flores-Villela, O., França, F.G.R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S.R., Garcia, M. a., García-Pérez, J.E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J.C.T., Gower, D.J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A.M., Hare, K., Hedges, S.B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F.M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J.S., Köhler, G., Kuchling, G., Kumlutaş, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A.S., López-Luna, M. a., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W.E., Mahler, D.L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O. a V, Márquez, R., Martins, M., Masterson, G., Mateo, J. a., Mathew, R., Mathews, N., Mayer, G., McCranie, J.R., Measey, G.J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D. a., Montgomery, C., Morato, S. a a, Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T.Q., Nilson, G., Nogueira, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, J., Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O.S.G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E.R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G.E., Radder, R., Ramer, J., Rasmussen, A.R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E.L., Riservato, E., Rivas, G., da Rocha, P.L.B., Rödel, M.O., Rodríguez Schettino, L., Roosenburg, W.M., Ross, J.P., Sadek, R., Sanders, K., Santos-Barrera, G., Schleich, H.H., Schmidt, B.R., Schmitz, A., Sharifi, M., Shea, G., Shi, H.T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H.J., Tognelli, M.F., Tolley, K., Tolson, P.J., Tuniyev, B., Tuniyev, S., Üzüm, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Veselý, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R.C., Wearn, O.R., Werner, Y.L., Whiting, M.J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K., Zug, G., 2013. The conservation status of the world's reptiles. Biol. Conserv. 157, 372–385. doi:10.1016/j.biocon.2012.07.015

Brown, G., Dorrough, J., Ramsey, D., 2011. Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. Landsc. Urban Plan. 103, 277–288. doi:10.1016/j.landurbplan.2011.08.002

Burnham, K.P., Anderson, D.R., 2002. Formal Inference From More Than One Model: Multimodel Inference (MMI), in: Burnham, K.P., Anderson, D.R. (Eds.), Model Selection and Multimodel Inference. Springer, New York, pp. 149–205. doi:10.1016/j.ecolmodel.2003.11.004

Cliff, A.D., Ord, J.K., 1981. Spatial Processes: Models & Applications. Pion, London.

Commonwealth of Australia, 2014. Australia's Bioregions (IBRA) [WWW Document]. URL http://www.environment.gov.au/land/nrs/science/ibra (accessed 3.10.14).

Commonwealth of Australia, 2013. Environmental Stewardship [WWW Document]. URL http://www.nrm.gov.au/national/continuing-investment/environmental-stewardship

Commonwealth of Australia, 2009. Environmental Stewardship Strategic Framework. Department of the Environment, Water, Heritage and the Arts, Canberra.

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., Diaz, M., Baldi, A., Batary, P., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J. Appl. Ecol. 49, 695–705. doi:10.1111/j.1365-2664.2012.02131.x

Cossins, A.R., Bowler, K., 1987. Temperature biology of animals. Chapman and Hall, London, UK.

Cunningham, R.B., Lindenmayer, D.B., Crane, M., Michael, D.R., Barton, P.S., Gibbons, P., Okada, S., Ikin, K., Stein, J.A.R., 2014. The law of diminishing returns: woodland birds respond to native vegetation cover at multiple spatial scales and over time. Divers. Distrib. 20, 59–71. doi:10.1111/ddi.12145

Cushman, S.A., McGarigal, K., 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landsc. Ecol. 17, 637–646. doi:10.1023/A:1021571603605

Dorrough, J., Mcintyre, S., Brown, G., Stol, J., Barrett, G., Brown, A., 2012. Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. Austral Ecol. 37, 569–582. doi:10.1111/j.1442-9993.2011.02317.x

Duckett, P.E., Stow, A.J., 2013. Higher genetic diversity is associated with stable water refugia for a gecko with a wide distribution in arid Australia. Divers. Distrib. 19, 1072–1083. doi:10.1111/ddi.12089

European Commission, 2014. Agri-environment measures [WWW Document]. URL http://ec.europa.eu/agriculture/envir/measures/index_en.htm (accessed 2.10.14).

Fabricius, C., Burger, M., Hockey, P.A.R., 2003. Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: arthropods and reptiles. J. Appl. Ecol. 40, 392–403. doi:10.1046/j.1365-2664.2003.00793.x

Fischer, J., Lindenmayer, D.B., 2005. The sensitivity of lizards to elevation: A case study from south-eastern Australia. Divers. Distrib. 11, 225–233. doi:10.1111/j.1366-9516.2005.00139.x

Fischer, J., Zerger, A., Gibbons, P., Stott, J., Law, B.S., 2010. Tree decline and the future of Australian farmland biodiversity. Proc. Natl. Acad. Sci. U. S. A. 107, 19597–19602. doi:10.1073/pnas.1008476107

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.-Y., Iverson, A.L., Batáry, P., Rudolphi, J., Tscharntke, T., Cardinale, B.J., Perfecto, I., 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proc. Biol. Sci. 281, 20141358. doi:10.1098/rspb.2014.1358

Guisan, A., Hofer, U., 2003. Predicting reptile distributions at the mesoscale: relation to climate and topography. J. Biogeogr. 30, 1233–1243. doi:10.1046/j.1365-2699.2003.00914.x

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29. doi:10.1111/j.1461-0248.2004.00686.x

Howland, B., Stojanovic, D., Gordon, I., Manning, A., Fletcher, D., Lindenmayer, D., 2014. Eaten Out of House and Home: Impacts of Grazing on Ground-Dwelling Reptiles in Australian Grasslands and Grassy Woodlands. PLoS One 9, (e105966) DOI:10.1371/journal.pone.0105966. doi:10.1371/journal.pone.0105966

Huang, I.B., Keisler, J., Linkov, I., 2011. Multi-criteria decision analysis in environmental sciences: ten years of applications and trends. Sci. Total Environ. 409, 3578–94. doi:10.1016/j.scitotenv.2011.06.022

Hutchinson, M., Mcintyre, S., Hobbs, R., Stein, J., Garnett, S., Kinloch, J., 2005. Integrating a global agro-climatic classification with bioregional boundaries in Australia. Glob. Ecol. Biogeogr. 14, 197–212. doi:10.1111/j.1466-822x.2005.00154.x

Hutchinson, M., Stein, J., Stein, J., 2011. GEODATA 9 Second Digital Elevation Model (DEM-9S) Version 3 [WWW Document]. URL http://www.ga.gov.au/meta/ANZCW0703011541.html (accessed October 2014).

IUCN, 2010. Countdown 2010 [WWW Document]. URL http://www.countdown2010.net/ (accessed 10.19.14).

Kay, G.M., Michael, D.R., Crane, M., Okada, S., MacGregor, C., Florance, D., Trengove, D., McBurney, L., Blair, D., Lindenmayer, D.B., 2013. A list of reptiles and amphibians from Box Gum Grassy Woodlands in south-eastern Australia. Check List 9, 476–481.

Kleijn, D., Baquero, R. a, Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243–257. doi:10.1111/j.1461-0248.2005.00869.x

Kleijn, D., Sutherland, W.W., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40, 947–969.

Lindenmayer, D., Bennett, A., Hobbs, R., 2010. Temperate Woodland Conservation and Management. CSIRO Publishing, Melbourne.

Lindenmayer, D.B., Zammit, C., Attwood, S.J., Burns, E., Shepherd, C.L., Kay, G., Wood, J., 2012. A Novel and Cost-Effective Monitoring Approach for Outcomes in an Australian Biodiversity Conservation Incentive Program. PLoS One 7, (e50872). DOI: 10.1371/journal.pone.0050872. doi:10.1371/journal.pone.0050872

Liu, Y., Rothenwöhrer, C., Scherber, C., Batáry, P., Elek, Z., Steckel, J., Erasmi, S., Tscharntke, T., Westphal, C., 2014. Functional beetle diversity in managed grasslands: Effects of region, landscape context and land use intensity. Landsc. Ecol. 29, 529–540. doi:10.1007/s10980-014-9987-0

Lüscher, G., Jeanneret, P., Schneider, M.K., Hector, A., Arndorfer, M., Balázs, K., Báldi, A., Bailey, D., Choisis, J.-P., Dennis, P., Eiter, S., Elek, Z., Fjellstad, W., Gillingham, P.K., Kainz, M., Kovács-Hostyánszki, A., Hülsbergen, K.-J., Paoletti, M.G., Papaja-Hülsbergen, S., Sarthou, J.-P., Siebrecht, N., Wolfrum, S., Herzog, F., 2015. Strikingly high effect of geographic location on fauna and flora of European agricultural grasslands. Basic Appl. Ecol. 16, 281–290. doi:10.1016/j.baae.2015.04.003

Lüscher, G., Jeanneret, P., Schneider, M.K., Turnbull, L.A., Arndorfer, M., Balázs, K., Báldi, A., Bailey, D., Bernhardt, K.G., Choisis, J.-P., Elek, Z., Frank, T., Friedel, J.K., Kainz, M., Kovács-Hostyánszki, A., Oschatz, M.-L., Paoletti, M.G., Papaja-Hülsbergen, S., Sarthou, J.-P., Siebrecht, N., Wolfrum, S., Herzog, F., 2014. Responses of plants, earthworms, spiders and bees to geographic location, agricultural management and surrounding landscape in European arable fields. Agric. Ecosyst. Environ. 186, 124–134. doi:10.1016/j.agee.2014.01.020

Magurran, A.E., McGill, B.J., 2011. Biological diversity: frontiers in measurement and assessment, Challenges. Oxford University Press, Oxford.

McCain, C.M., 2010. Global analysis of reptile elevational diversity. Glob. Ecol. Biogeogr. 19, 541–553. doi:10.1111/j.1466-8238.2010.00528.x

McCullagh, P., Nelder, J., 1989. Generalized linear models, 2nd ed, lavoisier.fr. Chapman & Hall, London.

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2006. Fauna-habitat relaionships: A basis for identifying key stand structural attributes in temperate Australian eucalypt forests and woodlands. Pacific Conserv. Biol.

Michael, D., Cunningham, R.B., Donnelly, C., Lindenmayer, D.B., 2012. Comparative use of active searches and artificial refuges to survey reptiles in temperate eucalypt woodlands. Wildl. Res. 39, 149–162.

Michael, D.R., Wood, J.T., Crane, M., Montague-Drake, R., Lindenmayer, D.B., 2014. How effective are agri-environment schemes for protecting and improving herpetofaunal diversity in Australian endangered woodland ecosystems? J. Appl.

Ecol. 51, 494–504. doi:10.1111/1365-2664.12215

Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S. a., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., Rillig, M.C., 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecol. Evol. 4, 3514–3524. doi:10.1002/ece3.1155

Perkins, A., Maggs, H., Watson, A., Wilson, J., 2010. Adaptive management and targeting of agri-environment schemes does benefit biodiversity: A case study of the corn bunting Emberiza calandra. J. Appl. Ecol. 48, 514–522.

Pike, D.A., Webb, J.K., Shine, R., 2011. Removing forest canopy cover restores a reptile assemblage. Ecol. Appl. 21, 274–280. doi:10.1890/09-2394.1

Ribeiro, R., Santos, X., Sillero, N., Carretero, M. a., Llorente, G.A., 2009. Biodiversity and Land uses at a regional scale: Is agriculture the biggest threat for reptile assemblages? Acta Oecologica 35, 327–334. doi:10.1016/j.actao.2008.12.003

Rodríguez, M.Á., Belmontes, J.A., Hawkins, B.A., 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. Acta Oecologica 28, 65–70. doi:10.1016/j.actao.2005.02.006

Schutz, A.J., Driscoll, D. a., 2008. Common reptiles unaffected by connectivity or condition in a fragmented farming landscape. Austral Ecol. 33, 641–652. doi:10.1111/j.1442-9993.2007.01830.x

Seebacher, F., Franklin, C.E., 2005. Physiological mechanisms of thermoregulation in reptiles: a review. J. Comp. Physiol. B. 175, 533–541. doi:10.1007/s00360-005-0007-1

Thackway, R., Cresswell, I.D., 1995. An interim biogeographic regionalization for Australia: a framework for establishing the national system of reserves. Canberra.

USDA, 2014. 2014 Farm Act Continues Most Previous Trends In Conservation. United States Department of Agriculture, Washington.

Whittingham, 2011. The future of agri-environment schemes: Biodiversity gains and ecosystem service delivery? J. Appl. Ecol. 48, 509–513. doi:10.1111/j.1365-2664.2011.01987.x

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D., Freckleton, R.P., 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. Ecol. Lett. 10, 25–35. doi:10.1111/j.1461-0248.2006.00992.x

Wilson, S., Swan, G., 2013. Complete Guide to Reptiles of Australia, 4th ed. New Holland Publishers, Sydney.

Xu, T., Hutchinson, M.F., 2013. New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. Environ. Model. Softw. 40, 267–279. doi:10.1016/j.envsoft.2012.10.003

Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. Mixed effects models and extensions in ecology with R. Springer, Newburgh.

Supporting Information

Appendix S1. Calculation of Growth Index variable

The Growth Index is calculated within the GROCLIM package of ANUCLIM (Xu and Hutchinson, 2013). The Growth Index is a measure that summarises several broad environmental and climatic variables into one biologically-meaningful productivity-related metric. Designed initially as a generalized growth model for vegetation response to light, thermal and water regimes, growth index calculates weekly indices of light, temperature, moisture availability and applies them to models of plant growth based on input climate surfaces for Australia. The output is a comprehensive set of raster layers, which can be built under current, or projected future climates.

For ecological examinations, the use of the growth index metric presents significant advantages over other environmental and climatic measures available including latitude, longitude, temperature and rainfall and hence was used in this study. First, although geographically descriptive, the use of latitude/longitude has limited ecological and biological meaning. Latitude/longitude is often used to reflect gradients in temperature, aridity and ecosystem change however in our study these gradients were better represented using the combined model of growth index. Second, combining environmental and climatic measures into one productivity-based model of growth index allowed us to combine the likely influences of several variables into one variable suitable for modelling. Third, the measures of growth index (daylight, temperature, and moisture) are relevant to reptiles as thermoregulatory ectotherms sensitive to basking opportunity, thermal conditions and moisture-limiting attributes like vegetation cover and prey availability.

Table S1. *Description of each region including the broad agro-climate (from Hutchinson et al., 2005), topographic and dominant land use features (from OEH, 2014).*

Region	Agro-climate	Annual Temp. (ºC)	Annual rainfall (mm)	Mean elevation (m a.s.l)	General Topography	Dominant Land Use
Northern Region	Most plant growth in summer, although summers are moisture limiting. Temperature limits plant growth in winter	10-19	449-1015	540	Inland Slopes	Summer crops; native pasture grazing
Northern Slopes	Most plant growth in summer, although summers are moisture limiting. Temperature limits plant growth in winter	10-16	500 – 1150	431	Tablelands / Plains	Winter cereals and summer crops; native pasture grazing
Southern Slopes	Moisture availability high in winter-spring, moderate in summer, most plant growth in spring	9-15	500 – 1150	427	Inland Slopes	Spring crops; improved and native pastures
Southern Highlands	Moisture availability high in winter-spring, moderate in summer, most plant growth in spring	6-16	460-1883	733	Elevated Ranges	Horticulture; improved and native pasture grazing

Supporting Information References

OEH, 2014. Bioregions of New South Wales [WWW Document]. URL http://www.environment.nsw.gov.au/bioregions/Bioregions.htm (accessed 7.13.14).

Hutchinson, M.F., Mcintyre, S., Hobbs, R.J., Stein, J.L., Garnett, S., Kinloch, J., 2005. Integrating a global agro-climatic classification with bioregional boundaries in Australia. Glob. Ecol. Biogeogr. 14, 197–212.

Table S2*. List of all reptile individuals surveyed for each species, summed for the entire study area (Study) and each study region: Northern (North), Northern Slopes (NS), Southern Slopes (SS), Southern Highlands (SH).*

Family	Scientific name	Totals				
		Study	North	NS	SH	SS
Agamidae	*Amphibolurus burnsi*	1	1	0	0	0
	Amphibolurus muricatus	6	1	0	5	0
	Diporiphora nobbi	1	1	0	0	0
	Intellagama lesueurii	1	1	0	0	0
	Pogona barbata	18	3	2	8	5
Carphodactylidae	*Underwoodisaurus milii*	11	0	0	0	11
Cheluidae	*Chelodina longicollis*	2	0	0	2	0
Diplodactylidae	*Amalosia rhombifer*	1	1	0	0	0
	Lucasium steindachneri	1	1	0	0	0
	Nebulifera robusta	3	3	0	0	0
	Oedura tryoni	1	1	0	0	0
	Strophurus intermedius	2	0	2	0	0
Elapidae	*Cryptophis nigrescens*	2	2	0	0	0
	Demansia psammophis	3	2	1	0	0
	Furina diadema	1	1	0	0	0
	Notechis scutatus	1	0	0	1	0
	Parasuta dwyeri	27	5	6	7	9
	Pseudechis porphyriacus	2	0	0	1	1
	Pseudonaja textilis	17	1	6	1	9
Gekkonidae	*Christinus marmoratus*	46	0	13	9	24
	Diplodactylus vittatus	37	2	6	8	21
	Gehyra dubia	1	0	1	0	0
	Gehyra variegata	7	0	2	4	1
	Heteronotia binoei	7	7	0	0	0
Pygopodidae	*Aprasia parapulchella*	32	0	9	14	9
	Delma inornata	14	2	2	2	8
	Delma plebeia	9	7	2	0	0
	Delma tincta	2	2	0	0	0
Scincidae	*Acritoscincus platynotum*	6	0	0	6	0
	Anomalopus leuckartii	15	10	5	0	0
	Carlia pectoralis	1	1	0	0	0
	Carlia sp	10	10	0	0	0
	Carlia tetradactyla	88	12	11	10	55
	Carlia vivax	3	3	0	0	0
	Cryptoblepharus pannosus	67	2	16	0	49
	Cryptoblepharus pulcher	34	34	0	0	0
	Cryptoblepharus sp	92	14	48	0	30
	Ctenotus spaldingi	163	36	41	10	76
	Ctenotus taeniolatus	39	0	2	15	22
	Egernia cunninghami	27	1	7	9	10
	Egernia striolata	49	14	7	0	28
	Eulamprus quoyii	1	1	0	0	0
	Hemiergis talbingoensis	134	28	0	87	19
	Lampropholis delicata	123	8	10	74	31
	Lampropholis guichenoti	22	8	0	13	1
	Lerista bougainvillii	5	0	1	1	3
	Lerista timida	13	6	7	0	0
	Lygisaurus foliorum	9	8	1	0	0
	Menetia greyii	12	7	0	4	1
	Morethia boulengeri	438	34	61	78	265
	Saiphos equalis	1	1	0	0	0
	Tiliqua rugosa ssp aspera	10	0	0	3	7
	Tiliqua scincoides ssp scincoides	13	4	1	6	2
Typhlopidae	*Ramphotyphlops nigrescens*	2	1	1	0	0
	Ramphotyphlops sp	1	1	0	0	0
	Ramphotyphlops wiedii	5	5	0	0	0
Varanidae	*Varanus varius*	2	0	1	0	1

Table S3. *Observed species richness, estimated richness and the percentage of observed to the estimated species richness (pcnt value) for the whole study area and each of the four study regions.*

	Observed richness	Estimated richness	Pcnt value
Whole study area	57	72	79.7%
Northern	43	59	72.4%
Northern Slopes	28	34	82.9%
Southern Slopes	26	30	87.5%
Southern Highlands	25	27	92.9%

Table S4. *The best-ranked generalised linear mixed models (GLMMs) investigating the role of eight predictor variables (growth index [Gr_id], northerly aspect [Asp_N], elevation [Elev], richness of native groundcover [NGR], length of log cover [LgL], rock cover [Rock], bare ground cover [BG] and native overstorey cover [NOS]) plus interaction with region (Reg) as predictors of four measures of reptile community assembly (total richness, rare species richness, abundance, evenness) for the whole study area. Outputs from both the (i) unstandardized and (ii) standardized variables are given. Selected models are indicated by bold text.*

(i) Unstandardized

Response	Included variables															Model rank		
	(Int)	Asp_N	Reg	BG	Elev	Gr_id	LgL	NGR	NOS	Rock	Reg* Elev	Reg* Asp_N	Reg* NGR	Reg* LgL	df	logLik	AICc	delta	weight
Species Richness	1.09	-0.06			-0.07	0.10	0.10	0.11	-0.08	0.10					9	-419.47	857.7	0.00	0.108
	1.09	-0.07				0.12	0.09	0.08	-0.07	0.10					8	-420.70	858	0.30	0.093
	1.09	-0.06				0.12	0.06	0.07		0.11					7	-421.84	858.2	0.45	0.087
	1.09				-0.07	0.11	0.11	0.11	-0.07	0.10					8	-420.80	858.2	0.50	0.084
	1.09	-0.06			-0.06	0.12	0.06	0.09		0.11					8	-420.90	858.4	0.71	0.076
	1.09				-0.06	0.12	0.07	0.09		0.11					7	-422.03	858.6	0.83	0.072
	1.09	-0.08				0.14		0.07		0.11					6	-423.16	858.7	0.95	0.067
	1.09					0.13	0.07	0.07		0.11					6	-423.21	858.8	1.05	0.064
	1.09					0.12	0.10	0.08	-0.06	0.10					7	-422.28	859.1	1.33	0.056
	1.09	-0.07			-0.06	0.13		0.09		0.11					7	-422.29	859.1	1.35	0.055
	0.92	**-0.07**	**+**		**-0.12**	**0.19**	**0.09**	**0.12**	**-0.07**	**0.10**					**12**	**-416.85**	**859.1**	**1.37**	**0.055**
	0.92	-0.08	+		-0.11	0.21		0.10		0.11					10	-419.08	859.1	1.41	0.053
	0.94	-0.07	+		-0.11	0.19	0.05	0.10		0.11					11	-418.07	859.3	1.60	0.049
	1.09	-0.06				0.13	0.06			0.12					6	-423.62	859.6	1.87	0.042
	0.90	-0.23	+		-0.10	0.21		0.10		0.12		+			13	-416.087	859.8	2.1	0.038
Rare Species Richness	-0.18		+		0.17			0.17	-0.09	0.11	+				12	-333.21	691.8	0.00	0.149
	-0.15		+		0.16			0.15		0.12	+				11	-334.44	692.1	0.24	0.132
	-0.20		+		0.16		0.07	0.17	-0.13	0.10	+				13	-332.75	693.2	1.32	0.077
	-0.18	-0.05	+		0.18			0.17	-0.10	0.11	+				13	-332.87	693.4	1.55	0.069
	-0.06		**+**		**0.28**			**-0.27**	**-0.11**	**0.12**	**+**		**+**		**15**	**-330.61**	**693.4**	**1.59**	**0.067**
	-0.39		+		0.19	0.11		0.16	-0.10	0.11	+				13	-332.97	693.6	1.76	0.062
	-0.15		+		0.18			0.18	-0.11		+				11	-335.21	693.6	1.78	0.061
	-0.21		+	0.04	0.19			0.17	-0.09	0.11	+				13	-333.08	693.8	1.97	0.056
	-0.19		+	0.05	0.19			0.15		0.12	+				12	-334.21	693.8	1.99	0.055
	-0.33		+		0.18	0.09		0.14		0.12	+				12	-334.279	694	2.13	0.051
Abundance	**1.85**	**-0.24**	**+**		**0.29**			**-0.14**		**0.11**	**+**	**+**	**+**		**18**	**-680.94**	**1401.1**	**0.00**	**0.223**
	1.47	-0.23	+		0.31	0.19		-0.13		0.11	+	+	+		19	-679.95	1401.5	0.39	0.183
	1.85	-0.23	+		0.29			-0.13	-0.02	0.11	+	+	+		19	-680.849	1403.2	2.19	0.075

Response	Included variables																Model rank		
											Reg* Elev	Reg* Asp_N	Reg* NGR	Reg* LgL					
	(Int)	Asp_N	Reg	BG	Elv	Gr_id	LgL	NGR	NOS	rck					df	logLik	AICc	delta	weight
Evenness	0.72					0.08				0.05					5	-78.55	167.4	0.00	0.138
	0.72				**-0.04**	**0.07**		**0.04**		**0.04**					**7**	**-76.69**	**167.9**	**0.52**	**0.107**
	0.72				-0.03	0.08				0.05					6	-77.93	168.2	0.86	0.09
	0.72					0.08		0.02		0.04					6	-78.01	168.4	1.01	0.083
	0.72					0.08	0.02			0.05					6	-78.12	168.6	1.24	0.074
	0.72	-0.02				0.08				0.05					6	-78.23	168.8	1.47	0.066
	0.72				-0.04	0.08		0.04							6	-78.44	169.2	1.87	0.054
	0.72				-0.04	0.07	0.02	0.04		0.04					8	-76.31	169.3	1.88	0.054
	0.72			0.01		0.08				0.05					6	-78.47	169.3	1.94	0.052
	0.72					0.08			0.01	0.05					6	-78.47	169.3	1.95	0.052
	0.72					0.09									4	-80.58	169.3	1.97	0.051
	0.72				-0.03	0.07	0.02			0.05					7	-77.518	169.5	2.16	0.047

(ii) Standardized

Response	Included variables																Model rank		
											Reg* Elev	Reg* Asp_N	Reg* NGR	Reg* LgL					
	(Int)	Asp_N	Reg	BG	Elv	Gr_id	LgL	NGR	NOS	rck					df	logLik	AICc	delta	weight
Species Richness	**1.38**	**-0.07**	**+**		**-0.08**	**0.08**	**0.09**	**0.11**	**-0.07**	**0.10**					**12**	**-416.85**	**859.1**	**0.00**	**0.092**
	1.39	-0.08	+		-0.07	0.09		0.10		0.11					10	-419.08	859.1	0.04	0.09
	1.38	-0.07	+		-0.08	0.08	0.05	0.10		0.11					11	-418.07	859.3	0.23	0.082
	1.37	-0.23	+		-0.07	0.09		0.09		0.12		+			13	-416.09	859.8	0.73	0.064
	1.39		+		-0.08	0.08	0.07	0.09		0.11					10	-419.56	860.1	1.00	0.056
	1.38		+		-0.08	0.08	0.10	0.11	-0.07	0.10					11	-418.51	860.2	1.10	0.053
	1.37		+		-0.10	0.06	0.18	0.11		0.11				+	13	-416.39	860.4	1.34	0.047
	1.37		+		-0.11		0.20	0.11		0.11				+	12	-417.52	860.4	1.34	0.047
	1.39	-0.08	+			0.10		0.08		0.11					9	-420.84	860.5	1.38	0.046
	1.39	-0.08	+		0.02	0.09		0.09		0.11	+				13	-416.48	860.6	1.51	0.043
	1.37	-0.23	+			0.10		0.07		0.12		+			12	-417.62	860.6	1.55	0.042
	1.37		+		-0.11		0.23	0.13	-0.07	0.11				+	13	-416.53	860.7	1.61	0.041
	1.37	-0.24	+		0.04	0.09		0.09		0.12	+	+			16	-413.13	860.8	1.66	0.04
	1.36		+		-0.10	0.06	0.21	0.12	-0.06	0.10				+	14	-415.43	860.8	1.68	0.04
	1.36	-0.06	+		-0.10	0.06	0.19	0.12	-0.07	0.11				+	15	-414.33	860.9	1.77	0.038
	1.36	-0.05	+		-0.10	0.06	0.16	0.11		0.11				+	14	-415.49	860.9	1.80	0.037
	1.39	-0.08	+		-0.07	0.09		0.10	-0.03	0.10					11	-418.87	860.9	1.83	0.037
	1.38	-0.08	+		0.01	0.08	0.08	0.11	-0.08	0.10	+				15	-414.38	861	1.86	0.036
Species Richness (cont.)	1.38	-0.07	+			0.09	0.08	0.09	-0.07	0.10					11	-418.92	861	1.92	0.035
	1.36	-0.05	+		-0.11		0.22	0.13	-0.07	0.11				+	14	-415.63	861.2	2.07	0.033

Response	**Included variables**																**Model rank**		
	(Int)	**Asp_N**	**Reg**	**BG**	**Elv**	**Gr_id**	**LgL**	**NGR**	**NOS**	**rck**	**Reg* Elev**	**Reg* Asp_N**	**Reg* NGR**	**Reg* LgL**	**df**	**logLik**	**AICc**	**delta**	**weight**
Rare Species	-0.07		+		0.12			0.16	-0.09	0.11		+			12	-333.21	691.8	0.00	0.149
	-0.07		+		0.11			0.14		0.12		+			11	-334.44	692.1	0.24	0.132
	-0.07		+		0.11		0.06	0.16	-0.13	0.10		+			13	-332.75	693.2	1.32	0.077
	-0.07	-0.05	+		0.13			0.16	-0.10	0.11		+			13	-332.87	693.4	1.55	0.069
	-0.07		**+**		**0.19**			**-0.26**	**-0.11**	**0.12**		**+**	**+**		**15**	**-330.61**	**693.4**	**1.59**	**0.067**
	-0.07		+		0.13	0.05		0.16	-0.10	0.11		+			13	-332.97	693.6	1.76	0.062
	-0.06		+		0.12			0.17	-0.11			+			11	-335.21	693.6	1.78	0.061
	-0.07		+	0.03	0.13			0.16	-0.09	0.11		+			13	-333.08	693.8	1.97	0.056
	-0.07		+	0.04	0.13			0.14		0.12		+			12	-334.21	693.8	1.99	0.055
	-0.07		+		0.12	0.04		0.14		0.12		+			12	-334.28	694	2.13	0.051
Abundance	**1.87**	**-0.23**	**+**		**0.20**			**-0.13**		**0.11**	**+**	**+**	**+**		**18**	**-680.94**	**1401.1**	**0.00**	**0.223**
	1.87	-0.23	+		0.22	0.08		-0.13		0.11	+	+	+		19	-679.95	1401.5	0.40	0.183
	1.87	-0.23	+		0.21			-0.13	-0.02	0.11	+	+	+		19	-680.85	1403.2	2.19	0.075
Evenness	**0.86**		**+**		**-0.04**	**0.05**		**0.03**		**0.04**					**10**	**-75.50**	**172**	**0.00**	**0.119**
	0.86		+		-0.04	0.06				0.05					9	-76.61	172	0.03	0.118
	0.86		+			0.06				0.05					8	-77.82	172.3	0.28	0.104
	0.86		+		-0.04	0.05	0.03			0.05					10	-75.95	172.9	0.90	0.076
	0.86		+		-0.05	0.05	0.02	0.03		0.05					11	-74.94	173.1	1.08	0.07
	0.86		+			0.06		0.02		0.04					9	-77.25	173.3	1.30	0.062
	0.86	-0.02	+		-0.04	0.05		0.03		0.04					11	-75.09	173.4	1.39	0.06
	0.86	-0.02	+		-0.04	0.06				0.05					10	-76.21	173.4	1.41	0.059
	0.86		+			0.05	0.02			0.05					9	-77.32	173.4	1.45	0.058
	0.86		+		-0.04	0.06		0.04							9	-77.37	173.5	1.55	0.055
	0.86	-0.02	+			0.06				0.05					9	-77.45	173.7	1.71	0.051
	0.86		+		-0.04	0.06			0.01	0.05					10	-76.51	174	2.01	0.044

Figure S1. *Example of a site from our study area showing the open woodland structure that is typical of the box-gum grassy woodland ecological community.*

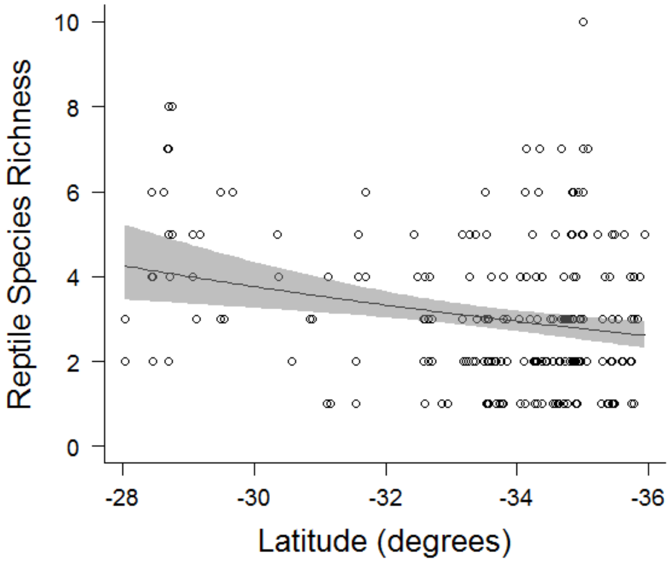

Figure S2. *Relationship between reptile species richness and latitude (degrees) gradient evident across the whole study, indicating confidence interval (shaded) and raw data (points)*

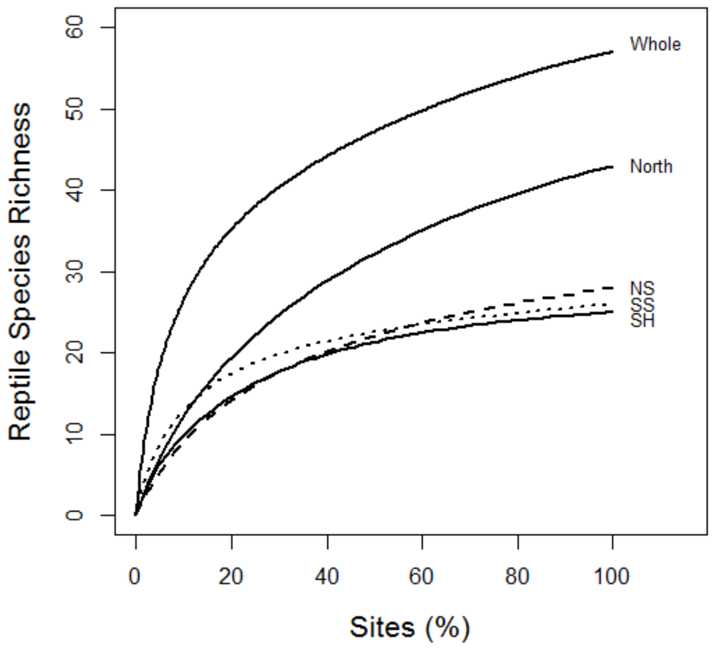

Figure S3. *Species accumulation curves for the observed species richness for the whole study and the four study regions.*

PAPER IV. EFFECTS OF PAST AND PRESENT LIVESTOCK GRAZING ON HERPETOFAUNA IN A LANDSCAPE-SCALE EXPERIMENT.

Central to obtaining effective agri-environment scheme outcomes is the use of carefully prescribed site-level management actions, as these counteract the negative influence of agriculture on biodiversity. Livestock grazing is a widely used management action in agri-environment scheme design, yet its impact on a variety of fauna remain poorly resolved. In this paper, we demonstrate how knowledge of grazing impacts – both present and past grazing – has important impact on reptile fauna.

Appendicies 2 and 3 reveal additional impacts of grazing across the same study but for a range of other taxa (invertebrates and birds).

Livestock graze a field neighbouring Box Gum Grassy Woodland.

Kay, G.M., Mortelliti, A., Tulloch, A.I., Barton, P.S., Florance, D., Cunningham, S.A., Lindenmayer, D.B., 2016. Effects of past and present livestock grazing on herpetofauna in a landscape-scale experiment. Conserv. Biol. 31, 446-4584. doi:10.1111/cobi.12779.

Effects of past and present livestock grazing on herpetofauna in a landscape-scale experiment.

Abstract

Livestock grazing is the most widespread land use on Earth and can have negative effects on biodiversity. Yet, many of the mechanisms by which grazing leads to changes in biodiversity remain unresolved. One reason is that conventional grazing studies often target broad treatments rather than specific parameters of grazing (e.g., intensity, duration, and frequency) or fail to account for historical grazing effects. We conducted a landscape-scale replicated grazing experiment (15,000 km^2, 97 sites) to examine the impact of past grazing management and current grazing regimes (intensity, duration, and frequency) on a community of ground-dwelling herpetofauna (39 species). We analyzed community variables (species richness and composition) for all species and built multiseason patch-occupancy models to predict local colonization and extinction for the 7 most abundant species. Past grazing practices did not influence community richness but did affect community composition and patch colonization and extinction for 4 of 7 species. Present grazing parameters did not influence community richness or composition, but 6 of the 7 target species were affected by at least one grazing parameter. Grazing frequency had the most consistent influence, positively affecting 3 of 7 species (increased colonization or decreased extinction). Past grazing practice affected community composition and population dynamics in some species in different ways, which suggests that conservation planners should examine the different grazing histories of an area. Species responded differently to specific current grazing practices; thus, incentive programs that apply a diversity of approaches rather than focusing on a change such as reduced grazing intensity

should be considered. Based on our findings, we suggest that determining fine-scale grazing attributes is essential for advancing grazing as a conservation strategy.

Introduction

Domestic livestock grazing is a major driver of ecosystem degradation and affects more of Earth's surface than any other human land use (Erb et al. 2007). To date, 25% of the total extent of terrestrial ecosystems, an area larger than the combined European and North American continents, has been altered by livestock grazing (Asner et al. 2004), and further expansion and intensification is anticipated (Alexandratos & Bruinsma 2012). Thus, mitigating the impacts of grazing on ecosystems, such as through conservation incentive programs, requires understanding the responses of different components of biodiversity to alternative grazing regimes (Tscharntke et al. 2005).

Despite over a half century of research investigating biodiversity responses to grazing, clear patterns have not emerged, fuelling debate on the suitability of different grazing approaches for conservation and restoration (Briske et al. 2011). This is likely due to 2 major shortcomings in the understanding of the influence of livestock grazing on biodiversity. First, the legacy of past grazing management may have large effects on contemporary biodiversity (Donihue et al. 2013; Valls-Fox et al. 2015), but the nature of this influence is poorly understood (McIntyre et al. 2003). Effects can be long-lasting, reflecting cumulative and slow degradation of agroecosystems through altered vegetation patterns and nutrient distribution (Denslow 1980). Second, the influence of livestock grazing arises from the collective influence of multiple parameters that define the grazing regime (Briske et al. 2008; Denmead et al. 2015), but studies have generally ignored this complexity and instead examined broad categories of grazing management (e.g., continuous vs. rotational

[Dorrough et al. 2012]). Important parameters include the intensity, duration, and frequency of disturbance events, which affect the structure and condition of faunal habitat (Miller et al. 2011). Where detailed grazing data are available, studies have tended to focus solely on measures of grazing intensity (e.g., McIntyre & Lavorel 2001; Fischer et al. 2009; Howland et al. 2014). Isolating the relative importance of multiple individual parameters is extremely important but requires carefully designed studies with large data sets of detailed grazing data, which are rarely available (but see Dorrough et al. 2004a).

Previous researchers examining biodiversity responses to grazing have focused on vegetation (Díaz et al. 2007; Dorrough & Scroggie 2008), soil biota (Teague et al. 2011), and highly mobile fauna (Martin & McIntyre 2007). Ground-dwelling fauna with low mobility and often low detectability rates (e.g., reptiles, amphibians, some invertebrates, and mammals) has attracted less attention (Dorrough et al. 2012; Howland et al. 2014; Larson 2014; Barton et al. 2016). Results of the few existing studies of herpetofauna show limited effects of grazing (review by Howland et al. [2014]), although the limited mobility and strong habitat associations of herpetofauna suggest that they might be particularly responsive to both direct (e.g., trampling and browsing) and indirect (e.g., changes to microclimate and cascading food webs) impacts of grazing (Larson 2014; Denmead et al. 2015). The limited effects may be because studies are commonly conducted at small spatial scales (field-level) and in isolation from other interacting disturbances (Briske et al. 2008). However, grazing represents only one of many potential contributors to species decline in agricultural landscapes (Tscharntke et al. 2005) and therefore should be explored in the context of other abiotic (e.g., climatic) and biotic (e.g., habitat modification) drivers (Brown et al. 2011). This requires large-scale studies to examine grazing effects against a background of natural variation (Briske et al. 2008; Barton et al. 2016). Many studies explore responses to grazing at the community or species level (e.g., Dorrough et al. 2012; Howland et al. 2014) without considering more subtle influences that could be acting on populations. Studies examining population dynamics (e.g., patch colonization and extinction [Mortelliti et al. 2015]) as well as community responses to grazing are therefore needed.

We investigated the impacts of past and present grazing management on ground-dwelling herpetofauna (reptiles and amphibians) in a landscape-scale experiment in southeastern Australia (15,000 km^2, 97 sites, Fig. 1). We focused on a diverse herpetofaunal community encompassing several microhabitat guilds defined by a wide range of ecological and life-history traits (Michael et al. 2015). We quantified the relative importance of parameters of contemporary grazing regimes (intensity, duration, and frequency) across a range of past grazing contexts in a farming landscape. We examined the response to grazing and nongrazing drivers of herpetofaunal community characteristics (richness and composition) as well as population turnover (patch colonization and extinction processes). Understanding the effects of past grazing and parameters of present grazing regimes has important implications for conservation. It can help identify areas where particular grazing regimes may be useful for restoring or maintaining populations and determine drivers of biodiversity decline. To address this conservation need, we considered how past grazing practices and parameters of present grazing regimes (intensity, duration, and frequency of grazing) influence community richness and composition and patch occupancy by individual species.

Methods

Study Design

Our study was conducted in a grazing-dominated landscape spanning approximately 100 km east-west and 150 km north-south in southeastern Australia (Fig. 1). We established 97 sites on 29 different farms in 2011. Sites were located within a critically endangered Box Gum Grassy Woodland ecological community (Supporting Information) of which <3% remains following 230 years of broad-scale clearing for agriculture (Lindenmayer et al. 2012). We grouped farms into 4 blocks that represented past grazing practices: continuous grazing for >10 years (prolonged continuous); recent (<5 years) long-duration rotational grazing following continuous grazing (modified low rotational); high-intensity short-duration grazing for >10 years (prolonged high rotational); and recent (<5 years) high-intensity short-duration grazing following previous continuous grazing (modified high rotational) (Fig. 1b). Within each farm, we selected 2–4 sites to represent different within-farm grazing strategies ranging from complete grazing exclusion to continuous stocking (Fig. 1c). We matched sites within farms on the basis of topography, past land use (cultivation, grazing, and fertilizer history), and tree cover. This allowed us to capture an intensification gradient from little cleared or grazed, unfertilized, and uncultivated woodlands to intensively cleared, grazed, fertilized, and cultivated fields.

Our experimental design allowed us to test both past and present grazing in the same landscape. First, we examined the effect of past grazing practices by comparing richness and composition of herpetofaunal communities and individual species patch-occupancy in groupings of farms comprising the 4 unique grazing management histories. We then examined individual grazing-regime parameters by combining data from the 97 sites in

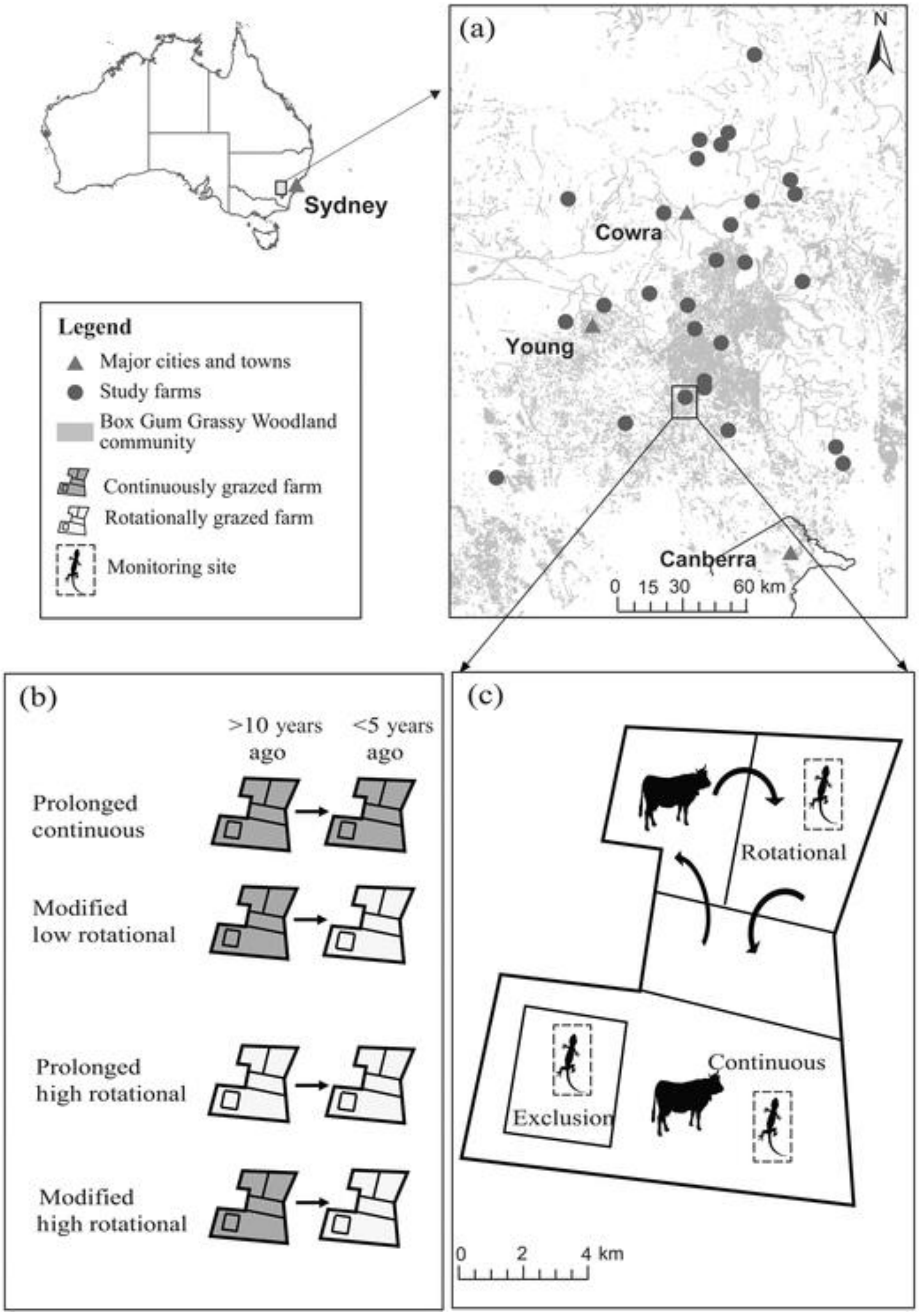

Figure 1. *Study area and experimental design of the grazing study: (a) location of farms, (b) 4 groups of past grazing practices defined by duration and type of management (prolonged continuous, continuous grazing for >10 years; modified low rotational, recent [< 5 years] long-duration rotational grazing following continuous grazing; prolonged high rotational, high-intensity short-duration grazing for >10 years; modified high rotational, recent [<5 years] high-intensity short-duration grazing following previous continuous grazing), and (c) typical farm with the monitoring site nested within a gradient of present grazing strategies used to ascertain the full range of specific grazing parameters.*

models of herpetofauna responses to the continuous grazing variables while controlling for differences in past grazing management.

Grazing and Ecological Variables

The predominant livestock on farms were sheep (*Ovis aries*) and cattle (*Bos taurus*). We collected data on the duration, frequency, and intensity of every grazing event for each site and summarized these into 4 grazing parameters for analysis (Table 1): duration, the average number of days grazed per stocking rotation; frequency, the total number of destocked periods per year; and intensity, the total daily dry sheep equivalent (a standardized measure of feed requirements by different kinds of livestock [McLaren 1997]) averaged across the entire year. We also calculated a second intensity measure that represented the average daily dry sheep equivalent for only the grazed days of the year (excluding days when the pasture was rested). We also included environmental predictor variables to determine whether these had more of an effect than grazing factors on herpetofaunal response (Table 1). Within a 250-m radius of each site, we collected 2 continuous landscape-level variables that are important to biodiversity in Australian fragmented landscapes (Dorrough & Scroggie 2008; Fischer et al. 2010): amount of tree cover and land area modified by frequent fertilization or cultivation. We considered 250 m an appropriate distance given the scale of movement of herpetofauna in these landscapes (Brown et al. 2011).

We recorded the time of each survey event. We used remotely sensed data for 5 site-scale abiotic environmental variables: elevation, aspect, rainfall, and landscape position (i.e., topographic wetness index). We measured air temperature during each survey. We collected data on 11 site-scale habitat and vegetation variables in field surveys from

January to March of each survey year following the protocol of Kay et al. (2016) (see Supporting Information for details). We used principal components analysis to reduce these 11 variables to 2 new variables to remove redundancy among correlated (r>0.6) variables (Ford 2005). The first 2 principal components (pc1 and pc2 represented 47% of variation) were used in all subsequent analyses. Principal component 1 represented a gradient of available grass sward structure from sites dominated by dense grassy tussocks to less-grassy log and rock-dominated sites, whereas pc2 represented a gradient of grass sward composition ranging from exotic-dominated to native-dominated swards (Supporting Information). Overall, this resulted in a complete set of 16 (5 grazing and 11 ecological) predictor variables (Table 1). We examined all data for correlations, log-transformed them if necessary to reduce skewness and the influence of extreme values, and standardized data to a mean of zero for analysis (Supporting Information).

Herpetofauna Surveys

At each site, we established 2 monitoring plots (0.4 ha) 100 m apart. For each plot, we surveyed herpetofauna with a repeated time- and area-constrained (10 min × 0.4 ha) active search of natural habitat and inspections of artificial refuge arrays (Supporting Information). Active searches involved scanning each plot for basking or moving animals, raking through leaf litter and grass tussocks, lifting logs and surface rocks, and inspecting exfoliating bark. Each artificial array consisted of 4 ceramic tiles (32 × 42 cm), 2 sheets of corrugated iron (1 × 1 m) stacked on top of each other, and 4 wooden posts (1.2-m long). Surveys were conducted across all 97 sites during spring (September) of 2011, 2012, and 2013 on clear days with minimal wind from 0900 to 1600 by the same group of experienced field ecologists. Taxonomy follows Wilson and Swan (2013) and Anstis

(2013). Individuals were released once recorded, in accordance with Australian National University ethics guidelines (protocols F.ES.04.10 and A2013/38).

Statistical Analyses

We examined both community and individual species patch-occupancy measures to determine impacts of past and present grazing on herpetofauna. Community analyses were conducted using the full set of species observations, whereas patch-occupancy models were fitted using detection (presence or absence) of the 7 species with the highest (>5%) detection rate (number of detections or number of visits): the skinks *Carlia tetradactyla* (n = 76), *Cryptoblepharus pannosus* (n = 79), *Ctenotus spaldingi* (n = 93), *Hemiergis talbingoensis* (n = 142), *Morethia boulengeri* (n = 402), gecko *Christinus marmoratus* (n = 43), and frog *Limnodynastes tasmaniensis* (n = 273) (Supporting Information).

We analyzed community response to grazing in 2 ways so that we could explore both richness and composition. First, we fitted generalized linear mixed models (GLMMs) (Zuur et al. 2009) with Poisson distribution (log link) to test for response in 3 richness measures: total species richness, richness of species occurring at <5% of all sites (hereafter rare species richness), and richness of species in each microhabitat guild. We assigned explanatory variables to 4 categories (or hypotheses) that we used to explain richness response: site-scale abiotic factors, site-scale habitat factors, landscape-scale habitat factors, and site-scale grazing factors (Table 1). To address our questions about past and present grazing, we fitted past and present grazing variables independently. Both grazing intensity measures (annual stocking rate and event stocking rate) were highly correlated (r>0.6; Supporting Information), so we examined them separately as 2 independent models (grazing 1 and grazing 2). When testing for past grazing effects, we fitted farm, time, and year as random effects. When testing for present grazing effects, we fitted farm, time, year, and past grazing as random effects. We ranked models based on Akaike information criterion (AIC) (Burnham & Anderson 2002) and considered all models within 2ΔAIC of the top model. We fitted models using the lme4 package for R (Bates et al. 2015).

In addition to richness, we tested for statistical differences in assemblage composition among past grazing categories with a multiresponse permutation procedure (MRPP) (Zimmerman et al. 1985). We examined the influence of current grazing parameters with Mantel tests (Sokal & Rohlf 1995) to test for correlation in overall among-site dissimilarity in herpetofauna versus grazing variables and by comparing this result to dissimilarity in herpetofauna versus environmental variables. We also explored important drivers in community composition by conducting principle coordinates analysis (McCune & Grace

Table 1. *Predictor variables used to assess herpetofaunal response to past and present grazing*

Category of Predictor	**Predictor (abbreviation)**	**Description**	**Source**	**Parameters for prediction** [a]
Time	Year (year)	Year (categorical) accounts for unmeasured year-specific factors	NA	*p*
	Time (time)	Time of day survey was conducted	NA	*p*
Site-scale Abiotic	Rainfall (rain)	Total rainfall (mm) for 2 months prior to survey period	Spatial data[b]	*p*
	Temperature (temp)	Air temperature (ºC) at time of survey (4 levels; <15ºC, 15-20ºC, 20-25ºC, >25ºC)	Habitat surveys (this study)	*p*
	Aspect (aspn)	Northerly Aspect	Spatial data[b]	Ψ
	Elevation (elev)	Elevation (m above sea level)	Spatial data[b]	Ψ
	Landscape Position (TWI)	Position in landscape given by Topographic Wetness Index	Spatial data[b]	Ψ

Category of Predictor	**Predictor (abbreviation)**	**Description**	**Source**	**Parameters for prediction [a]**
Site-scale habitat	pc1	Gradient of grassy habitat elements (dense grass tussocks to open, log and rock dominated sites).	Habitat surveys (this study)	Ψ, ϒ, ε
	pc2	Gradient of grass composition (native grass swards to exotic grass swards).	Habitat surveys (this study)	Ψ, ϒ, ε
Landscape-scale habitat	LU250	Area of modified (fertilized) pasture within 250 m radius of site	Spatial data[c]	Ψ, ϒ, ε
	tree250	Amount of tree cover within 250 m radius of site	Spatial data[d]	Ψ, ϒ, ε
Past Grazing	PastGraz	Past grazing as categorical covariate	Landholder surveys (this study)	Ψ, ϒ, ε
Present Grazing	Duration[e] (edg)	Average duration of each grazing event (days)	Landholder surveys (this study)	ϒ, ε
	Frequency[e] (nde)	Number of resting events per year	Landholder surveys (this study)	ϒ, ε
	Intensity 1[e] (asr)	Grazing intensity (DSEdays) per day on average, across whole year	Landholder surveys (this study)	ϒ, ε
	Intensity 2[e] (esr)	Grazing intensity (DSEdays) per day on average, across stocked events	Landholder surveys (this study)	ϒ, ε

[a] *Parameters for prediction: detection probability p, probability of a site being occupied during the first survey Ψ; probability of a site being colonized by the target species between sampling sessions ϒ; and probability of the target species becoming locally extinct between sampling sessions ε.*

[b] *9-second resolution Digital Elevation Model* (Hutchinson et al., 2011)

[c] *SCALD (Standard Classification for Attributes of Land) Classification (provided on 04/08/2011 by Office of Environment and Heritage)*

[d] *FPC Foliage Proportion of Cover (provided on 07/09/2014 by Office of Environment and Heritage)*

[e] *Variables log-transformed*

2002) and fitting environmental and grazing variables as biplot vectors. We repeated analyses separately for all species as a set and for only common species (detection rate>2.5 [Supporting Information]) to determine whether there was an effect of rare species on the apparent community. Analyses were conducted in PC-ORD version 6, MjM software (McCune & Mefford 2011). We used Bray–Curtis dissimilarity metrics calculated from presence-absence data to minimize the influence of highly abundant species.

To explore species-level grazing effects, we fitted multiseason patch-occupancy models (MacKenzie et al. 2003) to presence-absence data (the sequence of detection or nondetection in each site) from each of the 7 most abundant species from our herpetofaunal surveys. The multiseason framework is useful for accounting for imperfect species detection, a source of bias particularly for studies examining distributions of terrestrial vertebrate species (MacKenzie 2005). The multiseason patch-occupancy model estimates 4 parameters: species detectability, P; probability of a site being occupied during the first survey, Ψ; probability of species colonization of a patch between sampling visits, ϒ; and probability of species extinction of a patch between sampling visits, ε.

For our occupancy models, we treated each of the 97 monitored woodland patches as a site (MacKenzie et al. 2003). We considered a visit to be an inspection of one of the 2 monitoring plots within each site; thus, each site was surveyed twice on the same day during the same year. We followed the protocol of Mortelliti et al. (2015) for fitting models.

We started by modeling detectability (P), fitting 5 models reflecting effects of time (survey year and time of survey) or abiotic conditions (total rainfall during previous 2 months [rain] and current temperature [temp] at the time of sampling) on detectability. We then selected the variables that most affected site occupancy (Ψ). We restricted these to 8 historical landscape-level factors (Table 1) and retained all predictors <2ΔAIC.

To determine the influence of grazing history, we modeled the probabilities of colonization (ϒ) and extinction (ε) as functions of past grazing (4 levels; categorical) along with 6 nongrazing variables: elevation, aspect, landscape position, tree cover (within 250 m), modified land use (within 250 m), and grass structure (pc1) and composition (pc2). To determine the influence of present grazing parameters, we replaced past grazing with the 4 grazing parameters (asr, esr, nde, and edg); thus, there were 10 terms in each model (Table 1).

Our inference was based on model-averaged estimates of all models within 2ΔAIC (Burnham & Anderson 2002), and we measured goodness-of-fit with Nagelkerke's (1991) R^2. We classified species as positively (beneficially) influenced by grazing if the extinction parameter was negative or the colonization parameter was positive and as negatively influenced if species showed a negative colonization or positive extinction parameter. To avoid overfitting models, we used additive models rather than fitting interactions. We assumed that sites on different farms were independent and checked for spatial dependence in the residuals of the most parameterized model with a spline correlogram (Zuur et al. 2009), which consistently revealed no evidence of spatial autocorrelation. We fitted occupancy models with the unmarked package for R (Fiske & Chandler 2011).

Results

We detected 1439 individuals across 97 sites, 29 reptile and 10 amphibian species across 8 microhabitat guilds (Supporting Information).

Past Grazing

Past grazing did not influence herpetofaunal community richness, but it did influence community composition. Past grazing was not included in any of the top-ranked GLMMs for herpetofaunal species richness (Table 2); no hypotheses explained variability in species richness and guild richness more than the null model (i.e., model with no predictor variables). Rare species richness was best explained by landscape habitat variables of surrounding tree cover and modified land use. In contrast, community composition differed significantly among sites (MRPP: $T = 13.11$, $A = 0.023$, $p<0.001$) (Supporting Information) grouped by past grazing history for all pair-wise comparisons (Supporting Information). Analyzing common and rare species separately produced similar results, so we considered only results from the whole community.

Past grazing also affected individual species' population processes. Multiseason patch-occupancy models revealed a response to past grazing for 4 of 7 species (Table 3). No single past grazing practice influenced all species in a consistently positive (i.e., high colonization or low extinction) or negative (i.e., low colonization or high extinction) way (Fig. 2).

Colonization probability was higher in modified high rotational and modified low rotational treatments for *M. boulengeri* and *C. tetradactyla*, whereas *C. spaldingi* was more likely to show patch extinction in these treatments (Fig. 2). In contrast, prolonged high rotational grazing resulted in highest patch colonization for *L. tasmaniensis*. Prolonged continuous grazing resulted in lower colonization probabilities for all species except *C. spaldingi*, which was found to do better in this treatment (zero probability of extinction) than in most other types of past grazing. Further details of patch-occupancy analyses are provided in Supporting Information.

Present Grazing Parameters

As with past grazing, no individual parameters describing present grazing practice influenced overall herpetofaunal species richness (Table 2). Top-ranked models for species richness and guild richness were again the null model, whereas rare species richness was again explained by the landscape variables surrounding tree cover and modified land use. Mantel tests showed that the correlation between present grazing parameters and herpetofauna composition was very low and nonsignificant (r = 0.008, p = 0.291) compared with herpetofauna composition and environmental variables (r = 0.1433, p = 0.001). Principal coordinates ordinations (not shown) were consistent with this finding, revealing that environment variables had a greater (but still weak) effect on herpetofaunal composition than present grazing variables (Supporting Information).

Multiseason occupancy models revealed that present grazing parameters affected 6 of 7 species; the exception was *H. talbingoensis* (Fig. 3, Table 3). Top-ranked models included a mix of grazing parameters. Two species were influenced by grazing intensity (*C. spaldingi* and *L. tasmaniensis*) and another 2 by duration (*C. pannosus* and *M. boulengeri*); both variables demonstrated a mix of positive effects (i.e., increasing the probability of a woodland treatment site being colonized or decreasing extirpation risk) and negative effects

Table 3. *Results of the generalized linear mixed models, including top-ranked model (bold), for herpetofaunal community response variables (species richness, rare species richness, microhabitat guild richness) for each model examining past grazing and specific parameters of present grazing*[a]. *Models with no predictor variables are given as null model.*

Response Variable	Category of Predictor	Predictor variables[b]	ΔAIC[c]	R[2d]
PAST GRAZING				
Species richness	**null**		**0**	**0.184**
	Landscape habitat	LU250 + tree250	5.344	0.184
	Local habitat	pc1 + pc2	5.649	0.182
	Grazing management	PastGraz	6.762	0.156
	Abiotic	aspn + Elev + rain + TWI	8.302	0.148
Rare species richness	**Landscape habitat**	**LU250 + tree250**	**0**	**0.282**
	null		5.396	0.235
	Local habitat	pc1 + pc2	5.554	0.253
	Grazing management	PastGraz	7.435	0.227
	Abiotic	aspn + elev + rain + TWI	8.978	0.227
Microhabitat guild richness	**null**		**0**	**0.276**
	Grazing management	PastGraz	2.111	0.163
	Local habitat	pc1 + pc2	2.163	0.239
	Landscape habitat	LU250 + tree250	3.568	0.26
	Abiotic	aspn + elev + rain + TWI	4.6	0.165
PRESENT GRAZING PARAMETERS				
Species richness	**null**		**0**	**0.184**
	Landscape habitat	LU250 + tree250	2.214	0.184
	Local habitat	pc1 + pc2	2.476	0.182
	Grazing 2	esr + nde + edg	2.949	0.182
	Grazing 1	asr + nde + edg	4.165	0.169
	Abiotic	aspn + elev + rain + TWI	5.127	0.148
Rare species richness	**Landscape habitat**	**LU250 + tree250**	**0**	**0.282**
	null		5.396	0.235
	Local habitat	pc1 + pc2	5.512	0.25
	Grazing 2	esr + nde + edg	7.315	0.264
	Grazing 1	asr + nde + edg	8.398	0.248
	Abiotic	aspn + elev + rain + TWI	8.978	0.227
Microhabitat guild richness	**null**		**0**	**0.276**
	Local habitat	pc1 + pc2	2.097	0.234
	Landscape habitat	LU250 + tree250	3.568	0.26
	Abiotic	aspn + elev + rain + TWI	4.6	0.165
	Grazing 1	asr + nde + edg	5.373	0.24
	Grazing 2	esr + nde + edg	5.446	0.267

[a] *A separate model was fitted to test effects of grazing and other alternative hypotheses*

[b] *Predictor variables: northerly aspect (aspn), elevation (elev), rainfall over preceding 2 months (rain), position in landscape (TWI), structural groundcover habitat gradient (pc1), native-exotic groundcover composition gradient (pc2), surrounding land-use improved (LU250), surrounding tree cover (tree250), past grazing as categorical covariate (PastGraz), annual stock rate (asr), event stocking rate (esr), number of resting events (nde), number of days grazed per event (edg)*

[c] *Delta Akaike information criterion (difference between each model and the top ranked model). Top ranked model bolded.*

[d] *Nagelkerke's coefficient of determination*

Table 4. *Top-ranked multi-season patch-occupancy models for each of the seven herpetofaunal species (ranked by taxonomy, T) examined for past grazing and specific parameters of present grazing.*

Species	**T**[a]	**df**	**ΔAIC**[b]	**R^2**[c]	**Model**[d]	**Response**[e]
PAST GRAZING						
Carlia tetradactyla	S	10	0	0.300	Ψ(pc1) ϒ(PastGraz) ε(.) p(year)	1
Cryptoblepharus pannosus	S	8	0	0.383	Ψ(elev) ϒ(pc2) ε(tree250) p(temp)	0
Ctenotus spaldingi	S	7	0	0.250	Ψ(elev) ϒ(pc2) ε(pc1) p(.)	1
		6	1.33	0.220	Ψ(elev) ϒ(pc2) ε(.) p(.)	
		7	1.44	0.240	Ψ(elev) ϒ(tree250) ε(pc1) p(.)	
		9	1.84	0.270	Ψ(elev) ϒ(pc2) ε(PastGraz) p(.)	
Hemiergis talbingoensis	S	8	0	0.671	Ψ(elev) ϒ(.) ε(pc1) p(year)	0
Morethia boulengeri	S	10	0	0.376	Ψ(elev) ϒ(PastGraz) ε(tree250) p(time)	1
Christinus marmoratus	G	7	0	0.136	Ψ(aspn) ϒ(.) ε(tree250) p(time)	0
		6	0.68	0.108	Ψ(.) ϒ(.) ε(tree250) p(time)	
Limnodynastes tasmaniensis	F	10	0	0.282	Ψ(pc2) ϒ(PastGraz) ε(pc2) p(temp)	1
PRESENT GRAZING PARAMETERS						
Carlia tetradactyla	S	8	0	0.115	Ψ(pc1) ϒ(nde) ε(.) p(year)	1+
		9	0.85	0.125	Ψ(pc1) ϒ(nde) ε(edg) p(year)	
		7	0.97	0.086	Ψ(pc1) ϒ(.)ε(.) p(year)	
		9	1.76	0.117	Ψ(pc1) ϒ(nde) ε(pc2) p(year)	
		8	1.78	0.098	Ψ(pc1) ϒ(tree250) ε(.) p(year)	
		9	1.8	0.116	Ψ(pc1) ϒ(nde) ε(nde) p(year)	
		9	1.92	0.115	Ψ(pc1) ϒ(nde) ε(pc1) p(year)	
		9	1.93	0.115	Ψ(pc1) ϒ(nde) ε(asr) p(year)	
		9	1.97	0.115	Ψ(pc1) ϒ(nde) ε(esr) p(year)	
		9	1.98	0.115	Ψ(pc1) ϒ(nde) ε(tree250) p(year)	
		9	1.99	0.115	Ψ(pc1) ϒ(nde) ε(LU250) p(year)	
Cryptoblepharus pannosus	S	7	0	0.380	Ψ(elev) ϒ(.) ε(edg) p(temp)	1-
		8	0.07	0.400	Ψ(elev) ϒ(pc2) ε(edg) p(temp)	
Ctenotus spaldingi	S	7	0	0.250	Ψ(elev) ϒ(pc2) ε(pc1) p(.)	1-
		6	1.33	0.220	Ψ(elev) ϒ(pc2) ε(.) p(.)	
		7	1.45	0.240	Ψ(elev) ϒ(pc2) ε(esr) p(.)	
Hemiergis talbingoensis	S	8	0	0.650	Ψ(elev) ϒ(.) ε(pc1) p(year)	0
Morethia boulengeri	S	8	0	0.242	Ψ(elev) ϒ(pc2) ε(tree250) p(time)	1+
		7	0.76	0.221	Ψ(elev) ϒ(.) ε(tree250) p(time)	
		8	1.42	0.231	Ψ(elev) ϒ(edg) ε(tree250) p(time)	
		8	1.61	0.230	Ψ(elev) ϒ(LU250) ε(tree250) p(time)	
Christinus marmoratus	G	8	0	0.127	Ψ(aspn) ϒ(nde) ε(pc2) p(time)	1+
		8	0.63	0.120	Ψ(aspn) ϒ(nde) ε(tree250) p(time)	
		8	1.93	0.107	Ψ(aspn) ϒ(nde) ε(asr) p(time)	

Species	T[a]	df	ΔAIC[b]	R^2[c]	Model[d]	Response[e]
Limnodynastes tasmaniensis	F	7	0	0.180	Ψ(pc2) ϒ(.) ε(pc2) p(temp)	1+
		8	1.58	0.180	Ψ(pc2) ϒ(nde) ε(pc2) p(temp)	
		7	1.83	0.160	Ψ(pc2) ϒ(.) ε(asr) p(temp)	

[a] *Key: Skink (S); Gecko (G); Frog (F).*

[b] *Delta Akaike information criterion (difference between each model and the top ranked model). Only models <2 ΔAIC are shown.*

[c] *Nagelkerke's coefficient of determination*

[d] *Key:probability of a site being occupied during the first survey (Ψ); probability of colonization (ϒ); probability of extinction (ε); detection probability (p); northerly aspect (aspn); elevation above sea level (elev); tree cover within 250 m of site (tree250); area of modified land-use within 250 m of site (LU250); year as categorical covariate (Y); past grazing as categorical covariate (PastGraz); livestock stocking rate per year (asr); livestock stocking rate per event (esr); mean duration (days) of grazed event (edg); number of livestock resting events (nde); time of day survey conducted (time); ordination of grassy to non-grassy ground habitat (pc1); ordination of exotic to native grassland composition (pc2); category of air temperature at survey (temp); constant model with no covariate (.).*

[e] *Response (to grazing); 1, present; 0, absent; +, positive effect; -, negative effect.*

(i.e., decreasing the probability of a woodland treatment site being colonized or increasing extirpation risk). Grazing frequency was the only variable to act in a consistent way; *C. tetradactyla*, *C. marmoratus*, and *L. tasmaniensis* responded positively to this measure.

Discussion

Past grazing did not influence herpetofaunal richness measures (Table 2) but did affect community composition and patch colonization and extinction for 4 of 7 species examined (Fig. 2). Present grazing parameters did not influence community richness or composition (Supporting Information). However, 6 of 7 species responded to individual grazing parameters (intensity, duration, and frequency); grazing frequency was the most common factor across all species (Fig. 3). Using this combination of community and dynamic occupancy approaches, we have provided compelling evidence for effects of both past and present grazing that have previously been overlooked relative to herpetofauna.

Effects of Past Grazing Practices on Herpetofauna

Despite strong ecological reasons for expecting past grazing practices to influence herpetofauna, studies have been confined to analyses of communities as a whole (e.g., richness [Dorrough et al. 2012]), and evidence for individual species responses appears limited to a single study of an African gecko (Donihue et al. 2013). We found for the first time that past grazing practices alter herpetofaunal community composition (but not richness) and result in distinct treatment-specific

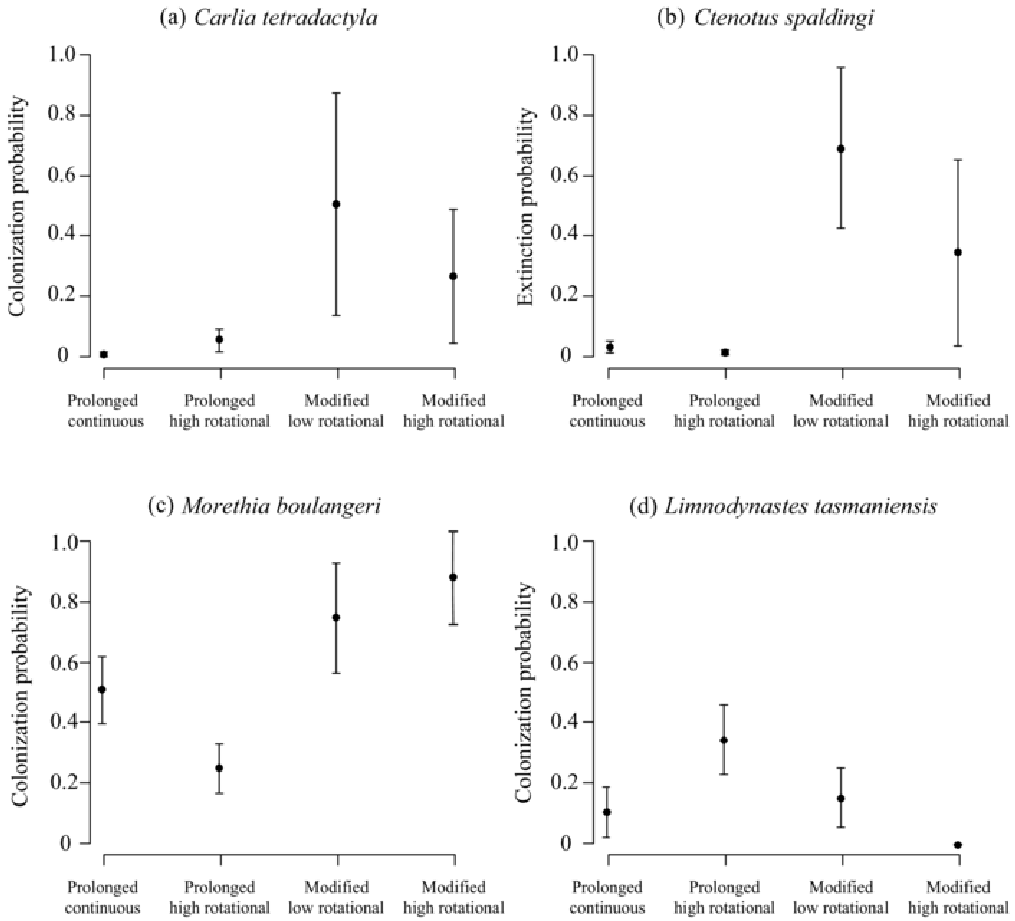

Figure 2. *Model predictions (SE) based on model-averaged estimates of top-ranked models (ΔAIC<2) that examined the effect of past grazing practice (4 levels, x-axis) on patch colonization of 3 and extinction of 1 herpetofaunal species.*

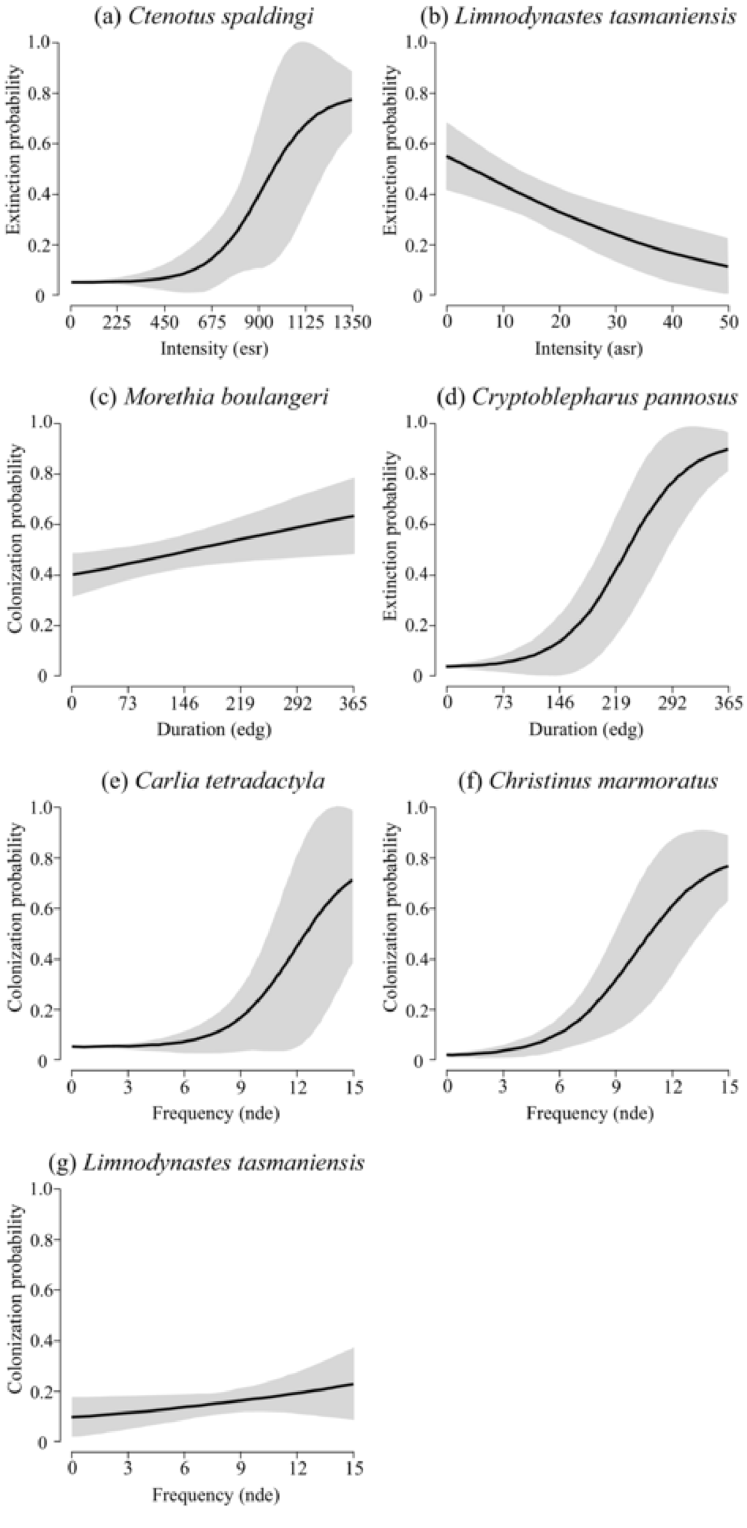

Figure 3. *Model predictions (SE) of (a, b, and d) extinction of and (c, e, f, and g) colonization by 6 herpetofaunal species relative to grazing intensity, duration, and frequency based on model-averaged estimates of top-ranked models (ΔAIC<2) (asr, annual stocking rate as dry sheep equivalents; esr, event stocking rate as dry sheep equivalents; edg, mean duration in days of grazing event; nde, number of destocked events [i.e., periods of no grazing]).*

communities (Supporting Information). We suggest the lack of studies identifying the impact of past grazing on herpetofauna to date may be due to their focus on species richness and abundance (e.g., Dorrough et al. 2012) over compositional analyses as was our focus here. A focus on species richness and abundance can mask informative compositional patterns in a community that although explored for some taxa (Barton et al. 2016) have remained undetected for herpetofauna. By exploring composition and single-species population processes under alternative past grazing regimes, our results emphasize the importance of assessing the impacts of anthropogenic processes at the community and the species level.

Past grazing influenced population processes of colonization and extinction and provided insights into the mechanisms driving faunal response to grazing. This lends important empirical support to untested but widely accepted views (Brown et al. 2011) that historical grazing can be an agent for filtering herpetofaunal assemblages in agricultural landscapes. However, these effects were variable at the species level (Fig. 2), resulting in complex species-specific interpretation. Species-specific responses can be expected for taxonomic groups with strong habitat associations because past grazing management can strongly affect the ecological condition (e.g., vegetation and soil attributes) of a patch (Folke et al. 2004). This could result in cascading effects on resources such as food, shelter, and thermoregulatory opportunity that benefit some species over others (Dennis et al. 1998; Woinarski & Ash 2002).

Interpreting and managing complex multispecies responses to grazing is a major challenge for implementing grazing regimes that sustain biodiversity as a whole (Dorrough et al. 2012). Our examination of dynamic occupancy models represents a novel approach to examining nuanced impacts on population dynamic processes across multiple species of herpetofauna and adds to recent support for this approach for examining impacts of grazing on other taxa (e.g., birds [Tulloch et al. 2016]). Our occupancy model focuses on a few relatively common species whose prevalence in the study area possibly reflects tolerance of grazing. We suggest caution in generalizing our interpretation of our species-specific results to the entire community, specifically because community-level analyses did not reveal the effects of specific current grazing parameters that were important in our species-specific models. Although our study was designed to select large numbers of the highest quality sites encompassing a range of habitats to maximize detection of less-common species, amassing data sets for a larger range of less-common species would improve ones' ability to make inferences across the community. This could be achieved by increasing sampling effort within each season to strengthen models for less-common species or by applying whole-community analytical approaches (i.e., hierarchical multispecies occupancy models [Ruiz-Gutierrez et al. 2010]), although such approaches require sampling beyond practical limitations of our large-scale multiyear study. Addressing these limitations in future studies would enable a wider community-level interpretation.

Effects of Present Grazing Practices on Herpetofauna

Evidence for consistent effects of contemporary grazing parameters on herpetofauna is limited. Previous studies, mostly in Australian woodland ecosystems, support a negative effect of grazing intensity on reptile richness and abundance (Brown et al. 2011; Dorrough et al. 2012; Larson 2014). Weak but positive effects of livestock density on reptile abundance also have been found (Howland et al. 2014), and we are not aware of any studies examining the effects of grazing frequency on herpetofauna.

Present grazing parameters did not affect community richness or composition. Instead, specific grazing parameters affected the population dynamics of 6 of 7 individual species in different ways (Table 3). Grazing intensity and duration were important, but the direction of influence was inconsistent across the species studied. Grazing frequency was important in a consistent (positive) manner despite this variable being implicated as having a negative influence on vegetation (Dorrough et al. 2004a). Grazing frequency is rarely examined in the grazing-ecology literature, yet our results suggest that it could be an important positive influence for ground-dwelling fauna that has not been explored previously. Frequent grazing (i.e., a state of ongoing disturbance) could stimulate the growth of structurally complex grasses without the prolonged impacts to terrestrial fauna predicted from complete destocking or continuous grazing (Dorrough et al. 2004b). Structurally complex grass swards can provide thermoregulatory, food, and shelter resources for herpetofauna (Howland et al. 2014), although not all species are likely to respond equally (as our results demonstrate). Further research investigating physiological tolerances of species in disturbed landscapes (Kearney & Porter 2009) would help clarify the impact on ground-dwelling fauna of grazing strategies with frequent alternation between grazing and resting periods.

Conservation Implications

Grazing by livestock threatens biodiversity in many parts of the world (Asner et al. 2004), challenging conservation managers with decisions about how to integrate biodiversity conservation into production landscapes. Three important implications for the conservation of ground-dependent herpetofauna in other grazing systems emerge from our landscape-scale study.

First, past grazing management needs to be considered in assessments of grazing impacts on biodiversity. This is because it changes the set of species likely to benefit from any current grazing strategy and thereby affects the likely biodiversity outcomes of the current management regime. Developing restorative grazing programs across a mosaic of past grazing practices will ensure that more species surviving under different management regimes receive benefits.

Second, targeting explicit grazing management parameters directly can help conserve or restore particular species but not all species. Because of variability in the way species respond to grazing parameters (e.g., Fig. 3), focusing on a specific variable to develop a one-size-fits-all approach to grazing will not be useful. Instead, land managers and practitioners will have to make trade-offs in terms of the grazing practices that they recommend to farmers for promoting biodiversity. No single regime will help all species, and some regimes, while increasing particular species, are likely to cause declines in others. This highlights a fundamental dilemma: How can conservation managers develop suitable one-size-fits-all grazing recipes that benefit all species in the community? Although a simple management approach may be to develop incentive programs that promote a diversity of grazing management (encompassing a range of parameters), managers will likely have greater impact if they promote particular strategies in some places to recover particular species and other strategies elsewhere to recover other species.

To ensure that the grazing practices being promoted are targeting the right species, managers and researchers must prioritize the gathering of detailed grazing measurements (i.e., livestock weights and daily movements) that allow for investigating the impacts of specific variables rarely accommodated in previous grazing studies. Access to such data is rare without landholder engagement. We recommend that in future researchers consider the importance of accurate current and historical grazing data to enable informed recommendations for grazing management as a tool for biodiversity conservation.

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References

Alexandratos N, Bruinsma J. 2012. World agriculture towards 2030/2050: the 2012 revision. Food and Agriculture Organization of the United Nations, Rome.

Anstis M. 2013. Tadpoles and frogs of Australia. New Holland Publishers, Sydney.

Asner G, Elmore A, Olander L, Martin R, Harris A. 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources 29:261–299.

Barton PS, Sato CF, Kay GM, Florance D, Lindenmayer DB. 2016. Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodlands. Insect Conservation and Diversity 9:124–134.

Bates D, Maechler M, Bolker B, Walker S. 2015. Package “lme4”.

Briske D, Derner J, Brown J, Fuhlendorf S, Teague W, Havstad K, Gillen R, Ash A, Willms W. 2008. Rotational grazing on rangelands: reconciliation of perception and experimental evidence. Rangeland Ecology & Management 61:3–17.

Briske D, Sayre N, Huntsinger L, Fernandez-Gimenez M, Budd B, Derner J. 2011. Origin, persistence, and resolution of the rotational grazing debate: integrating human dimensions into rangeland research. Rangeland Ecology & Management 64:325–334.

Brown G, Dorrough J, Ramsey D. 2011. Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. Landscape and Urban Planning 103:277–288.

Burnham K, Anderson D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Model selection and multimodel inference. Springer-Verlag, New York.

Denmead L, Barker G, Standish R, Didham R. 2015. Experimental evidence that even minor livestock trampling has severe effects on land snail communities in forest remnants. Journal of Applied Ecology 52:161–170.

Dennis P, Young M, Gordon I. 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23:253–264.

Denslow J. 1980. Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46:18–21.

Díaz S, et al. 2007. Plant trait responses to grazing: a global synthesis. Global Change Biology 13:313–341.

Donihue C, Porensky L, Foufopoulos J, Riginos C, Pringle R. 2013. Glade cascades: indirect legacy effects of pastoralism enhance the abundance and spatial structuring of arboreal fauna. Ecology 94:827–837.

Dorrough J, Ash J, McIntyre S. 2004a. Plant responses to livestock grazing frequency in an Australian temperate grassland. Ecography 27:798–810.

Dorrough J, Mcintyre S, Brown G, Stol J, Barrett G, Brown A. 2012. Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. Austral Ecology 37:569–582.

Dorrough J, Scroggie M. 2008. Plant responses to agricultural intensification. Journal of Applied Ecology 45:1274–1283.

Dorrough J, Yen A, Turner V, Clark SG, Crosthwaite J, Hirth JR. 2004b. Livestock grazing management and biodiversity conservation in Australian temperate grassy landscapes. Australian Journal of Agricultural Research 55:279–295.

Erb K-H, Gaube V, Krausmann F, Plutzar C, Bondeau A, Haberl H. 2007. A comprehensive global 5 min resolution land-use data set for the year 2000 consistent with national census data. Journal of Land Use Science 2:191–224.

Fischer J, Stott J, Zerger A, Warren G, Sherren K, Forrester RI. 2009. Reversing a tree regeneration crisis in an endangered ecoregion. Proceedings of the National Academy of Sciences of the United States of America 106:10386–10391.

Fischer J, Zerger A, Gibbons P, Stott J, Law BS. 2010. Tree decline and the future of Australian farmland biodiversity. Proceedings of the National Academy of Sciences of the United States of America 107:19597–19602.

Fiske I, Chandler R. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Folke C, Carpenter SR, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS.

2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Ford D. 2005. A primer of ecological statistics. The American Statistician 59:350.

Howland B, Stojanovic D, Gordon I, Manning A, Fletcher D, Lindenmayer D. 2014. Eaten out of house and home: impacts of grazing on ground-dwelling reptiles in Australian grasslands and grassy woodlands. PLOS ONE 9:(e105966) DOI:10.1371/journal.pone.0105966.

Hutchinson M, Stein J, Stein J. 2011. GEODATA 9 second digital elevation model (DEM-9S) version 3. Available from http://www.ga.gov.au/meta/ANZCW0703011541.html (accessed October 2014).

Kay G, Barton P, Driscoll D, Cunningham S, Blanchard W, McIntyre S, Lindenmayer D. 2016. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. Animal Conservation In Press:1–11. DOI:10.1111/acv.12267.

Kearney M, Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Larson D. 2014. Grassland fire and cattle grazing regulate reptile and amphibian assembly among patches. Environmental Management 54:1434–1444.

Lindenmayer DB, Zammit C, Attwood SJ, Burns E, Shepherd CL, Kay G, Wood J. 2012. A novel and cost-effective monitoring approach for outcomes in an Australian Biodiversity Conservation Incentive Program. PLOS ONE 7:(e50872) DOI: 10.1371/journal.pone.0050872.

MacKenzie D. 2005. What are the issues with presence-absence data for wildlife managers? Journal of Wildlife Management 69:849–860.

MacKenzie D, Nichols J, Hines J. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Martin T, McIntyre S. 2007. Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. Conservation Biology 21:504–514.

McCune B, Grace JB. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune B, Mefford MJ. 2011. PC-Ord: multivariate analysis of ecological data. MjM Software, Gleneden Beach, Oregon.

McIntyre S, Heard K, Martin T. 2003. The relative importance of cattle grazing in subtropical grasslands: Does it reduce or enhance plant biodiversity? Journal of Applied Ecology 40:445–457.

McIntyre S, Lavorel S. 2001. Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. Journal of Ecology 89:209–226.

Mclaren C. 1997. Dry sheep equivalents for comparing different classes of livestock. Department of Primary Industries, Victoria. Available from http://www.agronomy.com.au/download/dseratings.pdf (accessed June 2014).

Michael DR, Kay GM, Crane M, Florance D, MacGregor C, Okada S, McBurney L, Blair D, Lindenmayer DB. 2015. Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: implications for natural resource management in endangered grassy woodland ecosystems. Austral Ecology 40:651–660.

Miller A, Roxburgh S, Shea K. 2011. How frequency and intensity shape diversity-disturbance relationships. Proceedings of the National Academy of Sciences of the United States of America 108:5643–5648.

Mortelliti A, Michael D, Lindenmayer D. 2015. Contrasting effects of pine plantations on two skinks: results from a large-scale “natural experiment” in Australia. Animal Conservation 18:433–441.

Nagelkerke N. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Ruiz-Gutierrez V, Zipkin E, Dhondt A. 2010. Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species. Journal of Applied Ecology 47:621–630.

Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practice of statistics in biological research. WH Freeman and Company, San Francisco, California.

Teague W, Dowhower S, Baker S, Haile N, DeLaune P, Conover D. 2011. Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. Agriculture, Ecosystems & Environment 141:310–322.

Tscharntke T, Klein A, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. Ecology Letters 8:857–874.

Tulloch AIT, Mortelliti A, Kay GM, Florance D, Lindenmayer D. 2016. Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies. Conservation Biology 30:867–882.

Valls-Fox H, Bonnet O, Cromsigt J, Fritz H, Shrader A. 2015. Legacy effects of different land-use histories interact with current grazing patterns to determine grazing lawn soil properties. Ecosystems 18:720–733.

Wilson S, Swan G. 2013. Complete guide to reptiles of Australia, 4th edition. New Holland Publishers, Sydney.

Woinarski JCZ, Ash AJ. 2002. Responses of vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. Austral Ecology 27:311–323.

Zimmerman G, Goetz H, Mielke P. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology 66:606–611.

Zuur A, Ieno E, Walker N, Saveliev A, Smith G. 2009. Mixed effects models and extensions in ecology with R. Springer, Newburgh.

Supporting Information

Appendix S1. Details of the study area

Our study was located within an important grazing district in south-eastern Australia that coincides with an endangered woodland ecosystem (Figure S1). This woodland community is characterised by an understorey of native tussock grasses, herbs and scattered shrubs, and an open tree strata that was originally dominated by white box (*Eucalyptus albens*), yellow box (*E. melliodora*) and Blakely's red gum (*E. blakelyi*) (Commonwealth of Australia, 2013). Due to clearing of woodland on fertile soils, this community has been reduced to <4% of its original extent over the past 150 years (Lindenmayer et al., 2010). The community also supports a rich woodland-dependent herpetofauna, with over 120 species of reptiles and 40 species of frog recorded across the extent of the study area (Anstis, 2013; Kay et al., 2016a; Kay et al., 2013; Wilson and Swan, 2013).

Figure S1. *Photo of typical Box Gum Grassy Woodland, the critically endangered ecosystem targeted in this study*

Appendix S2. Ecological monitoring and grazing management details.

We conducted field surveys of herpetofauna (involving active searches and inspections of artificial arrays, Figure S2) and ground-layer ecological variables at each site every year from 2011 to 2013. Summary statistics for grazing (Table S1) and habitat (Table S2) variables are provided, as well as Pearsons correlations for each variable (Table S3). Values >0.6 were considered highly correlated.

Grazing variables

Grazing variables for each site were gathered from annual landholder surveys conducted over the three-year duration of this study. For each livestock grazing event we gathered data on: (i) the type and number of livestock (which we used to gather the Dry Sheep Equivalent index sensu Mclaren, 1997), and (ii) the precise start and end dates of the grazing event. These data were used to determine the livestock grazing parameters used in the study (intensity, duration and frequency of grazing). Summary statistics for grazing parameters are provided in Table S1.

Ecological habitat variables

We followed the protocol of Kay et al. (2016) for detailed measurement of ecological habitat variables. Sites consisted of a 40 x 200 m fixed monitoring area (0.8 ha) with two smaller monitoring plots (20 m x 40 m) nested within for measuring habitat-based variables, vegetation and percentage of ground cover. These plots were located at 0-50 m and 150-200 m along the overall monitoring site. Within each of these 20 x 50 m plots we recorded length of logs, regenerating saplings, and diameter at breast height of any trees > 5 cm. A 50 m transect was located down the centre of each plot with presence/absence measurements taken every metre to assess ground layer vegetation cover and composition for: native and exotic grass, native and exotic shrubs (including subshrubs), bare ground, soil crust, leaf litter, overstorey and mid-storey canopy. In addition, ground-layer plant biomass was assessed using a rising plate pasture meter to determine average height of ground cover present (Filip's Manual Folding Plate Meter, New Zealand; Correll et al., 2003). Percentage cover of native midstorey and overstorey was also assessed at each plot. Summary statistics for the ecological habitat variables are provided in Table S2.

We summarise 11 environment and habitat variables using Principal Components Analysis (PCA) into two Principal Component axes which accounted for approximately 47% of variation (Table S2). The first axis (pc1) had negative loadings in the amount and structural diversity of grassy biomass but positive loadings for tree, log and litter cover. This represents a gradient of available habitat structure ranging from grass-dominated structure to less-grassy tree-dominated (with high litter) sites. The second axis (pc2) had negative loadings of native groundcover vegetation components (e.g. grass and forb cover) but positive loadings for exotic groundcover vegetation components. This represents a gradient of sward composition, ranging from native dominated to exotic dominated.

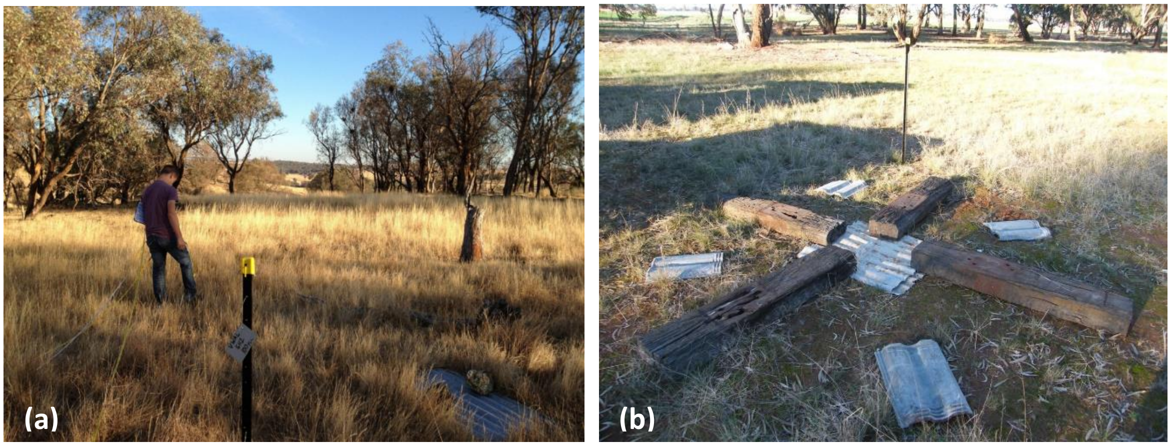


Figure S2. *Depiction of the (a) active search and (b) artificial refuge array used in herpetofaunal surveys*

Table S1. *Summary statistics for each of the four present grazing parameters used.*

Grazing variable	Mean of variable	S.D. of variable	Range of variable
Grazing Intensity (Annual DSE rate)	5.65	7.77	0 – 47.07
Grazing Intensity (Event DSE rate)	101.32	177.65	0 – 1355.45
Grazing Frequency (annual number of destocked events)	1.81	2.17	0 – 13
Grazing Duration (average number of days grazed per event)	176.20	131.92	0 – 365

Table S2. *Summary statistics for habitat variables recorded, including Principal Component loadings for the two most influential axes (pc1 and pc2).*

Habitat variable	Mean of variable	S.D. of variable	Range of variable	pc1	pc2
Bare ground cover (%)	2.64	3.85	0-21	0.286	-0.324
Coarse woody debris cover (m)	19.08	25.82	0-253	**0.301**	-0.016
Exotic herb and forb cover (%)	27.26	23.66	0-95	-0.271	**0.347**
Exotic perennial grass cover (%)	6.87	14.21	0-89	-0.117	**0.456**
Leaf litter and fine debris (%)	28.84	23.12	0-88	**0.418**	0.17
Mean ground-layer biomass height (cm)	14.54	8.54	2-45	**-0.481**	-0.057
Native herb and forb cover (%)	7.78	11.07	0-73	-0.064	**-0.397**
Native perennial grass cover (%)	62.00	22.80	2-100	-0.212	**-0.474**
Rock cover (%)	1.05	2.90	0-18	0.035	-0.385
Tree cover (%)	26.00	20.00	0-79	**0.349**	0.031
Variation in ground-layer biomass height (cm)	7.19	4.12	1-25	**-0.404**	-0.056
Variation explained by Principal Components				31.984	15.468

***Table S3**. Pearson's correlations for all variables*[a] *explored in the study, with values >0.6 (bold) considered highly correlated.*

	aspn	elev	TWI	rain	temp	pc1	pc2	LU250	tree250	asr[b]	esr[b]	edg[b]	nde[b]
aspn	1.00												
elev	0.02	1.00											
TWI	0.00	-0.33	1.00										
rain	0.03	0.46	-0.14	1.00									
temp	-0.05	-0.09	-0.01	-0.03	1.00								
pc1	-0.10	0.10	-0.05	0.17	0.06	1.00							
pc2	-0.10	0.25	-0.09	0.10	0.05	0.00	1.00						
LU250	0.01	-0.16	0.29	-0.15	-0.01	-0.05	0.21	1.00					
tree250	-0.10	0.35	-0.10	0.19	-0.01	0.39	-0.15	-0.25	1.00				
asr[b]	-0.02	0.02	-0.07	0.03	0.08	-0.04	0.21	0.20	-0.19	1.00			
esr[b]	0.01	0.00	-0.07	0.05	0.06	-0.18	0.19	0.13	-0.34	**0.78**	1.00		
edg[b]	-0.11	-0.07	0.01	-0.05	-0.01	0.16	0.10	0.07	0.02	0.57	0.29	1.00	
nde[b]	0.02	0.14	-0.05	0.12	-0.02	-0.08	0.09	0.01	-0.17	0.34	0.57	-0.05	1.00

[a] *Key: northerly aspect (aspn); elevation above sea level (elev); topographic wetness index (TWI); rainfall over preceding 2 months (rain); category of air temperature at survey (temp); ordination of grassy to non-grassy ground habitat (pc1); ordination of exotic to native grassland composition (pc2); area of modified land-use within 250 m of site (LU250); tree cover within 250 m of site (tree250); livestock stocking rate per year (asr); livestock stocking rate per event (esr); mean duration (days) of grazed event (edg); number of livestock resting events (nde).*

[b] *Indicates log-transformed variable.*

Figure S3. *Photos from sites representing the four different habitat types summarised by two dominant Principal Components. Principal component 1 (pc1) axis from (a) non-grassy habitat structure to (b) grassy habitat structure. Principal component 2 (pc2) axis from (c) native-dominated to (d) exotic-dominated groundcover grassy habitats*

Table S4. *Taxonomic and microhabitat guilds of the species surveyed. Microhabitat guild were assigned from Michael et al. (2015) and Anstis (2013). Species with * were retained for multi-season patch-occupancy analysis with detection rates (number of detections/number of visits) of >5%.*

Species	Taxon	Family	Guild	Status	Abundance	Detection rate
Litoria latopalmata	Amphibian	HYLIDAE	Terrestrial	Rare	15	1.3
Litoria peronii	Amphibian	HYLIDAE	Terrestrial	Common	19	2.5
Crinia parinsignifera	Amphibian	MYOBATRACHIDAE	Terrestrial	Rare	8	0.8
Crinia signifera	Amphibian	MYOBATRACHIDAE	Terrestrial	Rare	21	2.3
Limnodynastes dumerilii	Amphibian	MYOBATRACHIDAE	Burrowing	Rare	2	0.3
Limnodynastes fletcheri	Amphibian	MYOBATRACHIDAE	Terrestrial	Rare	1	0.2
Limnodynastes interioris	Amphibian	MYOBATRACHIDAE	Burrowing	Rare	2	0.3
Limnodynastes peronii	Amphibian	MYOBATRACHIDAE	Semi-aquatic	Rare	4	0.3
*Limnodynastes tasmaniensis**	Amphibian	MYOBATRACHIDAE	Terrestrial	Common	273	13.2
Uperoleia laevigata	Amphibian	MYOBATRACHIDAE	Terrestrial	Common	74	4.7
Amphibolurus muricatus	Reptile	AGAMIDAE	Semi-arboreal	Rare	3	0.5
Pogona barbata	Reptile	AGAMIDAE	Semi-arboreal	Rare	13	2.2
Demansia psammophis	Reptile	ELAPIDAE	Cryptozoic	Rare	1	0.2
Parasuta dwyeri	Reptile	ELAPIDAE	Cryptozoic	Rare	12	1.5
Pseudechis porphyriacus	Reptile	ELAPIDAE	Cryptozoic	Rare	1	0.2
Pseudonaja textilis	Reptile	ELAPIDAE	Terrestrial	Rare	12	1.3
*Christinus marmoratus**	Reptile	GEKKONIDAE	Arboreal	Common	43	5.1
Diplodactylus vittatus	Reptile	GEKKONIDAE	Cryptozoic	Rare	9	1.3
Underwoodisaurus milii	Reptile	GEKKONIDAE	Cryptozoic	Rare	1	0.2
Aprasia parapulchella	Reptile	PYGOPODIDAE	Cryptozoic	Common	35	2.5
Delma inornata	Reptile	PYGOPODIDAE	Cryptozoic	Rare	12	1.5
Acritoscincus duperreyi	Reptile	SCINCIDAE	Terrestrial	Rare	5	0.5
*Carlia tetradactyla**	Reptile	SCINCIDAE	Terrestrial	Common	76	8.5
*Cryptoblepharus pannosus**	Reptile	SCINCIDAE	Semi-arboreal	Common	79	6.8
Ctenotus orientalis	Reptile	SCINCIDAE	Terrestrial	Rare	2	0.3
*Ctenotus spaldingi**	Reptile	SCINCIDAE	Cryptozoic	Common	93	6.5
Ctenotus taeniolatus	Reptile	SCINCIDAE	Cryptozoic	Rare	14	1.0
Egernia cunninghami	Reptile	SCINCIDAE	Saxicolous	Rare	26	2.0
Egernia striolata	Reptile	SCINCIDAE	Saxicolous	Rare	12	1.0
*Hemiergis talbingoensis**	Reptile	SCINCIDAE	Fossorial	Common	142	9.0
Lampropholis delicata	Reptile	SCINCIDAE	Terrestrial	Common	39	3.5
Lampropholis guichenoti	Reptile	SCINCIDAE	Terrestrial	Rare	23	1.2
Lerista bougainvillii	Reptile	SCINCIDAE	Cryptozoic	Rare	16	0.8
Lerista timida	Reptile	SCINCIDAE	Fossorial	Rare	8	0.8
*Morethia boulengeri**	Reptile	SCINCIDAE	Terrestrial	Common	402	22.3
Tiliqua rugosa	Reptile	SCINCIDAE	Terrestrial	Rare	14	1.7
Tiliqua scincoides	Reptile	SCINCIDAE	Fossorial	Rare	16	2.2
Ramphotyphlops nigrescens	Reptile	TYPHLOPIDAE	Fossorial	Rare	2	0.5

Appendix S3. Details of the community analyses.

We analysed two aspects of the herpetofaunal community for this paper: richness, and composition.

Community Richness Analysis

We found no significant difference (see main text; Fig. S4) between past grazing treatments over the duration of the study for any measure of community richness (total species, rare species, microhabitat guild richness).

Compositional analysis

We used multi-variate analyses to test for differences in composition. To address our first question examining past grazing categories, we used a multi-response permutation procedure (MRPP) to test for differences in reptile assemblage composition among the four categories of grazing history (see main text). This test compares the average among-site similarity within each group with the overall similarity among all sites, with greater within-group similarity indicating samples are distinct from the overall set of samples (McCune and Mefford, 2011; Zimmerman et al., 1985). We found community composition differed significantly among sites grouped by past grazing history, including all pairwise comparisons between past grazing histories (Table S5). We used Principal Coordinates Analysis (McCune and Grace, 2002) to describe these results visually (Fig. S5a). A significant difference between Past Grazing treatments was also evident when analysing all species (MRPP: $T=-12.92$, $A=0.044$, $P<0.001$) and common species (MRPP: $T=-4.10$, $A=0.020$, $P<0.001$) separately, indicating compositional differences were not simply due to the occurrence of rare taxa in some sites but not others.

To address our second question examining present grazing parameters, we fitted Mantel Tests (Sokal and Rohlf, 1995) to test for correlation in overall among-site dissimilarity in herpetofauna versus grazing variables, and compare this to dissimilarity in herpetofauna

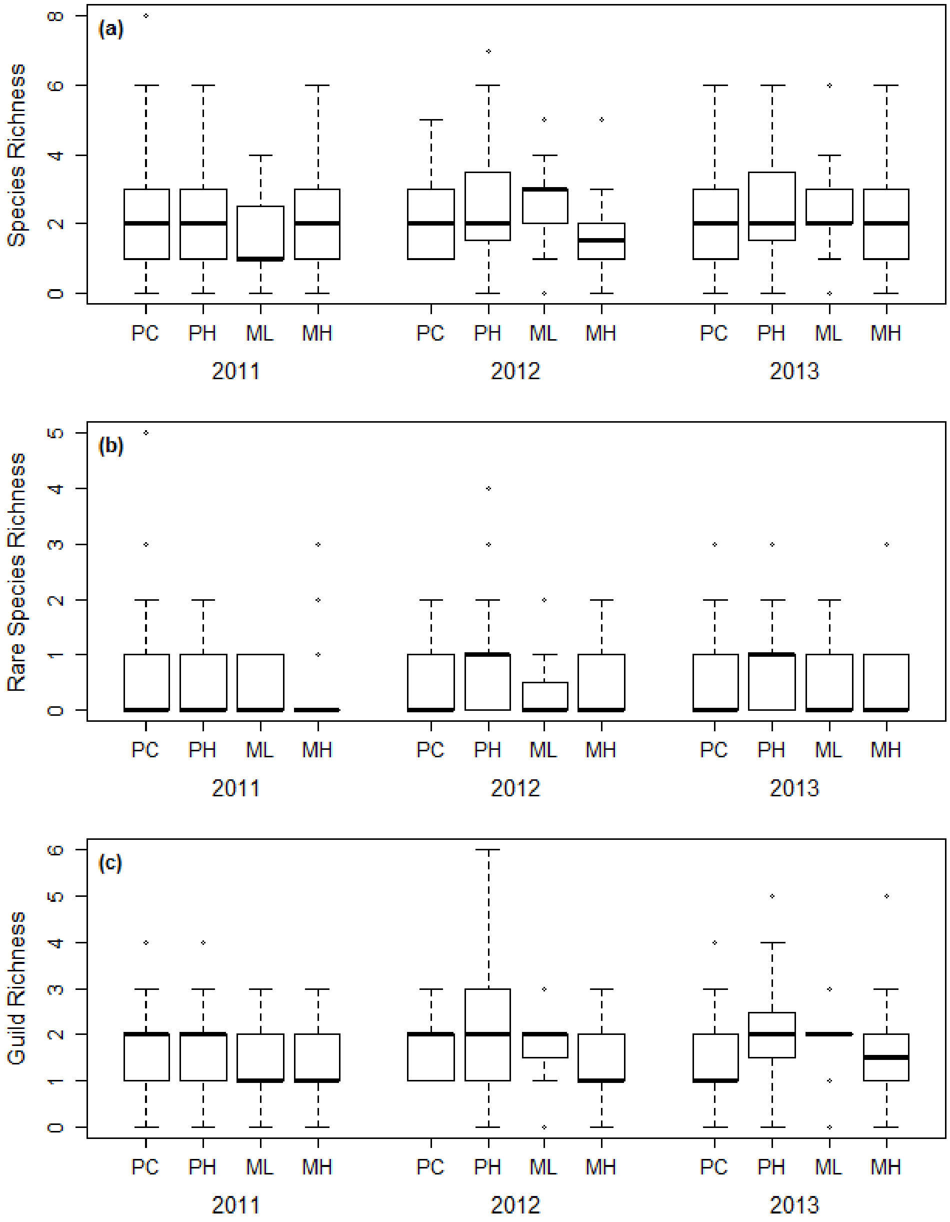


Figure S4. *Average (a) number of species, (b) richness of rare species, (c) richness of microhabitat guilds detected each year in the four past grazing management treatments: Prolonged Continuous (PC), Prolonged High-rotational (PH), Modified Low-rotational (ML), Modified High-rotational (MH). (box, defined by the 25th and 75th percentile; whiskers, maximum and minimum observed value excluding outliers; line within boxes, median value; circles, outliers)* versus environmental variables. We found that the correlation between present grazing parameters and among-site composition of the overall herpetofauna was comparatively lower (mantel: r=0.008, p=0.291) than that for the environmental variables (r=0.1433, p<0.001), indicating no effect on herpetofaunal community composition. We repeated these analyses for the common species data set and revealed a similar effect (grazing: r=0.007, p=0.321; environment: r=0.1308, p=0.002) once again indicating that the occurrence of rare taxa in some sites and not others had no influence on the result. Again, we used Principal Coordinates Analysis (PCoA; McCune and Grace, 2002) to describe these results visually (Fig. S5b), fitting all environmental and present grazing variables as vectors on biplots. PCoA ordinations revealed the influence of several environmental variables, and no present grazing variables, although these influences were very small overall (biplot $r^2>0.05$).

Table S5: *Multi-response Permutation Procedure analysis of pair-wise differences between past grazing treatments (MH = Modified High-rotational; ML = Modified Low-rotational; PC = Prolonged Continuous; PH = Prolonged High-rotational), indicating the test statistic (T), chance – corrected within-group agreement (A), and significance (p).*

Treatment comparison	T	A	P
MH vs. PC	-9.26697696	0.02586213	0.00000299
MH vs. PH	-15.32819278	0.04105180	0.00000000
MH vs. ML	-6.87350873	0.02644306	0.00008249
PC vs. PH	-3.67228803	0.00866095	0.00644603
PC vs. ML	-4.24225265	0.01369043	0.00252960
PH vs. ML	-5.55477575	0.01691886	0.00050543

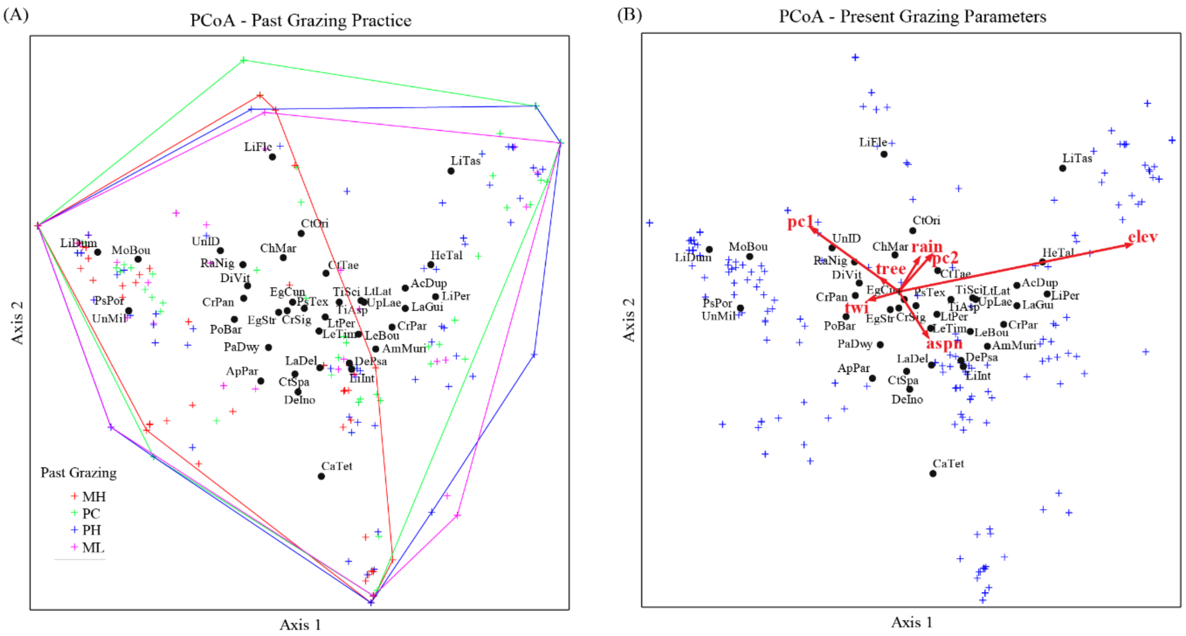


Figure S5: *Principal Coordinates Analysis ordination showing the influence of (A) past grazing practice and (B) present grazing parameters on variation in species composition of all herpetofauna (black dots) among sites (crosses). All sites comprising the four past grazing categories (Modified High-rotational [MH], Prolonged Continuous [PC], Prolonged High-rotational [PH], Modified Low-rotational [ML]) are bound by respective polygons. Biplots for the most influential environmental and present grazing variables (with* $r^2>0.05$*) only are drawn (key: northerly aspect [aspn]; elevation above sea level [elev]; topographic wetness index [TWI]; rainfall over preceding 2 months [rain]; ordination of grassy to non-grassy ground habitat [pc1]; ordination of exotic to native grassland composition [pc2]; tree cover within 250 m of site [tree]). Species codes are the first two characters of Genus name followed by three characters of Species name.*

Appendix S4. Details of the patch-occupancy colonization and extinction models.

Results for the colonization and extinction models that directly relate to grazing are included in Table 3 (main text). We also provide a summary of the past and present grazing effects for each of the species targeted in this study (Table S6). Additional detail for the set of models are provided below for analyses of both past grazing and present grazing parameters.

Analysis 1: Past grazing management

Several factors affected the probability of a site being occupied in the first season of sampling including elevation (four species: *C. pannosus*, *C. spaldingi*, *H. talbingoensis*, *M. boulengeri*), aspect (one species: *C. marmoratus*), grass sward structure – pc1 (one species: *C. tetradactyla*) and grass sward composition – pc2 (one species: *L. tasmaniensis*). Patterns of detectability varied strongly between species and included the time of day the survey was conducted (two species: *C. marmoratus*, *M. boulengeri*), the survey year (two species: *C. tetradactyla*, *H. talbingoensis*), the temperature at the time of the survey (two species: *C. pannosus*, *L. tasmaniensis*) and a constant (one species: *C. spaldingi*).

Analysis 2: Present grazing parameters

Once again several factors affected the probability of a site being occupied in the first season of sampling including mostly elevation (four species: *C. pannosus, C. spaldingi, H. talbingoensis, M. boulengeri*) but also grass sward structure – pc1 (one species: *C. tetradactyla*), grass sward composition – pc2 (one species: *L. tasmaniensis*) and aspect (one species: *C. marmoratus*). Patterns of detectability were retained from the first analysis for the second analysis and so are as above.

Table S6. *Summary of past and present grazing effects on target species by microhabitat guild.*

Species	Microhabitat Guild		Present Grazing Parameters[b]		
		Past Grazing[a]	Intensity	Duration	Frequency
Carlia tetradactyla	Terrestrial	1			+
Christinus marmoratus	Arboreal	0			+
Cryptoblepharus pannosus	Semi-arboreal	0		-	
Ctenotus spaldingi	Cryptozoic	1	-		
Hemiergis talbingoensis	Fossorial	0			
Limnodynastes tasmaniensis	Terrestrial	1	+		+
Morethia boulengeri	Terrestrial	1		+	

[a] *Response (to grazing); 1, present; 0, absent;*

[b] *Effect direction;+, positive effect (increase in patch colonization or decrease in patch extinction); -, negative effect (decrease in patch colonization or increase in patch extinction).*

Supporting References

Anstis, M. 2013. Tadpoles and frogs of Australia. New Holland, Sydney.

Commonwealth of Australia. 2013. Environmental Stewardship. Available from http://www.nrm.gov.au/national/continuing-investment/environmental-stewardship.

Correll, O., J. Isselstein, and V. Pavlu. 2003. Studying spatial and temporal dynamics of sward structure at low stocking densities: The use of an extended rising-plate-meter method. Grass and Forage Science 58:450–454.

Kay, G., P. Barton, D. Driscoll, S. Cunningham, W. Blanchard, S. McIntyre, and D. Lindenmayer. 2016. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. Animal Conservation In Press:1–11.

Kay, G. M., D. R. Michael, M. Crane, S. Okada, C. MacGregor, D. Florance, D. Trengove, L. McBurney, D. Blair, and D. B. Lindenmayer. 2013. A list of reptiles and amphibians from Box Gum Grassy Woodlands in south-eastern Australia. Check List 9:476–481.

Lindenmayer, D., A. Bennett, and R. Hobbs. 2010. Temperate Woodland Conservation and Management. CSIRO Publishing, Melbourne.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. Structural Equation Modeling 28:300.

McCune, B., and M. Mefford. 2011. PC-ORD: Multivariate Analysis of Ecological Data. Version 6.

McLaren, C. 1997. Dry Sheep Equivalents for comparing different classes of livestock. Available from http://www.agronomy.com.au/download/dseratings.pdf.

Michael, D. R., G. M. Kay, M. Crane, D. Florance, C. MacGregor, S. Okada, L. McBurney, D. Blair, and D. B. Lindenmayer. 2015. Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems. Austral Ecology 40:651–660.

Sokal, R., and F. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. New York.

Wilson, S., and G. Swan. 2013. Complete Guide to Reptiles of Australia, 4th edition. New Holland Publishers, Sydney.

Zimmerman, G., H. Goetz, and P. Mielke. 1985. Use of an Improved Statistical Method for Group Comparisons to Study Effects of Prairie Fire. Ecology 66:pp. 606–611.

PAPER V. SPECIES CO-OCCURRENCE NETWORKS REVEAL PATTERNS OF COMMUNITY RESTRUCTURE UNDER LANDSCAPE MODIFICATION.

The context of the surrounding landscape can have strong influence on the biodiversity response to agri-environment schemes. A better understanding of "how" surrounding land-use influences biodiversity is needed. In this paper, we explore how modification of the surrounding landscape can impact on community structure. Our study reveals a novel value of using co-occurrence analysis to uncover the impacts of land modification that may be masked in conventional studies of species richness and community composition.

A

Canola crop (flowering yellow) surround a patch of native vegetation.

Kay, G.M., Tulloch, A., Barton, P., Cunningham, S.A., Driscoll, D.A., Lindenmayer, D.B., 2016. Species co-occurrence networks reveal patterns of community restructure under landscape modification. Ecography. 40, 1-13. doi:10.1111/ecog.03079.

Species co-occurrence networks show reptile community reorganization under agricultural transformation.

Abstract

Agricultural transformation represents one of the greatest threats to biodiversity, causing degradation and loss of habitat, leading to changes in the richness and composition of communities. These changes in richness and composition may, in turn, lead to altered species co-occurrence, but our knowledge of this remains limited. We used a novel co-occurrence network approach to examine the impact of agricultural transformation on reptile community structure within two large (>172 000 km^2; 224 sites) agricultural regions in southeastern Australia. We contrasted assemblages from sites surrounded by intact and modified landscapes and tested four key hypotheses that agricultural transformation leads to (H1) declines in species richness, (H2) altered assemblages, (H3) declines in overall co-occurrence, and (H4) complex restructuring of pairwise associations. We found that modified landscapes differed in composition but not richness compared with intact sites. Modified landscapes were also characterized by differences in co-occurrence network structure; with species sharing fewer sites with each other (reduced co-occurrence connectance), fewer highly-connected species (truncation of the frequency distribution of co-occurrence degree) and increased modularity of co-occurrence networks. Critically, overall loss of co-occurrence was underpinned by complex changes to the number and distribution of pair-wise co-occurrence links, with 41-44% of species also gaining associations with other species. Change in co-occurrence was not correlated with changes in occupancy, nor by functional trait membership, allowing a novel classification of species susceptibility to agricultural transformation. Our study reveals the value of using co-

occurrence analysis to uncover impacts of agricultural transformation that may be masked in conventional studies of species richness and community composition.

Introduction

Agricultural transformation is a major driver of biodiversity decline (Newbold et al., 2015; Sala et al., 2000; Tscharntke et al., 2005). This process, driven by the replacement of natural environments with human-modified landscapes such as agricultural fields, impacts >50% of all ice-free land (Hooke, 2012) – an area set to increase as global demand for agriculture increases (Alexandratos and Bruinsma, 2012; Tscharntke et al., 2012a, 2012b). Studies of the impacts of agricultural transformation on biodiversity routinely identify loss of local-scale (α) and landscape-scale (γ) diversity (Fig 1A; Liu et al., 2014; Newbold et al., 2015) as well as changes in community composition (β) (Fig 1B; Karp et al., 2012; Solar et al., 2016). However, other more subtle changes to the way biota coexist and interact are likely (Bascompte, 2010; Poisot et al., 2015), even before discernable changes in richness or composition occur (Morriën et al., 2017; Tylianakis et al., 2007). For example, agricultural transformation may lead to changes in the occupancy of species among sites, thus altering coexistence among species, even though overall richness might not change. Identifying nuanced changes in the structure of a community could provide an important opportunity to anticipate negative consequences to biodiversity before species are lost or communities irreversibly restructured.

One approach to characterizing more subtle changes to communities is through quantifying species co-occurrence. Co-occurrence has long been used to examine community structure (Gotelli and McCabe, 2002) by describing how species within a community coexist. Species co-occurrence is often represented by a network of nodes (species) linked by vectors (edges) of varying strength corresponding to the frequency of paired species presence at a site (Araújo et al., 2011; Newman et al., 2001). Several processes could be responsible for species associations, such as shared environmental requirements, ecological interactions or other higher order processes (e.g. two species sharing a common predator). Our understanding of co-occurrence networks is founded mainly on studies examining biotic interaction theory like food webs (Berlow et al., 2009) or plant-pollinator networks (Burkle et al., 2013). These biotic interaction studies have demonstrated a number of useful ways to summarize complex network topology into network metrics that can be used to track community change over time, or across different regions (Tylianakis et al., 2010; Urban and Keitt, 2008). For example, network 'connectance' – the proportion of realized interactions from the pool of all possible interactions between the species of a network (May, 1973) – is considered an important indicator of community complexity (Gilbert, 2009; Tylianakis et al., 2010). Similarly, measuring the distribution of species associations can reveal the nature of community change, for example from one composed mainly of many species with few links and a few species with many links, to one with randomly distributed or truncated link distributions (Thébault and Fontaine, 2010; Tylianakis et al., 2010). These advancements in co-occurrence theory have prompted an interest in co-occurrence networks to evaluate impacts of anthropogenic processes like climate or land-use change on community structure (Araújo et al., 2011; Burkle et al., 2013; Morriën et al., 2017; Poisot et al., 2015). Such studies have provided promising opportunities to identify community assembly processes.

Some challenges, however, surround the use of network metrics for interpreting anthropogenic impacts with co-occurrence networks. One challenge is that the structure (topology) of different types of networks varies (Thébault and Fontaine, 2010), and so interpreting what each network means in the context of different threats remains problematic (Cazelles et al., 2016). For example, biotic interaction networks, which are built from (or imply) interactions between species, will differ with co-occurrence networks which are built from shared site occupancy without implying any direct interaction. Another challenge is that network metrics summarize ecological communities assuming a universal response of all species within that network to environmental changes (e.g. Burkle et al., 2013). However, environmental and anthropogenic changes rarely act evenly across all species in a community. For example, anthropogenic impacts of livestock grazing have revealed differential species-specific impacts for woodland reptile and bird communities within the same study region (Geoffrey M Kay et al., 2016; Tulloch et al., 2016c). Subsequently, we know far less about *how* structural changes in the networks occur, preventing most studies from providing useful guidance to conservation managers interested in identifying how and what aspects of the community to manage for.

A finer-scale understanding of co-occurrence among species may improve predictions of how and why communities respond to anthropogenic processes like agricultural transformation (Blois et al., 2014; Borthagaray et al., 2014; Veech, 2013, 2014). If a species declines in abundance or distribution in a landscape (a common symptom of agricultural transformation), we might expect habitat availability for other similar species to increase (Levin, 1970; MacArthur and Levins, 1964), potentially influencing species co-occurrence in a number of ways. For example, consider a community of co-occurring arboreal mammals that share the same habitat such as trees in a forest. Agricultural transformation (i.e. deforestation) would cause a loss of the amount or quality of tree habitats, such that some species lose a critical resource (e.g. tree cavities) but others do not. This loss of resources could reduce the co-occurrence of species within the community (Fig 1C), an effect that has been documented through universal change in single network metrics previously (e.g. Burkle et al., 2013). However, agricultural transformation may lead to restructuring of the community without noticeable change in co-occurrence (Fig 1D; Thébault and Fontaine, 2010). Loss of trees may cause extinctions from the site and hence lose connections with unaffected species (Fig 1D a-b). Alternatively, tree loss may cause the affected species to switch resources to another tree or refugial site (possible if they are generalists). This, in turn, could lead to coexistence with previously non co-occurring species within the ecosystem (Fig 1D a-c), or increased (strengthened) coexistence between previously co-occurring species (Fig 1D a-d), either by shifting in habitat-use requirements or partitioning use of the resource. The type of outcome will vary for each species, depending on their ability to share the available niche (Connor and Simberloff, 1979). These kinds of changes are important to decipher but this is not possible from simple species richness or species composition analyses.

Previous studies suggest that agricultural transformation will lead to (H1) reductions in species richness (Fig 1A; Ruffell et al., 2017) and (H2) changes in species composition (Fig 1B; Solar et al., 2016). However, recent advances in co-occurrence theory suggest that agricultural transformation may also lead to (H3) a change in co-occurrence reflected across the entire network, with declines in connectance and changes in the distribution of co-occurrence among species (Araújo et al., 2011; Blois et al., 2014; Fig 1C; Tylianakis et al., 2010). This may in turn lead to greater segregation of the community, and hence increased modularity of the network (Garay-Narváez et al., 2014; Valdovinos et al., 2009).

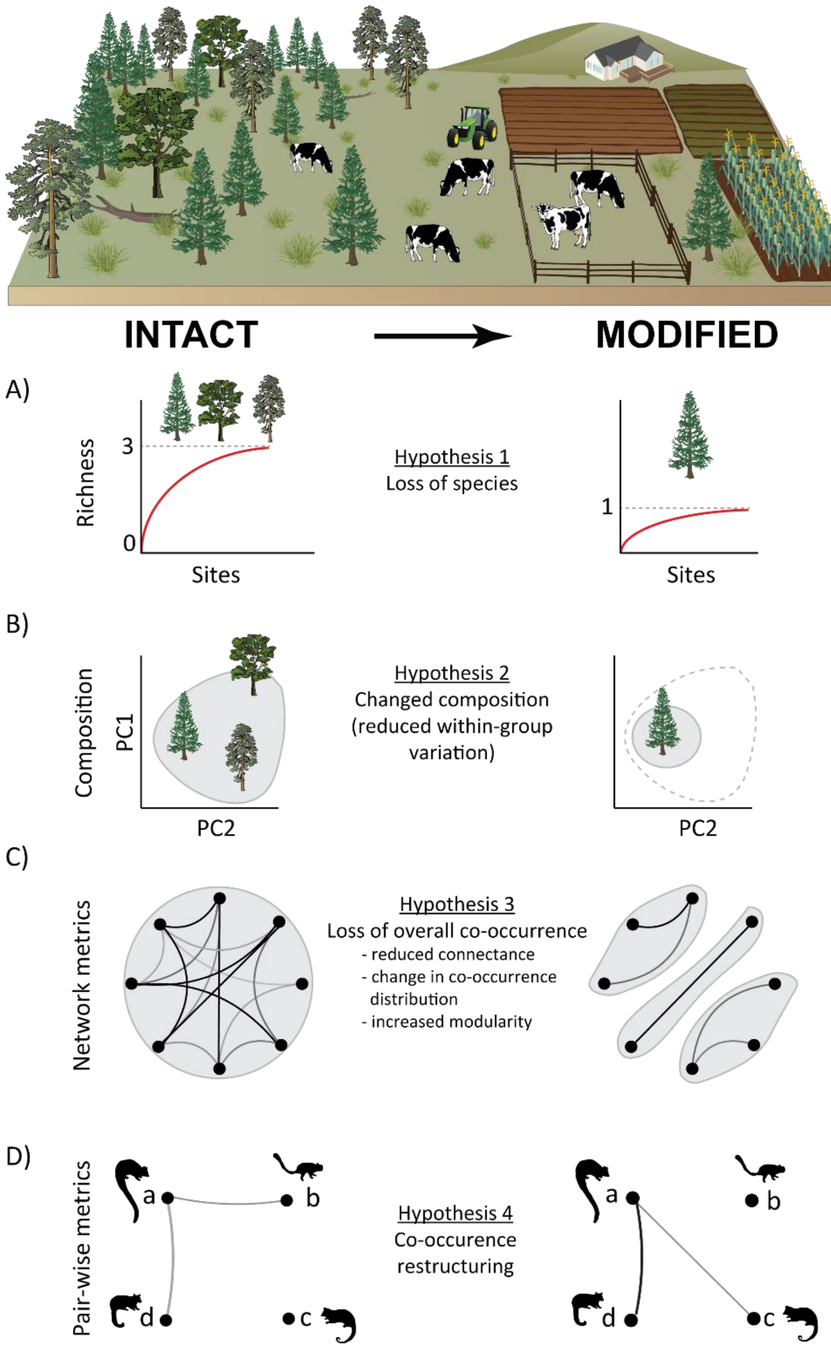


Figure 1. *Conceptual diagram describing known and anticipated effects of agricultural transformation. (A) Species richness decline. (B) Community composition change. (C) Loss of co-occurrence as measured by a range of network metrics (connectance, link distribution and modularity). (D) Restructuring of pairwise associations between species without changes to total network co-occurrence. Increasing line darkness represents increasing co-occurrence strength (i.e. likelihood of co-occurrence). Grey polygons represent species associations (with increasing modularity under agricultural transformation).*

For instance, human impacts can be advantageous for certain members of a community due to presence of certain functional traits or characteristics which result in these sub-communities becoming less associated with other members of the community (Sebastián-González et al., 2015; Takemoto et al., 2016). Additionally, we may expect (H4) species-specific responses that lead to restructuring of species-pair associations within the network, rather than a network-wide response, such that some species-pairs lose associations while others gain associations (Fig 1D). Characterizing species by their potential to lose, gain or restructure co-occurrence links provides a powerful opportunity to identify components of the community that are more at risk from anthropogenic change and could benefit most from targeted management (Arita and Peres-Neto, 2016). Furthermore, because changes to network connectance could be a result of factors such as lower site occupancy across the landscape (Tylianakis et al., 2010), or particular functional trait associations (e.g. habitat guild, body size, taxonomy), these factors should be examined.

Here, we combine co-occurrence network analysis with traditional community richness and compositional analyses to explore the above hypotheses (H1-H4) that species co-occurrence may reveal overlooked effects of agricultural transformation. We gathered a large-scale (224 sites spanning >172,000 km^2) empirical dataset of species occupancy and agricultural transformation within a critically endangered woodland ecosystem of south-eastern Australia. We focused on characterizing differences in the reptile community (42 species) across sites classified by the level of agricultural transformation for two distinct agro-climatic regions. Reptiles are particularly vulnerable to agricultural transformation due to their relatively low mobility and high reliance on groundcover habitats (Brown et al., 2011; Fischer et al., 2004; Jellinek et al., 2004; Schutz and Driscoll, 2008). Despite this, few studies document the impacts of agricultural transformation or other threats on reptile communities (Bland and Böhm, 2016) and so we used this group to address the following four questions:

i) Does species richness decline under agricultural transformation? (H1; Fig 1A),

ii) Does the community composition change under agricultural transformation? (H2; Fig 1B),

iii) Does agricultural transformation lead to a change in species co-occurrence reflected across the entire network (in terms of network connectance, degree distribution and network modularity)? (H3; Fig 1C), and

iv) Does agricultural transformation lead to alteration of individual species-pair associations within the network that might be masked in network-wide measures of co-occurrence? (H4; Fig 1D)

Methods

We surveyed reptiles between 2011 and 2014 across 224 woodland patches spanning 99 farms within the critically endangered Box Gum Grassy Woodland ecological community of south-eastern Australia (172,000 km^2, Supplementary material Appendix 1, Fig A1). We grouped sites into two broad agro-climatic systems (GM Kay et al., 2016a) that were expected to host different assemblages (Supplementary material Appendix 1): a winter-rainfall mixed grazing and cropping system (Tablelands Region, 147 sites), and a low-rainfall cropping system (Western Region, 77 sites).

Each reptile survey consisted of a time-constrained and area-constrained (20 minute x 0.8 ha) active search of natural habitat and inspection of artificial refuge arrays within each site (GM Kay et al., 2016a; Supplementary material Appendix 1). We conducted five surveys with a total effort of 1120 site-visits over spring (September 2011, 2012, 2014) and autumn (March 2012, 2014) to maximize sampling of the assemblage, recording 59 species in total. Occupancy for all reptiles was combined into a single site-visit by species matrix. We removed species with <1% occupancy across each landscape (17 out of 59 species) leaving 42 species for analysis. For most species abundance was low at the site level (1-2 individuals) so we converted abundances to presence-absence to reduce the influence of highly abundant species.

Fertilization and cultivation are major drivers of agricultural transformation (Emmerson et al., 2016). These activities have immense impact on the structure and type of ground layer vegetation and other resources necessary to reptiles (Brown et al., 2011; Jellinek et al., 2014 and references within). To quantify agricultural transformation throughout our study area, we interviewed farmers to determine the area of the landscape within 0.5 km radius of each site that had been fertilized or cultivated in the past 15 years (Supplementary material Appendix 1). We considered this distance appropriate because (i) reptiles are highly sensitive to immediate surrounding vegetation due to high habitat specificity, often have small home ranges and limited dispersal (Schutz and Driscoll, 2008), and (ii) larger (>1km) distances would sometimes confound site-level effects within farms.

Thresholds defining ecosystem vulnerability have been recently developed in a review of global ecosystem health for the IUCN Red List of Ecosystems (Bland et al., 2016; Keith et al., 2013). Natural ecosystems modified by present and ongoing agricultural activities, such as cultivation and fertilizer enrichment, are vulnerable to collapse when reduced in extent by >30% (Keith et al., 2013). Subsequently, we defined sites as intact as those with ≥70% cover unmodified by these activities within the 500m buffer (supporting communities potentially less prone to collapse) and sites with >30% modified cover (i.e. fertilized or cultivated within 15 years) as modified (and supporting communities potentially more prone to collapse). We repeated our analyses using a range of threshold values to explore the sensitivity of our results (Supplementary material Appendix 7).

Species richness and community composition

We examined differences in species richness within intact and modified landscapes for each region separately using Generalized Linear Mixed Models (GLMM) with Poisson distribution (log link). Because our analyses focused on whole assemblages at the site level, we pooled observations within sites and across time to compile an assemblage at every site. For each subset of sites within intact and modified landscapes, we modelled richness as the response variable, with the proportion of agricultural transformation as a continuous predictor and site as a random effect. We tested for spatial dependence in the model residuals using a Moran's I test (AD Cliff and Ord, 1981) to ensure that sites within farms were sufficiently spaced to meet assumption of independence, and found no evidence of spatial autocorrelation in either region (p_t=0.454; p_w=0.318).

We explored differences in assemblage composition between intact and modified landscapes for both the Western and Tablelands regions using Multi-Response Permutation Procedure (MRPP; Mielke et al., 2007) in PC-ORDv6 (McCune and Mefford, 2011); a nonparametric multivariate test of differences between groups. We determined statistical significance using 9,999 permutations of the species data among sites and calculated pairwise site differences using the Bray-Curtis dissimilarity metric using the *vegan* package (v2.3.3; Oksanen et al., 2015) for R v3.3.1. We visualized assemblage differences among agricultural transformation categories using Principal Coordinates Analysis ordinations (PCoA; McCune and Mefford, 2011).

Constructing networks of species co-occurrence

We used the approach of Lane et al. (2014), as adopted in Tulloch et al. (2016a), to build species co-occurrence networks for reptiles surveyed in intact and modified landscapes in both regions. We calculated the co-occurrence between each pair of species using the *sppairs* package (v1.0; Westgate and Lane, 2015) in R v3.3.1. The strength of co-occurrence (frequency of paired species presence at a site) was quantified from the slope (coefficient) of a logistic generalized linear mixed model for each pair of species, where species A was the response and species B the predictor (Lane et al., 2014; Tulloch et al., 2016a). We fitted site as a random effect to account for temporal dependency due to repeated observations across years, and excluded pairwise co-occurrence relationships that were not statistically significant at $\alpha = 0.05$ (Araújo et al., 2011). To fit the models we initially used the pooled species by site presence-absence dataset applied in the richness and compositional analyses. Due to low reptile occupancy at each site, the models failed to converge when run using the 224 sites. Therefore, we treated each of the survey repetitions as unique events to generate sufficient power to run co-occurrence models, generating each of the four networks by inputting a presence/absence dataset of species by site-visit (1120 site-visits in total).

Because the large number of pairwise models considered inflates the chance of spurious results and over-estimation of the number of significant connections, we also conducted a parallel study of co-occurrence significance using the probabilistic approach described by Veech et al (2013). Whilst there were some differences in the strength of co-occurrence of individual species, the overall patterns of relationships between landscape transformation and co-occurrence metrics did not change (Supplementary material Appendix 5). This is most likely due to the fact that with the large amount of data from our surveys, individual pairwise co-occurrences were very likely to be statistically significant even if adjusted for multiplicity (Lane et al. 2014).

Sampling intensity is known to influence some network indices (Dormann et al., 2009; Goldwasser and Roughgarden, 1997; Nielsen and Bascompte, 2007). We accounted for differences in sampling effort between intact and modified landscape types by randomly selecting an equal subset of sites within each agro-climatic region (equal to the minimum number of sites present in intact or modified treatments for each region; Western = 25 sites, Tablelands = 57 sites), and generating 100 random networks. We calculated the mean strength of all significant co-occurrence relationships between each species pair across each of the 100 random networks to create the final species-by-species co-occurrence matrix for the intact and modified landscape in each region (4 meta-networks in total). Where mean values equaled zero, we included rather than omitted them to ensure underestimation rather than overestimation of strength values. The temporal extent of data used to build networks was relatively short (4 years; 2011-2014) and therefore we did not account for the temporal dynamics known to influence in co-occurrence at longer time-scale dynamics (i.e. community succession) (Poisot et al., 2015; Tulloch et al., 2016a).

Network co-occurrence metrics

We examined several complimentary and universally applied network metrics to quantify the impacts of agricultural transformation on reptile species co-occurrence (Tylianakis et al., 2010). First, we quantified the degree (number of positive co-occurrence relationships; Dunne et al., 2002; Tylianakis et al., 2010) for each species, and summed them to obtain the total number of positive co-occurrence links, k, for each network. Because degree is sensitive to the number of species in each network and to sampling effort (Dormann et al., 2009; Goldwasser and Roughgarden, 1997; Nielsen and Bascompte, 2007), we used network connectance as a measure that accounts for network size, k/n^2, where n is the number of network nodes (sensu Gilbert, 2009).

Second, we examined whether there was change between intact and modified landscapes in the distribution of co-occurrence measures (degree and strength) (Araújo et al., 2011; Dunne et al., 2002; Tylianakis et al., 2010). We did this by characterizing the architecture of each network by examining the frequency distribution of species degree and strength (sensu Tylianakis et al., 2010).

Third, we examined whether the modularity of co-occurrence networks differed under agricultural transformation. Because human impacts can lead to greater segregation of ecological communities (sensu Sebastián-González et al., 2015; Takemoto et al., 2016), we examined whether co-occurrence networks in modified landscapes exhibited more modular structure than those in intact landscapes. To characterize differences in modularity, we quantified and plotted the modularity of each network using the igraph package (v1.0.1; Csárdi and Nepusz, 2006) in R v.3.3.1, using the ‘modularity’ function to find network modules. We considered networks with modularity values of >0.4 as having a modular structure, following Newman (2006).

Pairwise associations

We examined species pairwise associations to reveal effects of agricultural transformation on community restructuring that could be masked by network metrics. For each association, we classified change in each link between intact and modified communities as either lost (significant positive co-occurrence to no co-occurrence), gained (no positive co-occurrence to significant positive co-occurrence) or stable (positive co-occurrence link maintained). Of the three classifications here, we considered only lost or gained links to represent changes in network structure.

There is a range of conditions that might result in restructured associations (Connor and Simberloff, 1979; Levin, 1970; MacArthur and Levins, 1964). Species may lose or gain connections due to changes in spatial occupancy (even if overall populations are stable), or population asynchrony among species pairs. To test whether co-occurrence changes were simply related to species' occupancy of the landscape, we constructed simple linear models relating each species' change in occupancy to changes in co-occurrence (in terms of species link density – the relative number of significant links that a species had from all possible links – as well as mean strength). Doing so allowed us to determine if the species becoming rarer in the landscape were the ones losing co-occurrence, and vice versa, and to classify species as having: (1) both increased co-occurrence and prevalence ("increaser"); (2) reduced co-occurrence but greater prevalence ("pioneer"); (3) both reduced co-occurrence and prevalence ("decliner"), and; (4) greater co-occurrence but reduced prevalence ("refugial").

Finally, we examined whether co-occurrence differed among particular functional groups, and if this could be used to predict how a network might restructure under modification (e.g. Borthagaray et al., 2014). We examined the proportion of each species' susceptibility classification ("increaser", "pioneer", "decliner", "refugial") within key functional groups considered important for reptiles. We included microhabitat guild (terrestrial, saxicolous, fossorial, arboreal and semi-arboreal, following Michael et al., 2015), body size (large [≥50cm], medium [10-50cm], small [<10cm]; Borthagaray et al. 2014), taxonomic guild (following Wilson and Swan, 2013), habitat specialization (specialist, generalist following Michael et al. 2015) and dietary guild (following Wilson and Swan, 2013). We then explored whether assigned susceptibility classifications differed among these functional groups.

Results

Community richness and composition

Our analyses included 2,869 individuals from 42 reptile species (Supplementary material Appendix 2). Individual species occupancy was lower in modified landscapes for 24 (62%) and 21 (78%) species in the Western and Tablelands communities, and higher for 15 (38%) and 8 (30%) species respectively. Species richness per site was not significantly different across landscapes in either region (Table 1, GLMM; p_w=0.749; p_t=0.484; Supplementary material Appendix 3, Fig. A5, Table A3). We found a significant difference in the composition of reptile communities between intact and modified landscapes in both regions (MRPP; p_w=0.019; p_t<0.001; Supplementary material Appendix 3, Fig. A6, Table A4).

Network co-occurrence metrics

Co-occurrence networks from modified landscapes revealed lower degree and lower average links per species compared with intact landscapes (Table 1). We found connectance was lower for sites in modified landscapes in both regions, indicating that reduction in the number of co-occurrences occurred independently of differences in network size (Table 1).

Table 1. *Summary statistics of (i) site-level agricultural transformation attributes, (ii) reptile richness and composition variables, and (iii) co-occurrence network variables for both intact (>70% unmodified) and modified (<70% unmodified) sites across the two agro-climatic regions within the study area.*

	Western Region		Tablelands Region	
	intact	modified	intact	modified
Site characteristics				
Number of sites	52	25	90	57
Mean percentage of modified landscape within 500m buffer (± sd)	4.8 (8.3)	64.5 (22.2)	9.4 (10.1)	58.3 (19.7)
Reptile Richness and composition				
Species richness (mean/site)	39 (4.58)	27 (4.36)	27 (3.63)	24 (3.40)
Number (%) of species increasing in occupancy	15 (38%)		8 (30%)	
Number (%) of species declining in occupancy	24 (62%)		21 (78%)	
Co-occurrence networks				
Total positive links per network	200	51	162	22
Links per species	5.13	1.89	6.00	0.92
Connectance (# links/spp^2)	0.13	0.07	0.22	0.04
Network modularity index	0.21	0.54	0.17	0.52

The distributions of both degree and strength were considerably different between intact and modified landscapes (Supplementary material Appendix 4, Fig. A7). Modified landscapes had a truncated degree distribution, with the loss of well-connected nodes. Networks in modified landscapes were considerably more modular than in intact landscapes (Table 1; Supplementary material Appendix 6). Values >0.4 suggest that the network has a modular structure (Newman, 2006).

Pairwise associations

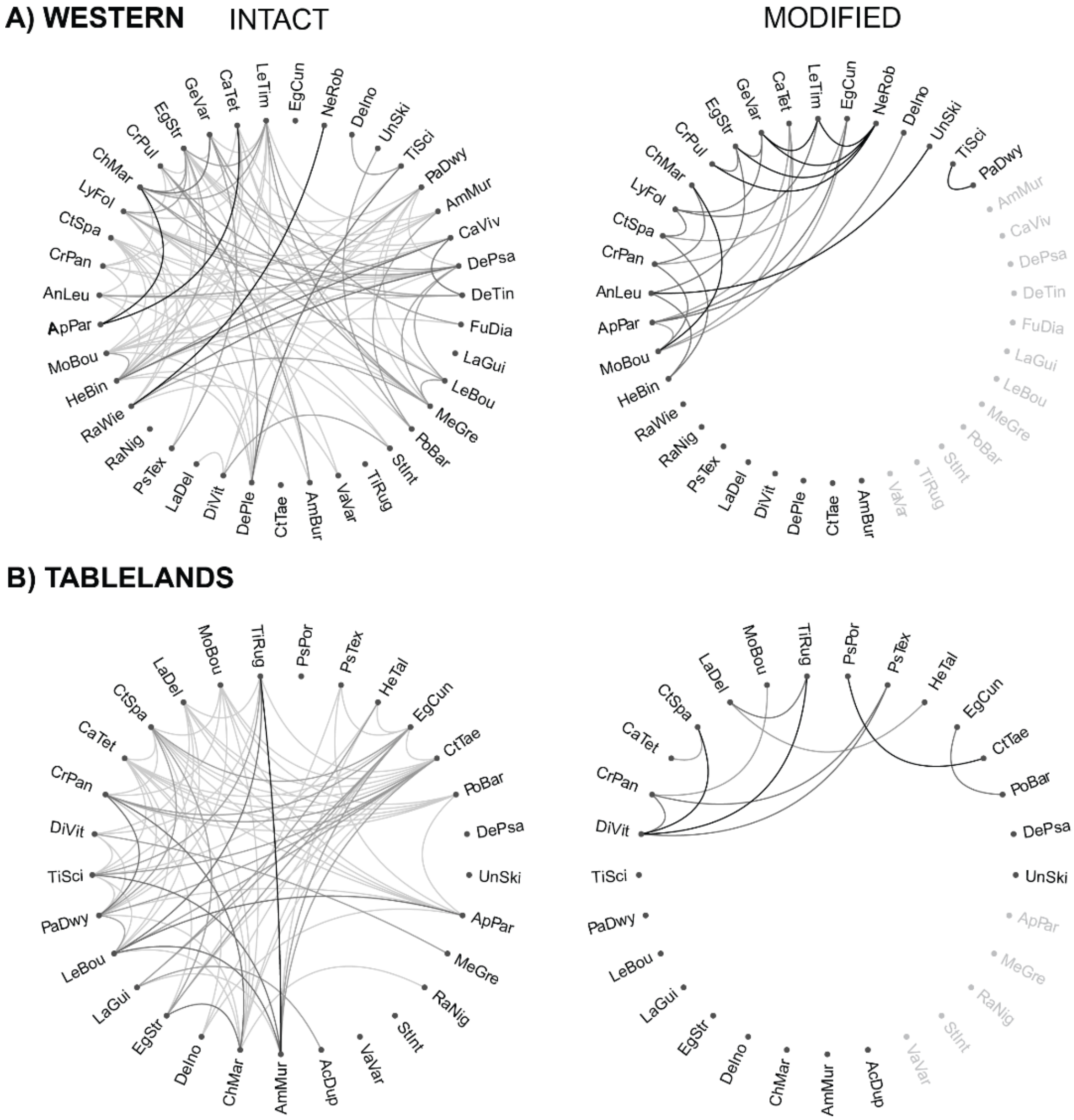
Relatively few species associations were constant across landscapes, with the vast majority restructuring (92% and 96% of links in Western and Tablelands respectively) mostly through losing rather than gaining connections (Table 2). The majority of pairwise associations (75% and 91% of restructured links) were either lost or gained by species that persisted across landscape types (Table 2), with a smaller percentage permanently lost due to a loss of one or both species (25% and 8% of restructured links). Few species gained associations due to the presence of a species in modified but not intact landscapes (0% and 1% of links in Western and Tablelands respectively; Table 2).

Almost all pairwise associations changed in strength (98% for both regions; Table 2). This change was mostly attributed to a loss (79% and 88% of all restructured links in Western and Tablelands respectively) – and to a lesser extent gain (21% and 12%) – in associations, rather than a change in strength of maintained associations (Table 2). Where pairwise associations were maintained in intact and modified landscapes, these nearly always had higher strength in modified landscapes (Table 2).

In total, 17 (44%) and 12 (41%) species gained at least one association for both the Western and Tablelands regions, with 6 species in each region (15% and 22%) establishing completely novel co-occurrences (e.g. *Egernia cunninghamiana* Fig. 2). No species that had multiple co-occurrence connections in intact landscapes maintained all co-occurrences in modified landscapes. Six (16%) and 9 (31%) species from the Western and Tablelands lost all existing connections (e.g. *Parasuta dwyeri* Fig. 2B) under agricultural transformation. There was little consistency between regions in the species that established, lost or maintained connections (Fig. 2).

Table 2. *Summary of the changes in individual species pairwise co-occurrence link dynamics (degree and strength) between sites within intact and modified landscapes for the two study regions. Changes in degree and strength are classified as either lost, gained or changed (restructured) under agricultural transformation.*

Pairwise species co-occurrences	**Western**		**Tablelands**	
	n	% links	n	% links
Change in pairwise species co-occurrence connections (degree)				
Stable (or no link)	20	8%	8	4%
Links restructured	218	92%	170	96%
- Links lost (because species lost from modified landscape)	54	25%	13	8%
- Links gained (because species gain in modified landscape)	0	0%	2	1%
- Links lost (species present across both landscapes)	130	60%	143	83%
- Links gained (species present across both landscapes)	34	15%	14	8%
Change in pairwise species co-occurrence strength				
Stable (or no strength)	4	2%	4	2%
Strength changed	234	98%	176	98%
- Decreased strength (because the link was removed)	182	78%	154	88%
- Increased strength (because the link was formed)	34	15%	14	8%
- Decreased strength (of an existing link)	2	1%	0	0%
- Increased strength (of an existing link)	16	7%	8	5%



A) WESTERN INTACT

MODIFIED

B) TABLELANDS

Figure 2. *Species co-occurrence networks derived from reptile communities in sites within intact and modified landscapes across the (A) Western and (B) Tablelands study regions. Nodes represent species present (with >1% occupancy) in each landscape. Vectors between nodes represent significant positive co-occurrence relationships, with vector strength proportional to line darkness (lightest grey -= low strength, black = high strength). Species codes represent first two letters of the genus and last three letters of species name. Greyed names represent species absent (locally extinct) from landscape type*

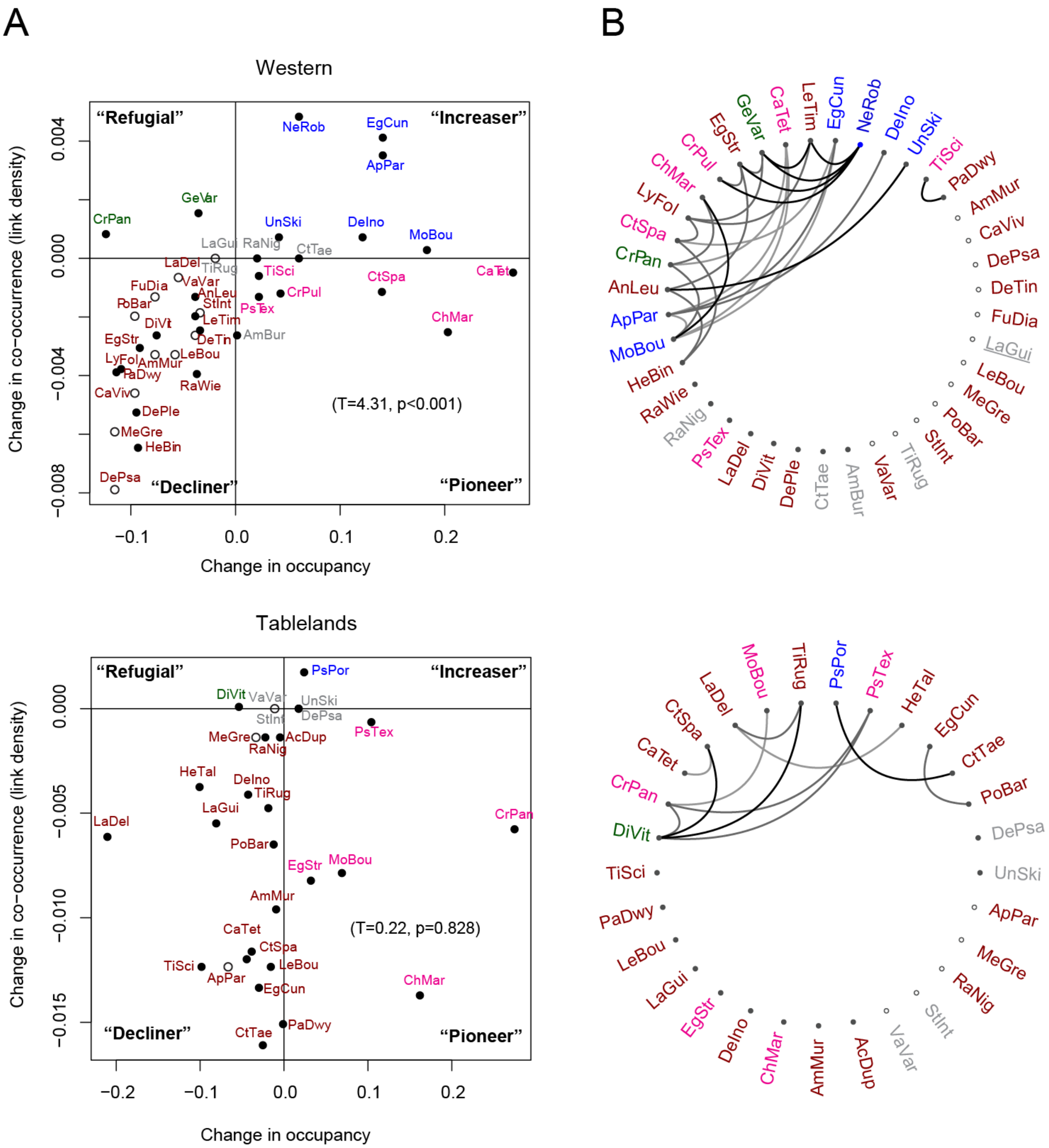


Figure 3. *(A) Relationships (plus significance values) between change in occupancy and change in average co-occurrence link density (links/species^2) for species within intact and modified landscapes for each case study region. Dots represent individual species (codes represent the first two letters of the genus and second three letters for the species names). Hollow circles represent species no longer present in modified landscapes. (B) Relevant quadrants superimposed onto network structure, with color codes representing plot quadrants; species that increase in occupancy and increase in connectance ("Increaser", blue), species that increase in occupancy but decrease in connectance ("Pioneer", gold), species that decrease in occupancy but increase in connectance ("Refugial", green), species that decrease in occupancy and connectance ("Decliner", red), and species that do not deviate either in occupancy or connectance (black).*

Changes in co-occurrence (in terms of link density) were not correlated with changes in occupancy in the Tablelands (p_t=0.828) but were positively associated in the Western region (p_w<0.001; Fig. 3, Supplementary material Appendix 4, Table A6). The majority of species had both lower link density and occupancy under agricultural transformation (i.e. met our definition of "decliners"; 52% and 66% of species in Western and Tablelands respectively), with only 1 – 2 species decreasing in occupancy but increasing in link density ("refugial", Fig. 3). Other species either increased in both occupancy and link density with others ("increaser", 16% and 4% of Western and Tablelands respectively) or increased in occupancy while decreasing in link density ("pioneers",16% of Western and 19% of Tablelands community). There were no significant relationships between changes in species occupancy and changes in co-occurrence strength in either region (p_w=0.248, p_t=0.874; Supplementary material Appendix 4, Fig. A8).

Grouping co-occurrence effects by species functional groups (i.e. microhabitat guild, body size, habitat specialization, taxonomic guild, and dietary guild) did not reveal any functional groups that might be used to predict the sensitivity of a species' co-occurrence relationships to agricultural transformation (Supplementary material Appendix 4, Fig. A9).

Discussion

In this study we tested hypotheses (Fig. 1) regarding the well-established impact of agricultural transformation on (H1) species richness and (H2) composition, and a less explored response in species co-occurrence (H3) across the entire network, and (H4) individual species-pair associations within the network. Our first hypothesis that agricultural transformation would result in reduced mean site-level richness was not upheld. However, we found agricultural transformation significantly altered species composition of reptile communities in woodland remnants, supporting our second hypothesis. Similarly, our third hypothesis that overall declines in species co-occurrence are reflected across the entire network by a decline in network connectance, change in degree distribution as well as increased modularity was upheld. Finally, we found that overall loss of co-occurrence was not due to an even loss across all species, supporting our fourth hypothesis, and instead changes were complex and involved gains and switches in species co-occurrence. Our study demonstrates how examination of co-occurrence can reveal new insights into the impact of agricultural transformation on biodiversity, providing a different perspective to traditional richness and compositional approaches. Our findings provide a novel set of information that can feed back into conservation decisions capable of identifying impacts before species are lost and communities irreversibly change.

Loss of species richness and changes in community composition as a result of agricultural transformation is well documented (Liu et al., 2014; Newbold et al., 2015; Ruffell et al., 2017), albeit less so for reptiles than other taxonomic groups (Trimble and van Aarde, 2012). Our results support hypotheses for compositional change, but departed from expectations of reduced site-level richness and join others (e.g. Tylianakis et al., 2007) in highlighting apparent challenges with using simple diversity metrics like richness to quantify impacts of anthropogenic change on biodiversity. One problem with relying on detecting change in species richness is that effects generally occur over long time-periods (decades/centuries) (e.g. Helm et al., 2006). Similarly, changes in richness may already be manifest in extant populations long exposed to anthropogenic impacts making observable differences impossible to detect (e.g. prior-filtering of sites; Brown et al., 2011; Jellinek et al., 2014). A second problem is that detecting statistical change in richness will be challenging for some groups with inherently low site-level diversity (like reptiles). This is because models quantifying the loss of a single species from a starting point of only 2-3 species (as in our study) requires a far greater number of replicates than models from a starting point of 15-20 species. The absence of change in richness observed in our study, which represents one of the largest investigations of the effects of any anthropogenic threat on reptiles to date (1120 visits of 224 sites over 4 years), underscores the difficulty in obtaining sufficiently large datasets capable of detecting changes in richness. Despite many conservation efforts to track and manage changes in diversity (Lindenmayer and Fischer, 2006), increasing evidence suggests that other important changes are occurring to community structure due to anthropogenic change (e.g. Dornelas et al., 2014). Our data support this by identifying the role of anthropogenic-related assemblage restructuring in the absence of species loss.

Examining co-occurrence proved useful for identifying other aspects of changes in community composition under agricultural transformation. Network analysis revealed a lower connectance, fewer well-associated species with loss of weak links, and increased network modularity under agricultural transformation (Table 1, Fig. 2; Supplementary material Appendix 6). Characterizing these changes in network structure allowed us to detect changes in species distributions that we might anticipate under agricultural transformation. Loss of connectance, and increased modularity of networks, may drive reduction of resilience or function under the target threat (Fournier et al., 2016; Gilbert, 2009; Heleno et al., 2012; Thébault and Fontaine, 2010). Similarly, fewer well associated species suggest a loss of keystone species critical to the functioning of ecosystems (Fournier et al., 2016; Tulloch et al., 2016a). These interpretations are consistent with studies examining co-occurrence response to other anthropogenic threats (Araújo et al., 2011; Morriën et al., 2017), but are largely founded on what we know from biotic interaction networks (Thébault and Fontaine, 2010). Caution is, however, required in the interpretation of co-occurrence network analysis (Cazelles et al., 2016; Tylianakis et al., 2010). For example, even if network metrics are useful for a general description of co-occurrence, they are not necessarily useful for identifying the causes of change in co-occurrence due to the difficulty of replicating networks (especially for vertebrates that require a high degree of sampling effort) to achieve sufficient power for statistical analysis (but see Horner-Devine et al., 2007 for an example of replicated vertebrate co-occurrence networks using a meta-analysis). For this reason, most co-occurrence network analysis to date has focused more on genetic and microbial communities where replication of communities is easier (Li et al., 2015; e.g. Williams et al., 2014). In addition, the standard statistical machinery available for richness and composition analyses is not well developed and as readily available for comparing networks (although methods to model the likelihood of different sets of predictors in explaining patterns in community structure are increasing, see for example Peres-Neto et al., 2006). A critical next step is to understand the functional implications of differences in co-occurrence network topology, as well as the development of standardized statistical approaches for comparing multiple networks of species co-occurrence and relating differences to environmental or landscape change.

Our examination of pairwise connections appear very useful for providing detailed insight into *how* communities may respond to agricultural transformation (Arita and Peres-Neto, 2016; Veech, 2013). Nearly all pairwise connections restructured (i.e. were lost or gained), with a considerably high number of species (41-44%) demonstrating ability to gain new associations (e.g. *Nebulifera robusta*, Fig 2A). Although restructured associations may in some cases be random and not ecologically meaningful, developing knowledge about how many and what type of species exhibit ability for restructuring associations can help reveal a species' unique vulnerability to the target threat. For example, species-level restructuring did not conform to any functional grouping in this study (Supplementary material Appendix 4, Fig. A9). Despite growing interest in the role of functional traits on summarizing outcomes (Lindenmayer et al., 2015; Thompson et al., 2016), our results clearly show that there is no relation between the role of the species (i.e. 'decliner', 'refugial', 'increaser' and 'pioneer') and any of their known properties (e.g. microhabitat, size, family, feeding guild etc). Ergo, addressing threats like agricultural transformation cannot rely on broad/universal responses at the whole community level, which is often the lens of examination (e.g. Burkle et al., 2013). Instead, approaches capable of identifying species-level responses, such as co-occurrence analysis, may significantly advance our ability to address such threats.

Implications for management

Our observation that changes to co-occurrence within the community are not universal (Fig. 3) represents a novel and useful opportunity to inform biodiversiy conservation management in the context of anthropogenic changes. For example, consider a group of organisms for which information is limited but that are vital to some ecosystem functions (e.g. an insect pollinator). Identifying components of the communities more or less vulnerable to a particular threat allows us to act before damage is done through irreversible species loss and reduced ecosystem functioning (Gilbert, 2009; Heleno et al., 2012). Combining knowledge of occupancy with co-occurrence enabled us to characterize species by their distinctive response to agricultural transformation. We identified species that have become less common and also exhibit lower co-occurrence (i.e. reduced link density) under agricultural transformation (Fig. 3 bottom left quadrant). These 'decliner' species are more vulnerable to stochastic climatic and environmental threats (Lindenmayer and Fischer, 2006) and could represent a "red flag" for possible local extinction risk to managers. Conservation strategies protecting species-rich sites would likely miss the remnant patches for these species and so fail to adequately protect them. Instead, targeted species management strategies would be better. Species declining in occupancy but gaining co-occurrence (Fig. 3 top left quadrant) represent another possible "at risk" group. This is because increased co-occurrence among particular sets of species could indicate groups being forced into refugia with other species that are declining (Tylianakis et al., 2010). Alternatively, it could indicate the invasion of one species' habitat by another species leading to transient co-occurrence. Importantly, our study also has identified species that may respond neutrally or even positively to agricultural transformation. Species that are increasing and losing co-occurrence (Fig. 3 bottom right quadrant) most likely represent those dispersing into novel unoccupied environments (because of loss of another species or change in environmental conditions), and may not require urgent management. Furthermore, species that are increasing in both co-occurrence and occupancy (Fig. 3 top right quadrant) represent those expanding their distributions into occupied sites. Determining whether the expansion of these species under agricultural transformation represents a beneficial (e.g. restoration of a species with important functional role or conservation listing) or negative (e.g. domination by an aggressive competitor) ecological outcome is important for guiding management for these species. For some groups (e.g.

reptiles) this will likely require gathering additional ecological data to ascertain (Bland and Böhm, 2016; Tingley et al., 2016).

Our approach reveals change in species associations under agricultural transformation but there remains a clear need for deeper ecological inference (Cazelles et al., 2016; Fournier et al., 2016). Increasingly, studies are finding non-random changes in co-occurrence networks in response to environmental changes (Morriën et al., 2017; Tulloch et al., 2016a). Burkle et al. (2013) showed that both interactions and co-occurrence changed over time under anthropogenic influences, while Morriën et al. (2017) found co-occurrence networks of soil micro organisms changed under land restoration. Only some of these studies have been able to explicitly link interactions such as competition or mutualism with the changes in co-occurrence. We stress that the patterns found in our study, as well as in others, require deeper understanding of the driver of association change. For example, our measure of transformation (proportion of surrounding area either fertilized or cultivated) combined a subset of possible, interacting threats to biodiversity that blur the precise mechanism of change. To better understand the drivers of association change, we suggest that researchers studying interaction networks work alongside community ecologists studying co-occurrence to understand how changes in species interactions might be explained by co-occurrence networks, and in turn, whether co-occurrence networks adequately describe community function and change in resilience.

Our study highlights the value of co-occurrence networks to identify the impacts of agricultural transformation on biodiversity. Importantly, our study also presents several potential research opportunities to advance the usage of co-occurrence networks. First, our study is based on a simplified binary classification of agricultural transformation. However, our approach may be readily transferred to categorical classifications of land-use, or even continuous data, where sufficient co-occurrence data exists. Although reptiles represent a key component of biodiversity (Bland and Böhm, 2016), they differ in α, β, and γ diversity to other vertebrate groups (Gaston, 2000). Replication of our approach for other α-diverse taxonomic groups would provide generality to our findings, and help determine the extent to which co-occurrence networks reliably reveal community restructuring. Second, experimental tests aiming to tease apart underpinning processes driving co-occurrence (e.g. competition, resource availability) should be conducted to help develop a stronger ecological understanding of these differences. Importantly, our analyses focussed on positive co-occurrence associations and could be repeated for negative associations if managers are interested in investigating the effects of particular threats suspected to result in species avoidance (e.g. predators or invasive competitors). Third, our study deliberately used a measure of agricultural transformation that comprised multiple threatening actions facing in-situ communities (e.g. fertilization, habitat removal, invasive species), motivated by an increasing need for holistic strategies that address multiple threats (Tulloch et al., 2016a). A useful next step would be to isolate the independent effects of the various processes to further refine management recommendations. Fourth, species co-occurrence may be influenced by temporal dynamics (such as community succession) over extended timeframes (Poisot et al., 2015; Tulloch et al., 2016a). We limited the temporal extent of our data (to 4 years) to reduce this influence, however a better understanding of how temporal dynamics influence co-occurrence and particularly species co-occurrence restructure is needed. Long-term monitoring studies would prove useful for examining these important aspects.

Conclusions

Agricultural transformation is a global driver of biodiversity decline in agro-ecosystems (Sala et al., 2000). Previous examinations of its impact on biodiversity have largely focused on identifying changes in species richness and community composition. Our large-scale examination of species co-occurrence networks builds on this work to give more comprehensive insight into the impact of agricultural transformation on biodiversity that is not possible in conventional studies of species richness and community composition. In particular, agricultural transformation led to complex changes in species associations, with many species gaining and losing association with other species rather than a uniform loss throughout the community. Considering co-occurrence at the species-level in conjunction with species occupancy allowed stratification of assemblages by their distinctive response to the threat of agricultural transformation. This allowed us to identify those species at most risk of future decline as well as those for which targeted monitoring is required. Wider examination of species co-occurrence networks to expose the ecological impacts of a range of other pervasive anthropogenic threats (e.g. climate change) is needed.

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References

Alexandratos, N. and Bruinsma, J. 2012. World agriculture towards 2030/2050: the 2012 revision. - Food and Agriculture Organization of the United Nations, Rome.

Araújo, M. B. et al. 2011. Using species co-occurrence networks to assess the impacts of climate change. - Ecography (Cop.). 34: 897–908.

Arita, H. T. and Peres-Neto, P. 2016. Species co-occurrence analysis: pairwise versus matrix-level approaches. - Glob. Ecol. Biogeogr. 25: 1397–1400.

Bascompte, J. 2010. Structure and dynamics of ecological networks. - Science(Washington) 329: 416–419.

Berlow, E. L. et al. 2009. Simple prediction of interaction strengths in complex food webs. - Proc. Natl. Acad. Sci. 106: 187–91.

Bland, L. M. and Böhm, M. 2016. Overcoming data deficiency in reptiles. - Biol. Conserv. 204: 16–22.

Bland, L. M. et al. 2016. Guidelines for the application of IUCN Red List of Ecosystems Categories and Criteria Guidelines for the application of IUCN Red List of Ecosystems Categories and Criteria. - Gland, Switzerland: IUCN.

Blois, J. L. et al. 2014. A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary. - Ecography (Cop.). 37: 1095–1108.

Borthagaray, A. I. et al. 2014. Inferring species roles in metacommunity structure from species co-occurrence networks. - Proc. Biol. Sci. 281: 20141425-.

Brown, G. et al. 2011. Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. - Landsc. Urban Plan. 103: 277–288.

Burkle, L. A. et al. 2013. Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. - Science (80-.). 339: 1611–1615.

Cazelles, K. et al. 2016. A theory for species co-occurrence in interaction networks. - Theor. Ecol. 9: 39–48.

Cliff, A. D. and Ord, J. K. 1981. Spatial and temporal analysis: autocorrelation in space and time. - In: Quantitative Geography A British View. pp. 104–110.

Connor, E. F. and Simberloff, D. 1979. The assembly of species communities - chance or competition. - Ecology 60: 1132–1140.

Csárdi, G. and Nepusz, T. 2006. The igraph software package for complex network research. - InterJournal Complex Syst. 1695: 1695.

Dormann, C. F. et al. 2009. Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. - Open Ecol. J. 2: 7–24.

Dornelas, M. et al. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. - Science (80-.). 344: 296–299.

Dunne, J. a. et al. 2002. Network structure and biodiversity loss in food webs: Robustness increases with connectance. - Ecol. Lett. 5: 558–567.

Emmerson, M. et al. 2016. Chapter Two – How Agricultural Intensification Affects Biodiversity and Ecosystem Services. - Adv. Ecol. Res. 55: 43–97.

Fischer, J. et al. 2004. The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. - J. Appl. Ecol. 41: 32–44.

Fournier, B. et al. 2016. Multiple assembly rules drive the co-occurrence of orthopteran and plant species in grasslands: combining network, functional and phylogenetic approaches. - Front. Plant Sci. 7: 1–12.

Garay-Narváez, L. et al. 2014. Food web modularity and biodiversity promote species persistence in polluted environments. - Oikos 123: 583–588.

Gaston, K. J. 2000. Global patterns in biodiversity. - Nature 405: 220–227.

Gilbert, A. J. 2009. Connectance indicates the robustness of food webs when subjected to species loss. - Ecol. Indic. 9: 72–80.

Goldwasser, L. and Roughgarden, J. 1997. Sampling effects and the estimation of food-web properties. - Ecology 78: 41–54.

Gotelli, N. J. and McCabe, D. J. 2002. Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. - Ecology 83: 2091–2096.

Heleno, R. et al. 2012. Connectance of species interaction networks and conservation value: Is it any good to be well connected? - Ecol. Indic. 14: 7–10.

Helm, A. et al. 2006. Slow response of plant species richness to habitat loss and fragmentation. - Ecol. Lett. 9: 72–77.

Hooke, R. 2012. Land Transfomation by Humans: A Review. - GSA Today 22: 4–10.

Horner-Devine, M. C. et al. 2007. A comparison of taxon co-occurrence patterns for macro- and microorganisms. - Ecology 88: 1345–1353.

Jellinek, S. et al. 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. - Austral Ecol. 29: 294–304.

Jellinek, S. et al. 2014. Reptiles in restored agricultural landscapes: the value of linear strips, patches and habitat condition. - Anim. Conserv. 17: 544–554.

Karp, D. S. et al. 2012. Intensive agriculture erodes β-diversity at large scales. - Ecol. Lett. 15: 963–970.

Kay, G. M. et al. 2016a. Effects of past and present livestock grazing on herpetofauna in a landscape-scale experiment. - Conserv. Biol. 31: 446–458.

Kay, G. M. et al. 2016b. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. - Anim. Conserv. 19: 515–525.

Keith, D. A. et al. 2013. Scientific Foundations for an IUCN Red List of Ecosystems. - PLoS One 8: e62111.

Lane, P. W. et al. 2014. Visualization of species pairwise associations: A case study of surrogacy in bird assemblages. - Ecol. Evol. 4: 3279–3289.

Levin, S. A. 1970. Community Equilibria and Stability, and an Extension of the Competitive Exclusion Principle. - Am. Nat. 104: 413.

Li, B. et al. 2015. Metagenomic and network analysis reveal wide distribution and co-occurrence of environmental antibiotic resistance genes. - ISME J. 9: 2490–2502.

Lindenmayer, D. and Fischer, J. 2006. Habitat fragmentation and landscape change: an ecological and conservation synthesis. - Island Press.

Lindenmayer, D. et al. 2015. Richness is not all: how changes in avian functional diversity reflect major landscape modification caused by pine plantations. - Divers. Distrib.: 1–12.

Liu, Y. et al. 2014. Functional beetle diversity in managed grasslands: Effects of region, landscape context and land use intensity. - Landsc. Ecol. 29: 529–540.

MacArthur, R. and Levins, R. 1964. Competition, habitat selection, and character displacement in a patchy environment. - Proc. Natl. Acad. Sci. U. S. A. 51: 1207–1210.

May, R. M. 1973. Stability and complexity in model ecosystems. - Monogr. Popul. Biol. 6: 1–235.

McCune, B. and Mefford, M. J. 2011. PC-Ord: Multivariate analysis of ecological data. - MjM Software.

Michael, D. R. et al. 2015. Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems. - Austral Ecol. 40: 651–660.

Mielke, P. W. et al. 2007. Permutation Methods: A Distance Function Approach. - Springer.

Morriën, E. et al. 2017. Soil networks become more connected and take up more carbon as nature restoration progresses. - Nat. Commun. 8: 14349 doi: 10.1038/ncomms14349.

Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. - Nature 520: 45–50.

Newman, M. E. J. 2006. Modularity and community structure in networks. - Proc. Natl. Acad. Sci. 103: 8577.

Newman, M. E. J. et al. 2001. The structure and function of complex networks. - Phys. Rev. E 64: 26118.

Nielsen, A. and Bascompte, J. 2007. Ecological networks, nestedness and sampling effort. - J. Ecol. 95: 1134–1141.

Oksanen, A. J. et al. 2015. Package "vegan" (R package). - Version 2.3-0, <http://cran.r-project.org, https://github.com/vegandevs/vegan>.

Peres-Neto, P. R. et al. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. - Ecology 87: 2614–2625.

Poisot, T. et al. 2015. Beyond species: why ecological interaction networks vary through space and time. - Oikos 124: 243–251.

Ruffell, J. et al. 2017. The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. - Ecography (Cop.). 40: 171–178.

Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. - Science (80-.). 287: 1770–4.

Schutz, A. J. and Driscoll, D. A. 2008. Common reptiles unaffected by connectivity or condition in a fragmented farming landscape. - Austral Ecol. 33: 641–652.

Sebastián-González, E. et al. 2015. Macroecological trends in nestedness and modularity of seed-dispersal networks: human impact matters. - Glob. Ecol. Biogeogr. 24: 293–303.

Solar, R. et al. 2016. Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. - Biol. Conserv. 197: 98–107.

Takemoto, K. et al. 2016. Human Impacts and Climate Change Influence Nestedness and Modularity in Food-Web and Mutualistic Networks (A Belgrano, Ed.). - PLoS One 11: e0157929.

Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. - Science (80-.). 329: 853–856.

Thompson, M. E. et al. 2016. The importance of defining focal assemblages when evaluating amphibian and reptile responses to land use. - Conserv. Biol. 30: 249–258.

Tingley, R. et al. 2016. Addressing knowledge gaps in reptile conservation. - Biol. Conserv. in press.

Trimble, M. J. and van Aarde, R. J. 2012. Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. - Ecosphere 3: 1–16.

Tscharntke, T. et al. 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. - Ecol. Lett. 8: 857–874.

Tscharntke, T. et al. 2012a. Global food security, biodiversity conservation and the future of agricultural intensification. - Biol. Conserv. 151: 53–59.

Tscharntke, T. et al. 2012b. Landscape moderation of biodiversity patterns and processes - eight hypotheses. - Biol. Rev. 87: 661–685.

Tulloch, A. I. T. et al. 2016a. Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies. - Conserv. Biol. 30: 867–882.

Tulloch, A. I. T. et al. 2016b. Dynamic Species Co-Occurrence Networks Require Dynamic Biodiversity Surrogates. - Ecography (Cop.). 39: 1185–1196.

Tylianakis, J. M. et al. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. - Nature 445: 202–205.

Tylianakis, J. M. et al. 2010. Conservation of species interaction networks. - Biol. Conserv. 143: 2270–2279.

Urban, D. and Keitt, T. 2008. Landscape Connectivity: A Graph-Theoretic Perspective. - Ecology 82: 1205–1218.

Valdovinos, F. S. et al. 2009. Structure and dynamics of pollination networks: The role of alien plants. - Oikos 118: 1190–1200.

Veech, J. A. 2013. A probabilistic model for analysing species co-occurrence. - Glob. Ecol. Biogeogr. 22: 252–260.

Veech, J. A. 2014. The pairwise approach to analysing species co-occurrence. - J. Biogeogr. 41: 1029–1035.

Westgate, M. J. and Lane, P. W. 2015. sppairs: Species Pairwise Association Analysis in R (R package). - Version 1.0, < https://github.com/ mjwestgate/sppairs>.

Williams, R. J. et al. 2014. Demonstrating microbial co-occurrence pattern analyses within and between ecosystems. - Front. Microbiol. 5: 1–10.

Wilson, S. and Swan, G. 2013. Complete Guide to Reptiles of Australia. - New Holland Publishers.

Supplementary Material

Appendix 1. Details of the study region.

Our study is set within a broad agricultural landscape of southeastern Australia, spanning approximately >1000 km north-to-south from Warwick in southern Queensland (28°1’32”S, 152°12’22”E) to Albury in southern New South Wales (36°4’47”S, 146°54’59”E) (Figure A1). This area supports some of the most productive landscapes for cereal cropping and livestock grazing in Australia on account of moderate rainfall (400 – 1200 mm per annum) and moderate to highly fertile soils (Commonwealth of Australia, 2013). The dominant vegetation of this region is the critically endangered Box Gum Grassy Woodland (BGGW) ecological community (Figure A2), of which <4% remains following 230 years of broad-scale clearing for agriculture (Lindenmayer et al., 2010). This woodland community comprises a diverse vegetation assemblage consisting of an open tree strata that was originally dominated by white box *Eucalyptus albens*, yellow box *E. melliodora* and Blakely’s red gum *E. blakelyi* and an understorey of native tussock grasses, herbs and scattered shrubs (Commonwealth of Australia, 2013).

Two broad agro-climatic systems have been defined across this study area (Kay et al., 2016b), based on previous classifications of landscapes with similar climate, vegetation and common land-use (Hutchinson et al. 2005). These systems include a winter-rainfall mixed grazing and cropping system (termed Tablelands Region in the main text), and a low-rainfall cropping system (termed Western Region in the main text). Within each region, dominant land-uses include wheat and canola cropping, grazing of improved (exotic) pastures, and grazing of native pastures. The predominant livestock on farms were sheep

(*Ovis aries*) and cattle (*Bos taurus*). Farm sizes ranged from 100 Ha to in some cases > 5000 ha, with the average closer to 1-2,000 Ha.

Specifics of the land-use data

For this study system, we considered transformed landscapes as those which had experienced any combination of two key threats in the recent (within 50 year) past: cultivation and fertilization. A critical aspect of our ‘natural’ study is that we combine these key transformation threats (cultivation and fertilization) into a single value used to represent transformation. While understanding the nature of both threats would be useful, combining key threats in this way provides a means to explore the impacts of transformation in a broad sense, acknowledging that such threats rarely interact in isolation.

We obtained site-level agricultural transformation data by conducting a survey of landholders to identify the cultivation and fertilization histories of landscapes surrounding each of 224 available sites. We classified all areas within 500m radius of each site as either: (i) native (areas with little fertilizer application, with less than 3 applications in total and not fertilized in the previous 15 years), (ii) improved (areas with some history of fertilization or cultivation in the past 15 years), (iii) cropped (five or more crops in the past 15 years), and (iv) other (e.g. infrastructure, water etc) (Figure A4). We removed any sites from further analysis which contained incomplete data (either from the land-use or ecological surveys) or comprised >5% of surrounding area as “other”.

We digitized this data using ArcGIS and calculated the proportional area of native, improved and cropped landscapes within 500m radius of each site. We calculated a “proportion unmodified” measure for each site as:

$$\propto unmodified = \frac{\propto native}{\propto total} \text{ x } 100$$

where $\propto native$ is the proportional surrounding area classified as native and $\propto total$ is the total area within 500m radius of each site. As mentioned in the main text, we defined sites with ≥70% proportion unmodified as intact and sites with >30% modified (i.e. fertilized or cultivated within 15 years) as modified following classifications of ecosystem threat by Keith et al. (2013). The mean area of surrounding (<500 m) modified landscape for intact sites was 4.8 ± 8.3% and 9.4 ± 10.1% for the Western and Tablelands agro-climatic regions respectively, and 64.5 ± 22.2% and 58.3 ± 19.7% for modified landscapes for the same regions (Table 1, main text).

Specifics of the reptile data

Reptile surveys were conducted using a repeated time- and area-constrained (20-min x 0.8 ha) active search of natural habitats and inspections of artificial refuge arrays (Figure A4) within each site. Active searches of natural habitat involved scanning each plot for basking or moving animals, raking through leaf litter and grass tussocks, lifting logs and surface rocks and inspecting exfoliating bark. Each array consisted of four roof tiles (32 cm x 42 cm), two sheets of corrugated iron (1 m x 1 m) stacked on top of each other, and four wooden sleepers (1.2 m long). We conducted surveys on clear days with minimal wind between 0900 and 1600 hours by the same group of experienced field ecologists. We identified species using Wilson & Swan (2012), releasing animals once recorded in accordance with Australian National University ethics guidelines (protocols F.ES.04.10 and A2013/38).

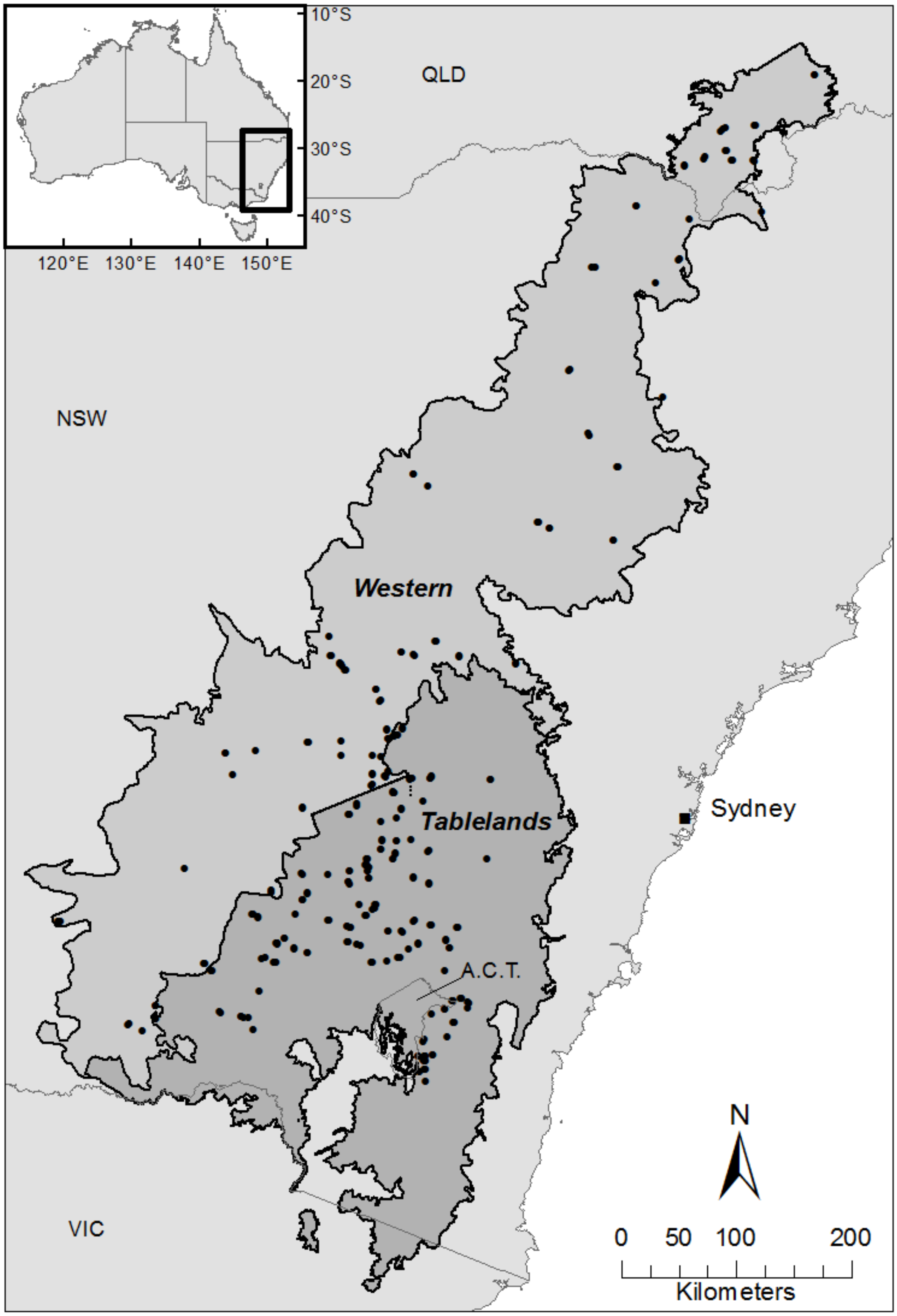


Figure A1. Location of the study area spanning New South Wales (NSW) and southern Queensland (QLD) of south-eastern Australia showing the location of monitoring sites (n=224) surveyed across the two agro-climatic systems (grey filled).

Figure A2. *Example of a site from our study area showing the open woodland structure that is typical of the box-gum grassy woodland ecological community.*

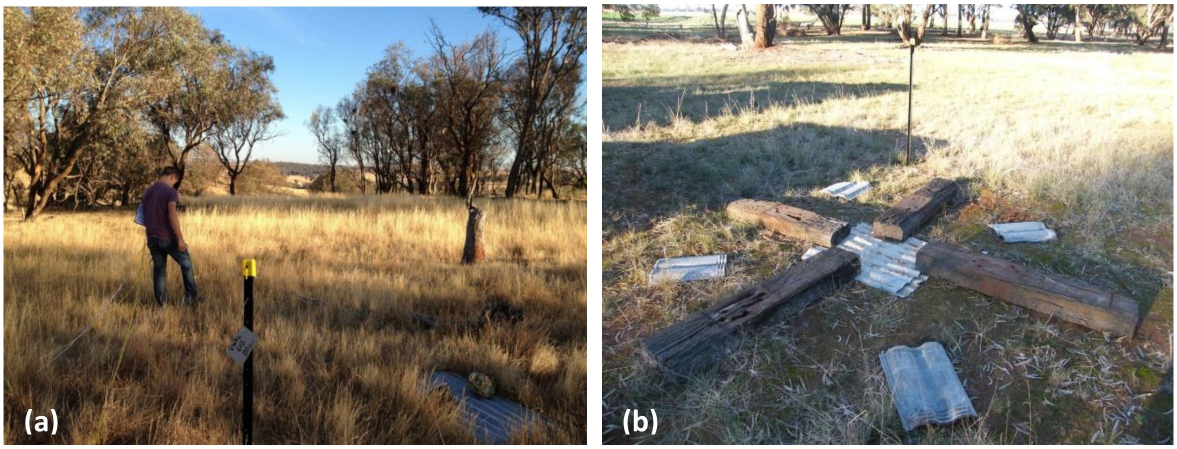


Figure A3. *Depiction of the (a) active search and (b) artificial refuge array used in herpetofaunal surveys*

Figure A4. *Example of a completed landuse survey, with different categories of land-use demarked. (Green polygon = remnant woodland, 2 = Native, 3 = Improved, 4 = Cropped landscape).*

Appendix 2: Species occupancy and functional trait information

Table A1. *Species list including total abundance (Abund) and occurrence ('Occur.'; number of site-level occurrences / total number of sites) for intact and modified (mod) landscapes within the two agro-climatic regions across the whole study. Key;* ▲ *denotes increase,* ▼ *denotes decrease and* – *denotes absent (and stable)*

Family	**Scientific Name**	**Abund**	**Occur.**	**Occurrence**					
		Whole Study		Western Region			Tablelands Region		
				intact	mod		intact	mod	
Agamidae	*Amphibolurus burnsi*	3	1%	3.8%	4.0%	▲	0.0%	-	–
	Amphibolurus muricatus	10	4%	7.7%	-	▼	4.4%	3.5%	▼
	Pogona barbata	22	8%	9.6%	-	▼	10.0%	8.8%	▼
Elapidae	*Demansia psammophis*	7	3%	11.5%	-	▼	-	1.8%	▲
	Furina diadema	4	2%	7.7%	-	▼	-	-	–
	Parasuta dwyeri	37	10%	15.4%	4.0%	▼	8.9%	8.8%	▼
	Pseudechis porphyriacus	3	1%	-	-	–	1.1%	3.5%	▲
	Pseudonaja textilis	32	11%	5.8%	8.0%	▲	8.9%	19.3%	▲
Gekkonidae	*Christinus marmoratus*	82	21%	7.7%	28.0%	▲	18.9%	35.1%	▲
	Diplodactylus vittatus	42	8%	11.5%	4.0%	▼	8.9%	3.5%	▼
	Gehyra variegata	11	4%	11.5%	8.0%	▼	-	-	–
	Heteronotia binoei	19	5%	17.3%	8.0%	▼	-	-	–
	Nebulifera robusta	5	1%	1.9%	8.0%	▲	-	-	–
	Strophurus intermedius	4	1%	3.8%	-	▼	1.1%	-	▼
Pygopodidae	*Aprasia parapulchella*	67	5%	1.9%	16.0%	▲	6.7%	-	▼
	Delma inornata	19	7%	3.8%	16.0%	▲	7.8%	3.5%	▼
	Delma plebeia	14	4%	13.5%	4.0%	▼	-	-	–
	Delma tincta	3	1%	3.8%	-	▼	-	-	–
Scincidae	*Acritoscincus duperreyi*	4	1%	-	-	–	2.2%	1.8%	▼
	Anomalopus leuckartii	16	5%	15.4%	12.0%	▼	-	-	–
	Carlia tetradactyla	145	31%	13.5%	40.0%	▲	37.8%	33.3%	▼
	Carlia vivax	6	2%	9.6%	-	▼	-	-	–
	Cryptoblepharus pannosus	178	27%	40.4%	28.0%	▼	11.1%	38.6%	▲
	Cryptoblepharus pulcher	21	3%	7.7%	12.0%	▲	-	-	–
	Ctenotus spaldingi	283	35%	50.0%	64.0%	▲	26.7%	22.8%	▼
	Ctenotus taeniolatus	39	6%	1.9%	8.0%	▲	7.8%	5.3%	▼
	Egernia cunninghami	47	8%	1.9%	16.0%	▲	10.0%	7.0%	▼
	Egernia striolata	62	11%	21.2%	12.0%	▼	5.6%	8.8%	▲
	Hemiergis talbingoensis	285	18%	-	-	–	31.1%	21.1%	▼
	Lampropholis delicata	147	21%	13.5%	8.0%	▼	33.3%	12.3%	▼
	Lampropholis guichenoti	61	7%	1.9%	-	▼	13.3%	5.3%	▼
	Lerista bougainvillii	23	3%	5.8%	-	▼	3.3%	1.8%	▼
	Lerista timida	18	5%	15.4%	12.0%	▼	-	-	–
	Lygisaurus foliorum	44	8%	26.9%	16.0%	▼	-	-	–
	Menetia greyii	9	4%	11.5%	-	▼	3.3%	-	▼
	Morethia boulengeri	1028	73%	57.7%	76.0%	▲	75.6%	82.5%	▲
	Tiliqua rugosa	18	6%	1.9%	-	▼	8.9%	7.0%	▼
	Tiliqua scincoides	30	8%	5.8%	8.0%	▲	13.3%	3.5%	▼
	Unidentified skink	6	2%	3.8%	8.0%	▲	-	1.8%	▲
Typhlopidae	*Ramphotyphlops nigrescens*	4	2%	1.9%	4.0%	▲	2.2%	-	▼
	Ramphotyphlops wiedii	8	2%	7.7%	4.0%	▼	-	-	–
Varanidae	*Varanus varius*	3	1%	3.8%	-	▼	1.1%	-	▼

Table A2. *List of traits for all species surveyed across the study.*

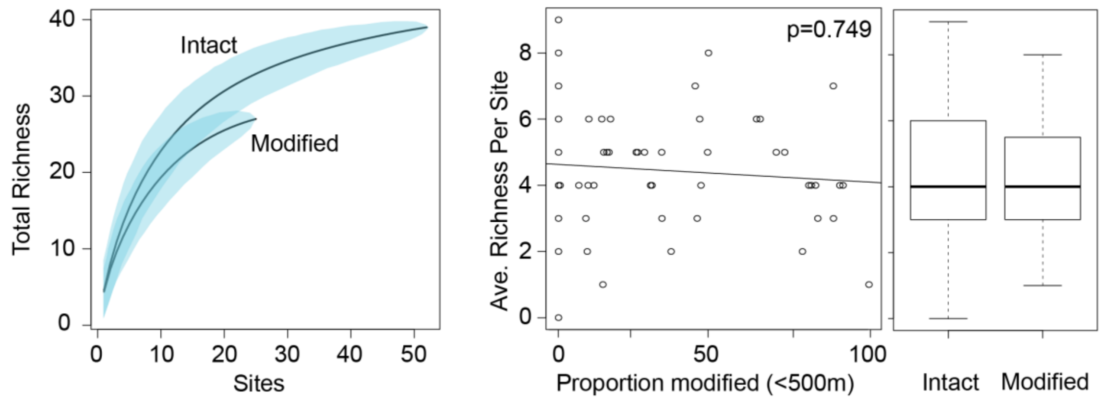
Taxonomy	**Species**	**Code**	**Guild**	**Size**[a]	**Specialization**	**Diet**
Agamidae	*Amphibolurus burnsi*	AmBur	Semi-arboreal	Medium	Specialist	Insects
	Amphibolurus muricatus	AmMur	Semi-arboreal	Small	Generalist	Insects
	Pogona barbata	PoBar	Semi-arboreal	Medium	Generalist	Insects
Elapidae	*Demansia psammophis*	DePsa	Cryptozoic	Large	Specialist	Reptiles
	Furina diadema	FuDia	Cryptozoic	Medium	Generalist	Reptiles
	Parasuta dwyeri	PaDwy	Cryptozoic	Medium	Specialist	Reptiles
	Pseudechis porphyriacus	PsPor	Cryptozoic	Large	Generalist	Reptiles
	Pseudonaja textilis	PsTex	Terrestrial	Large	Generalist	Reptiles
Gekkonidae	*Christinus marmoratus*	ChMar	Arboreal	Small	Generalist	Insects
	Diplodactylus vittatus	DiVit	Cryptozoic	Small	Generalist	Arthropods
	Gehyra variegata	GeVar	Arboreal	Small	Generalist	Arthropods
	Heteronotia binoei	HeBin	Fossorial	Small	Generalist	Insects
	Nebulifera robusta	NeRob	Arboreal	Small	Generalist	Insects
	Strophurus intermedius	StInt	Arboreal	Small	Specialist	Insects
Pygopodidae	*Aprasia parapulchella*	ApPar	Cryptozoic	Medium	Specialist	Ants
	Delma inornata	DeIno	Terrestrial	Medium	Generalist	Insects
	Delma plebeia	DePle	Terrestrial	Medium	Generalist	Insects
	Delma tincta	DeTin	Terrestrial	Medium	Generalist	Insects
Scincidae	*Acritoscincus duperreyi*	AcDup	Terrestrial	Small	Specialist	Arthropods
	Anomalopus leuckartii	AnLeu	Fossorial	Medium	Generalist	Insects
	Carlia tetradactyla	CaTet	Terrestrial	Small	Generalist	Ants
	Carlia vivax	CaViv	Terrestrial	Small	Generalist	Insects
	Cryptoblepharus pannosus	CrPan	Semi-arboreal	Small	Generalist	Insects
	Cryptoblepharus pulcher	CrPul	Semi-arboreal	Small	Specialist	Insects
	Ctenotus spaldingi	CtSpa	Cryptozoic	Small	Generalist	Arthropods
	Ctenotus taeniolatus	CtTae	Cryptozoic	Small	Generalist	Arthropods
	Egernia cunninghami	EgCun	Saxicolous	Medium	Generalist	Vegetation
	Egernia striolata	EgStr	Saxicolous	Medium	Specialist	Insects
	Hemiergis talbingoensis	HeTal	Fossorial	Small	Generalist	Arthropods
	Lampropholis delicata	LaDel	Terrestrial	Small	Generalist	Arthropods
	Lampropholis guichenoti	LaGui	Terrestrial	Small	Generalist	Arthropods
	Lerista bougainvillii	LeBou	Cryptozoic	Small	Specialist	Arthropods
	Lerista timida	LeTim	Fossorial	Small	Specialist	Arthropods
	Lygisaurus foliorum	LyFol	Terrestrial	Small	Generalist	Insects
	Menetia greyii	MeGre	Terrestrial	Small	Specialist	Ants
	Morethia boulengeri	MoBou	Terrestrial	Small	Generalist	Arthropods
	Tiliqua rugosa	TiRug	Terrestrial	Medium	Generalist	Vegetation
	Tiliqua scincoides	TiSci	Fossorial	Medium	Specialist	Insects
	Unidentified skink	UnSki	Terrestrial	Small	Specialist	Insects
Typhlopidae	*Ramphotyphlops nigrescens*	RaNig	Fossorial	Medium	Generalist	Ants
	Ramphotyphlops wiedii	RaWie	Cryptozoic	Medium	Generalist	Ants
Varanidae	*Varanus varius*	VaVar	Semi-arboreal	Large	Generalist	Reptiles

[a] *Key: small is <10cm, medium is 10-50cm, large is >50cm*

[b] *Diet class Insects includes arthropods and ants.*

Appendix 3: Additional species richness and composition results

A) Western



B) Tablelands

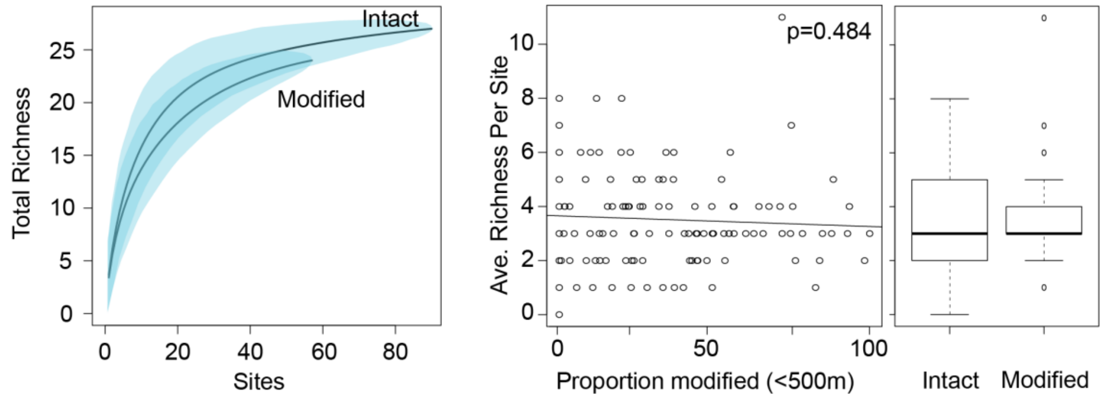


Figure A5. *Species richness summary statistics for (A) Western and (B) Tablelands regions. Showing accumulation curves for the whole species set (with 95% confidence interval), mean (per site) species richness regression plots, and mean (per site) species richness boxplots demonstrating non-significant differences in mean richness between intact and modified landscapes*

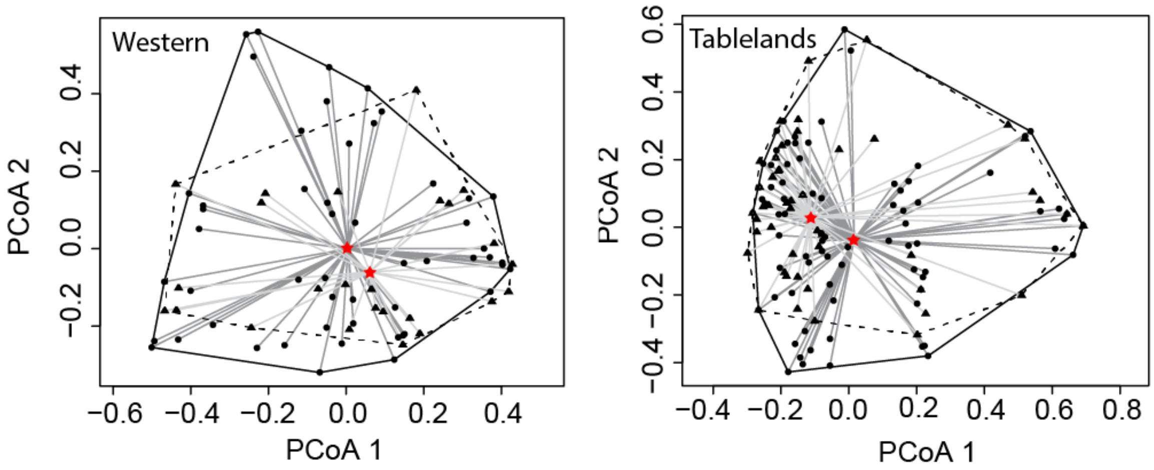


Figure A6. *Ordination plots of the Principal Coordinates Analysis describing overlap in reptile assemblages for intact and modified landscapes throughout the two study regions. For each ordination, circles represent intact sites and triangles represent modified sites displayed in ordinate space, connected by lines to the centroid (red star) of each group. Sites close together have more similar species than sites far apart. Polygons represent the convex hull of the groups of sites in intact (solid) and modified (dotted) landscapes.*

Table A3. *Summary of generalised linear mixed effect model for reptile species richness as predicted by proportion of modification (mod) by factor and continuous variable for both agro-climatic regions throughout the study area.*

Model	Estimate	SE	F	P
WESTERN:				
Species Richness ~ mod (factor) + (1|Farm)	-0.04	0.12	-0.32	0.749
Species Richness ~ mod (continuous) + (1|Farm)	0.03	0.05	0.62	0.535
TABLELANDS:				
Species Richness ~ mod (factor)	-0.06	0.09	-0.70	0.484
Species Richness ~ mod (continuous)	0.03	0.05	0.70	0.485

Table A4. *Summary of reptile community (a) composition (MRPP) and (b) permanova effects across both regions.*

	MRPP			PERMDISP		
	T	A	P	F	d.f.	P
WESTERN: intact vs modified	-2.56	0.01	**0.019**	5.055	1	**0.027**
TABLELANDS: intact vs modified	-6.26	0.01	**0.001**	3.137	1	0.077

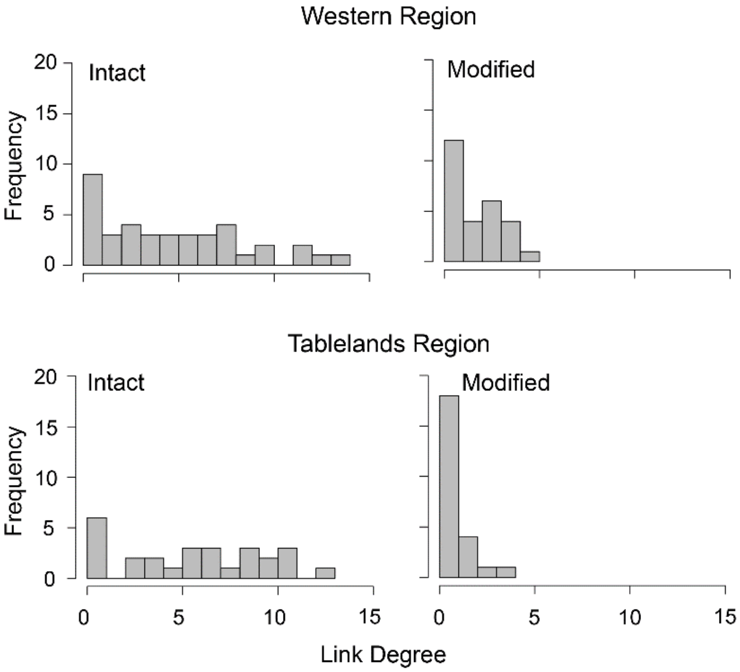
Appendix 4: Additional detail and results for co-occurrence analysis

Details of network analysis methodology and supporting data

A tutorial for using the R sppairs library (Westgate and Lane 2015) to derive species co-occurrence is available here: http://martinwestgate.com/software/sppairs/tutorial/. When calculating co-occurrence between each pair of species to derive co-occurrence networks, we used the default setting of contingency tables (or.contingency()), but with no rarity cutoff (i.e. no species excluded from analysis, including species that occurred only once in the dataset). For this study, we ignored any information provided by negative associations between species.

Additional co-occurrence results

a) Degree Distribution



b) Strength Distribution

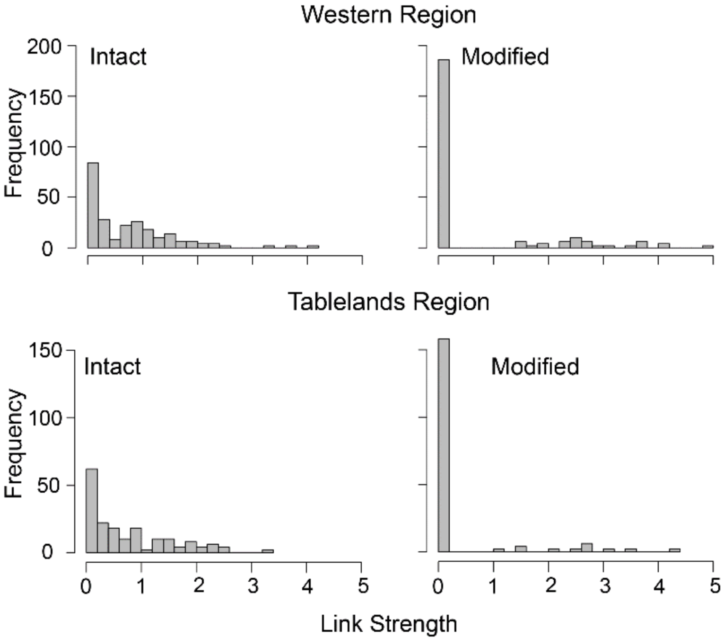


Figure A7. *Frequency distribution of significant positive co-occurrence (a) degree and (b) strength for both intact and modified landscapes across the two study regions.*

Table A5. *Network metric results for the co-occurrence network of 39 species in the Western and 29 species in the Tablelands regions. Showing changes in species degree and strength between co-occurrence networks representing intact and modified treatments.*

Species	Western Region				Tablelands Region			
	intact		modified		intact		modified	
	Degre	Strengt	Degre	Strengt	Degre	Strengt	Degre	Strengt
Acritoscincus duperreyi	*	*	*	*	1	1.373	0	0.000
Amphibolurus burnsi	4	0.488	0	0.000	*	*	*	*
Amphibolurus muricatus	5	0.638	*	*	7	1.835	0	0.000
Anomalopus leuckartii	7	0.597	2	2.573	*	*	*	*
Aprasia parapulchella	3	2.333	4	2.000	9	0.590	*	*
Carlia tetradactyla	7	1.036	3	1.598	10	0.254	1	1.596
Carlia vivax	7	1.053	*	*	*	*	*	*
Christinus marmoratus	8	1.582	2	2.715	10	0.786	0	0.000
Cryptoblepharus	5	0.238	3	2.036	8	1.160	3	1.916
Cryptoblepharus pulcher	6	1.009	2	3.131	*	*	*	*
Ctenotus spaldingi	8	0.069	3	2.290	11	0.748	2	2.355
Ctenotus taeniolatus	0	0.000	0	0.000	13	0.859	1	4.245
Delma inornata	1	1.657	1	2.234	3	0.409	0	0.000
Delma plebeia	8	0.860	0	0.000	*	*	*	*
Demansia psammophis	12	0.906	*	*	*	*	0	0.000
Delma tincta	4	1.564	*	*	*	*	*	*
Diplodactylus vittatus	4	0.815	0	0.000	5	0.484	4	2.947
Egernia cunninghami	0	0.000	3	2.011	11	0.874	1	2.621
Egernia striolata	13	0.629	4	2.956	6	1.278	0	0.000
Furina diadema	2	0.788	*	*	*	*	*	*
Gehyra variegata	6	1.504	4	3.296	*	*	*	*
Hemiergis talbingoensis	*	*	*	*	4	0.609	1	1.496
Heteronotia binoei	14	0.785	2	2.509	*	*	*	*
Lampropholis delicata	1	0.792	0	0.000	7	0.158	2	2.098
Lampropholis guichenoti	0	0.000	*	*	4	1.159	0	0.000
Lerista bougainvillii	5	1.064	*	*	9	1.400	0	0.000
Lerista timida	10	0.712	3	3.398	*	*	*	*
Lygisaurus foliorum	12	0.647	3	2.718	*	*	*	*
Menetia greyii	9	0.939	*	*	1	1.563	*	*
Morethia boulengeri	10	0.223	5	2.048	7	0.349	1	1.113
Nebulifera robusta	1	4.066	4	3.896	*	*	*	*
Parasuta dwyeri	8	0.617	1	4.804	11	0.852	0	0.000
Pogona barbata	3	1.056	*	*	6	0.171	1	2.621
Pseudechis porphyriacus	*	*	*	*	0	0.000	1	4.245
Pseudonaja textilis	2	0.936	0	0.000	3	0.417	2	2.265
Ramphotyphlops	0	0.000	0	0.000	1	0.833	*	*
Ramphotyphlops wiedii	6	1.563	0	0.000	*	*	*	*
Strophurus intermedius	3	0.572	*	*	0	0.000	*	*
Tiliqua rugosa	0	0.000	*	*	6	1.375	2	3.124
Tiliqua scincoides	3	1.533	1	4.804	9	0.847	0	0.000
Unidentified skink	1	1.103	1	3.689	*	*	0	0.000
Varanus varius	2	0.503	*	*	0	0.000	*	*

Table A6. *Summary of linear model for the change in occurrence and change in average co-occurrence connectance for both agro-climatic regions throughout the study area.*

Model	Estimate	SE	T	P
WESTERN:				
Change in connectance ~ change in occurrence	0.016	0.004	4.31	<0.001
TABLELANDS:				
Change in connectance ~ change in occurrence	0.003	0.01	0.22	0.828

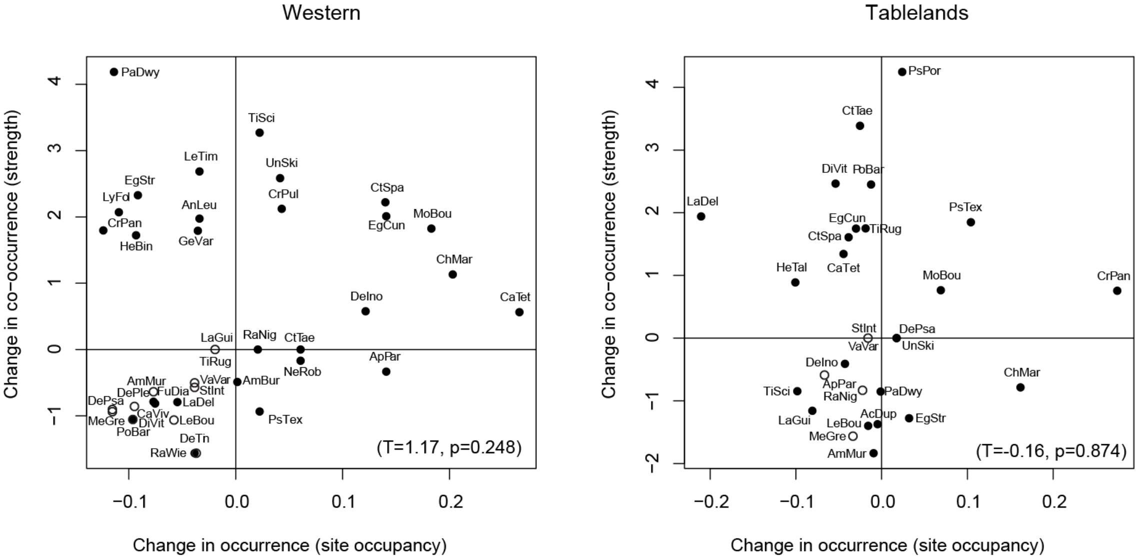


Figure A8. *Relationships (plus significance values) between change in occurrence and change in average co-occurrence strength for species within intact and modified landscapes for each case study region. Dots represent individual species (codes represent the first two letters of the genus and second three letters for the species names). Hollow circles represent species no longer present in modified landscapes.*

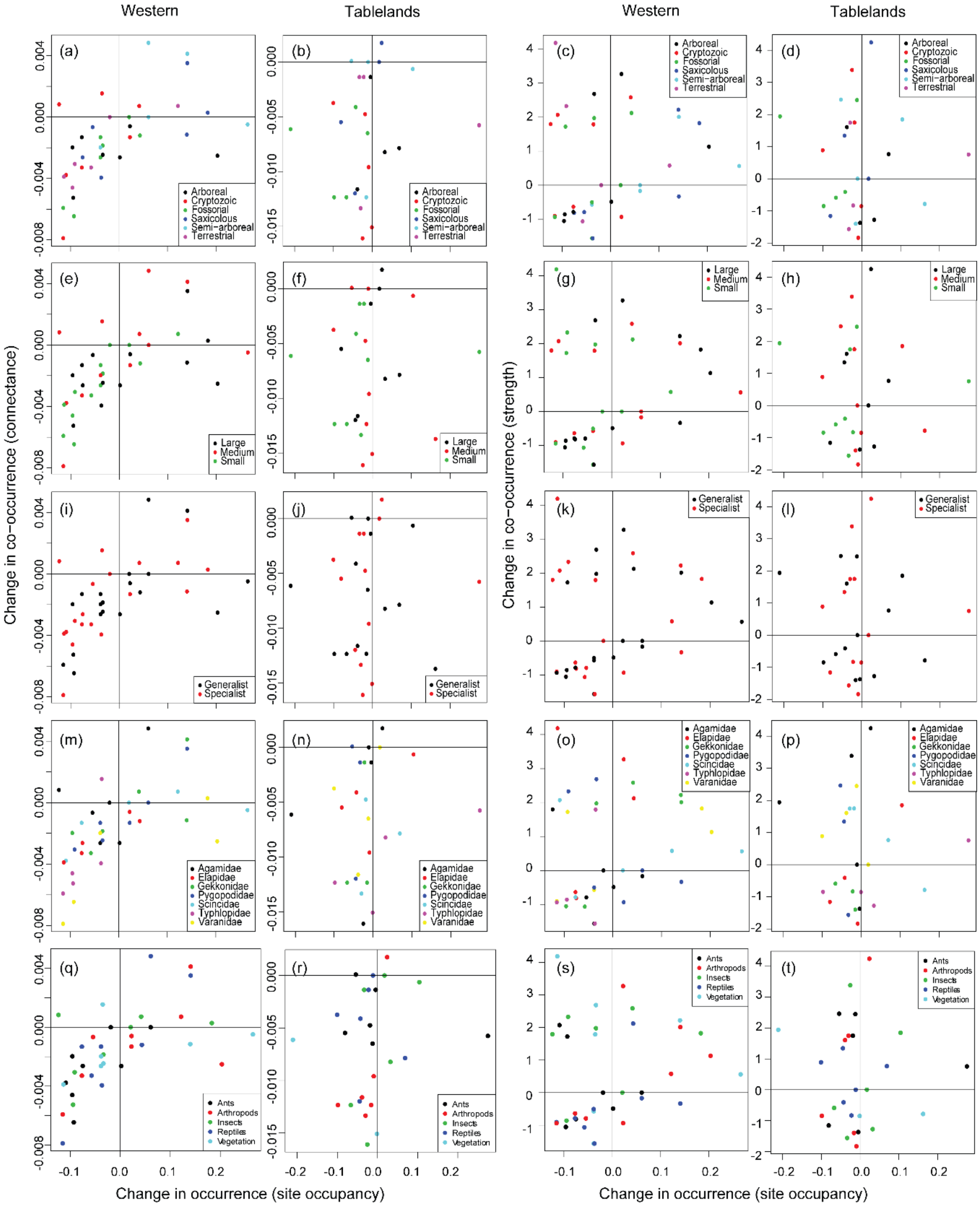


Figure A9. *Relationship between change in occurrence and change in co-occurrence connectance (links/sp^2) and strength, color coded by main species trait groups, for Western and Tablelands co-occurrence networks. Showing species traits of (a-d) microhabitat guild, (e-h) body size, (i-l) habitat specialization, (m-p) taxonomic guild, and (q-t) dietary guild. Dots represent species.*

Appendix 5: Comparison of co-occurrence results with alternative probabilistic analysis.

We tested the validity of our approach against an alternative probabilistic co-occurrence quantification method presented by Veech (2013). This approach calculates pairwise species co-occurrence by deriving exact probabilities that two species should co-occur either more or less frequently than they actually do, and returns a more conservative network than other matrix randomization procedures.

Importantly, whilst there were some differences in the strength of co-occurrence of individual species under the Veech (2013) approach compared with the odds-ratio procedure adopted in the main text, the overall patterns of relationships between landscape modification and co-occurrence metrics did not change. As found in the original odds-ratio analyses, network connectance was lower in modified than intact landscapes for both regions (Table A7). Similarly, network modularity was greater in modified than intact landscapes for both regions (Table A7). Examining pair-wise associations under the Veech (2013) approach, a similar number of links remained stable under modification (i.e. 3-7% compared with 4-8% in the odds-ratio approach) and restructured (i.e. 93-97% compared to 92-96% in the odds-ratio approach) under modification (Table A8; Table 2 main text). Finally, as found in the original odds-ratio analysis, changes in occupancy were not correlated with changes in co-occurrence connectance for the Tablelands region (p_t=0.754) but were for the Western region (p_w=0.043) (Figure A10).

Table A7. *Summary statistics of co-occurrence network variables calculated using the probabilistic approach of Veech (2013), for both intact (>70% unmodified) and modified (<70% unmodified) sites across the two agro-climatic regions within the study area.*

	Western Region		Tablelands Region	
	intact	modified	intact	modified
Co-occurrence networks				
Total positive degree	188	40	154	22
Links per species	4.82	1.48	5.70	0.92
Connectance (# links/spp^2)	0.12	0.05	0.21	0.04
Modularity	0.21	0.55	0.17	0.52

Table A8. *Summary of the change in individual species pairwise co-occurrence link dynamics (degree and strength) between sites within intact and modified landscapes for the two study regions. Changes in degree and strength are classified as either lost, gained or changed (restructured) under agricultural transformation.*

Pairwise species co-occurrences	**Western**		**Tablelands**	
	n	% links	n	% links
Change in pairwise species co-occurrence connections (degree)				
Stable (or no link)	7	3%	12	7%
Links restructured	218	97%	154	93%
- Links lost (because species lost from modified landscape)	44	20%	5	3%
- Links gained (because species gain in modified landscape)	0	0%	2	1%
- Links lost (species present across both landscapes)	174	80%	137	90%
- Links gained (species present across both landscapes)	34	16%	10	7%
Change in pairwise species co-occurrence strength				
Stable (or no strength)	3	1%	2	1%
Strength changed	222	99%	164	99%
- Decreased strength (because the link was removed)	182	82%	142	87%
- Increased strength (because the link was formed)	34	15%	10	6%
- Decreased strength (of an existing link)	0	0%	0	0%
- Increased strength (of an existing link)	6	3%	12	7%

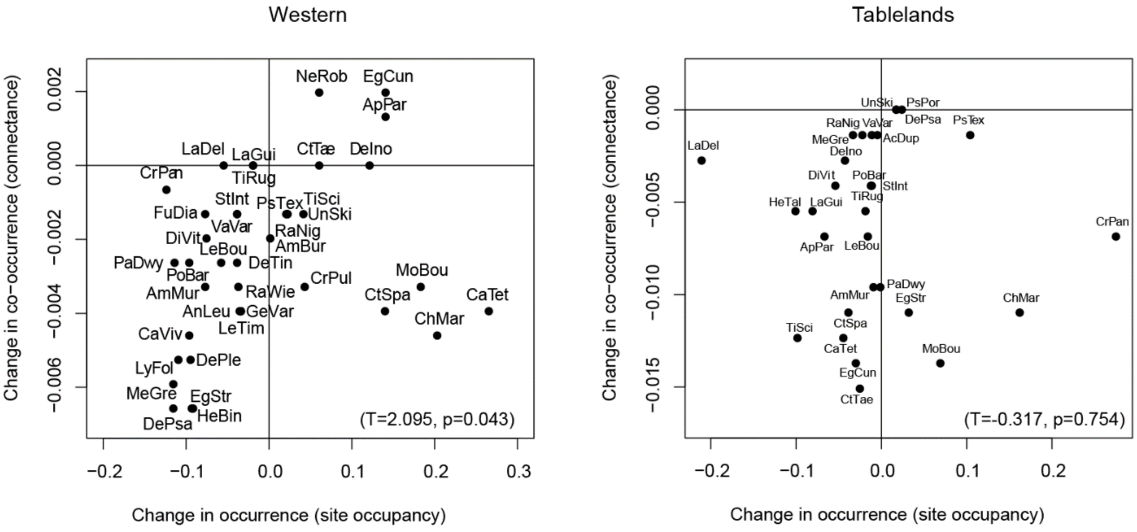


Figure A10: *Relationships (plus significance values) between change in occupancy and change in average co-occurrence link density (links/species^2) for species within intact and modified landscapes for each case study region. Dots represent individual species (codes represent the first two letters of the genus and second three letters for the species names).*

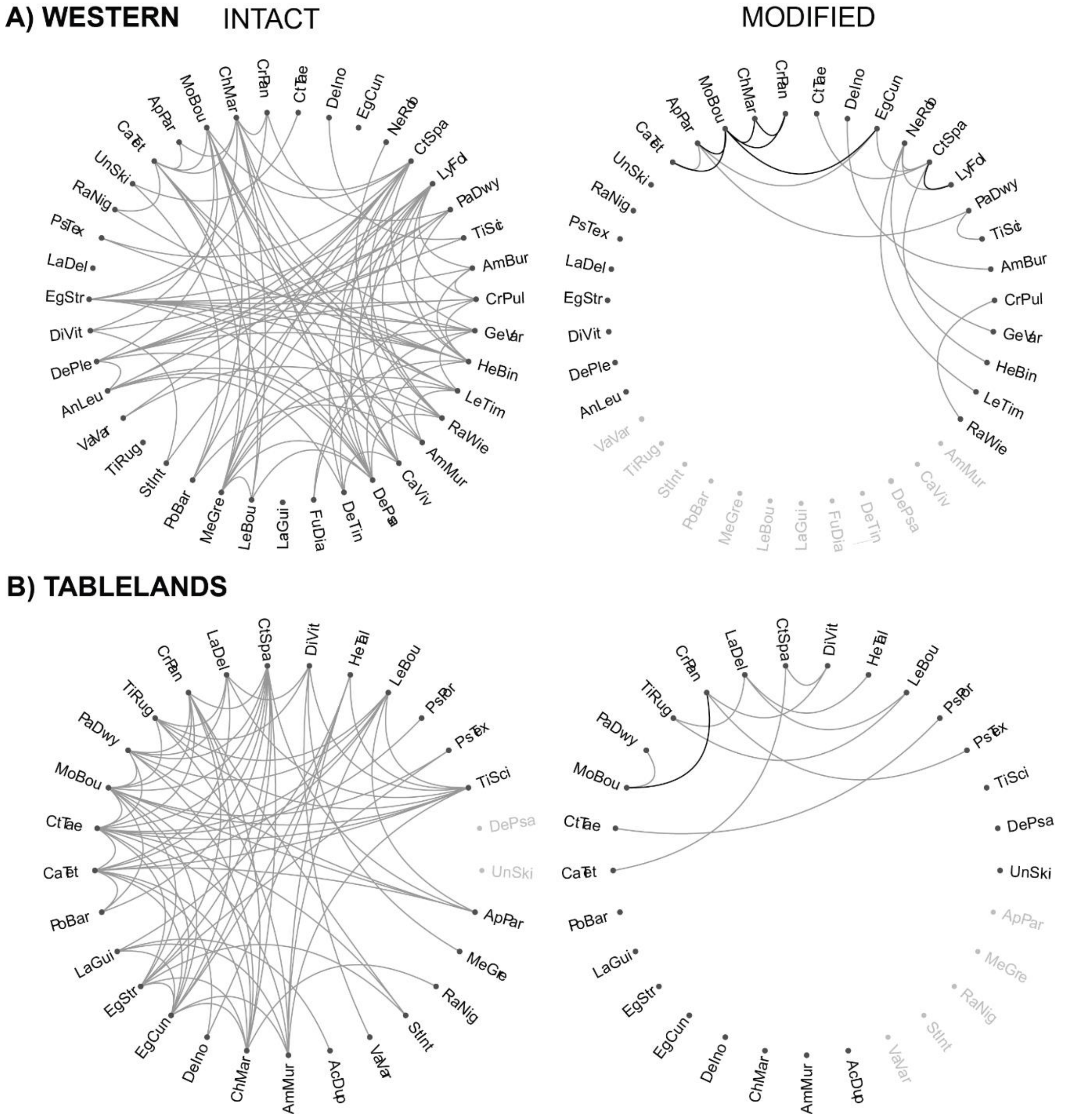


Figure A11: *Species co-occurrence networks using the Veech (2013) protocol for reptiles in sites within intact and modified landscapes across the (A) Western and (B) Tablelands study regions. Nodes represent species present (with >1% occupancy) in each landscape. Vectors between nodes represent significant positive co-occurrence relationships of varying strength, with line darkness proportional to effect size (with black>0.2). Greyed names represent species absent (locally extinct) from landscape type.*

Appendix 6: Results from the modularity analysis.

We examine several complimentary and universally applied network metrics to identify the impacts of agricultural transformation on species co-occurrence. A useful approach is to identify whether the network becomes more modular, because there are some good theoretical reasons (Tylianakis et al., 2010) and some evidence from the biotic interactions literature (Garay-Narváez et al., 2014; e.g. Valdovinos et al., 2009) why network modularity should change under agricultural transformation.

Network modularity is an approach designed to measure the strength of division of a network into modules (also called groups, clusters or communities). Networks with high modularity have dense connections between the nodes within modules but sparse connections between nodes in different modules. We hypothesized in this study that agricultural transformation would lead to greater segregation of the community, and hence greater modularity (Figure 1, Main text).

We examined network modularity using the igraph package in R v3.3.1 (Csárdi and Nepusz, 2006). We input a matrix of species-species co-occurrences (the verticies of the modularity graph) and their associated strengths (edges or arrows of the modularity graph).

The output is a value summarizing modularity for each of the four networks constructed (Table 1, Main text). Values >4 are suggestive of modular networks (Newman, 2006). We plot the arrangements of vertices (species; yellow circles) and edges (co-occurrence strength; arrows) (Figure A12).

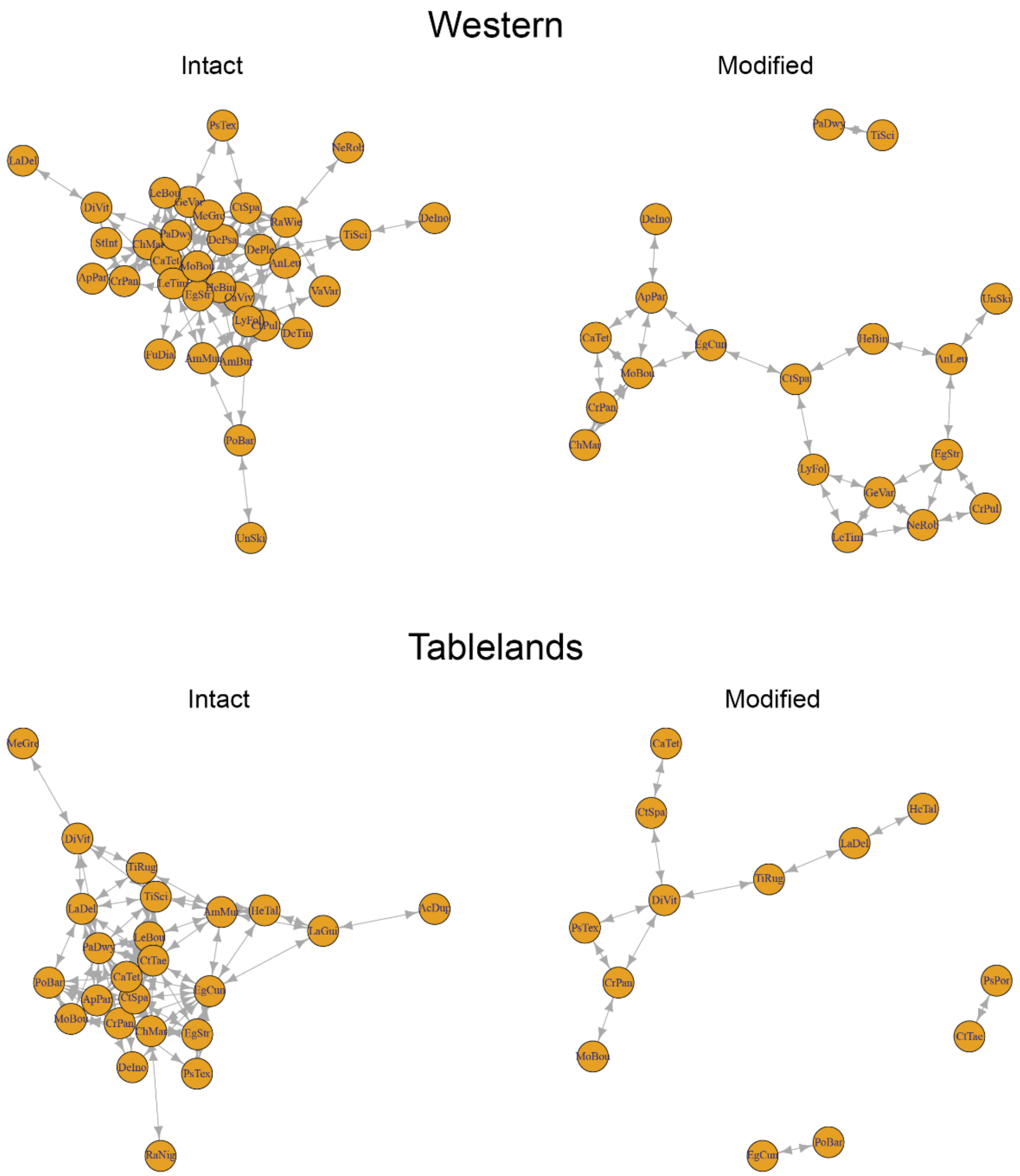


Figure A12. *Modularity of the four reptile co-occurrence networks. Sites in modified landscapes exhibit greater modularity than sites in intact landscapes, with greater edge distance (arrows; co-occurrence strength) between vertices (species; yellow circles).*

Appendix 7: Threshold sensitivity analysis.

We categorised landscapes as either intact or modified based on a threshold value defining the vulnerability of ecosystems to collapse developed by the IUCN Red List of Ecosystems (Bland et al., 2016). We considered sites with ≥70% unmodified within the surrounding 500m buffer as intact because natural ecosystems modified by present and ongoing agricultural processes, such as cultivation and fertilizer enrichment, are vulnerable to collapse when reduced in extent by >30% (Bland et al., 2016; Keith et al., 2013).

To explore the sensitivity of our results to different threshold values, we reran analyses for a range of thresholds; ≥50%, ≥60%, ≥80% and ≥90% of unmodified surrounding landscape. Adjusting the threshold value altered the number of sites classified as intact or modified for both regions (Table A9), but not the overall result for difference in species richness (Table A10). Similarly, overall result for composition remained unaltered, with significant effects for all thresholds in both regions, with the exception of near-significant effects for the 50 and 90% thresholds in the Western region (Table A11).

Furthermore, the overall structure of co-occurrence networks remained consistent. Linear models for the change in occupancy and change in average co-occurrence connectance under each threshold exhibiting similar patterns as the selected 70% threshold, with the exception of the 50 and 90% thresholds in the Western region. Critically, for each threshold examined, the overall loss of co-occurrence was not due to an even loos across all species, and that changes were complex and involved gains and switches in species co-occurrence (Figure A21).

Table A9: *Number of sites per treatment for each threshold value of unmodified surrounding landscape*

Threshold (%)	**Western**		**Tablelands**	
	Intact	**Modified**	**Intact**	**Modified**
≥90	42	35	55	92
≥80	49	28	70	77
≥70	52	25	90	57
≥60	57	20	100	47
≥50	63	14	116	31

Table A10: *Summary of generalised linear mixed effect models for reptile species richness as predicted by proportion of modification (mod) by continuous variable and factor (for each threshold value) for both agro-climatic regions throughout the study area.*

Region	Model	Threshold	Estimate	SE	F	P
Western	Species Richness ~ mod (continuous) + (1|Farm)		0.03	0.05	0.62	0.535
	Species Richness ~ mod (factor) + (1|Farm)	50	-0.10	0.15	-0.66	0.507
		60	0.02	0.13	0.12	0.907
		70	-0.05	0.13	-0.38	0.707
		80	-0.02	0.12	-0.18	0.857
		90	-0.01	0.11	-0.11	0.912
Tablelands	Species Richness ~ mod (continuous) + (1|Farm)		0.03	0.05	0.7	0.485
	Species Richness ~ mod (factor) + (1|Farm)	50	0.04	0.11	0.37	0.709
		60	-0.09	0.10	-0.92	0.359
		70	-0.06	0.09	-0.70	0.484
		80	-0.07	0.09	-0.78	0.438
		90	-0.05	0.09	-0.56	0.577

Table A11: *Summary of reptile community composition (MRPP) results for each threshold, across both agro-climatic regions.*

Region	Threshold	T	A	P
Western	50	0.04	0.07	0.058
	60	-4.02	0.01	0.005
	70	-2.56	0.01	0.019
	80	-1.98	0.01	0.036
	90	-0.03	-0.11	0.053
Tablelands	50	-8.07	0.01	0.003
	60	-10.46	0.02	0.000
	70	-6.26	0.01	0.001
	80	-7.66	0.01	0.004
	90	-7.29	0.01	0.005

Table A12: *Summary of linear models for the change in occupancy and change in average co-occurrence link density (links/species^2) for both agro-climatic regions throughout the study area.*

Model	Threshold	Estimate	SE	T	P
WESTERN:					
Change in connectance ~ change in occupancy	50	0.003	0.004	0.846	0.403
	60	0.011	0.004	2.92	0.006
	70	0.016	0.004	4.31	<0.001
	80	0.010	0.004	2.72	0.010
	90	0.008	0.004	1.91	0.064
TABLELANDS:					
Change in connectance ~ change in occupancy	50	0.008	0.012	0.71	0.484
	60	0.004	0.01	0.40	0.696
	70	0.003	0.01	0.22	0.828
	80	-0.006	0.007	-0.86	0.396
	90	-0.003	0.007	-0.40	0.693

Supporting References

Bland, L. M. et al. 2016. Guidelines for the application of IUCN Red List of Ecosystems Categories and Criteria Guidelines for the application of IUCN Red List of Ecosystems Categories and Criteria. - Gland, Switzerland: IUCN.

Commonwealth of Australia 2013. Environmental Stewardship. - Department of the Environment, Water, Heritage and the Arts. Date Acessed 12/3/2014, <http://www.nrm.gov.au/national/continuing-investment/environmental-stewardship>.

Csárdi, G. and Nepusz, T. 2006. The igraph software package for complex network research. - InterJournal Complex Syst. 1695: 1695.

Garay-Narváez, L. et al. 2014. Food web modularity and biodiversity promote species persistence in polluted environments. - Oikos 123: 583–588.

Kay, G. M. et al. 2016. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. - Anim. Conserv. 19: 515–525.

Keith, D. A. et al. 2013. Scientific Foundations for an IUCN Red List of Ecosystems. - PLoS One 8: e62111.

Lindenmayer, D. et al. 2010. Temperate Woodland Conservation and Management. - CSIRO Publishing.

Newman, M. E. J. 2006. Modularity and community structure in networks. - Proc. Natl. Acad. Sci. 103: 8577.

Tylianakis, J. M. et al. 2010. Conservation of species interaction networks. - Biol. Conserv. 143: 2270–2279.

Valdovinos, F. S. et al. 2009. Structure and dynamics of pollination networks: The role of alien plants. - Oikos 118: 1190–1200.

Veech, J. A. 2013. A probabilistic model for analysing species co-occurrence. - Glob. Ecol. Biogeogr. 22: 252–260.

Wilson, S. and Swan, G. 2013. Complete Guide to Reptiles of Australia. - New Holland Publishers.

PAPER VI. PASTURE HEIGHT AND CROP DIRECTION INFLUENCE REPTILE MOVEMENT IN AN AGRICULTURAL MATRIX.

In addition to understanding *how* landscape context can affect agri-environment schemes success, it is important to know *why* landscape context may affect agri-environment schemes success. One of the key assumptions in agri-environment scheme policy is that investment will promote propagation of biodiversity into the broader landscape evenly, although it is clear that dispersal into surrounding landscapes for some species (e.g. ground dependent species such as reptiles) will be more challenging than others. For agri-environment schemes to better support the conservation of such species in the broader landscape, it is crucial that a greater understanding of how these species disperse in different matrix environments is gained. In this paper, we demonstrate that the type and structure of surrounding landscapes (matrix) do influence the ability of species to navigate, and hence connect, between habitat patches.

A fluorescent trail blazes through the night, marking the path of a dispersing gecko.

Kay, G.M., Driscoll, D.A., Lindenmayer, D.B., Pulsford, S.A., Mortelliti, A., 2016. Pasture height and crop direction influence reptile movement in an agricultural matrix. *Agriculture, Ecosystems & Environment*. 235, 164–171.

Pasture height and crop direction influence reptile movement in an agricultural matrix.

Abstract

Tackling the global threat of habitat fragmentation on biodiversity requires knowledge of how species move within agricultural landscapes. However, the specific mechanisms influencing dispersal within such landscapes remain poorly understood. The objective of our study was to assess how matrix type (improved pasture, native pasture or crop) and structure (grass height) influence fine-scale reptile movement, as well as influences of crop sowing direction and setting-sun position. In an agricultural region of south-eastern Australia, we first released 20 individuals of an arboreal gecko (*Christinus marmoratus*) at set distances from trees to determine the distance at which they could perceive their tree habitat (perceptual range). We then translocated 36 individuals into six matrix environments within their perceptual range of isolated trees to examine how gecko movement was modified by the type and structure of the matrix. We also recorded crop sowing direction and setting-sun position and examined all recorded tracks using angular statistics. We found that geckos exhibited a perceptual range of 40-80m. Short matrix environments promoted direct movements towards trees, irrespective of matrix type. Furthermore, movements were significantly affected by crop sowing direction with individuals following the planted lines. Our study has three significant implications: (i) restoring mature tree spacing to 80m apart will assist gecko movements, (ii) targeted management for low pasture height, such as by maintaining directional narrow strips of low vegetation among taller pastures, might assist movement and facilitate increased

connectivity, (iii) directional sowing of crops between habitat patches presents a simple but potentially effective tool for reconnecting fragmented landscapes.

Introduction

Globally, expanding agricultural practices are creating increasingly fragmented landscapes, with patches of habitat that can support high biodiversity becoming interspersed with a matrix of crops and pastures (Alexandratos and Bruinsma, 2012). The persistence of biodiversity in these fragments depends crucially on an individual's capacity to move through the agricultural matrix (Ricketts, 2001; Zollner and Lima, 2005). The degree to which the matrix genuinely represents a barrier to movement has therefore been the focus of intense research effort in recent years (Anderson et al., 2015; Cooney et al., 2015; Driscoll et al., 2014; Malekian et al., 2015; Rodríguez-San Pedro and Simonetti, 2015; e.g. Smith et al., 2013; Sozio et al., 2013). Landscape-scale occupancy studies, as well as expert opinion, have dominated assessments of species movements (Driscoll et al., 2014). More recently, mark-recapture and molecular studies have also shown that certain matrix environments represent a barrier to movement for many species (Anderson et al., 2015; e.g. Prevedello and Vieira, 2010a). Despite increasing evidence for the impact of the matrix on some elements of biodiversity, previous studies have tended to remain correlative, focused on broad (>1km) movements and have rarely identified the specific mechanisms that influence fine-scale movement (Lechner et al., 2015). Understanding specific mechanisms explaining why movement might be poorer in some matrix environments at fine-scales would allow us to implement effective management strategies to improve biodiversity conservation (Hawkes, 2009).

The type and structure of the matrix represents a key factor influencing the fine-scale movements of terrestrial animals through agricultural landscapes (Driscoll et al., 2013). The composition and height of vegetation can greatly influence the distance at which individuals may perceive neighboring habitat – its perceptual range (Pe’er and Kramer-Schadt, 2008; Prevedello et al., 2010). For example, lower vegetation obstruction associated with certain land-use types (i.e. grazed pastures) support greater perceptual range in some Brazilian marsupials (Prevedello et al., 2011). Despite the important role of the matrix on perceptual range, empirical data quantifying this impact is lacking for most taxa. Additionally, the type and structure of the matrix can directly influence a species’ ability to orientate and move, even when within the perceived range of habitat. For example, the fine-scale movements of some small mammals are strongly guided by the linear structure of cereal crops despite proximity to habitat (Prevedello and Vieira, 2010b; Sozio et al., 2013) but this important effect has not been examined for any other terrestrial fauna in cropping landscapes. Comprehensive examinations of the effects of matrix type and structure on the fine-scale movements of small, ground-dwelling organisms would be useful but are rare (but see Haynes and Cronin, 2006; Sozio et al., 2013). Additionally, how the fine-scale movements of non-mammalian organisms are affected by a broad suite of different agricultural environments has yet to be explored.

Understanding fine-scale movements within different matrix environments could be particularly useful for enhancing connectivity for reptiles (Southwood and Avens, 2010) and amphibians (Pittman et al., 2014b), both of which are undergoing major declines in agricultural landscapes globally (Böhm et al., 2013; Gibbon et al., 2000). These groups are consistently under-studied in connectivity science (Driscoll et al., 2013), yet are likely to show strong movement patterns between different matrix environments due to their direct associations with management-specific groundcover habitats (Moore et al., 2008; Schutz and Driscoll, 2008). For example, cultivated pasture and crop matrices generally support fewer micro-habitat features critical for many reptiles (Kay et al., 2016) and may illicit more "directed" movements than required in native pastures where these micro-habitat features are more common. Our understanding of reptile navigation has mostly focused on long-range movements of marine turtles (Rivas et al., 2015; Southwood and Avens, 2010) and a crocodilians (Read et al., 2007), while our knowledge of the specific cues terrestrial reptiles use for guiding fine-scale movements is comparatively limited. For example, extensive review of the literature reveals evidence only for the role of sun position in orienting movements in some terrestrial turtles (DeRosa and Taylor, 1978) and lizards (Beltrami et al., 2010; Freake, 2001), as well as homing ("map and compass") senses in some pythons (Pittman et al., 2014a) and geckos (Marek et al., 2010). A further examination of the influence of matrix and non-matrix cues on the perceptual range and movement of small terrestrial reptiles within agricultural landscapes is needed.

Here, we provide a novel examination of the influence of a range of matrix environments on the fine-scale movements of small terrestrial reptiles to better understand mechanisms guiding habitat perception and orientation within the matrix. First, we examined the impact of a range of matrix types (native pasture, improved pasture, and cropped landscapes) and structures (tall or short) on habitat detection and orientation. Visual cues are thought to be most important for guiding fine-scale movements for small terrestrial reptiles (e.g. Freake, 2001; Gruber and Henle, 2004), and so we expect the structure (specifically short pastures) would have strongest influence on habitat perception and movement. Second, we examined the influence of crop sowing direction on fine-scale movements. Based on strong effects observed for small mammals (Prevedello and Vieira, 2010b; Sozio et al., 2013), we hypothesized crop sowing direction would also strongly influence reptile orientation.

We selected a nocturnal arboreal gecko (*Christinus marmoratus*) as a model species to test the influence of the matrix because it is arboreal with limited dispersal capability. Translocation experiments are an ideal approach to test orientation ability (Betts et al., 2015; Wiltschko and Wiltschko, 1999), and so we used field experiments to address the following two questions:

i) How does the type (improved pasture, native pasture or crop) and structure (pasture height) of different agricultural matrix environments influence the fine-scale habitat detection and movement of reptiles?
ii) How does crop sowing direction influence fine-scale movement of reptiles?

Methods

Study area and design

Our study was conducted in the highly fragmented mixed cropping/grazing agricultural landscape near Boorowa (-34.437°S, 148.717°E), south-eastern Australia (Fig. 1a). The predominant form of agriculture in this area is pasture dominated by native groundcovers with no or infrequent fertilization (native pasture), pasture dominated by exotic groundcovers and a regular history of fertilization (exotic pastures), and cereal cropping of either wheat (*Triticum vulgare*) or canola (*Brassica napus*) (see Appendix A for details).

We undertook movement experiments during October-November 2014 within fields comprising six different matrix environments: short native pasture, short exotic pasture, long native pasture, and long exotic pastures plus two cereal crops: wheat and canola (Fig. A.1). We replicated these treatments three times in separate fields (spaced >2 km to ensure spatial independence) giving a total of 18 sites. We measured pasture height at each site using a rising-plate pasture meter (Correll et al., 2003) and defined short pastures where the site mean height was <10 cm and long pastures where the mean height was >20 cm (Appendix A). Both crops (canola and wheat) were cultivated along rows spaced approximately 20 cm apart, with plants closer within lines creating semi-permeable guides without acting as a barrier for movement. We examined two crops with contrasting growth-form to provide a wider test of the general influence of crops on species movement that was not possible in previous studies that examine only a single crop type (Prevedello and Vieira, 2010b; Sozio et al., 2013). At ground-level, both crops formed visible lines of planted stems although wheat crops were more closely planted (1-2 cm apart) than canola crops (5-10 cm apart) and allowed greater ground-level visibility than within the leafy multi-stem branching canola crops. For both native and exotic pastures, the distribution of plants did not follow any regular pattern.

Movement experimental protocol

Our experiment involved releasing individuals of a nocturnal arboreal gecko (*Christinus marmoratus*) into fields comprising an isolated tree surrounded by different matrix environments and recording the direction of movement (or orientation). Trees are key habitat structures for this species (Michael et al., 2015; Taylor et al., 2015; Wilson and Swan, 2013) and we therefore expected animals would move quickly towards them if released within their perceptual range. We therefore considered all groundcovers as

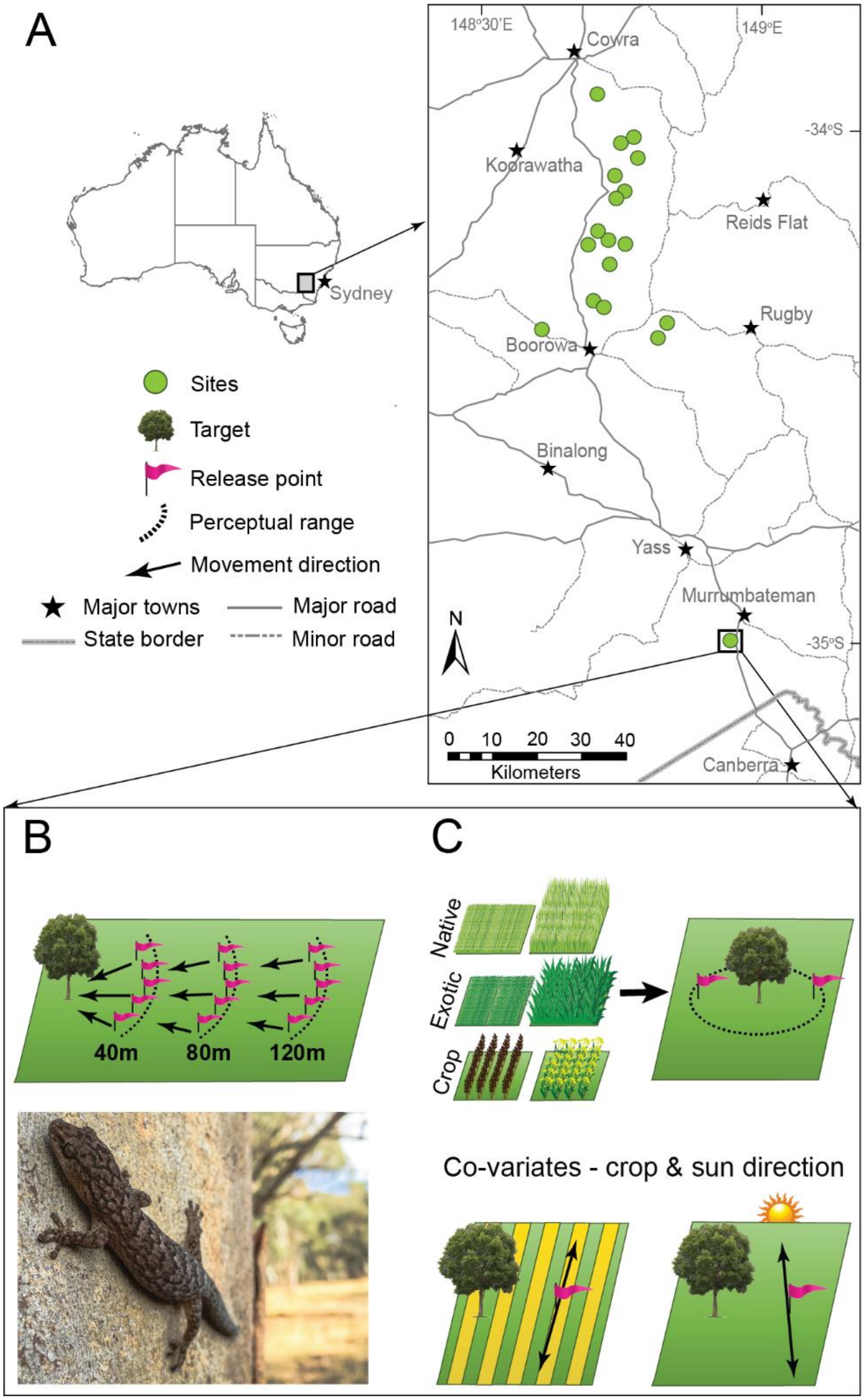


__Figure 1.__ Study area and experimental design of the movement study. (A) Location of sites. (B) Design used to identify the perceptual range for C. marmoratus (pictured). (C) Design used to identify influence of type and structure of the 6 matrix treatments (short native, long native, short exotic, long exotic, wheat crop, canola crop) on movement when released within their perceptual range (Question 1) and to test co-variate cues (crop-sowing and sun direction) influencing C. marmoratus movement (Question 2).

"matrix" given the non-core use of this environment by the target species (following the definition of Driscoll et al., 2013).

A critical first step was to identify the perceptual range of *C. marmoratus* to determine the distance for release in subsequent experiments. Perceptual range of a species cannot be considered absolute, and will vary depending on the matrix context (Pe'er and Kramer-Schadt, 2008). We interpreted perceptual range relative to short pastures to find the maximum possible distance our target species may realistically detect habitat within our study environment (i.e. pastures where no visual obstruction is present given the environmental conditions). To quantify this, we released animals into short (<10 cm high) pastures (representing a mix of both native and exotic pastures) with no visual obstruction at set distances (40 m, 80 m and 120 m) from isolated "target" trees (Fig. 1b). Each target tree was isolated from the nearest tree by a distance of >250 m, and occurred on flat landscapes presenting similar horizons for all released animals. Five animals were released at each distance interval simultaneously, separated by 10 m to minimize conspecific interference. We repeated this at two trees. The release position for all distance categories was kept constant (due west of the target tree) to minimize the influence of confounding cues (e.g. the visual silhouette of the target tree) and animals were carried to the release point in a dark bag that was gently spun to ensure disorientation prior to release. Animals were released by hand, with the observer moving quickly away in a consistent direction (south) for all releases, in order to reduce their influence on subsequent movements of lizards.

To examine the impact of matrix type (native pasture, improved pasture, and cropped landscapes) and structures (tall or short grass) on habitat detection and orientation

(Question 1), we selected three target trees for each of the six treatments, resulting in a total of 18 sites. At each site, we released two animals at a distance of 40 m (the perceptual range in short pastures), one due east and one due west of the target tree (Fig. 1c), once again keeping release positions consistent and disorientating individuals to minimize confounding influences. To explore the influence of crop plantings on orientation (Question 2), at each point we recorded the bearing of sowing direction. Because sun position can influence orientation in some reptiles (Beltrami et al., 2010; DeRosa and Taylor, 1978), we also measured the direction of sun-down so that we could control for this effect (Fig. 1c).

Animals were hand caught in remnant fragments within the same landscape but more than 5 km distant from the release landscape to remove any influence of learnt behavior on movements. Individuals were fed and housed for a maximum of 72 hours before being released to ensure optimal physiological condition and minimal stress (sensu Betts et al., 2015). Each animal was released only once. Prior to release, animals were marked with fluorescent powders of different colors. Animals were released at dusk, on evenings with no wind, clear skies and at the new moon-phase to maximize perceptual ability of animals and reduce confounding non-target factors able to influence navigation (Dacke et al., 2003; Rivas et al., 2015). We tracked animals six hours after release, recording the movements of each individual using a hand-held GPS from the release point until no additional powder was detected or until reaching the target tree. We defined this as an individuals' "track" (i.e. the path between an individuals' release point and the tree or final point of powder detection).

Data analysis

We use circular statistics (Batschelet, 1981) to quantify the orientation of individuals by subdividing entire tracks (i.e. entire path from release to final detection) into vectors recording the distance and direction of each composite movement (Appendix B). We corrected each track and subsequent vectors to have the same position relative to the tree (e.g. tracks in the west were reflected to the east). We then calculated weighted mean vectors of each track (at least 1 m long), with segment lengths as weights (following Sozio et al., 2013) to provide a series of directional and weighted vectors per track. We calculated the perceptual range as the maximum distance at which released animals demonstrated they had perceived the target tree by heading directly towards it (V-test for the significance of mean angles around a specified direction; Batschelet, 1981).

To test for the influence of type and structure of matrix on fine-scale movement (Question 1), we tested whether the target weighted mean vectors orientated towards the target tree in each of the six treatments. To test for the influence of crop plantation lines on movement (Question 2), we recorrected tracks relative to target directions of the crop sowing direction (V-test with mean angles as axial data; Sozio et al., 2013). We used the same approach to test for the influence of sun-setting direction. All analyses were performed using Oriana 4 software (Kovach, 1994).

Results

We captured and released 56 individuals: 20 to determine the perceptual range and 36 for the main movement experiment (six per treatment; Table 1). The mean track length was 32.7 m with minimum and maximum track lengths of 16.7 and 86.3 m.

Table 5. *Results of the V-tests performed on weighted mean vectors of individual movement, with the expected mean toward the focal tree, along the crop plantation row (crop; axial data) and in line with setting sun-position (sun-position; axial data). N= sample size (number of individuals); u = V-test statistic. Statistical significance (p<0.05) is in bold.*

Matrix type	Distance (m)	N	To tree		With crop		Sun-position	
			u	P	u	P	u	P
DISTANCE								
Short Pasture	40	5	3.135	**<0.001**	-	-	-	-
Short Pasture	80	10	-0.543	0.703	-	-	-	-
Short Pasture	120	5	1.000	0.165	-	-	-	-
MATRIX QUALITY								
Canola crop	40	6	-0.714	0.756	2.278	**0.01**	-0.223	0.586
Wheat crop	40	6	0.815	0.212	3.128	**<0.001**	0.084	0.467
Short native	40	6	3.432	**<0.001**	-	-	0.022	0.491
Long native	40	6	-0.916	0.814	-	-	-0.272	0.604
Short exotic	40	6	3.300	**<0.001**	-	-	-0.16	0.562
Long exotic	40	6	-1.883	0.971	-	-	-0.646	0.735

Matrix type and structure

The perceptual range trials revealed that all individuals released at 40 m moved towards the target tree (u=3.135, p<0.001; Table 1). There was no overall significant movement towards the tree at distances of either 80 m (u=-0.543, p=0.703) or 120 m (u=1.00, p=0.165). This suggests the perceptual range of *C. marmoratus* within short pastures is at least 40 m but less than 80 m.

For the main movement experiments, orientation within different matrix environments revealed that *C. marmoratus* oriented directly towards the target tree in matrix environments with short native pasture (u=3.43, p<0.001) and short exotic pasture (u=3.30, p<0.001), but not for long native pasture (u=-0.916, p=0.814), long exotic pasture (u=-

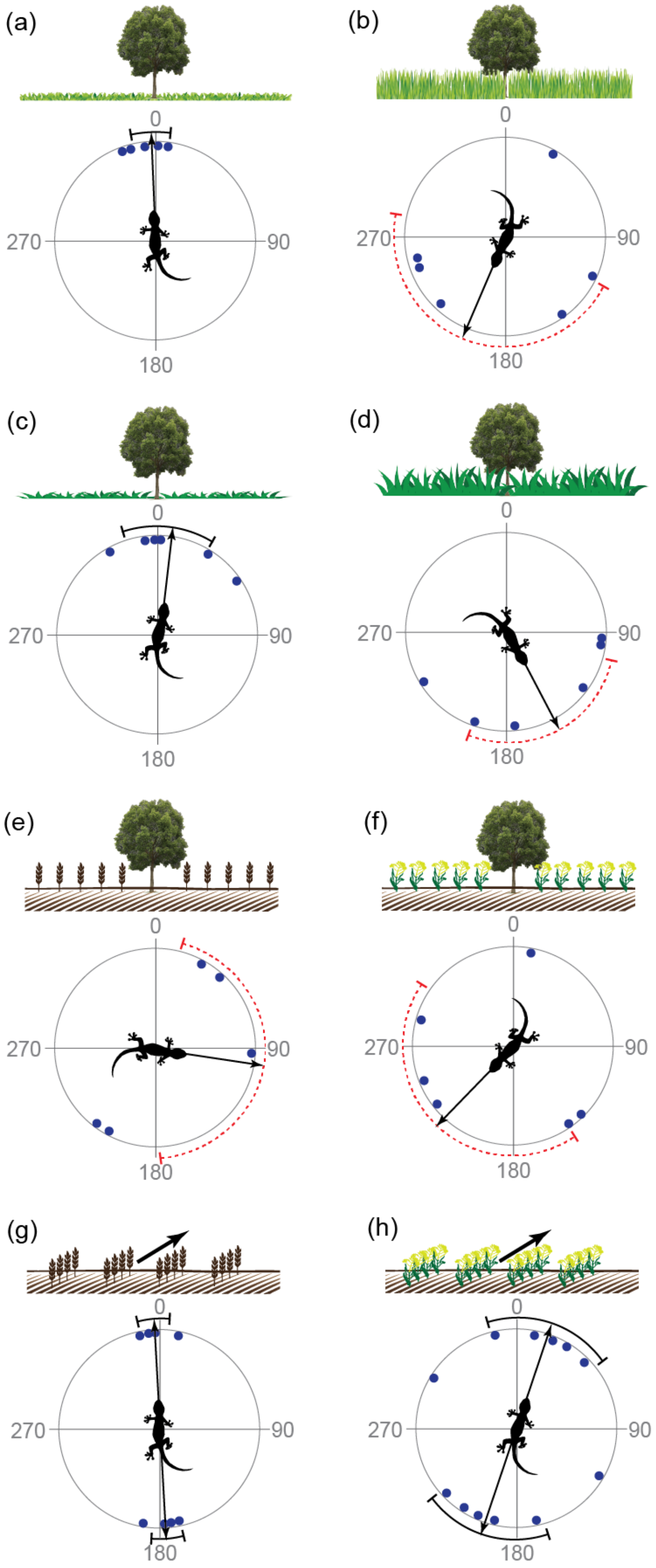


Figure 2. *Movement directions for C. marmoratus released into matrix treatments within perceived range of the target tree. Angular orientations by matrix type and structure (a-f) and axial (bi-directional) orientations relative to covariate crop sowing direction (g-h), where: (a) short native, (b) long native, (c) short exotic, (d) long exotic pastures, (e, g) wheat and (f, h) canola crops. Blue points around the circle represents the mean direction of an individual path relative to the release point (center cross-hairs); the zero represents the tree direction, the line represents the mean vector of each group of individuals and the circular arc represents the 95% confidence interval limits of significant (black solid) or insignificant (red dotted) orientations. Christinus marmoratus oriented towards the tree in short pasture of either type as well as along crop plantation rows, but did not in long pasture or any crop type.*

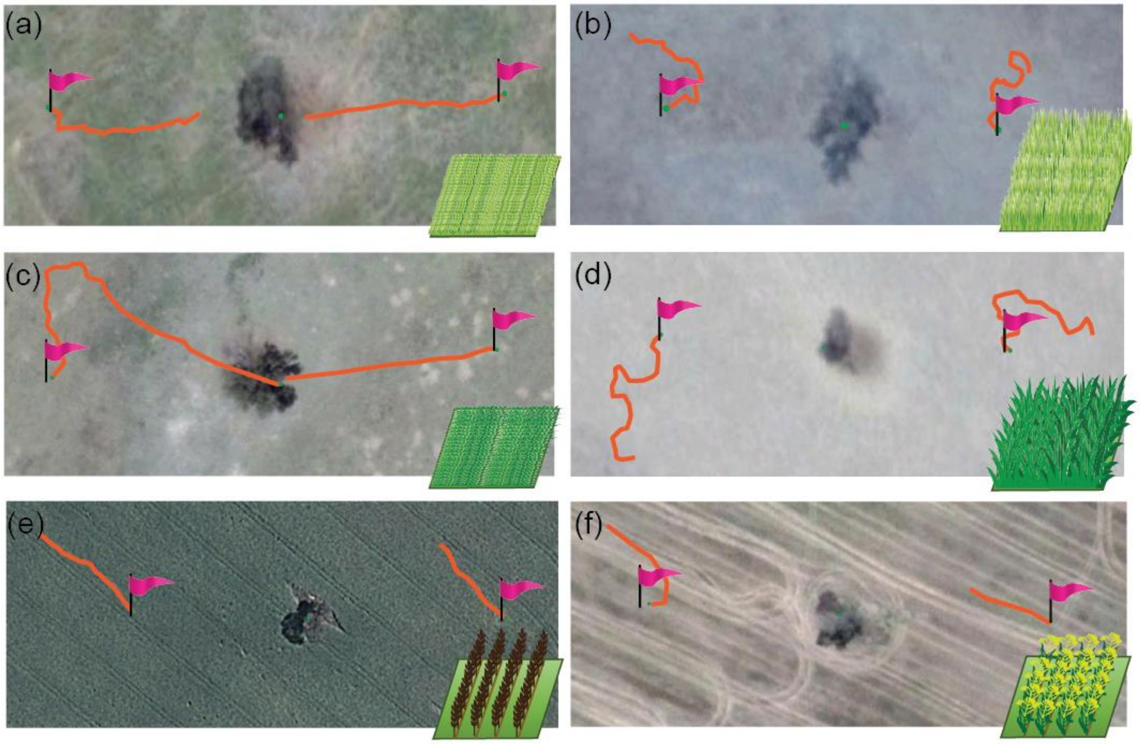


Figure 3. *A representative example of the tracks observed within different matrix environments. (a) Short native pasture, (b) long native pasture, (c) short exotic pasture, (d) long exotic pasture, (e) wheat, and (f) canola crop.*

1.883, p=0.971), or either wheat (u=0.815, p=0.212) or canola (u=-0.714, p=0.756) crops (Table 1, Fig. 2, Fig. 3).

Influence of crop sowing direction

Movement of *C. marmoratus* within crops was significantly oriented along the direction of the planted crop lines (Table 1, Fig. 2). This effect was present in both crop types but was stronger for wheat (u=3.128, p<0.001) compared to canola (u=2.278, p=0.01). The position of the setting sun did not influence *C. marmoratus* movement in any matrix environment (Table 1, Fig. 2).

Discussion

Our study aims to help fill a research gap examining the movement of reptiles within a range of different matrix environments, providing new insights into the role of matrix environments for fine-scale species movement and habitat connectivity. We found that *C. marmoratus* have a perceptual range of at least 40 m and less than 80 m within short pastures. Examining different matrix environments, we found that, when released within their perceptual range in short pastures (i.e. <40 m), the height of pasture rather than the type of matrix (native pasture, exotic pasture or crop) was the most important factor driving habitat detection. We also found that individuals strongly followed planted crop lines during their movement, irrespective of the direction of habitat, supporting previous studies of small-mammals to provide compelling evidence for the impact of crops on the movement of ground-dwelling fauna.

Ecological response to the matrix

Our result for a 40-80m perceptual range for *C. marmoratus* is consistent with the previous few examinations of perceptual range for arboreal geckos (Gruber and Henle, 2004). Although perceptual range may depend upon matrix context (Pe'er and Kramer-Schadt, 2008), our results indicate that effective movement within the matrix for this arboreal gecko may be achieved when mature trees are spaced at an equivalent (or reduced) distance. However, less than 3% of the original remnant vegetation persists across the landscapes examined here (Lindenmayer et al., 2012c; Sato et al., 2016) and our results suggest fine-scale orientation and dispersal capability could be eroded by historic and ongoing tree clearing. The loss of large old scattered trees is a pervasive issue across agricultural landscapes globally (Lindenmayer et al., 2012b and references therein). Our result highlights significant challenges to sustaining important connectivity processes relevant beyond the landscapes and taxa examined here. Restoring agricultural landscapes in ways that enhance perceptual range could address this issue in line with the recent call for incorporating fine-scale dispersal behavior into conservation planning (Lechner et al., 2015). Such restoration approaches could include establishment of "stepping stone" visual structures that could assist orientation (sensu Saura et al., 2014) and may enhance connectivity over relatively immediate (~1-10 years) timeframes compared to timeframes required to restore the target habitat (Sato et al., 2016). For example, natural (i.e. young planted trees) or even artificial (i.e. erected) structures (Goldingay et al., 2011) could be used but require testing.

Our study revealed clear patterns of reptile orientation in shorter rather than longer pastures, irrespective of whether this was native or exotic pasture. This supports vision as a primary tool for orientating between habitats for this species as found for another arboreal gecko species in this system (*Gehyra variagata*; Gruber and Henle, 2004). An ability to orientate and move decisively in short pastures has clear benefits when considering the multiple threats to ectothermic reptiles in exposed landscapes. For example, low vegetation could cause a loss of thermal buffering and a reduction in operative function in ectotherms, or subject individuals to a higher predation risk (e.g. Sato et al., 2014) causing a need to exit the matrix quickly. Moreover, short pastures provide limited apparent ecological benefit to arboreal geckos, but have been found to have negative impact on reptile occupancy (Howland et al., 2014) and landscape/ecosystem function generally (Gaitàn et al., 2014). Nevertheless, this 'substandard' matrix environment evidently assists orientation and so reconciling its utility for enhancing connectivity, as well as developing a better understanding of species’ motivations for movement, is critical. Importantly, while short pastures appear useful for individuals orientating within the matrix, we have not considered the edge permeability (or willingness of individuals/species to enter) of such environments (Youngquist and Boone, 2014). Doing so, for a range of taxa, will help determine the value of short pastures for enhancing connectivity, and for understanding the degree to which it also represents a dispersal barrier.

Although individuals were unable to move towards habitat in cropped environments, we found that movements were strongly aligned with crop plantation rows. This was true for two structurally different types of crop (wheat vs canola), suggesting the effects may be more general than previously known based on studies focusing on single crop types. Previous studies show orientation is driven by the visual effects of stem-lines (Prevedello and Vieira, 2010b). Our results support these findings (Table 1, Fig. 2g-h), revealing stronger influence within wheat crops which are visually clearer at ground-level compared to the “bushy” less clear rows within canola. Importantly, our finding for a small reptile concords with previous studies of some small mammals (Prevedello and Vieira, 2010b; Sozio et al., 2013) and has implications for theoretical movement ecology in matrix environments. That is, the influence of crops for guiding small mammal movements proposed by Prevedello and Vieira (2010b) and Sozio et al. (2013) appear applicable to a broader range of taxa, including small reptiles. Our results therefore contribute to a wider understanding of the impact of cropping on the movement of ground-dwelling fauna, which represent key groups associated with high conservation risk (e.g. small mammals, amphibians) in agricultural landscapes. A thorough investigation of this issue for additional species is required to further test the generality of this for ground-dwelling fauna in other agricultural landscapes globally.

Despite the clear findings of our study, a number of key questions remain. First, how does the perceived range of habitat change with (i) different matrix contexts, (ii) the characteristics of target habitat (i.e. age, size, type of tree in this study), (iii) the background (horizon) context, and (iv) the taxa examined? Second, how are our observations influenced by temporal dynamics of the matrix, such as the seasonality of pasture and crop growth (Bertrand et al., 2015), and how do these interact with temporal patterns (if present) in dispersal events? Third, we selected an arboreal species that uses trees which are generally visible landmarks at ground-level. However, it is less clear how species associated with "less-visual" habitats orientate. For example, outcrops and hilltops are critical habitat for many saxicolous (rock-dwelling) reptiles (Michael et al., 2008), yet the cues (if any) that individuals use to orientate towards such habitats remain unknown but are of key conservation significance.

Conservation implications

Understanding how species move through the agricultural matrix at fine-scales can help identify mechanisms influencing dispersal efficacy and inform decisions about the conservation of biodiversity in fragmented landscapes (Barton et al., 2015; Lechner et al., 2015). Our study highlights how different matrix environments influence the fine-scale movements of small terrestrial reptiles, a group of global conservation concern, to enhance connectivity and survival within fragmented agricultural landscapes. Considering the extent of agricultural modification of habitats globally (Alexandratos and Bruinsma, 2012) as well as the challenges facing conservation managers in these landscapes, our findings have three clear management implications relevant for the conservation of poor-dispersing fauna that extend beyond our system.

First, our results for perceptual range suggest that tree spacing should be close (i.e. <80 m) to facilitate direct movement. Our study provides novel evidence for the role of large mature trees in orienting reptiles, and although we acknowledge that our study focusses on a single species, our findings join a host of others advocating the ecological value of scattered trees (Allnutt et al., 2008; Gibbons, 2010; Lindenmayer et al., 2012b; Manning et al., 2006; Moga et al., 2016). Ongoing tree loss is a major issue in this landscape (Evans, 2016) and our study highlights risks associated with maintaining low tree densities within agricultural landscapes for maintaining important ecological function.

Second, targeted management of pasture height can influence species movements with potential to help facilitate increased connectivity yet is rarely considered in management plans tasked with reconnecting fragmented landscapes (Prevedello and Vieira, 2010a). Maintaining tall pastures is a targeted priority in many conservation programs because it benefits occupancy for poor-dispersing fauna at-risk of agricultural fragmentation (e.g. Howland et al., 2014), reduces threatening processes like predation (Sato et al., 2014; e.g. Schneider et al., 2012), and prevents loss of ecosystem function (Gaitàn et al., 2014). Our results suggest that species move directly towards habitat in low pastures, even in highly modified (non-native) landscapes. One opportunity for enhancing movement could be to maintain narrow strips of low vegetation among taller pastures to facilitate directional movement but that minimize predation and increase perceptual range. This could be achieved by strip grazing or mowing pastures directionally between habitat patches, but first needs to be experimentally tested.

Third, our study provides evidence for the influence of cropping on the fine-scale movements of small reptiles, suggesting that targeted management of cropping could enhance connectivity for at least some reptiles in fragmented landscapes. Specifically, directional sowing between habitats represents an important opportunity to link isolated habitat remnants to facilitate greater directional movements for species who otherwise remain exposed to hostile effects of the matrix. Our work corroborates recent studies that demonstrate similar effects for small mammals (Prevedello and Vieira, 2010b; Sozio et al., 2013), suggesting that directional cropping management can enhance connectivity for multiple taxa within two vertebrate groups of key conservation concern (Böhm et al., 2013; Ceballos et al., 2005). Furthermore, by revealing consistent response across two globally wide-spread crop types (wheat and canola), we provide important evidence for the generality of this response that is of increasing need as human demand for food continues to increase (Alexandratos and Bruinsma, 2012). Strategies that encourage directional cropping to link habitats therefore provide a promising approach for conserving some significant ground-dwelling fauna in cropping landscapes globally.

Acknowledgements

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References

Alexandratos, N., Bruinsma, J., 2012. World agriculture towards 2030/2050: the 2012 revision. Food and Agriculture Organization of the United Nations, Rome.

Allnutt, T.F., Ferrier, S., Manion, G., Powell, G.V.N., Ricketts, T.H., Fisher, B.L., Harper, G.J., Irwin, M.E., Kremen, C., Labat, J.-N.N., Lees, D.C., Pearce, T. a., Rakotondrainibe, F., 2008. A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. Conserv. Lett. 1, 173–181. doi:10.1111/j.1755-263X.2008.00027.x

Anderson, S.J., Kierepka, E.M., Swihart, R.K., Latch, E.K., 2015. Assessing the Permeability of Landscape Features to Animal Movement : Using Genetic Structure to Infer Functional Connectivity. PLoS One 1–20. doi:10.5061/dryad.p5hd0

Barton, P.S., Lentini, P.E., Alacs, E., Bau, S., Buckley, Y.M., Burns, E.L., Driscoll, D.A., Guja, L.K., Kujala, H., Lahoz-Monfort, J.J., Mortelliti, A., Nathan, R., Rowe, R., Smith, A.L., 2015. Guidelines for Using Movement Science to Inform Biodiversity Policy. Environ. Manage. 56, 791–801. doi:10.1007/s00267-015-0570-5

Batschelet, E., 1981. Circular Statistics in Biology. Technometrics 24, 371. doi:10.2307/1267831

Beltrami, G., Bertolucci, C., Parretta, a, Petrucci, F., Foà, a, 2010. A sky polarization compass in lizards: the central role of the parietal eye. J. Exp. Biol. 213, 2048–2054. doi:10.1242/jeb.040246

Bertrand, C., Burel, F., Baudry, J., 2015. Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. Landsc. Ecol. 451–466. doi:10.1007/s10980-015-0259-4

Betts, M.G., Gutzwiller, K.J., Smith, M.J., Robinson, W.D., Hadley, A.S., 2015. Improving inferences about functional connectivity from animal translocation experiments. Landsc. Ecol. 30, 585–593. doi:10.1007/s10980-015-0156-x

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., Rhodin, A.G.J., Stuart, S.N., van Dijk, P.P., Young, B.E., Afuang, L.E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L.R. V, Allison, A., Ananjeva, N., Anderson, S., Andrén, C., Ariano-Sánchez, D., Arredondo, J.C., Auliya, M., Austin, C.C., Avci, A., Baker, P.J., Barreto-Lima, A.F., Barrio-Amorós, C.L., Basu, D., Bates, M.F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M.D.R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J.R., Chapple, D.G., Cheylan, M., Cisneros-Heredia, D.F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G.C., Couper, P.J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P.A., Crother, B., Cruz, F., Daltry, J.C., Daniels, R.J.R., Das, I., de Silva, A., Diesmos, A.C., Dirksen, L., Doan, T.M., Dodd, C.K., Doody, J.S., Dorcas, M.E., Duarte de Barros Filho, J., Egan, V.T., El Mouden, E.H., Embert, D., Espinoza, R.E., Fallabrino, A., Feng, X., Feng, Z.J., Fitzgerald, L., Flores-Villela, O., França, F.G.R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S.R., Garcia, M. a., García-Pérez, J.E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J.C.T., Gower, D.J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A.M., Hare, K., Hedges, S.B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F.M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J.S., Köhler, G., Kuchling, G., Kumlutaş, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A.S., López-Luna, M. a., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W.E., Mahler, D.L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O. a V, Márquez, R., Martins, M., Masterson, G., Mateo, J. a., Mathew, R., Mathews, N., Mayer, G., McCranie, J.R., Measey, G.J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D. a., Montgomery, C., Morato, S. a a, Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T.Q., Nilson, G., Nogueira, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, J., Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O.S.G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E.R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G.E., Radder, R., Ramer, J., Rasmussen, A.R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E.L., Riservato, E., Rivas, G., da Rocha, P.L.B., Rödel, M.O., Rodríguez Schettino, L., Roosenburg, W.M., Ross, J.P., Sadek, R., Sanders, K., Santos-Barrera, G., Schleich, H.H., Schmidt, B.R., Schmitz, A., Sharifi, M., Shea, G., Shi, H.T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H.J., Tognelli, M.F., Tolley, K., Tolson, P.J., Tuniyev, B., Tuniyev, S., Üzüm, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Veselý, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R.C., Wearn, O.R., Werner, Y.L., Whiting, M.J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K., Zug, G., 2013. The conservation status of the world’s reptiles. Biol. Conserv. 157, 372–385. doi:10.1016/j.biocon.2012.07.015

Ceballos, G., Ehrlich, P.R., Soberón, J., Salazar, I., Fay, J.P., 2005. Global Mammal Conservation: What Must We Manage? Science (80-.). 309, 603–607. doi:10.1126/science.1114015

Cooney, S.A., Schauber, E.M., Hellgren, E.C., 2015. Comparing permeability of matrix cover types for the marsh rice rat (Oryzomys palustris). Landsc. Ecol. 30, 1307–1320. doi:10.1007/s10980-015-0185-5

Correll, O., Isselstein, J., Pavlu, V., 2003. Studying spatial and temporal dynamics of sward structure at low stocking densities: The use of an extended rising-plate-meter method. Grass Forage Sci. 58, 450–454. doi:10.1111/j.1365-2494.2003.00387.x

Dacke, M., Nilsson, D.-E., Scholtz, C.H., Byrne, M., Warrant, E.J., 2003. Insect orientation to polarized moonlight. Nature 424, 33. doi:10.1038/424033a

DeRosa, C.T., Taylor, D.H., 1978. Sun-compass orientation in the painted turtle, Chrysemys picta (Reptilia, Testudines, Testudinidae). J. Herpetol. 12, 25–28. doi:10.2307/1563498

Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., Smith, A.L., 2013. Conceptual domain of the matrix in fragmented landscapes. Trends Ecol. Evol. 28, 605–613. doi:10.1016/j.tree.2013.06.010

Driscoll, D. a., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., Lindenmayer, D.B., Smith, A.L., Berry, L.E., Burns, E.L., Edworthy, A., Evans, M.J., Gibson, R., Heinsohn, R., Howland, B., Kay, G., Munro, N., Scheele, B.C., Stirnemann, I., Stojanovic, D., Sweaney, N., Villaseñor, N.R., Westgate, M.J., 2014. The Trajectory of Dispersal Research in Conservation Biology. Systematic Review. PLoS One 9, e95053. doi:10.1371/journal.pone.0095053

Evans, M.C., 2016. Deforestation in Australia: drivers, trends and policy responses. Rev. Lit. Arts Am. 3, 2–40. doi:10.1071/PC15052

Freake, M.J., 2001. Homing behaviour in the sleepy lizard (Tiliqua rugosa): the role of visual cues and the parietal eye. Behav. Ecol. Sociobiol. 1–7. doi:10.1007/s002650100387

Gaitàn, J.J., Oliva, G.E., Bran, D.E., Maestre, F.T., Aguiar, M.R., Jobb??gy, E.G., Buono, G.G., Ferrante, D., Nakamatsu, V.B., Ciari, G., Salomone, J.M., Massara, V., 2014. Vegetation structure is as important as climate for explaining ecosystem function across patagonian rangelands. J. Ecol. 102, 1419–1428. doi:10.1111/1365-2745.12273

Gibbon, J., Scott, D., Ryan, T., Buhlmann, K., Tuberville, T., Metts, B., Greene, J., Mills, T., Leiden, Y., Poppy, S., Winne, C., 2000. The Global Decline of Reptiles, Déjà Vu Amphibians. Bioscience 50, 653–666.

Gibbons, P., 2010. Prioritising conservation in temperate woodlands, in: Lindenmayer, D.B., Bennett, A.F., Hobbs, R.J. (Eds.), Temperate Woodland Conservation and Management. CSIRO Publishing, pp. 15–21.

Goldingay, R.L., Taylor, B.D., Ball, T., 2011. Wooden poles can provide habitat connectivity for a gliding mammal. Aust. Mammal. 33, 36–43. doi:10.1071/AM10023

Gruber, B., Henle, K., 2004. Linking habitat structure and orientation in an arboreal species *Gehyra variegata* (Gekkonidae). Oikos 107, 406–414.

Hawkes, C., 2009. Linking movement behaviour, dispersal and population processes: Is individual variation a key? J. Anim. Ecol. doi:10.1111/j.1365-2656.2009.01534.x

Haynes, K.J., Cronin, J.T., 2006. Interpatch movement and edge effects: The role of behavioral responses to the landscape matrix. Oikos 113, 43–54. doi:10.1111/j.0030-1299.2006.13977.x

Howland, B., Stojanovic, D., Gordon, I., Manning, A., Fletcher, D., Lindenmayer, D., 2014. Eaten Out of House and Home: Impacts of Grazing on Ground-Dwelling Reptiles in Australian Grasslands and Grassy Woodlands. PLoS One 9, (e105966) DOI:10.1371/journal.pone.0105966. doi:10.1371/journal.pone.0105966

Kay, G.M., Barton, P.S., Driscoll, D.A., Cunningham, S.A., Blanchard, W., Mcintyre, S., Lindenmayer, D.B., 2016. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. Anim. Conserv. 19, 515–525. doi:10.1111/acv.12267

Kovach, W.L., 1994. Oriana. Oriana Wind. Version 1.01.

Lechner, A.M., Doerr, V., Harris, R.M.B., Doerr, E., Lefroy, E.C., 2015. A framework for incorporating fine-scale dispersal behaviour into biodiversity conservation planning. Landsc. Urban Plan. 141, 11–23. doi:10.1016/j.landurbplan.2015.04.008

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012a. Global decline in large old trees. Science (80-.). 338, 1305–1306. doi:10.1126/science.1231070

Lindenmayer, D.B., Zammit, C., Attwood, S.J., Burns, E., Shepherd, C.L., Kay, G., Wood, J., 2012b. A Novel and Cost-Effective Monitoring Approach for Outcomes in an Australian Biodiversity Conservation Incentive Program. PLoS One 7, (e50872). DOI: 10.1371/journal.pone.0050872. doi:10.1371/journal.pone.0050872

Malekian, M., Cooper, S.J.B., Saint, K.M., Lancaster, M.L., Taylor, A.C., Carthew, S.M., 2015. Effects of landscape matrix on population connectivity of an arboreal mammal, Petaurus breviceps. Ecol. Evol. 5, 3939–3953. doi:10.1002/ece3.1675

Manning, A., Fischer, J., Lindenmayer, D., 2006. Scattered trees are keystone structures–implications for conservation. Biol. Conserv. 132, 311–321. doi:10.1016/j.biocon.2006.04.023

Marek, C., Bissantz, N., Curio, E., Siegert, A., Tacud, B., Ziggel, D., 2010. Spatial orientation of the Philippine bent-toed gecko (Cyrtodactylus philippinicus) in relation to its home range. Salamandra 46, 93–97.

Michael, D.R., Cunningham, R.B., Lindenmayer, D.B., 2008. A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. J. Appl. Ecol. 45, 1742–1752. doi:10.1111/j.1365-2664.2007.0

Michael, D.R., Kay, G.M., Crane, M., Florance, D., MacGregor, C., Okada, S., McBurney, L., Blair, D., Lindenmayer, D.B., 2015. Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems. Austral Ecol. 40, 651–660. doi:10.1111/aec.12232

Moga, C.I., Samoilă, C., Öllerer, K., Băncilă, R.I., Réti, K.O., Craioveanu, C., Poszet, S., Rákosy, L., Hartel, T., 2016. Environmental determinants of the old oaks in wood-pastures from a changing traditional social-ecological system of Romania. Ambio 45, 480–489. doi:10.1007/s13280-015-0758-1

Moore, J.A., Miller, H.C., Daugherty, C.H., Nelson, N.J., 2008. Fine-scale genetic structure of a long-lived reptile reflects recent habitat modification. Mol. Ecol. 17, 4630–4641. doi:10.1111/j.1365-294X.2008.03951.x

Pe’er, G., Kramer-Schadt, S., 2008. Incorporating the perceptual range of animals into connectivity models. Ecol. Modell. 213, 73–85. doi:10.1016/j.ecolmodel.2007.11.020

Pittman, S.E., Hart, K.M., Cherkiss, M.S., Snow, R.W., Fujisaki, I., Smith, B.J., Mazzotti, F.J., Dorcas, M.E., 2014a. Homing of invasive Burmese pythons in South Florida: evidence for map and compass senses in snakes. Biol. Lett. 10, 20140040–20140040. doi:10.1098/rsbl.2014.0040

Pittman, S.E., Osbourn, M.S., Semlitsch, R.D., 2014b. Movement ecology of amphibians: A missing component for understanding population declines. Biol. Conserv. 169, 44–53. doi:10.1016/j.biocon.2013.10.020

Prevedello, J.A., Forero-Medina, G., Vieira, M.V., 2010. Movement behaviour within and beyond perceptual ranges in three small mammals: Effects of matrix type and body mass. J. Anim. Ecol. 79, 1315–1323. doi:10.1111/j.1365-2656.2010.01736.x

Prevedello, J.A., Forero-Medina, G., Vieira, M. V., 2011. Does land use affect perceptual range? Evidence from two marsupials of the Atlantic Forest. J. Zool. 284, 53–59. doi:10.1111/j.1469-7998.2010.00783.x

Prevedello, J.A., Vieira, M. V., 2010a. Does the type of matrix matter? A quantitative review of the evidence. Biodivers. Conserv. 19, 1205–1223. doi:10.1007/s10531-009-9750-z

Prevedello, J.A., Vieira, M. V., 2010b. Plantation rows as dispersal routes: A test with didelphid marsupials in the Atlantic Forest, Brazil. Biol. Conserv. 143, 131–135. doi:10.1016/j.biocon.2009.09.016

Read, M.A., Grigg, G.C., Irwin, S.R., Shanahan, D., Franklin, C.E., 2007. Satellite Tracking Reveals Long Distance Coastal Travel and Homing by Translocated Estuarine Crocodiles, Crocodylus porosus. PLoS One 2, 1–5. doi:10.1371/journal.pone.0000949

Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. Am. Nat. 158, 87–99. doi:10.1086/320863

Rivas, M.L., Tomillo, P.S., Uribeondo, J.D., Marco, A., 2015. Leatherback hatchling sea-finding in response to artificial lighting: Interaction between wavelength and moonlight. J. Exp. Mar. Bio. Ecol. 463, 143–149. doi:10.1016/j.jembe.2014.12.001

Rodríguez-San Pedro, A., Simonetti, J.A., 2015. The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? Landsc. Ecol. 30, 1561–1572. doi:10.1007/s10980-015-0213-5

Sato, C.F., Wood, J.T., Schroder, M., Green, K., Osborne, W.S., Michael, D.R., Lindenmayer, D.B., 2014. An experiment to test key hypotheses of the drivers of reptile distribution in subalpine ski resorts. J. Appl. Ecol. 51, 13–22. doi:10.1111/1365-2664.12168

Sato, C.F., Wood, J.T., Stein, J.A., Crane, M., Okada, S., Michael, D.R., Kay, G.M., Florance, D., Seddon, J., Gibbons, P., Lindenmayer, D.B., 2016. Natural tree regeneration in agricultural landscapes: The implications of intensification. Agric. Ecosyst. Environ. 230, 98–104. doi:10.1016/j.agee.2016.05.036

Saura, S., Bodin, Ö., Fortin, M.J., 2014. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. J. Appl. Ecol. 51, 171–182. doi:10.1111/1365-2664.12179

Schneider, N.A., Low, M., Arlt, D., Pärt, T., 2012. Contrast in edge vegetation structure modifies the predation risk of natural ground nests in an agricultural landscape. PLoS

One 7, e31517. doi:10.1371/journal.pone.0031517

Schutz, A.J., Driscoll, D. a., 2008. Common reptiles unaffected by connectivity or condition in a fragmented farming landscape. Austral Ecol. 33, 641–652. doi:10.1111/j.1442-9993.2007.01830.x

Smith, M.J., Forbes, G.J., Betts, M.G., 2013. Landscape configuration influences gap-crossing decisions of northern flying squirrel (Glaucomys sabrinus). Biol. Conserv. 168, 176–183. doi:10.1016/j.biocon.2013.10.008

Southwood, A., Avens, L., 2010. Physiological, behavioral, and ecological aspects of migration in reptiles. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 180, 1–23. doi:10.1007/s00360-009-0415-8

Sozio, G., Mortelliti, A., Boitani, L., 2013. Mice on the move: Wheat rows as a means to increase permeability in agricultural landscapes. Biol. Conserv. 165, 198–202. doi:10.1016/j.biocon.2013.05.022

Taylor, D., Daniels, C.B., Johnston, G., 2015. Habitat selection by an arboreal lizard in an urban parkland: not just any tree will do. Urban Ecosyst. 243–255. doi:10.1007/s11252-015-0480-6

Wilson, S., Swan, G., 2013. Complete Guide to Reptiles of Australia, 4th ed. New Holland Publishers, Sydney.

Wiltschko, R., Wiltschko, W., 1999. The orientation system of birds — I. Compass mechanisms. J. Ornithol. doi:10.1007/BF02462086

Youngquist, M.B., Boone, M.D., 2014. Movement of amphibians through agricultural landscapes: The role of habitat on edge permeability. Biol. Conserv. 175, 148–155. doi:10.1016/j.biocon.2014.04.028

Zollner, P.A., Lima, S.L., 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108, 219–230.

Supplementary Material

Appendix A: Details of the study area and agricultural matrix environments

Our study took place within an important agricultural region of New South Wales, south-eastern Australia. The dominant vegetation community of the region is the critically endangered Box Gum Grassy Woodlands. This woodland community is characterized by an understory of native tussock grasses, herbs and scattered shrubs, and an open tree strata that was originally dominated by white box *Eucalyptus albens*, yellow box *E. melliodora* and Blakely's red gum *E. blakelyi*. The region is characterized by a gently undulating landscape comprising foothills and ranges, with a complex geology typified by granites and meta-sediments. The average annual rainfall of the region is 585mm, peaking over winter and spring months. The annual mean minimum and maximum temperatures ranged from 11.0-31.3^{o}C in the summer to -1.0-13.9^{o}C in the winter (Bureau of Meteorology, 2016).

We examined movements within six types of matrix environment; Long native, short native, long exotic, short exotic pastures and two crops, wheat and canola (Fig. A.1). Both crop treatments demonstrated visible lines along planted rows (Fig. A.1f), and no crops oriented east-west were selected in this study to avoid confounding influences of animal movements towards habitat trees and along crop-rows.

We measured site-level pasture height using a rising-plate pasture meter (Correll et al., 2003) every meter along two 30m transects starting from the release points heading inwards towards the target tree. This gave us 60 measurements per site from which we calculated the mean (Table A.1) and used it to define short (mean<10cm height) and long (>20cm height) pastures.

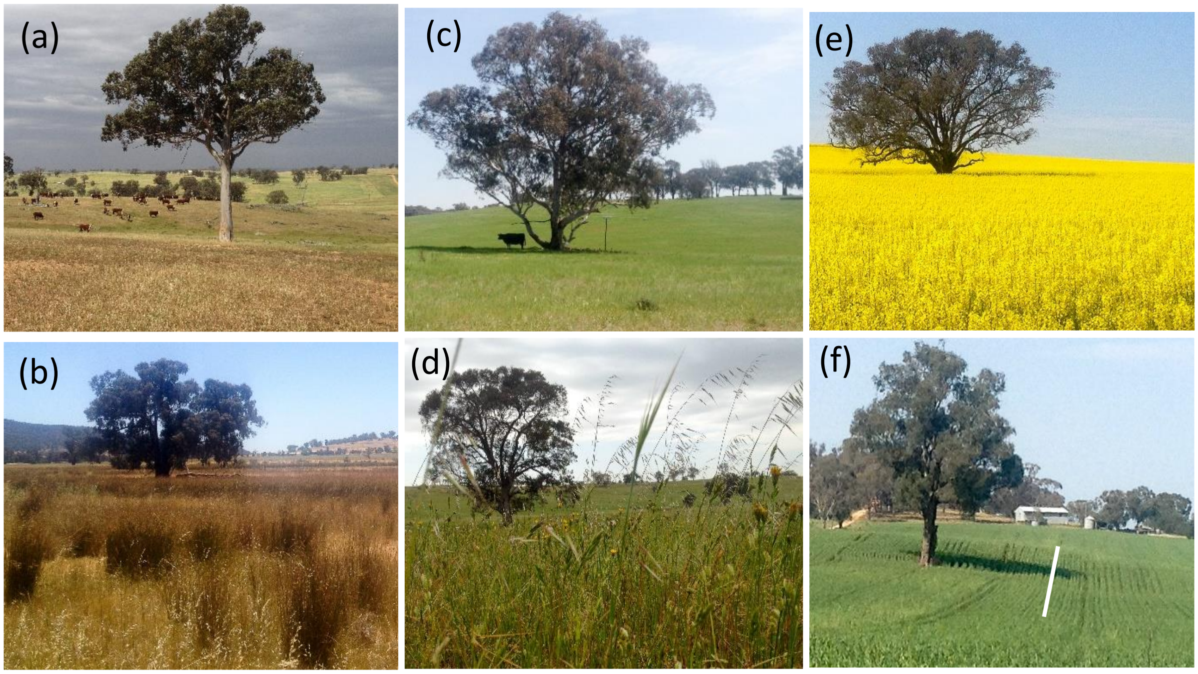

Figure A.1. *Typical images of different matrix environments (with target tree) including (a) short and (b) long native pasture, (c) short and (d) long exotic pasture, and (e) canola and (f) wheat crops. Typically observed sowing lines for crops are indicated (white line).*

Table A.1. *Mean pasture height per site per treatment*

Treatment	Site	Pasture Height (cm)	
		Mean	Std. Dev.
Canola	C1C	1.20	0.20
	C2C	1.20	0.20
	C3C	1.20	0.20
Wheat	C4W	1.20	0.20
	C5W	1.20	0.20
	C7W	1.20	0.20
Long Exotic	LE1	32.00	9.44
	LE2	47.40	10.56
	LE3	36.35	8.95
Long Native	LN1	25.25	9.68
	LN2	20.15	6.13
	LN3	21.15	8.61
Short Exotic	SE2	10.60	5.07
	SE3	9.49	3.73
	SE4	6.50	3.61
Short Native	SN1	6.20	3.03
	SN3	9.15	3.26
	SN4	10.45	3.47

Supporting References

Bureau of Meteorology, 2016. Bureau of Meteorology [WWW Document]. URL http://www.bom.gov.au/ (accessed 3.28.16).

Appendix B: Visual example of track quantification.

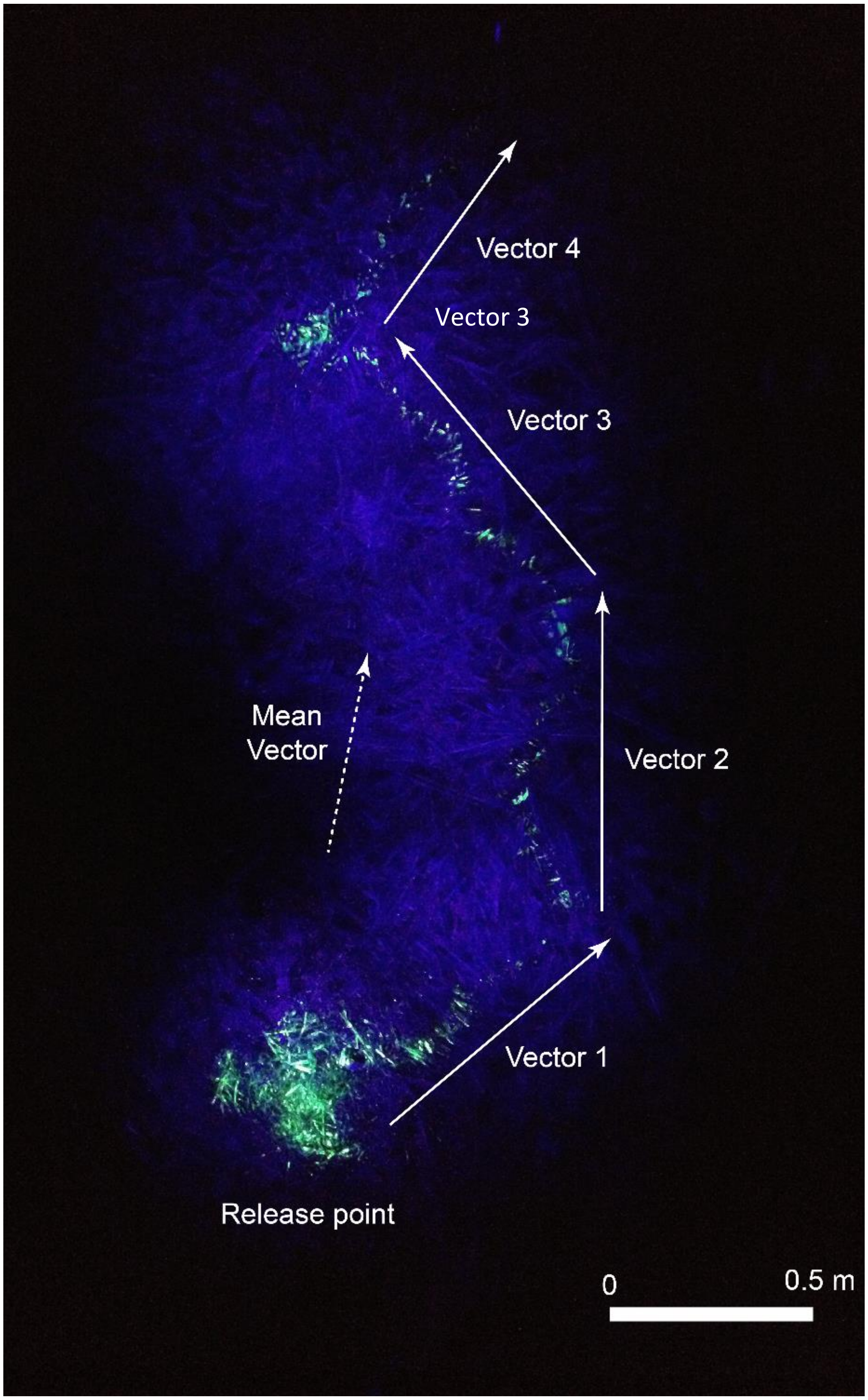

Figure B.1. *Photo of a track section (3m) as observed under ultraviolet light including the release point at the bottom of image. Individual vectors (and direction of mean vector) are indicated, whose distance and bearing are used in analyses.*

APPENDIX I. ECOLOGICAL NICHE BREADTH AND MICROHABITAT GUILD STRUCTURE IN TEMPERATE AUSTRALIAN REPTILES: IMPLICATIONS FOR NATURAL RESOURCE MANAGEMENT IN ENDANGERED GRASSY WOODLAND ECOSYSTEMS.

An assessment of species guilds and functional traits have increasingly proven useful for interpreting responses of large biotic communities to the impacts of land management, yet comprehensive assessments of guild designation for reptiles remains poorly resolved. In this paper, we use our comprehensive ecological dataset of reptiles within woodlands derived (in part) from the Environmental Stewardship biodiversity monitoring program to identify components of reptile niche breadth and microhabitat guild structure.

This paper was used to determine classifications used in other PhD chapters (papers III and V) although was considered adjunct to the main thesis.

Michael, D.R., Kay, G.M., Crane, M., Florance, D., MacGregor, C., Okada, S., McBurney, L., Blair, D., Lindenmayer, D.B., 2015. Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems. Austral Ecol. 40, 651–660. doi:10.1111/aec.12232.

Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems.

Abstract

Ecological theory predicts that species with narrow niche requirements (habitat specialists) are more vulnerable to anthropocentric disturbances than those with broad niche requirements (habitat generalists). Hence, understanding a species ecological niche and guild membership would serve as a valuable management tool for providing *a priori* assessments of a species extinction risk. It also would help to forecast a species capacity to respond to land use change, as what might be expected to occur under financial incentive schemes to improve threatened ecological vegetation communities. However, basic natural history information is lacking for many terrestrial species, particularly reptiles in temperate regions of the world. To overcome this limitation, we collated 3527 reptile observations from 52 species across an endangered woodland ecoregion in south-eastern Australia and examined ecological niche breadth and microhabitat guild structure. We found 30% of species had low ecological niche values and were classified as habitat specialists associated with large eucalypt trees, woody debris, surface rock or rocky outcrops. Cluster analysis separated species into six broad guilds based on microhabitat similarity. Approximately 80% of species belonged to guilds associated with old growth vegetation attributes or non-renewable litho-resources such as surface rock or rocky outcrops. Our results suggest that agri-environment schemes that focus purely on grazing management are unlikely to provide immediate benefits to broad suites of reptiles associated with old growth vegetation and litho-resources. Our classification scheme will be useful for identifying reptile species that are potentially vulnerable to anthropocentric disturbances and may require alternative

strategies for improving habitat suitability and reptile conservation outcomes in grassy woodland ecosystems.

Introduction

The application of theory in conservation biology provides a useful framework for understanding environmental complexity (Wiens 1995; Turner et al. 2001; McGlade 2009). However, Driscoll and Lindenmayer (2012) argue that many ecological theories are heuristic, poorly defined and narrowly focused, and fail to deliver adequate conservation outcomes. The 'niche' concept is one realm of theoretical ecology that has been the subject of much debate since its conception (Whittaker et al. 1973; Pianka 1976; Kearney 2006; Holt 2009; McInerny & Etienne 2012). The original concept, coined by Joseph Grinnell, used the term ecological niche to describe the basic habitat a species requires to survive and reproduce (Grinnell 1917). Elton (1927) further contextualized the concept of niche in terms of the trophic role of a species in the community. However, it was not until Hutchinson (1957) made the distinction between the fundamental (ecological) niche and the realized (actual) niche of a species (i.e. after resource competition and predator–prey interactions had taken place) that the concept became widely applied (reviewed by Whittaker et al. 1973; Leibold 1995; Austin 2007; Peterson 2011). Despite the growing literature on the application of niche theory in ecology, for many organisms, their fundamental niche remains poorly known.

Space, time and food are all important dimensions of the ecological niche of an organism (Pianka 1973; Peterson 2011). However, when applied to management, habitat descriptors are more important than time and food in explaining niche partitioning (Schoener 1974). This is because the ecological niche provides insights into a species extinction risk and vulnerability to anthropocentric disturbances (Owens & Bennett 2000; Botts et al. 2013). Several studies have found that species most at risk of decline or extinction are habitat specialists (Foufopoulos & Ives 1999; Owens & Bennett 2000; Lee & Jetz 2011). Reptiles as a group are perceived to be more susceptible to threat processes than birds or mammals because of their relatively narrow range distributions and niche requirements (Gibbons et al. 2000). However, managing multiple species over large spatial scales is problematic (Fischer et al. 2004), and strategies to improve biodiversity outcomes in human-modified landscapes are required. The strategy of mesofilter conservation may provide some solutions to this problem of managing multiple species (Hunter 2005). This strategy seeks to manage ecosystems to benefit many species simultaneously. The effectiveness of mesofilter conservation is dependent on the ability to identify key elements of a landscape that are critical to broad suites of species (Mac Nally 2004). Guild-based investigations that identify critical habitat components for groups of organisms can provide a mechanism for managing multiple species (Holmes et al. 1979; Mac Nally 1994; Kornan et al. 2013). However, to the best of our collective knowledge, no studies have explicitly quantified niche breadth and guild structure in temperate Australian reptiles. Thus, understanding a species ecological niche and guild membership not only provides a useful management tool for predicting species responses to disturbance, but can also provide an a priori assessment of a species capacity to respond to environmental change.

To provide critical information to guide reptile conservation in the context of native vegetation management, we examined ecological niche breadth and guild membership in a temperate woodland reptile community from south-eastern Australia. This broad region supports the critically endangered white box-yellow box-Blakely's red gum woodland (referred to as box gum grassy woodland) and derived native grassland ecological vegetation communities. These ecological vegetation communities are two of the most heavily cleared and modified bioregions in the world (Benson 2008). Furthermore, the region is rich in reptile diversity (Kay et al. 2013) and contains several threatened species, including the nationally vulnerable pink-tailed worm lizard Aprasia parapulchella (Environment Protection and Biodiversity Conservation Act 1999) and the endangered northern velvet gecko Amalosia rombifer (Threatened Species Conservation Act 1995). However, reptiles in the temperate woodlands of south-eastern Australia have been poorly studied, especially within the box gum grassy woodland, and little natural history information is available for the vast majority of species in the ecoregion.

In recent years, the Australian Government (Commonwealth of Australia 2009), Local Land Services in New South Wales and Catchment Management Authorities in Victoria have delivered market-based incentive schemes that pay private land managers (often farmers) to undertake specific conservation actions as part of funding agreements to improve box gum grassy woodland vegetation condition and extent (Lindenmayer et al. 2012). These instruments are referred to as agri-environment schemes. However, a key assumption of the agri-environment scheme is that changes in livestock grazing management and pest plant control will facilitate improvements in native vegetation condition. This will, in turn, enhance habitat for woodland fauna. However, recent studies that have evaluated reptile responses to agri-environment schemes and native vegetation management in general report limited success in terms of improving reptile species richness and diversity (Brown et al. 2011; Dorrough et al. 2012, Michael et al. 2013, 2014). A broader understanding of the mechanisms that drive species response to landscape change is required to inform and improve future management incentive schemes. With the aim of improving conservation outcomes, we sought to identify species with narrow niche requirements (habitat specialists) and microhabitat guilds associated with landscape elements that are not adequately captured under conventional management schemes. We use this information to determine which species are likely to require a targeted management approach to improve habitat suitability and reptile conservation outcomes in farming landscapes.

Methods

Study area

We conducted our study in the temperate eucalypt woodlands of south-eastern Australia and predominantly within the critically endangered white box *Eucalyptus albens*, yellow box *E. melliodora* and Blakely's red gum *E. blakelyi* grassy woodland and derived native grassland ecological vegetation communities. Our study region extended from Warwick in southern Queensland (28°01S 152°11E) to Merton in southern Victoria (36°58′ 145°42′), and spanned a latitudinal distance of approximately 1130 km (Fig. 1). The average annual rainfall in the region ranged from 696 mm in the north, peaking in the summer months (Warwick weather station No. 41525), to 710 mm in the south, peaking in the winter months (Alexandra weather station No. 88001). The average annual minimum and maximum summer temperatures ranged from 17.9–30.0°C in the north to 11.9–29.3°C in the south. The average annual minimum and maximum winter temperatures ranged from 2.9–17.9°C in the north to 2.5–11.2°C in the south (Bureau of Meteorology 2013).

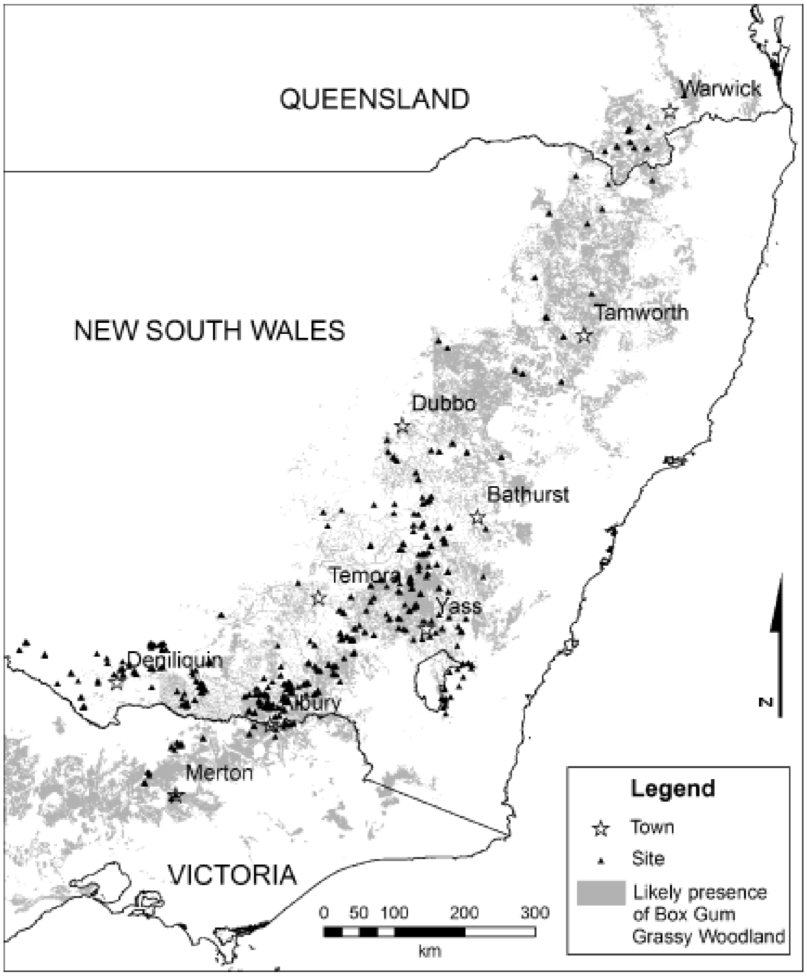

Figure 1. *Location of long-term temperate woodland biodiversity monitoring sites (triangles) and the likely extent of box gum grassy woodland in south-eastern Australia.*

Temperate eucalypt woodlands once formed a relatively continuous band of vegetation on fertile soils west of the Great Dividing Range from approximately 27°S in southern Queensland to the lower south-east of South Australia (Yates & Hobbs 2000). Today, more than 95% of the temperate woodland has been cleared and converted to agriculture (Lindenmayer et al. 2010). In recognition of the growing concern about biodiversity conservation issues in production landscapes, the Australian Government developed the Environmental Stewardship Program. This programme, which is congruent with the

European Union's agri-environment scheme, aims to maintain and/or improve the condition and extent of threatened woodland ecological vegetation communities under the Environment Protection and Biodiversity Conservation Act 1999. Agri-environment schemes provide private land managers with the financial incentive to undertake prescriptive management interventions, including modifying grazing regimes, reducing fertilizer use, undertaking exotic plant management, restricting timber and rock removal, and planting native understorey species.

Experimental design and survey protocol

We established 677 sites on private property across the region as part of five long-term biodiversity monitoring programmes (see Table 1 for a description of each programme). Each site consisted of a 200-m transect marked at the 0-, 100- and 200-m points. Grazing management varied at each site and included areas under set stocking, rotational grazing (e.g. spring – summer grazing exclusion) or total grazing exclusion. Between 2002 and 2012, we conducted 2652 site visits across the five programmes, representing between three and five survey periods (Table 1). We completed surveys between August and December and between 09.00 and 16.00 hours on clear, sunny days with minimal wind. At each site, one observer conducted a time- and area-constrained (30 min × 1 ha) active search of natural habitat (200 × 50 m), whereby reptiles were captured by hand or visually identified in situ. For each observation, we recorded the microhabitat (substrate) where the reptile was first sighted, assigning the record to one of eight microhabitat types: open ground = OG (including among grass), leaf litter = LL (beneath or on top), on log = OL (including fallen trees), on rock = OR (boulder or outcrop), tree trunk = TT (including tree stumps and dead trees), under bark of large trees = UB, under log = UL and under surface rock = UR.

Table 1. *Biodiversity monitoring programmes in the temperate woodland of south-eastern Australia showing the number of survey sites, survey year and survey effort (literature sources are provided for more information on the experimental design of each programme)*

Monitoring programme	**Number of sites**	**Year of survey**	**Survey effort (sites × year)**	**Literature**
South-west Slopes Restoration Study	219	2002, 2003, 2005, 2008, 2011	1095	Cunningham *et al.* 2007
Murray Biodiversity Monitoring Program	93	2008, 2009, 2010, 2012	372	Michael *et al.* 2014
North East/Goulburn Broken Biodiversity Monitoring Program	40	2010, 2011, 2012	120	Michael *et al.* 2013
Environmental Steward Program	325	2010, 2011, 2012	1065	Lindenmayer *et al.* 2012
Total	677		2652	

Data analysis

For each species, we calculated Levin's measure of niche breadth using the inverse of Simpson's diversity index (Simpson 1949):

$$B = 1 \Big/ \sum_{i=1}^{n} p_i^2 \quad (1)$$

Where B is the microhabitat niche breath value, i is the microhabitat category, n is the number of categories and p is the proportion of microhabitat category i. The form of the Simpson's diversity index varies from 1, which represents a single microhabitat category, to n, representing equal use of a given number of categories. We classified species with $B < 1.5$ as habitat specialists and species with $B > 1.5$ as habitat generalists based on a natural break in the histogram of niche values. To explore guild membership, we created a similarity matrix in Primer v6 (Clarke & Gorley 2006) and performed a cluster analysis using the Bray–Curtis similarity index on the standardized frequency distributions for species microhabitat use. Twelve species (23%) were recorded less than twice and were omitted from the cluster analysis.

Results

Summary statistics

Our data comprised 4287 observations from 52 species in ten families (Table 2). From the total number of observations, we obtained microhabitat data from 3527 individuals. The three most abundant species that accounted for over 65% of all observations were Boulenger's skink *Morethia boulengeri* ($n = 1159$, 32.8% of observations), ragged snake-eyed skink *Cryptoblepharus pannosus* ($n = 959$, 27.2% of observations) and the eastern striped skink *Ctenotus robustus* ($n = 238$, 6.7% of observations).

Niche breadth

Microhabitat niche breadth (B) ranged from 1.00 to 4.01 (Table 2). Mean niche breadth values were highest in the family Scincidae ($n = 22$ species, $B = 2.09$), followed by Agamidae ($n = 5$, $B = 1.92$), Pygopodidae ($n = 5$, $B = 1.83$), Elapidae ($n = 8$, $B = 1.7$), Gekkonidae ($n = 9$, $B = 1.66$) and Typhlopidae ($n = 2$, $B = 1.13$). Twenty-three species (44%) had niche values less than $B = 1.5$. After removing species with less than two observations, we classified 12 species (30%) as habitat specialists (Table 2). These included *Amphibolurus burnsi*, *A. muricatus*, *Hemiergis talbingoensis, Ramphotyphlops nigrescens, Tiliqua scincoides*, *Egernia cunninghami*, *A. parapulchella*, *Ctenotus teaniolatus*, *Diplodactylus vittatus*, *Lerista bougainvillii*, *R. wiedii* and *Underwoodisaurus milii* (Table 3).

***Table 2**. Temperate woodland reptiles observed in this study from south-eastern Australia, showing activity pattern (D = diurnal, N = nocturnal), niche breadth values (*B*) and microhabitat categories (OG: open ground, LL: leaf litter, OL: on log (including fallen trees), OR: on rock (including outcrops), TT: tree trunk (including tree stumps and dead trees), UB: under bark, UL: under log and UR: under surface rock)*

Common name	**Species**	**Number of observations**	***B*[a]**	**Microhabitat**
Agamidae				
Burn's Dragon	*Amphibolurus burnsi* (D)	3	1.00	OL
Jacky Dragon	*Amphibolurus muricatus* (D)	10	1.15	OL, OR, TT
Nobbi Dragon	*Diporiphora nobbi* (D)	6	2.57	LL, OL, OR
Eastern Water Dragon	*Intellagama lesueurii* (D)	1	1.00	OL
Eastern Bearded Dragon	*Pogona barbata* (D)	38	3.86	OG, LL, OL, OR, TT, UL
Gekkonidae				
Zig Zag Velvet Gecko	*Amalosia rhombifer* (N)	1	1.00	UB
Southern Marbled Gecko	*Christinus marmoratus* (N)	127	1.59	LL, OR, UB, UL
Eastern Stone Gecko	*Diplodactylus vittatus* (N)	41	1.50	LL, UL, UR
Tree Dtella	*Gehyra variegata* (N)	13	2.25	UB, UL, UR
Binoe's Gecko	*Heteronotia binoei* (N)	15	1.99	UB, UL, UR
Northern Velvet Gecko	*Nebulifera robusta* (N)	4	1.60	UB, UR
Southern Spotted Velvet Gecko	*Oedura tryoni* (N)	2	2.00	UB, UR
Southern Spiny-tailed Gecko	*Strophurus intermedius* (D/N)	26	1.83	UB, UL
Thick-tailed Gecko	*Underwoodisaurus milii* (N)	12	1.18	UL, UR
Pygopodidae				
Pink-tailed Worm Lizard	*Aprasia parapulchella* (D/N)	50	1.00	UR
Olive Legless Lizard	*Delma inornata* (D)	19	2.59	LL, UL, UR
Leaden Delma	*Delma plebeia* (D/N)	6	2.57	LL, UL, UR
Excitable Delma	*Delma tincta* (N)	2	2.00	UL, UR
Burton's Snake Lizard	*Lialis burtonis* (D)	1	1.00	UR
Scincidae				
Two-clawed Worm Skink	*Anomalopus leuckartii* (D)	12	1.80	UL, UR
Southern Rainbow Skink	*Carlia tetradactyla* (D)	114	4.01	OG,LL, OR, UB, UL, UR
Lively Rainbow Skink	*Carlia vivax* (D)	2	1.00	LL
Ragged Snake-eyed Skink	*Cryptoblepharus pannosus* (D)	959	2.41	OG, LL, OL, OR, TT, UB, UL, UR
Elegant Snake-eyed Skink	*Cryptoblepharus pulcher* (D)	46	2.31	OL, TT, UB

Common name	**Species**	**Number of observations**	***B*[a]**	**Microhabitat**
Eastern Ctenotus	*Ctenotus orientalis* (D)	2	1.00	UR
Eastern Striped Skink	*Ctenotus robustus* (D)	238	2.27	OG, LL, TT, UL, UR
Copper-tailed Skink	*Ctenotus taeniolatus* (D)	35	1.12	UL, UR
Cunningham's Skink	*Egernia cunninghami* (D)	35	1.41	OL, OR, UB
Tree Crevice Skink	*Egernia striolata* (D)	89	3.13	OL, OR, TT, UB, UR
Eastern Water Skink	*Eulamprus quoyii* (D)	1	1.00	OL
Three-toed Earless Skink	*Hemiergis talbingoensis* (D/N)	119	1.34	LL, UL, UR
Grass Skink	*Lampropholis delicata* (D)	62	3.73	OG, LL, UB, UL, UR
Garden Skink	*Lampropholis guichenoti* (D)	16	3.04	OG, LL, UB, UL, UR
South-eastern Slider	*Lerista bougainvillii* (D)	29	1.42	LL, UL, UR
Timid Slider	*Lerista timida* (D)	64	2.21	LL, UL, UR
White's Skink	*Liopholis whitii* (D)	1	1.00	UR
Litter Skink	*Lygisaurus foliorum* (D)	24	2.79	OG, LL, UL, UR
Grey's Skink	*Menetia greyii* (D)	34	2.82	LL, UL, UR
Boulenger's Skink	*Morethia boulengeri* (D)	1159	2.70	OG, LL, OL, TT, UB, UL, UR
Shingleback	*Tiliqua rugosa* (D)	14	2.18	OG, UL, UR
Common Blue-tongue	*Tiliqua scincoides* (D)	7	1.32	UL, UR
Varanidae				
Lace Monitor	*Varanus varius* (D)	8	1.68	LL, OR, TT
Typhlopidae				
Blackish Blind Snake	*Ramphotyphlops nigrescens* (D/N)	9	1.25	UL, UR
Brown-snouted Blind Snake	*Ramphotyphlops wiedii* (D/N)	12	1.00	UR
Pythonidae				
Inland Carpet Python	*Morelia spilota* (D/N)	1	1.00	OR
Elapidae				
Yellow-faced Whip Snake	*Demansia psammophis* (D)	9	1.97	OG, UL, UR
Red-naped Snake	*Furina diadema* (D/N)	2	2.00	UL, UR
Dwyer's Snake	*Parasuta dwyeri* (D/N)	22	1.72	LL, UL, UR
Red-bellied Black Snake	*Pseudechis porphyriacus* (D)	3	1.80	OG, UR
Eastern Brown Snake	*Pseudonaja textilis* (D)	18	2.41	OG, UL, UR
Curl Snake	*Suta suta* (D/N)	2	1.00	UL
Bandy Bandy	*Vermicella annulata* (D/N)	2	1.00	UR

[a] *Species with $B < 1.5$ were classified as habitat specialists and species with $B > 1.5$ were classified as habitat generalists.*

Guild classification

Our cluster analysis grouped species according to habitat similarity (number of microhabitats used and frequency of use) and produced six broad guilds: (i) saxicolous (outcrop-dwelling); (ii) arboreal; (iii) semi-arboreal; (iv) fossorial (log-dwelling); (v) cryptozoic (surface rock-dwelling); and (vi) four terrestrial sub-groups (Table 3). Saxicolous members included two species from Scincidae; arboreal guild members included four species from Gekkonidae; semi-arboreal members included seven species from Agamidae, Scincidae and Varanidae; fossorial members included six species from Scincidae, Gekkonidae and Typhlopidae; cryptozoic members included ten species from Pygopodidae, Scincidae, Gekkonidae, Typhlopidae and Elapidae; and the four terrestrial sub-groups included ten species from Pygopodidae, Scincidae and Elapidae (Table 3). Frequency distributions for all 52 reptile species according to their microhabitat categories are provided in the supporting information (Appendix S1–S7).

Discussion

We evaluated ecological niche values and habitat guild structure in a reptile community associated with the endangered box gum grassy woodland in south-eastern Australia. Our key findings were: (i) 30% of the reptile community had low ecological niche breadth values and were classified as habitat specialists. These species were associated with logs, surface rocks, rocky outcrops or mature trees. (ii) Eighty per cent of all species belonged to habitat guilds associated with old growth attributes or non-renewable litho-resources. We discuss the implications of our classification scheme in the context of vegetation management, market-based financial incentive programmes and agri-environment schemes.

Table 3. *Classification of temperate woodland reptiles in south-eastern Australia based on microhabitat guild membership, mode of thermoregulation and niche affiliation (species with <2 observations are not included)*

Guild	Niche	Species assemblage
Saxicolous (outcrop-dwelling)	Specialist	*Egernia cunninghami*
	Generalist	*Egernia striolata*
Arboreal (bark-dwelling)	Generalist	*Christinus marmoratus*, *Gehyra variegata*, *Nebulifera robusta*, *Strophurus intermedius*
Semi-arboreal (tree/log-dwelling)	Specialist	*Amphibolurus burnsi*, *A. muricatus*
	Generalist	*Cryptoblepharus pannosus*, *C. pulcher*, *Diporiphora nobbi*, *Pogona barbata*, *Varanus varius*
Fossorial (log-dwelling)	Specialist	*Hemiergis talbingoensis*, *Ramphotyphlops nigrescens*, *Tiliqua scincoides*
	Generalist	*Anomalopus leuckartii*, *Heteronotia binoei*, *Lerista timida*
Cryptozoic (surface rock-dwelling)	Specialist	*Aprasia parapulchella*, *Ctenotus taeniolatus*, *Diplodactylus vittatus*, *Lerista bougainvillii*, *Ramphotyphlops wiedii*, *Underwoodisaurus milii*
	Generalist	*Ctenotus robustus*, *Demansia psammophis*, *Parasuta dwyeri*, *Pseudechis porphyriacus*
Terrestrial (group 1: open ground)	Generalist	*Tiliqua rugosa*, *Pseudonaja textilis*
Terrestrial (group 2: rock/log/litter-dwelling)	Generalist	*Carlia tetradactyla*, *Lampropholis delicata*, *L. guichenoti*, *Morethia boulengeri*
Terrestrial (group 3: rock/log-dwelling)	Generalist	*Delma inornata*, *D. plebeia*
Terrestrial (group 4: litter-dwelling)	Generalist	*Menetia greyii*, *Lygisaurus foliorum*

Niche breadth

Habitat specialists are predicted to be more vulnerable to disturbance than habitat generalists (Brown et al. 1995; Thuiller 2004; Botts et al. 2013). In this study, many species were infrequently observed and for these species, niche breadth values should be interpreted with caution. Among those species with sufficient data, we classified 12 species as microhabitat specialists (Table 3). Five of these species were associated with attributes of old growth vegetation, such as large mature eucalypt trees and fallen timber. The remaining seven species were associated with non-renewable resources such as surface rock (bush rock) and insular rocky outcrops (predominantly granite) (Table 3).

Species that are adapted to specific environments over their geographical range (i.e. species with a narrow ecological niche) may not be able to respond to changes in the landscape that result from human disturbances (Gehring & Swihart 2003), including those that occur under traditional farming practices. Examples include incremental loss of large paddock trees (Fischer et al. 2009), loss of fallen timber (Mac Nally et al. 2001; Manning et al. 2013), and bush rock removal and outcrop degradation (Michael et al. 2010). Hence, species that rely on large trees, fallen timber or surface rocks are most vulnerable to local extinction because of the incremental loss of these critical habitats in agricultural landscapes. Once depleted, old growth resources such as fallen timber may take several decades to accumulate, and surface rock may never be replaced. A logical extension of this concept is that habitat specialists also may not respond immediately to improvements in native vegetation condition and extent, such as those reported to occur under agri-environment schemes (Lindenmayer et al. 2012; Michael et al. 2014) or land abandonment (Lunt et al. 2010). In one study, Michael et al. (2014) found that only habitat generalists such as *M. boulengeri* and *C. pannosus* responded to native vegetation management. Similarly, Dorrough et al. (2012) argue that most reptiles are unlikely to respond to the short-term benefits gained by rotational grazing management. Clearly, more work needs to be done to enhance conditions for habitat specialists.

Guild classification

Many ecological communities contain guilds (Pianka 1980), groups of organisms that strongly interact among themselves for the use of a common resource, but only weakly with members of other groups (Blaum et al. 2011; Peterson 2011). In the context of wildlife management, understanding how different communities are structured in terms of guild assemblages is important for determining which groups of species are reliant on resources that may be limited or depleted in the landscape. Our cluster analysis grouped 39 species based on microhabitat similarity (Fig. 2). From this we were able to distinguish six broad microhabitat guilds within the box gum grassy woodland (Table 3). Notably, 80% of all species belonged to guilds associated with old growth attributes (e.g. fallen timber and large old trees) or non-renewable resources (e.g. surface rocks and rocky outcrops).

The strong reliance on old growth trees and tree-related resources such as fallen timber by several guilds (arboreal, semi-arboreal and fossorial) raises an important issue in the conservation of reptiles in agricultural landscapes – the management of fallen timber and firewood collection. The collection of fallen timber for firewood or to simply clean up paddocks is a widespread and common practice in Australian grazing landscapes. This practice has significant negative outcomes for reptiles (Driscoll et al. 2000; Mac Nally et al.

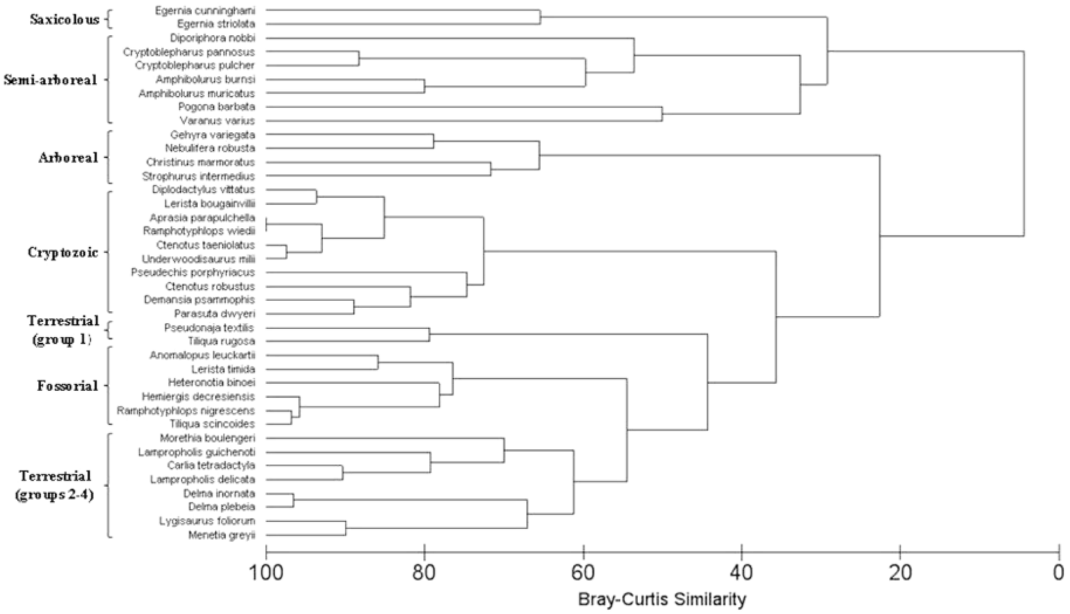

Figure 2. *Cluster analysis showing microhabitat relationships among 39 reptile species in the temperate woodlands of south-eastern Australia (note: excludes species with less than two observations).*

2001; Manning et al. 2013; Michael et al. 2014). More strategic policies on timber management are required given that so many reptile species are dependent on fallen timber for thermoregulation, shelter and foraging (Mac Nally et al. 2001; Manning et al. 2013). Furthermore, more research is required to evaluate threshold responses to amounts of fallen timber to develop ecologically sustainable prescriptions for timber collection on private property. A recent study in the Australian Capital Territory examined reptile responses to timber restoration and found that reptile abundance increased significantly over a 4-year period in response to the addition of timber into a grassy woodland reserve (Manning et al. 2013). That study suggested some reptile species (e.g. terrestrial generalists) may respond relatively quickly to timber retention and the strategic re-introduction of timber to grazing landscapes.

A second major issue in the conservation of woodland reptiles is the management of bush rock and insular rocky outcrops. Our classification scheme identified a wide variety of cryptozoic and saxicolous species associated with this non-renewable resource (Table 3). The cryptozoic guild also includes the nationally endangered pink-tailed worm lizard *A. parapulchella*. This species has a patchy distribution throughout the southern half of the box gum grassy woodland and the importance of shallowly embedded surface rocks in the ecology and conservation of this species is well established (reviewed by Wong et al. 2011). However, for the vast majority of other cryptozoic species, including *R. wiedii* (a small scolecophidian snake that occupies the same niche as *A. parapulchella*), habitat requirements are poorly known, and it is likely that their distribution is limited and strongly influenced by the presence of rocks in the landscape. From a management perspective, the collection of bush rock presents a major threat to temperate reptiles (Pike et al. 2010; Croak et al. 2013) but is an activity that is difficult to regulate (Shine et al. 1998). In the box gum grassy woodland, bush rock retention is primarily limited to short-term funding agreements under the Environmental Stewardship Program. Bush rock removal is listed as a threatening process under Schedule 3 of the New South Wales Threatened Species Conservation Act (1995). However, the listing exempts ‘the removal of rock from paddocks when it constitutes a necessary part of the carrying out of a routine agricultural activity’ (see supporting information for an example of bush rock removed from a paddock).

Because ‘bush rock’ is non-renewable and several key reptile guilds are dependent on this resource (Table 3), it should be a key component of environmental stewardship payments and other agri-environment schemes to address reptile conservation in agricultural landscapes. Furthermore, Australian states need to adopt policies on busk rock removal in the wider agricultural landscape to prevent incremental loss of this keystone resource. Michael et al. (2008, 2010) provide a case for managing rocky outcrops in agricultural landscapes, emphasizing the importance of protecting this resource to maintain and enhance reptile diversity. Rocky outcrops also provide important nodal points in the landscape from where restoration efforts could be focused. Physical restoration of rocky outcrops should also be considered. For example, in the Sydney region, artificial rocks have been used successfully to restore degraded habitat for threatened reptiles (Webb & Shine 1999; Croak et al. 2010, 2013). This method could be applied to granite outcrops, especially those where exfoliated surface rock has been removed or damaged by livestock. However, a major deficiency in agri-environment schemes and natural resource management in general in south-eastern Australia is the lack of policy guidelines on protecting and managing rocky outcrops.

Implications for natural resource management

A relatively recent initiative of State and Federal governments in Australia is to provide land managers with financial assistance to ‘improve the condition and extent of endangered ecological communities such as box gum grassy woodland’ by reducing stocking and grazing intensity, reducing fertiliser use, expanding weed management and replanting native species (Commonwealth of Australia 2009). Studies that evaluate the merits of native vegetation management interventions for improving faunal diversity are generally lacking in Australia (Lindenmayer et al. 2012). Two recent studies indicate that reptiles are unlikely to respond to short-term changes in grazing regimes (Dorrough et al. 2012; Michael et al. 2014), although medium- to longer-term benefits to arboreal and semi-arboreal guilds are predicted based on increases in native vegetation cover (Vesk & Dorrough 2006). We argue that grazing management alone is inadequate to protect and enhance approximately 80% of all reptile species associated with box gum grassy woodland, especially those reliant on old growth and non-renewable resources. Instead, we recommend that future agri-environment schemes place more emphasis on bush rock retention, rocky outcrop restoration and fallen timber management to improve reptile conservation outcomes in agricultural landscapes.

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References

Austin M. (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecol. Model. 200, 1–19.

Benson J. S. (2008) New South Wales vegetation classification and assessment part 2: plant communities of the NSW South-western slopes bioregion and update of NSW Western Plains plant communities, version 2 of the NSWVCA database. Cunninghamia 10, 599–672.

Blaum N., Mosner E., Schwager M. & Jeltsch F. (2011) How functional is functional? Ecological groupings in terrestrial animal ecology: towards an animal functional type approach. Biodivers. Conserv. 20, 2333–2345.

Botts E. A., Erasmus B. F. & Alexander G. J. (2013) Small range size and narrow niche breadth predict range contractions in South African frogs. Global Ecol. Biogeogr. 22, 567–576.

Bureau of Meteorology (2013) Bureau of Meterology. [Cited 17 October 2013.] Available from URL: http://www.bom.gov.au/

Brown G. W., Dorrough J. W. & Ramsey D. S. (2011) Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. Landscape Urban Plan. 103, 277–288.

Brown J. H., Mehlman D. W. & Stevens G. C. (1995) Spatial variation in abundance. Ecology 76, 2028–2043.

Clarke K. R. & Gorley R. N. (2006) PRIMER v6. Plymouth Marine Laboratory.

Commonwealth of Australia (2009) Environmental Stewardship Strategic Framework. Canberra: Commonwealth of Australia.

Croak B. M., Pike D. A., Webb J. K. & Shine R. (2010) Using artificial rocks to restore nonrenewable shelter sites in human-degraded systems: colonization by fauna. Restor. Ecol. 18, 428–438.

Croak B. M., Webb J. K. & Shine R. (2013) The benefits of habitat restoration for rock-dwelling velvet geckos Oedura lesueurii. J. Appl. Ecol. 50, 432–439.

Cunningham R. B., Lindenmayer D. B., Crane M., Michael D. & MacGregor C. (2007) Reptile and arboreal marsupial response to replanted vegetation in agricultural landscapes. Ecol. Appl. 17, 609–619.

Dorrough J., McIntyre S., Brown G., Stol J., Barrett G. & Brown A. (2012) Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. Austral Ecol. 37, 569–582.

Driscoll D. A. & Lindenmayer D. B. (2012) Framework to improve the application of theory in ecology and conservation. Ecol. Monogr. 82, 129–147.

Driscoll D., Freudenberger D. & Milkovits G. (2000) Impact and Use of Firewood in Australia. CSIRO Sustainable Ecosystems, Canberra.

Elton C. S. (1927) Animal Ecology. Sidgwick & Jackson, London.

Fischer J., Lindenmayer D. B. & Cowling A. (2004) The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. J. Appl. Ecol. 41, 32–44.

Fischer J., Stott J., Zerger A., Warren G., Sherren K. & Forrester R. I. (2009) Reversing a tree regeneration crisis in an endangered ecoregion. P. Natl. Acad. Sci. 106, 10386–10391.

Foufopoulos J. & Ives A. R. (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. Am. Nat. 153, 1–25.

Gehring T. M. & Swihart R. K. (2003) Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biol. Conser. 109, 283–295.

Gibbons J. W., Scott D. E., Ryan T. J. et al. (2000) The global decline of reptiles, déjà vu amphibians. Bioscience 50, 653–666.

Grinnell J. (1917) The niche-relationships of the California Thrasher. The Auk. 34, 427–433.

Holmes R. T., Bonney R. E. Jr. & Pacala S. W. (1979) Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 1979, 512–520.

Holt R. D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. P. Natl. Acad. Sci. 106, 19659–19665.

Hunter M. L. (2005) A mesofilter conservation strategy to complement fine and coarse filters. Conserv. Biol. 19, 1025–1029.

Hutchinson G. E. (1957) Concluding remarks – Cold Spring Harbour Symp. Quant. Biol. 22, 415–427.

Kay G., Michael D. R., Crane M. et al. (2013) A list of reptiles and amphibians from Box-Gum Grassy Woodlands in south-eastern Australia. Check List 9, 476–481.

Kearney M. (2006) Habitat, environment and niche: what are we modelling? Oikos 115, 186–191.

Kornan M., Holmes R. T., Recher H. F., Adamik P. & Kropil R. (2013) Convergence in foraging guild structure of forest breeding bird assemblages across three continents is related to habitat structure and foraging opportunities. Community Ecol. 14, 89–100.

Lee T. M. & Jetz W. (2011) Unravelling the structure of species extinction risk for predictive conservation science. P. Roy. Soc B-Biol. Sci. 278, 1329–1338.

Leibold M. A. (1995) The niche concept revisited: mechanistic models and community context. Ecology 76, 1371–1382.

Lindenmayer D. B., Zammit C., Attwood S. J. et al. (2012) A novel and cost-effective monitoring approach for outcomes in an Australian biodiversity conservation incentive program. PLoS ONE 7, e50872. doi: 10.1371/journal.pone.0050872

Lindenmayer D., Bennett A. & Hobbs R., eds (2010) Temperate Woodland Conservation and Management. CSIRO Publishing, Collingwood.

Lunt I. D., Winsemius L. M., McDonald S. P., Morgan J. W. & Dehaan R. L. (2010) How widespread is woody plant encroachment in temperate Australia? Changes in woody vegetation cover in lowland woodland and coastal ecosystems in Victoria from 1989 to 2005. J. Biogeogr. 37, 722–732.

Mac Nally R. (1994) Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective. J. Anim. Ecol. 63, 988–1001.

Mac Nally R., Fleishman E., Bulluck L. P. & Betrus C. J. (2004) Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. J. Biogeogr. 31, 917–929.

Mac Nally R., Parkinson A., Horrocks G., Conole L. & Tzaros C. (2001) Relationships between terrestrial vertebrate diversity, abundance and availability of coarse woody debris on south-eastern Australian floodplains. Biol. Conser. 99, 191–205.

McGlade J., ed. (2009) Advanced Ecological Theory: Principles and Applications. Wiley-Blackwell, Oxford.

McInerny G. J. & Etienne R. S. (2012) Ditch the niche – is the niche a useful concept in ecology or species distribution modelling? J. Biogeogr. 39, 2096–2102.

Manning A. D., Cunningham R. B. & Lindenmayer D. B. (2013) Bringing forward the benefits of coarse woody debris in ecosystem recovery under different levels of grazing and vegetation density. Biol. Conser. 157, 204–214.

Michael D. R., Cunningham R. B. & Lindenmayer D. B. (2008) A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. J. Appl. Ecol. 45, 1742–1752.

Michael D. R., Lindenmayer D. B. & Cunningham R. B. (2010) Managing rock outcrops to improve biodiversity conservation in Australian agricultural landscapes. Ecol. Manag. Restor. 11, 43–50.

Michael D. R., Lindenmayer D. B. & Wood J. (2013) Biodiversity baseline surveys: implications for threatened grassy woodland management in the North East and

Goulburn Broken ctachments, Victoria. Report to the North East Catchment Management Authority, Wodonga, Victoria.

Michael D. R., Wood J., Crane M., Montague-Drake R. & Lindenmayer D. B. (2014) How effective are agri-environment schemes for protecting and improving herpetofaunal diversity in Australian endangered woodland ecosystems? J. Appl. Ecol. 51, 494–505.

Owens I. P. E. & Bennett P. M. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. P. Natl. Acad. Sci. USA 97, 12144–12148.

Peterson A. T. (2011) Ecological niche conservatism: a time structured review of evidence. J. Biogeogr. 38, 817–827.

Pianka E. R. (1973) The structure of lizard communities. Annu. Rev. Ecol. Syst. 1973, 53–74.

Pianka E. R. (1976) Competition and niche theory. In: Theoretical Ecology: Principles and Applications (ed. R. M. May) pp. 114–141. Saunders, Philadelphia.

Pianka E. R. (1980) Guild structure in desert lizards. Oikos 1980, 194–201.

Pike D. A., Croak B. M., Webb J. K. & Shine R. (2010) Subtle – but easily reversible – anthropogenic disturbance seriously degrades habitat quality for rock-dwelling reptiles. Anim. Conserv. 13, 411–418.

Schoener T. W. (1974) Resource partitioning in ecological communities. Science 185, 27–39.

Shine R., Webb J. K., Fitzgerald M. & Sumner J. (1998) The impact of bush-rock removal on an endangered snake species, Hoplocephalus bungaroides (Serpentes: Elapidae). Wildl. Res. 25, 285–295.

Simpson E. H. (1949) Measurement of diversity. Nature 163, 688.

Thuiller W. (2004) Patterns and uncertainties of species' range shifts under climate change. Glob. Change Biol. 10, 2020–2027.

Turner M. G., Gardner R. H. & O'neill R. V. (2001) Landscape Ecology in Theory and Practice: Pattern and Process. Springer Verlag, New York.

Vesk P. A. & Dorrough J. W. (2006) Getting trees on farms the easy way? Lessons from a model of eucalypt regeneration on pastures. Aust. J. Bot. 54, 509–519.

Webb J. K. & Shine R. (1999) Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? Biol. Conser. 90, 93–99.

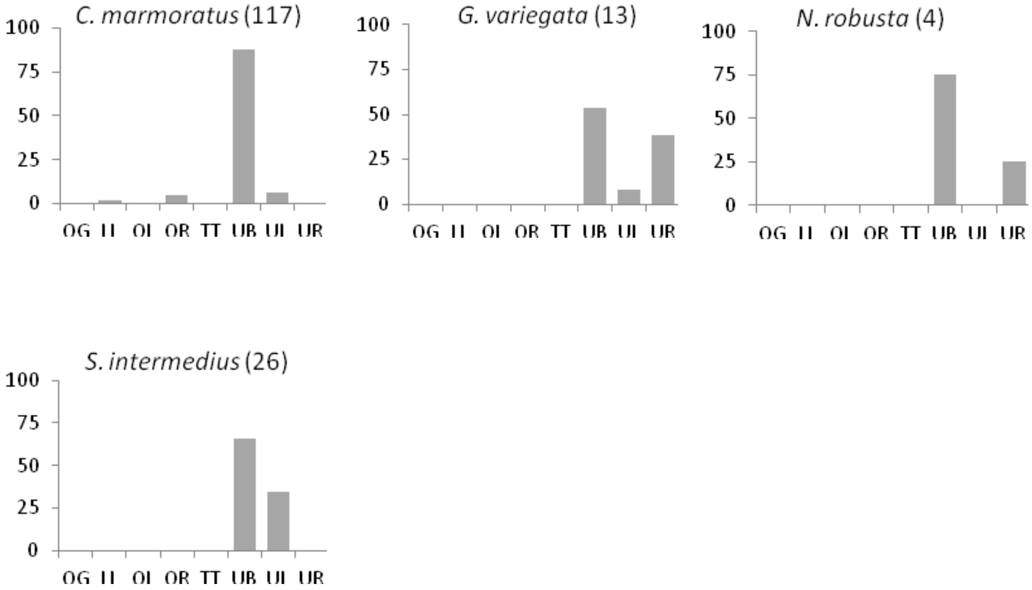
Whittaker R. H., Levin S. A. & Root R. B. (1973) Niche, habitat, and ecotope. Am. Nat. 1973, 321–338.

Wiens J. A. (1995) Landscape mosaics and ecological theory. In: Mosaic Landscapes and Ecological Processes (eds L. Hannson, L. Fahrig & G. Merriam) pp. 1–26. Springer, Verlag, New York.

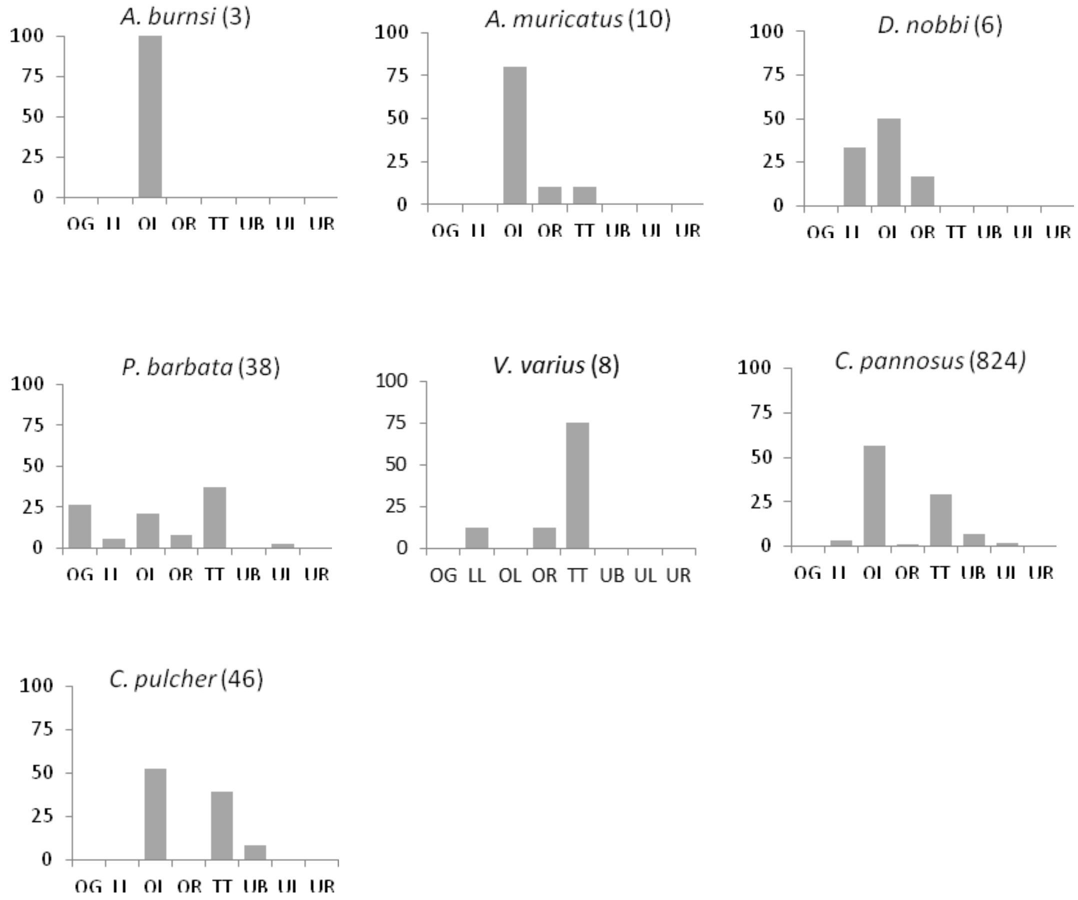
Wong D. T., Jones S. R., Osborne W. S. et al. (2011) The life history and ecology of the Pink-tailed Worm-lizard Aprasia parapulchella Kluge – a review. Aust. Zool. 35, 927–940.

Yates C. J. & Hobbs R. J. (2000) Temperate Eucalypt Woodlands in Australia: Biology, Conservation, Management and Restoration. Surrey Beatty & Sons, Chipping Norton, Sydney.

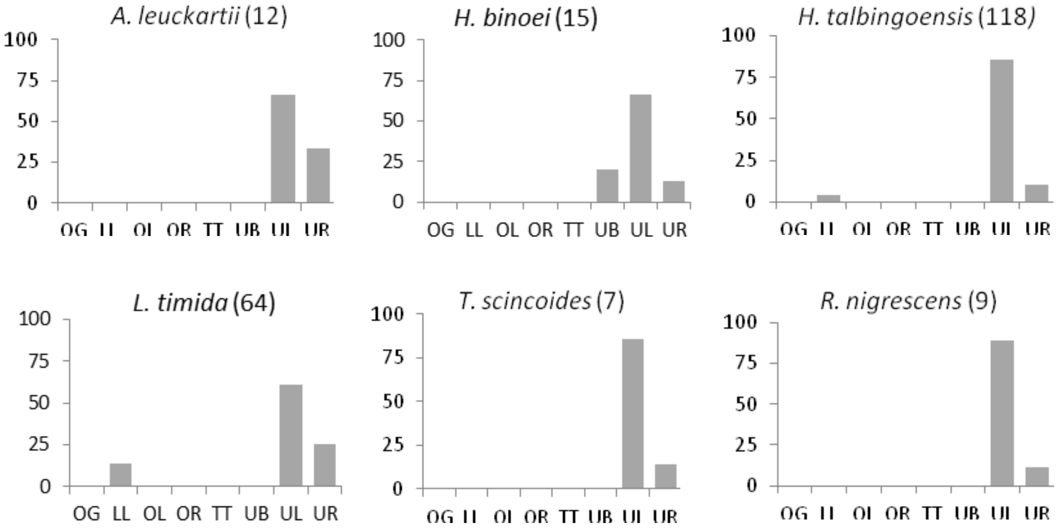
Supporting Information



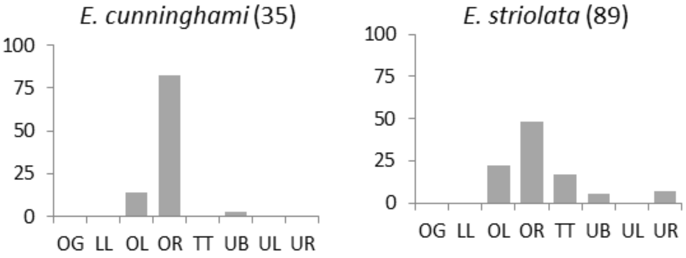
S1. *Frequency distribution of arboreal species in the box gum grassy woodland of south-eastern Australia·*



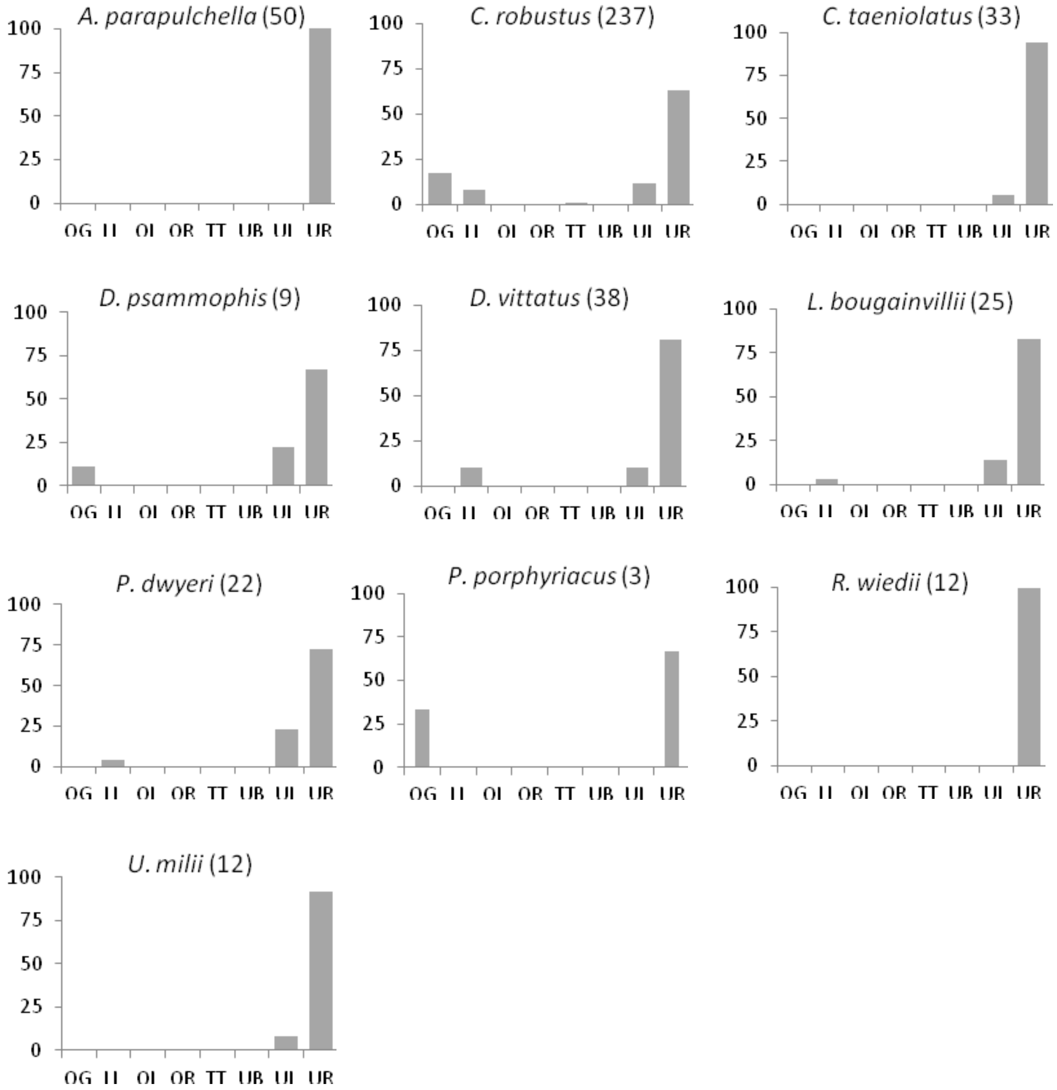
S2. *Frequency distribution of semi-arboreal species in the box gum grassy woodland of south-eastern Australia.*



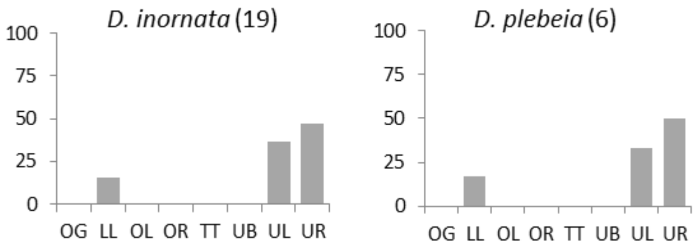
S3. *Frequency distribution of fossorial (log-dwelling) species in the box gum grassy woodland of south-eastern Australia.*



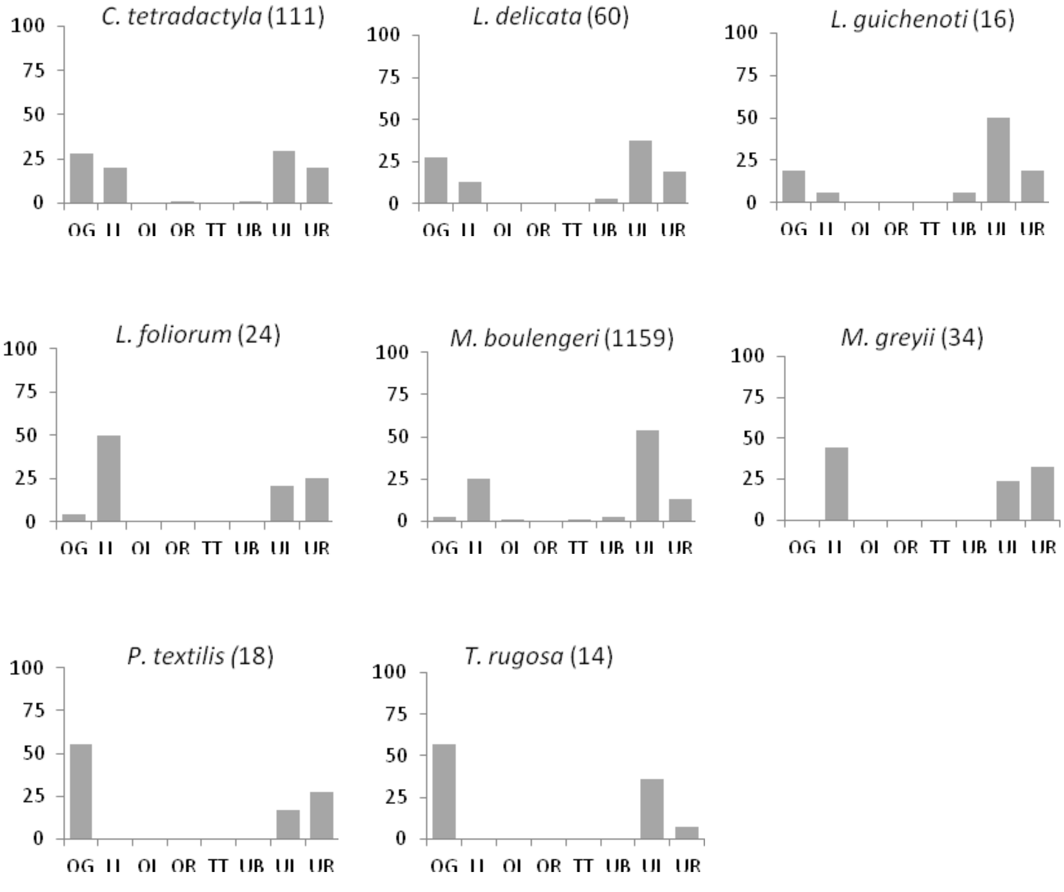
S4. *Frequency distribution of saxicolous (rocky outcrop-dwelling) species in the box gum grassy woodland of south-eastern Australia.*



S5. *Frequency distribution of cryptozoic (rock-dwelling) species in the box gum grassy woodland of south-eastern Australia.*



S6. *Frequency distribution of log/rock-dwelling species in the box gum grassy woodland of south-eastern Australia.*



S7. *Frequency distribution of terrestrial species in the box gum grassy woodland of south-eastern Australia.*

APPENDIX II. EFFECTS OF ENVIRONMENTAL VARIATION AND LIVESTOCK GRAZING ON ANT COMMUNITY STRUCTURE IN TEMPERATE EUCALYPT WOODLANDS.

Livestock grazing is recognised as a key management tool for the enhancement of biodiversity conservation value in private-protected areas. However, as highlighted in Paper IV in this thesis, little empirical evidence exists to support the ecological impacts of grazing.

In the following two papers, we explore the impacts of livestock grazing on alternative taxonomic groups to better understand the role of livestock grazing on broader biodiversity of production landscapes; namely invertebrates (ants) and birds.

Barton, P.S., Sato, C.F., Kay, G.M., Florance, D., Lindenmayer, D.B., 2016. Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodlands. Insect Conserv. Divers. 9, 124–134. doi:10.1111/icad.12151

Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodlands.

Abstract

- Grazing by livestock is a major ecological disturbance, with potential effects on vegetation, soil, and insect fauna. Ants are a diverse and functionally important insect group with many associations with the ground layer, yet recent global syntheses question the importance of grazing effects on ant communities relative to vegetation or soil.
- We examined the effects of vegetation, soil and grazing on the whole ant community, ant functional groups, and abundant species in temperate eucalypt woodlands, southeastern Australia.
- We found limited influence of grazing on our vegetation and soil measures, except for a positive association between grazing and exotic perennial grass cover. We also found that exotic grass cover had a negative effect on overall ant abundance and richness, but not functional groups or individual species. Soil C:N ratio had a positive effect on the subdominant Camponotini, and leaf litter cover had a positive effect on the abundance of cryptic species. Partial Mantel tests revealed an effect of both environmental and grazing measures on ant assemblage composition, but constrained ordination showed that leaf litter cover, grass biomass, and native and exotic perennial grass cover had stronger correlations with ant community structure than grazing.
- Our study shows that both environmental variation and grazing play a role in driving ant community structure, but that key environmental variables such as grass biomass and leaf litter cover are particularly important in temperate eucalypt woodlands. Monitoring of ant communities to measure the benefits of

changed grazing regimes for biodiversity should consider contemporary grazing pressure as well as the underlying effects of variation in plants and soils.

Introduction

Grazing by livestock can be a major disturbance in ecosystems due to its effects on soils and plant communities (Milchunas & Lauenroth, 1993; Hobbs, 1996; Schuman et al., 1999), as well as associated insect fauna (Seymour & Dean, 1999; Kruess & Tscharntke, 2002). As a consequence, the management of grazing is a priority for many land managers with responsibility for the conservation of biodiversity (Rook et al., 2004; Lunt et al., 2007).

Grazing can alter soil and plant attributes over prolonged periods (Milchunas & Lauenroth, 1993; Hobbs, 1996). For soils, this can include both physical and chemical aspects such as compaction from the impact of animal hooves, as well as altered phosphorus and nitrogen levels through plant consumption and redistribution via urine and dung (Yates et al., 2000; Beever et al., 2003). For plants, this can include the introduction and spread of exotic grass species (Driscoll et al., 2014), the selective grazing of different plant species (Dorrough et al., 2007), and changes in the structure, biomass, or composition of the ground-layer plant community (Yates et al., 2000). These changes to soils and plant communities have consequences for associated biota, both above and below ground, with many documented cases of changes in animal communities (Hobbs, 1996; Milchunas et al., 1998; Foster et al., 2014).

Ants are a major component of animal biomass and biodiversity in terrestrial ecosystems (Holldobler & Wilson, 1990), and play a critical role in soil health (de Bruyn, 1999) and ecosystem functioning (Evans et al., 2011). The important role of ants in ecosystems, and their often close association with soils (Bottinelli et al., 2015) and plant communities (Andersen, 1995) has led to their use as ‘indicators’ of ecosystem health (de Bruyn, 1999; Andersen & Majer, 2004; Barton & Moir, 2015). A major part of this work has been the use of ants as indicators of disturbance (King et al., 1998; Read & Andersen, 2000; Hoffmann & Andersen, 2003), particularly for grazing (Bestelmeyer & Wiens, 1996; Bromham et al., 1999; Hoffmann, 2010; Hoffmann & James, 2011).

There is a substantial literature on ant responses to grazing that has collectively shown location-specific and species-specific responses are common (e.g. Bromham et al., 1999; Whitford et al., 1999; Read & Andersen, 2000; Bestelmeyer & Wiens, 2001; Hoffmann, 2010). Significant effort, therefore, has been invested in the search for general responses of ants to disturbance and their use as bioindicators. This has been aided greatly by the use of ant functional groups, modelled after plant disturbance responses such as disturbance-opportunist species or disturbance-sensitive species (Andersen, 1995, 1997). Empirical studies and reviews of this approach have supported the use of ant functional groups insofar as providing a useful framework for building predictions about potential ant responses to disturbances, including grazing regimes (Hoffmann & Andersen, 2003; Hoffmann, 2010). Nevertheless, important knowledge gaps remain, including the context dependence of ant responses (Hoffmann, 2010), and the relative importance of fine-scale environmental features in influencing ant responses (Yates et al., 2011).

In this study, we examined ant assemblages from sites in a large-scale grazing experiment in a temperate agricultural region of southeastern Australia. Our objective was to examine the relative influence of a suite of grazing, plant, and soil variables on ants with the aim of better understanding which variables drive patterns of ant diversity in this region currently using grazing management to achieve biodiversity restoration. We split our objective into two main questions: (i) how does livestock grazing and environmental variation affect the abundance or species richness of functional groups and common species of ant? and, (ii) how does livestock grazing and environmental variation affect ant assemblage composition? Previous syntheses of ant responses to grazing have suggested that disturbance by grazing might be less important for structuring ant communities than natural variation in vegetation and soil (Hoffmann, 2010; Hoffmann & James, 2011). Put another way, the presence of livestock might not be as important as the presence of key habitat attributes in determining the composition of ant communities. We therefore interpreted our findings in light of this recent synthesis, as well as the generalised responses of ant functional groups to disturbance and the environment described by Hoffmann and Andersen (2003). Specifically, we predicted that opportunists (e.g. Rhytidoponera spp.) would respond positively to grazing disturbance (if any response), whereas other functional groups would show positive associations with features of the environment, such as cryptic species (e.g. Solenopsis spp.) preferring areas with leaf litter (Hoffmann & Andersen, 2003). We discuss how our findings might inform biodiversity monitoring in temperate landscapes being restored via changed livestock grazing regimes.

Methods

Study area and design

Our study area was located in southeastern Australia, and covers an area approximately 100 km east to west and 150 km north to south (Fig. S1). Within this area, 97 sites were established during 2010–2011 on 29 different farms. All sites were located in Red gum (*Eucalyptus blakelyi*) – Yellow box (*Eucalyptus melliodora*) grassy woodland, which is characterised by a heterogeneous distribution of eucalypt trees interspersed by open grassland (Fig. S2). This type of grassy woodland was once widespread in southeastern Australia, but is now a critically endangered ecological community as it has been greatly modified and reduced in extent due to agricultural practices including grazing (McIntyre et al., 2014). Farms were grouped into three blocks, each representing a historical grazing practice of either (i) continuous grazing, (ii) long-term holistic grazing (rotational grazing for greater than 10 years), or (iii) short-term holistic grazing (rotational grazing for less than 5 years). Farms with continuous grazing allow livestock access to sites all year round, whereas farms with holistic grazing typically rotate higher numbers of livestock through sites, but for a limited duration. On each farm, sites were established with one of three different treatments: (i) grazing exclusion; (ii) stewardship; and (iii) 'business as usual'. Sites with grazing exclusion were not grazed by any livestock. Stewardship sites must not be grazed for the 6 months of the year during spring and summer periods as part of a contractual obligation to the Environmental Stewardship Program of the Australian government (Lindenmayer et al., 2012). The business-as-usual sites continued grazing in line with the usual practices of the farm (viz. continuous grazing, long-term holistic or short-term holistic grazing). In the long term, these grazing treatments will be used to assess the effectiveness of the Australian Government Environmental Stewardship Program for a range of different biota (Lindenmayer et al., 2012).

Grazing and environmental variables

The predominant domestic livestock grazing on farms was by sheep *Ovis aries* and cattle *Bos taurus*. Two measures of livestock grazing pressure were obtained for each site in the previous 12 months as reported by individual landholders. These data were used to generate grazing variables that were used in our analyses: (i) number of days grazed per year; and (ii) annual stocking rate. Annual stocking rate was calculated by multiplying the total number of stock grazing on a site by the number of days they were present, and dividing by the area of the site (hectares), and then 365 to give a value per day. Livestock numbers were first standardised to ‘dry sheep equivalent’ to account for differences between sheep and cattle Dry sheep equivalent is a standardised measure of feed requirements that allows for comparisons of carrying capacity among different kinds of livestock (Mclaren, 1997). These two variables were used to represent differences in grazing between the treatments established on each farm.

Field surveys were conducted on each site during January and February 2012 to collect data on ground-layer ecological variables. Sites consisted of a 40 × 200 m fixed monitoring area (0.8 ha). Nested within each site were two smaller monitoring quadrats (20 × 50 m) for measuring vegetation variables. These plots were located at 0–50 m and 150–200 m along the monitoring site. Within each of these 20 × 50 m plots, all tree stems were recorded to 10 cm diameter classes (Lindenmayer et al., 2012). A 50 m transect was located down the centre of each plot with biometric measurements (Gibbons et al., 2008) taken every metre to assess ground layer native and exotic grass cover, and leaf litter cover. In addition, ground-layer plant biomass was assessed using a rising plate pasture meter to determine average height of ground cover present (Filip's Manual Folding Plate Meter, Jenquip, New Zealand (Correll et al., 2003).

Soil core samples were collected every 16.5 m (n = 12) along the centre of the 200 m transect of each site. Soil bulk density core samples (10 cm diameter × 5 cm height steel rings) were taken at 0–5 cm soil depth following careful removal of any surface plant and litter biomass present. Following collection, samples 1–4, 5–8, and 9–12 were pooled together to provide three bulked samples per depth per site (see Fig. S1). Analysis was performed for each of the three samples per site, and an average was then taken to give a per-site value used in subsequent analyses. Samples were air-dried at 35 °C for 48 h prior to processing and bulk density was calculated on a sub-sample dried at 105 °C for 48 h. Air-dried samples were subsequently crushed, passed through a 2 mm sieve, and retained for further chemical analysis. The >2 mm fraction was separated into organic and non-organic components and weighed and then discarded. Total carbon and nitrogen was determined with Dumas combustion analysis (Vario Max, Elementar, Germany) (Matejovic, 1997).

Ant sampling

We sampled ants using pitfall traps that were 250 ml plastic jars dug in flush with the ground surface, and half-filled with a non-toxic polyethylene glycol solution. Eight traps were placed in each site, with four traps at the corners of a 5 × 5 m square at each end of the site, and deployed for 2 weeks in December 2011 to collect ground-active arthropods. Three of the eight traps were randomly selected and had their ants removed and sorted, with these data pooled to give one sample per site. All sampling approaches have their limitations, and we recognise that our sampling approach favoured spatial replication over sampling intensity within sites, and favoured the more active species of the ant community.

All ant specimens were sorted to subfamily, genus, and species (or morphospecies) by a specialist at the Australian Museum, Sydney. We placed each ant species into a functional group using the classification scheme described by Andersen (1995, 1997) (see Table S1). These were as follows: (i) dominant Dolichoderinae, (ii) subdominant Camponotini, (iii) generalist Myrmecinae, (iv) opportunists, (v) hot climate specialists, (vi) cryptic species, and (vii) cold climate specialists.

Statistical analysis

A subset of 78 of the 97 possible sites had the full complement of soil, plant, grazing and ant data collected, and these sites formed the basis of all subsequent data analysis. It is well established that livestock grazing can affect soils and plants (Abbott et al., 1979; Yates et al., 2000), and we recognised that this might lead to confounding of grazing and environmental effects on ants. We therefore used multivariate analysis of variance (manova) to test for the effect of past grazing history on the eight-environmental variables, but found no significant overall effect (Rao F = 1.34, d.f. = 2, P = 0.182). This is not to say that past grazing has not had any effect on these variables, but that variation among sites within these broad groupings was not substantially different from variation among sites across all grazing histories. We performed a principle components analysis (PCA) of the eight plant and soil variables and two short-term grazing variables to identify potential co-linearity among variables and broad gradients in environmental variation (Gotelli & Ellison, 2004). We used a correlation matrix of the data as the plant, soil, and grazing variables were quantified using different methods and units.

Question 1: How does grazing and environmental variation affect the abundance and species richness of functional groups and individual species of ant? We addressed this first question by using all-subsets generalised linear regression to explore which set of environmental and grazing variables best explained the abundance and species richness of the whole ant assemblage and separate functional groups, as well as the abundance of some individual species. For each model, we used a quasi-Poisson error distribution and a logarithmic link function for ant response variables. Our explanatory variables included the three grazing variables (included grazing history, days grazed per year, stocking rate), three soil variables (soil bulk density, C:N ratio, fraction organic material >2 mm), and five vegetation variables (number of tree stems, grass biomass, native grass cover, exotic grass cover, leaf litter cover). We weighted our models using the Schwarz Information Criterion (SIC) (Schwarz, 1978), and present the best two candidate models. All models were run using GenStat 16 software (VSN International, 2013).

Question 2: How does grazing and environmental variation affect ant assemblage composition? To address this second question, we used three different multivariate analyses. First, we used a multi-response permutation procedure (MRPP) to test for a difference in ant assemblage composition among the three grazing history blocks. This test compares the average among-site similarity within each group with the overall similarity among all sites, with greater within-group similarity indicating samples are distinct from the overall set of samples (Zimmerman et al., 1985; McCune & Mefford, 2011). Second, we used partial Mantel tests (Sokal & Rohlf, 1995; McCune & Mefford, 2011) to test the null hypothesis of no correlation between among-site ant assemblage similarity and among-site variation in a second matrix (either environment or grazing) while controlling for a third matrix (either environment or grazing). This test enabled us to examine the independent effects of either the environment or grazing, while controlling for variation in the other. We also tested for a correlation with geographical proximity to see if there was any evidence of spatial autocorrelation in our ant data among sites. For these tests, we used Bray–Curtis distances (Bray & Curtis, 1957) for ant data, and Euclidean distances for our environmental, grazing, and geographical (easting/northing) variables, and determined significance using 9999 permutations of the data. Third, we used Canonical analysis of principal coordinates (Anderson & Willis, 2003) to examine how variation in ant assemblage composition was explained by variation in our grazing and environmental variables. This ordination technique uses correlation with continuous variables (our grazing and environmental variables) to constrain axes of variation in ant assemblage composition derived from Principal Coordinates Analysis (metric multidimensional scaling) (Anderson & Willis, 2003). We then used a biplot to identify which ant species were strongly correlated with variation among our sites. For all our multivariate analyses, we removed singletons and square-root transformed ant abundance data to reduce the influence of highly abundant species.

Results

Variation in grazing and the environment

Principle components analysis reduced our 10 vegetation, soil, and grazing measures to three new axes that accounted for approximately 63% of total variation in these variables (Table 1). The first axis (PC1) had a high negative loading for grass biomass, and positive loadings for leaf litter, number of tree stems, and C:N ratio, and indicates that most variation among sites can be attributed to co-variation among these variables. The sign of these loadings also indicate that grass biomass decreased when litter, tree stems, and soil C:N ratio increased. The second axis (PC2) had a high negative loading for large soil organic fragments, and positive loadings for soil bulk density and native grass cover. The sign of the loadings indicated that the soil organic fragments decreased when soil density and native grass cover increased. Notably, the third axis (PC3) had high positive loadings for exotic grass cover and both short-term grazing measures, indicating these variables co-varied with each other (but not with the other plant and soil measures).

Table 1. *Summary of principal component analysis of eight environmental and two grazing variables. Variables with strong axis loadings are shown in bold*

	PC1	**PC2**	**PC3**
Mean ground-layer biomass (kg ha^{-1})	**−0.454**	0.087	−0.148
Leaf litter cover (%)	**0.518**	−0.051	−0.018
Number of tree stems (per ha)	**0.451**	0.102	0.063
Soil C:N ratio	**0.482**	0.022	−0.164
Soil organic fragments (% >2 mm)	0.048	**−0.675**	0.099
Soil bulk density (g cm^{-3})	0.131	**0.533**	0.027
Native perennial grass cover (%)	−0.196	**0.397**	0.181
Exotic perennial grass cover (%)	−0.151	−0.262	**0.407**
Annual stocking rate (livestock ha^{-1} year^{-1})	0.054	0.093	**0.613**
Days grazed per year	0.080	0.066	**0.601**
Percentage variation explained	30.740	17.160	14.700

Question 1: Ant functional groups and individual species

We collected 87 species of ant (22 061 individuals) from 78 sites (Table S2). The most species-rich genera were the *Iridomyrmex* (13 species), *Monomorium* (11 species), *Melophorus* (10 species), *Camponotus* (9 species), and *Pheidole* (9 species), and the most abundant species were *Iridomyrmex rufoniger*, *Pheidole* sp B, *Monomorium sordidum*, and *Rhytidoponera metallica*. Functionally, the generalist myrmecines were the most diverse functional group (22 species), followed by the dominant dolichoderines (14 species).

All-subsets generalised linear regression revealed exotic perennial grass cover to be the best predictor of the abundance and species richness of the whole ant assemblage (Table 2, Fig. 1a, b). Soil C:N ratio was important for the abundance of the subdominant

Table 2. *Summary of generalised linear models with top two models of environmental and grazing variables describing the abundance and species richness of the whole ant assemblage, ant functional groups, and individual ant species*

	SIC	***R^2***	**Best model variables**	**SIC**	**R^2**	**Second model variables**
Whole assemblage						
Abundance	81.12	8.61	EPG	82.28	12.57	EPG + ASR
Species richness	88.31	11.55	EPG	88.88	15.70	NPG + EPG
Subdominant Camponotini						
Abundance	79.52	9.31	SCN	81.27	12.57	SCN + DGY
Species richness	87.59	17.70	SCN + ASR	86.54	23.61	SCN + ASR + DGY
Opportunists						
Abundance	93.45	39.86	TS + SD + NPG	94.29	42.59	TS + SO + SD + NPG
Species richness	84.24	31.28	SCN + EPG	87.66	32.13	SCN + EPG + ASR
Cryptic species						
Abundance	81.41	11.20	LL	82.52	9.86	GB
Species richness	76.91	4.77	SD	77.14	4.46	LL
Dominant Dolichoderinae						
Abundance	91.84	21.44	GH + SCN + SD	93.24	24.68	GH + SD + EPG + DGY
Species richness	83.25	11.91	GB + DGY	83.43	17.07	GB + NPG + DGY
Generalist Myrmicinae						
Abundance	88.60	34.64	LL + SCN + SO + ASR	90.15	37.33	LL + SCN + SO + EPG + ASR
Species richness	85.58	6.68	NPG	85.64	11.83	TS + NPG
Hot climate specialists						
Abundance	86.49	13.61	GB + DGY	87.21	17.82	GB + TS + DGY
Species richness	80.65	5.35	NPG	81.64	9.70	NPG + EPG
Cold climate specialists						
Abundance	75.10	8.34	ASR	77.15	5.51	DGY

	SIC	R^2	Best model variables	SIC	R^2	Second model variables
Species richness	75.17	5.22	SO	75.52	4.72	NPG
Individual species						
Rhytidopoera metallica	102.79	54.67	GH + TS + SO + SD + NPG	103.30	57.04	GH + TS + SCN + SO + SD + NPG
Iridomyrmex rufoniger	91.37	28.88	GB + LL + SCN + DGY	89.45	35.22	GB + LL + SCN + EPG + DGY
Iridomyrmex purpureus	93.97	41.07	GH + LL	92.19	45.74	GH + LL + NPG
Monomorium rothsteini	98.84	54.04	GB + LL + SD + ASR + DGY	98.88	56.73	GH + GB + LL + EPG + ASR
Monomorium sordidum	100.54	65.04	GH + LL + SCN + SO + NPG + ASR	101.61	64.47	GH + LL + TS + SCN + SO + NPG
Pheidole spB	96.45	36.97	GH + SCN + NPG + EPG + ASR	96.59	36.84	GH + SCN + SO + EPG + ASR
Nylanderia spA	85.27	16.98	TS	83.38	23.70	TS + SD
Notoncus ectatommoides	82.46	13.35	GB + DGY	83.03	12.65	GB + ASR
Camponotus consobrinus	95.29	53.32	GH + GB + LL + NPG	96.98	55.08	GH + GB + LL + SO + NPG

GH, grazing history; GB, grass biomass; LL, leaf litter cover; TS, tree stem count; SCN, Soil C:N ratio; SO, soil organic fragments >2 mm; SD, soil bulk density; NPG, native perennial grass cover; EPG, exotic perennial grass cover; ASR, annual stocking rate; DGY, days grazed per year; SIC, Schwarz Information Criterion.

Camponotini (Fig. 2a), the species richness of opportunists, and the abundance of the subdominant Camponotini, dominant Dolichoderinae and cryptic species. Leaf litter cover was an important predictor of the abundance of cryptic species (Fig. 2b). Annual stocking rate was found to be the single most important predictor of the abundance of cold climate specialists (Fig. 2c). For individual species, the best models were more complex than for functional groups. Although all best models of the individual species had at least one environmental predictor, seven of the eight models also had a grazing predictor, with grazing history the most commonly selected variable. For example, the number of days grazed had a negative effect on *I. rufoniger* (Fig. 3a). Native grass cover, in addition to grazing history, had a positive effect on the generalist *R. metallica* (Fig. 3b). The opportunist *Nylanderia* spA was the only individual species that had no grazing variable in the best model and was negatively associated with the number of tree stems (Fig. 3c). Additional details of models are given in Tables S3 and S4.

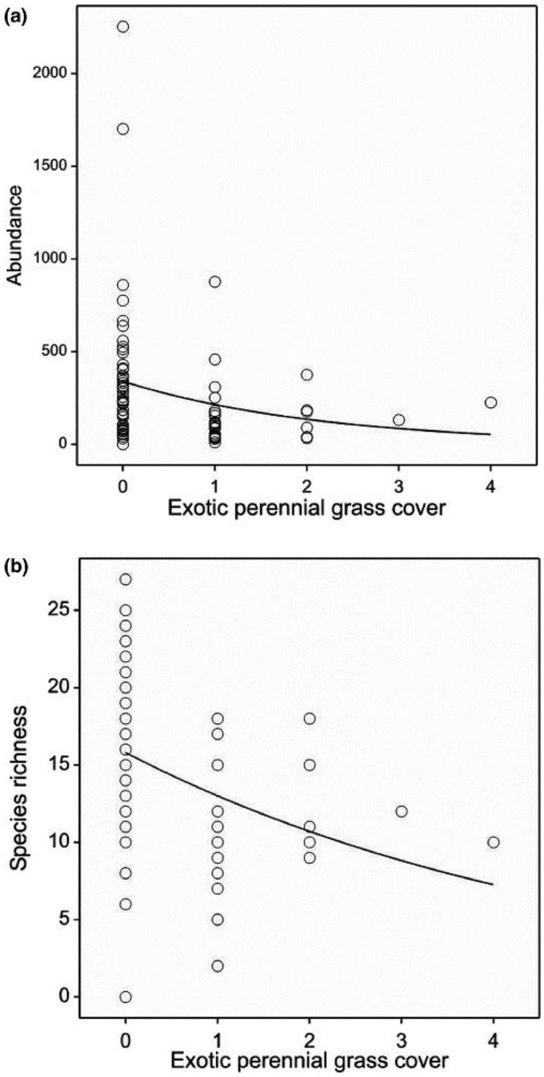


Figure 1. *Fitted models showing the relationship between percentage exotic perennial grass cover and (a) the abundance and (b) species richness of the ant assemblage. Predicted values are plotted on the original scale.*

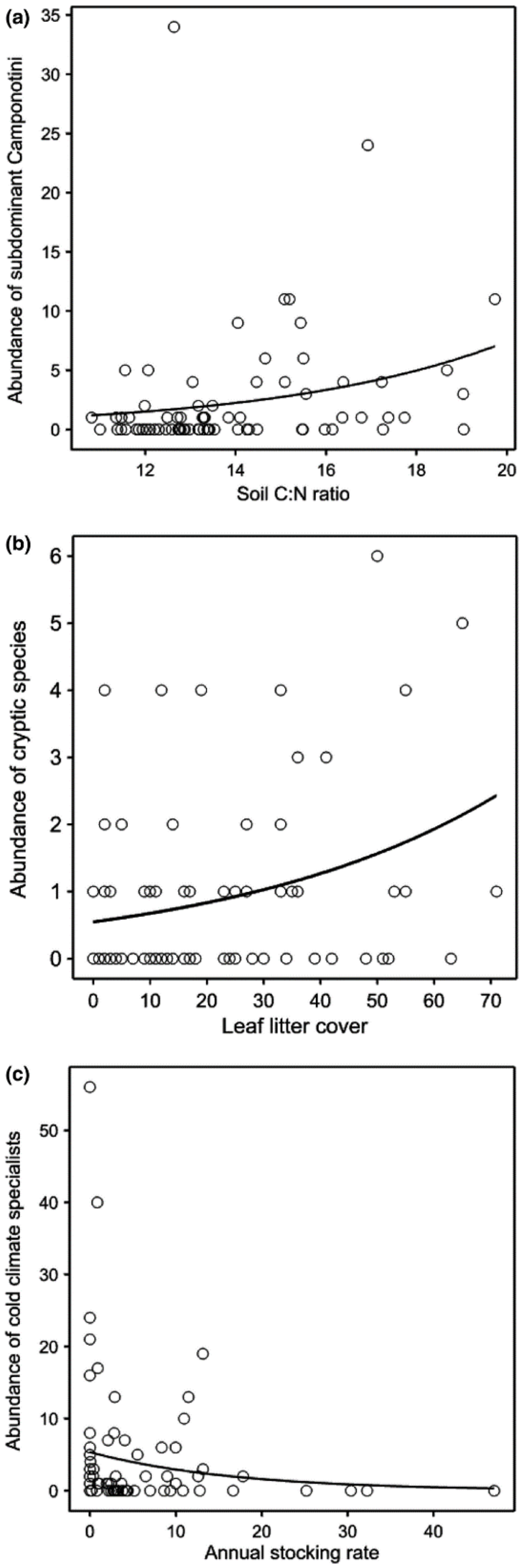


Figure 2. *Fitted models showing the relationship between soil nitrogen, leaf litter and stocking rate variables, and the abundance of (a) subordinate Camponotini, (b) cryptic species, and (c) cold climate specialists respectively. Predicted values are plotted on the original scale.*

Question 2: Ant composition

We found that ant assemblage composition was weakly significantly different among sites grouped by grazing history (MRPP: $T = -1.97$, $A = 0.007$, $P = 0.037$), but that pairwise comparisons between grazing blocks were not significant ($P > 0.05$).

Partial Mantel tests indicated a significant correlation between ant assemblage composition and environmental variation when controlling for grazing ($r = 0.161$, $P = 0.002$), and geographical proximity ($r = 0.156$, $P = 0.002$). We also found a significant correlation between ant composition and grazing when controlling for the environment ($r = 0.176$, $P = 0.012$). Notably, no significant correlation was observed for geographical proximity when controlling for the environmental ($r = -0.045$, $P = 0.206$). This shows there was structuring of the ant community by both the environment and grazing, but not by geographical proximity.

The first two axes of the principal coordinate analysis explained 14.3% and 11.2% of the variation in ant species composition respectively. Constraining these axes by the eight environmental and two grazing variables (Fig. 4) revealed that most of the environmental variables were more strongly correlated with variation in the ant community than the grazing variables. In particular, grass biomass and leaf litter cover were strongly correlated with ant assemblage structure along the axis 1, but in opposing directions. Similarly, native and exotic perennial grass cover were strongly correlated, but in opposing directions, with variation in ant composition along axis 2. Several ant species were strongly correlated with the ordination axes, and thus representative of distinct assemblages among our sites (Fig. 4). The generalist *M. sordidum* and the Dominant Dolichoderine *Iridomyrmex purpureus* were positively correlated with axis one, and thus characteristic of assemblages found at sites with higher leaf litter. The

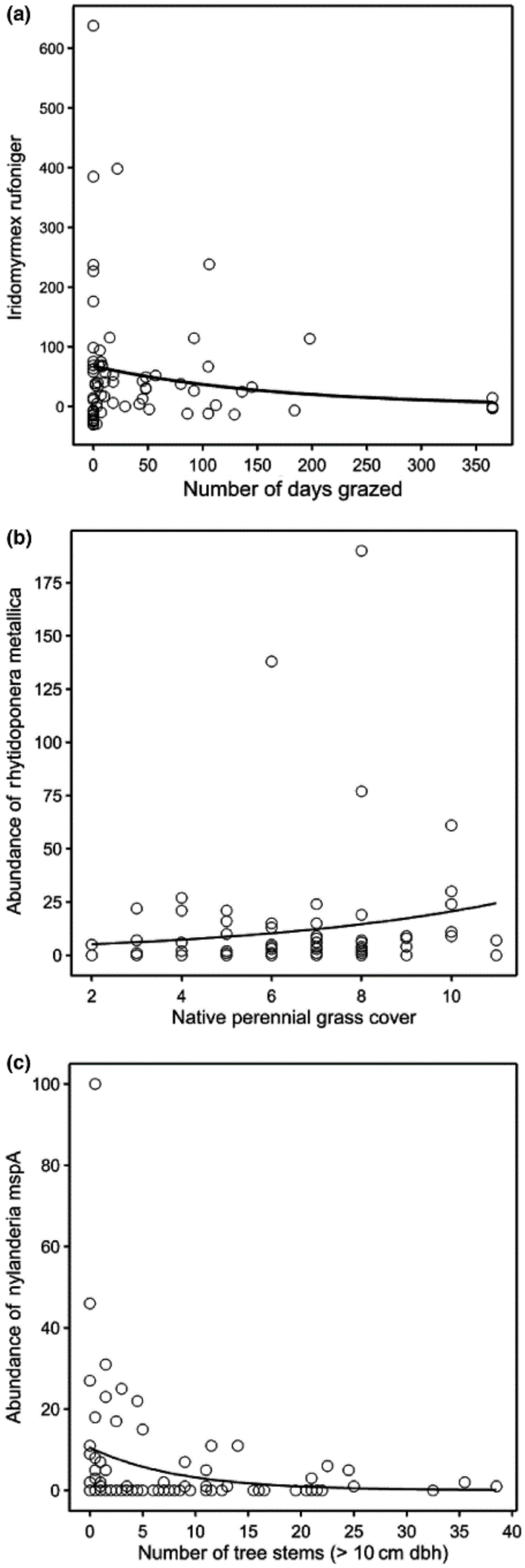


Figure 3. *Fitted models showing the relationship between grazing and environmental variables and the abundance of (a)* Iridomyrmex rufoniger*, (b)* Rhytidoponera metallica*, and (c)* Nylanderia *spA. predicted values are plotted on the original scale.*

opportunist *R. metallica*, generalist myrmecine *Monomorium rothsteini*, and dominant dolichoderine *I. rufoniger* had strong positive correlations with axis two, and thus characteristic of assemblages associated with sites with higher native grass cover. Notably, the cold climate specialist *Heteroponera imbellis* was the only species strongly negatively correlated with both axes 1 and 2, and was characteristic of assemblages associated with higher exotic perennial grass cover.

Discussion

In this study, we examined the influence of livestock grazing and environmental variation on ant assemblages from sites in a temperate agricultural region in southeastern Australia. Our results provide equivocal support for the global prediction that soil and vegetation have a greater effect on ant community composition than grazing (Hoffmann, 2010; Hoffmann & James, 2011). This is because we found that grazing history, stocking rate, and days grazed per year were also important for ant abundance, species richness, and compositional variation among sites, and suggests a more nuanced role for these different aspects of grazing pressure. Below we discuss our findings in light of the combined effects of the environment and grazing, and the implications of our findings for using reduced grazing to restore ant communities.

Environmental variation is a key driver of ant community structure

We found that at least one environmental variable occurred in all the best models we constructed, except for abundance of cold climate specialists. This includes the whole ant assemblage, different functional groups and individual species, and demonstrates the overall importance of plant and soil attributes on ant community structure. It is notable that exotic grass cover was an important driver of the abundance and richness of the whole ant assemblage (potentially influenced by outliers, Fig. 1a), but was not important for functional groups of individual species. This higher level response of the ant community, but not functional groups of individual species, suggests that exotic grass cover could be a general predictor of simpler ant communities with lower diversity. Our constrained ordination showed that grass biomass and leaf litter cover were strongly correlated (but in opposite directions) with the strongest gradient in ant compositional variation (axis 1, Fig. 4). This variation is typical of the structure of grassy eucalypt woodlands, where eucalypt trees are interspersed with patches of grassland (Yates & Hobbs, 1997). The heterogeneous structure of grassy woodlands therefore appears to be an important driver of overall assemblage composition as well as key functional groups. For example, the abundance of cryptic species was best explained by leaf litter (Fig. 2b), which is their preferred habitat (Bestelmeyer & Wiens, 1996; Hoffmann & Andersen, 2003). Leaf litter cover also was positively correlated with the number of tree stems, and soil C:N ratio. The abundance of the subdominant Camponotini was positively associated with C:N ratio, indicating they preferred more wooded areas. In contrast, *Nylanderia* spA (an opportunist) was negatively associated with the number of tree stems, indicating they prefer more open areas, and this was supported by our ordination showing a correlation between sites characterised by *Nylanderia* and higher grassy biomass and native grass cover.

A second important environmental gradient was obvious in our constrained ordination, and was represented by a change from high exotic perennial grass to high native perennial grass cover. Sites with high native grass cover were characterised by the occurrence of the opportunist *R. metallica*, whereas sites with exotic grass cover were characterised by the presence of the cold climate specialist *H. imbellis*. Notably, we also found that exotic grass cover was the best predictor of the abundance and richness of the overall ant community. Yet, this variable also was correlated with the two short-term

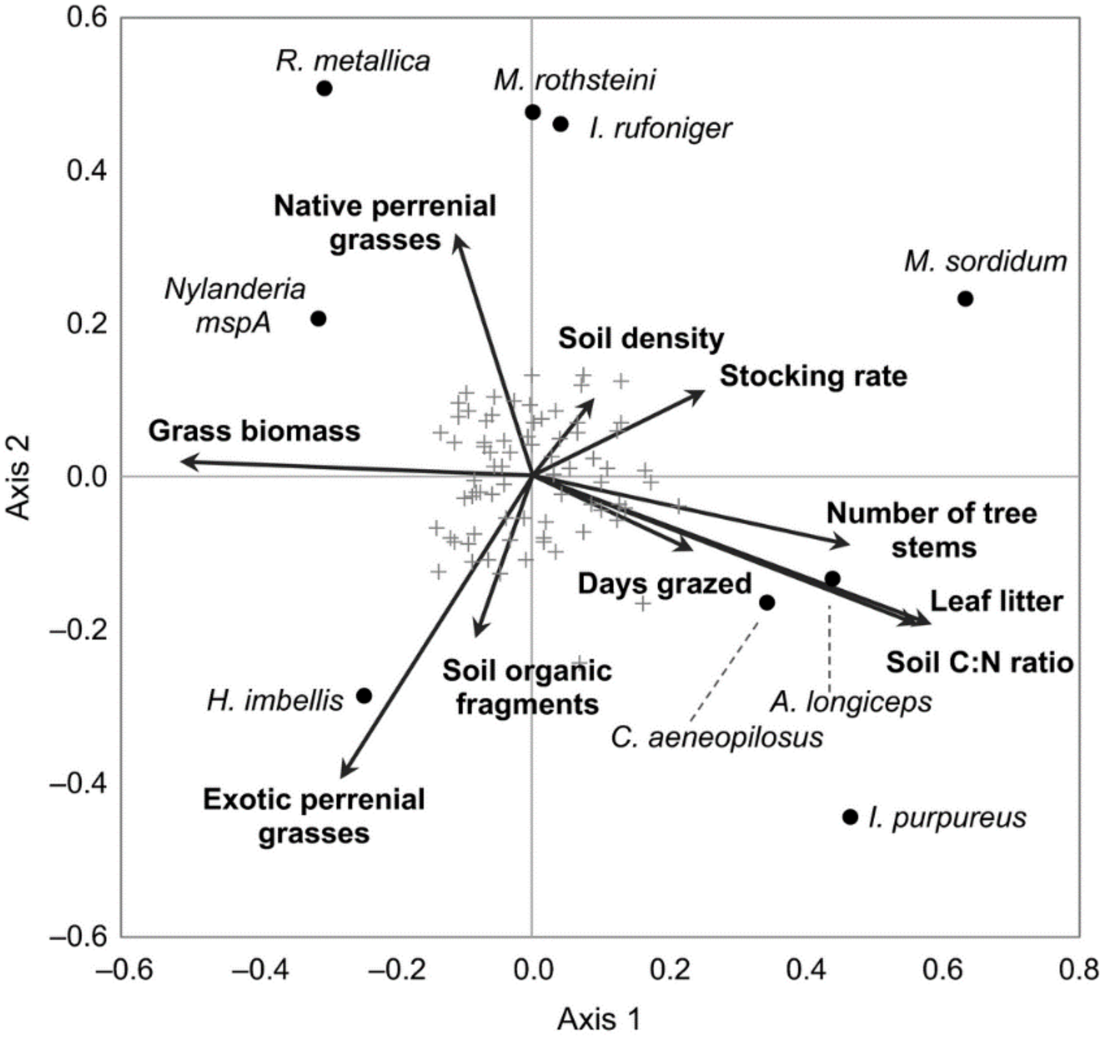


Figure 4. *Canonical Analysis of Principal Coordinates ordination showing variation in ant species composition among sites (crosses) and strength and direction of correlations of constraining environmental and grazing variables (dark arrows). Individual ant species (black dots) strongly correlated with the axes in each quadrant of the ordination are also shown to indicate their relative influence on species composition among sites.*

grazing measures, and highlights the difficulty in separating these confounded and co-linear measures.

Effects of grazing

In addition to environmental effects, we also found compelling evidence of both long-term (grazing history) effects and short-term (days grazed, stocking rate) effects of grazing on ant assemblages. Grazing history, stocking rate, or days grazed were frequently identified as important predictors of the abundance or species richness of ant functional groups we examined (but not the whole community). It has been suggested that coarse response metrics such as abundance or richness are often not suitable for detecting the responses of ants to grazing as they can mask the responses of individual species within the assemblage (Hoffmann, 2010). But, we also found a significant (albeit weak) difference in ant assemblage composition between the three grazing history blocks. Past grazing practices therefore appear to be an important driver of differences in ant assemblages. Variation in grazing pressure was also correlated with variation in ant assemblage composition, even after controlling for environmental variation, indicating it has a separate effect in addition to the environment.

We found that eight of the nine individual ant species we analysed had at least one grazing variable in the best model constructed for them. This is more than the general prediction that approximately one quarter to one third of common ant species will display a response to grazing (Hoffmann & James, 2011), although it was to possible to examine all species. Furthermore, the species for which grazing was important were from a mix of functional groups, and not just opportunists as might be expected. For example we found that *I. rufoniger*, a dominant dolichoderine, had a negative association with the number of days grazed. This contrasts with Lindsay *et al*. (2009), who found a positive effect of grazing on dominant dolichoderines (i.e. *Iridomyrmex* spp.) in grassy woodland remnants, although their result may have been driven by a different species of *Iridomyrmex*. These apparently idiosyncratic yet common responses to grazing may be due to the different measures of grazing used in our study compared with others (e.g. fixed treatments vs. continuous measures), or other interacting disturbances that may not be accounted for, such as fire history (Foster et al., 2014). A key conclusion from our study is that both historical and contemporary grazing practices appear to be important for shaping ant communities, but that these different measures of grazing may each be important in distinct ways. The builds on other studies of grazing impacts on ants (e.g. Bestelmeyer & Wiens, 1996; Hoffmann & James, 2011) by demonstrating that a single measure of grazing may be insufficient to characterise its influence on insect biodiversity.

Implications for biodiversity restoration

We have shown that grazing, vegetation, and soils were important drivers of ant community structure. Yet, it remains unclear the degree to which historical grazing practices may have altered the environment in our study area, and we found limited evidence of differences in key environmental variables across the three broad grazing history blocks in our study design. Nevertheless, our PCA did identify co-linearity between exotic perennial grass cover and short-term grazing measures, suggesting some important confounding among key grazing and environmental variables. It is well established that grazing changes soil and plant community attributes (Milchunas & Lauenroth, 1993; Yates et al., 2000), and the impact of grazing on temperate eucalypt woodlands has previously been demonstrated (Bromham et al., 1999; Eldridge et al., 2011; Prober & Wiehl, 2011). In contrast, little is known about the historical diversity patterns of ants in temperate woodlands of southeastern Australia, and it is difficult to conceptualise appropriate restoration goals for ant communities. What is clear, is that restoration actions that target reductions in livestock grazing should lead to improved tree regeneration (Fischer et al., 2009), subsequent increases in tree densities and leaf litter cover, and improved native ground cover and soil organic content (Yates et al., 2000; Prober & Wiehl, 2011). This will benefit some ant functional groups over others, such as cryptic species associated with litter and soil processes, and generalist myrmecines and subordinate camponotini linked to many other ecological processes (Bestelmeyer & Wiens, 1996; Folgarait, 1998; Hoffmann & Andersen, 2003).

Monitoring of ant communities to understand the benefits of changed grazing regimes to restore biodiversity should consider the historical context of gazing, contemporary grazing pressure, as well as the many underlying effects of plants and soils. A key challenge for ant biodiversity restoration in grazing-dominated landscapes will be disentangling grazing from environmental effects, and aligning this knowledge with restoration goals that focus on returning both ant biodiversity and their ecological functions.

Acknowledgements

We thank Derek Smith at the Australian Museum for sorting and identifying ants from our samples. Andrew Higgins at the Australian National University performed the soil chemistry analysis. DBL was funded by an Australian Research Council Laureate Fellowship. Ian Packer from the former Lachlan Catchment Management Authority provided invaluable advice in experimental design and sampling techniques.

References

Abbott, I., Parker, C.A. & Sills, I.D. (1979) Changes in the abundance of large soil animals and physical properties of soils following cultivation. Australian Journal of Soil Research, 17, 343–353.

Andersen, A.N. (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography, 22, 15–29.

Andersen, A.N. (1997) Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography, 24, 433–460.

Andersen, A.N. & Majer, J.D. (2004) Ants show the way Down Under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment, 2, 291–298.

Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology, 84, 511–525.

Barton, P.S. & Moir, M.L. (2015) Invertebrate indicators in restoration ecology. Surrogates and Indicators in Ecology, Conservation and Environmental Management. (ed. by D. Lindenmayer, J. Pierson and P. Barton), CSIRO Publishing, Melbourne, Victoria.

Beever, E.A., Tausch, R.J. & Brussard, P.F. (2003) Characterizing grazing disturbance in semiarid ecosystems across broad scales, using diverse indices. Ecological Applications, 13, 119–136.

Bestelmeyer, B.T. & Wiens, J.A. (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. Ecological Applications, 6, 1225–1240.

Bestelmeyer, B.T. & Wiens, J.A. (2001) Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. Ecological Applications, 11, 1123–1140.

Bottinelli, N., Jouquet, P., Capowiez, Y., Podwojewski, P., Grimaldi, M. & Peng, X. (2015) Why is the influence of soil macrofauna on soil structure only considered by soil ecologists? Soil & Tillage Research, 146, 118–124.

Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs, 27, 326–349.

Bromham, L., Cardillo, M., Bennett, A.F. & Elgar, M.A. (1999) Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Australian Journal of Ecology, 24, 199–207.

de Bruyn, L.A.L. (1999) Ants as bioindicators of soil function in rural environments. Agriculture Ecosystems & Environment, 74, 425–441.

Correll, O., Isselstein, J. & Pavlu, V. (2003) Studying spatial and temporal dynamics of sward structure at low stocking densities: the use of an extended rising-plate-meter method. Grass and Forage Science, 58, 450–454.

Dorrough, J.W., Ash, J.E., Bruce, S. & McIntyre, S. (2007) From plant neighbourhood to landscape scales: how grazing modifies native and exotic plant species richness in grassland. Plant Ecology, 191, 185–198.

Driscoll, D.A., Catford, J.A., Barney, J.N., Hulme, P.E., Inderjit, I., Martin, T.G., Pauchard, A., Pyšek, P., Richardson, D.M., Riley, S. & Visser, V. (2014) New pasture plants intensify invasive species risk. Proceedings of the National Academy of Sciences of the United States of America, 111, 16622–16627.

Eldridge, D.J., Val, J. & James, A.I. (2011) Abiotic effects predominate under prolonged livestock-induced disturbance. Austral Ecology, 36, 367–377.

Evans, T.A., Dawes, T.Z., Ward, P.R. & Lo, N. (2011) Ants and termites increase crop yield in a dry climate. Nature Communications, 2, 262.

Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K. & Forrester, R.I. (2009) Reversing a tree regeneration crisis in an endangered ecoregion. Proceedings of the National Academy of Sciences of the United States of America, 106, 10386–10391.

Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation, 7, 1221–1244.

Foster, C.N., Barton, P.S. & Lindenmayer, D.B. (2014) Effects of large native herbivores on other animals. Journal of Applied Ecology, 51, 929–938.

Gibbons, P., Briggs, S.V., Ayers, D.A., Doyle, S., Seddon, J., McElhinny, C., Jones, N., Sims, R. & Doody, J.S. (2008) Rapidly quantifying reference conditions in modified landscapes. Biological Conservation, 141, 2483–2493.

Gotelli, N.J. & Ellison, A.M. (2004) A Primer of Ecological Statistics. Sinauer Associates Inc, Sunderland, Vermont.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates. Journal of Wildlife Management, 60, 695–713.

Hoffmann, B.D. (2010) Using ants for rangeland monitoring: global patterns in the responses of ant communities to grazing. Ecological Indicators, 10, 105–111.

Hoffmann, B.D. & Andersen, A.N. (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecology, 28, 444–464.

Hoffmann, B.D. & James, C.D. (2011) Using ants to manage sustainable grazing: dynamics of ant faunas along sheep grazing gradients conform to four global patterns. Austral Ecology, 36, 698–708.

Holldobler, B. & Wilson, E.O. (1990) The Ants. Harvard University Press, Cambridge, Massachusetts.

King, J.R., Andersen, A.N. & Cutter, A.D. (1998) Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. Biodiversity and Conservation, 7, 1627–1638.

Kruess, A. & Tscharntke, T. (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conservation Biology, 16, 1570–1580.

Lindsay, E.A. & Cunningham, S.A. (2009) Livestock grazing exclusion and microhabitat variation affect invertebrates and litter decomposition rates in woodland remnants. Forest Ecology and Management, 258, 178–187.

Lindenmayer, D.B., Zammit, C., Attwood, S.J., Burns, E., Shepherd, C.L., Kay, G. & Wood, J. (2012) A novel and cost-effective monitoring approach for outcomes in an Australian biodiversity conservation incentive program. PLoS ONE, 7, e50872.

Lunt, I.D., Eldridge, D.J., Morgan, J.W. & Witt, G.B. (2007) A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. Australian Journal of Botany, 55, 401–415.

Matejovic, I. (1997) Determination of carbon and nitrogen in samples of various soils by the dry combustion. Communications in Soil Science and Plant Analysis, 28, 1499–1511.

McCune, B. & Mefford, M.J. (2011) PC-ORD. Multivariate Analysis of Ecological Data, Version 6.19. MjM Software, Gleneden Beach, Oregon.

McIntyre, S., Cunningham, R.B., Donnelly, C.F. & Manning, A.D. (2014) Restoration of eucalypt grassy woodland: effects of experimental interventions on ground-layer vegetation. Australian Journal of Botany, 62, 570–579.

Mclaren, C. (1997) Dry Sheep Equivalents for Comparing Different Classes of Livestock. Department of Primary Industries, Melbourne, Victoria.

Milchunas, D.G. & Lauenroth, W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs, 63, 327–366.

Milchunas, D.G., Lauenroth, W.K. & Burke, I.C. (1998) Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. Oikos, 83, 65–74.

Prober, S.M. & Wiehl, G. (2011) Resource heterogeneity and persistence of exotic annuals in long-ungrazed Mediterranean-climate woodlands. Biological Invasions, 13, 2009–2022.

Read, J.L. & Andersen, A.N. (2000) The value of ants as early warning bioindicators: responses to pulsed cattle grazing at an Australian arid zone locality. Journal of Arid Environments, 45, 231–251.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. & Mills, J. (2004) Matching type of livestock to desired biodiversity outcomes in pastures - a review. Biological Conservation, 119, 137–150.

Schuman, G.E., Reeder, J.D., Manley, J.T., Hart, R.H. & Manley, W.A. (1999) Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications, 9, 65–71.

Schwarz, G. (1978) Estimating the dimension of a model. Annals of Statistics, 6, 461–464.

Seymour, C.L. & Dean, W.R.J. (1999) Effects of heavy grazing on invertebrate assemblages in the Succulent Karoo, South Africa. Journal of Arid Environments, 43, 267–286.

Sokal, R.R. & Rohlf, F.J. (1995) Biometry: The Principles and Practice of Statistics in Biological Research, 3rd edn. W. H. Freeman and Co., New York City, New York.

VSN International. (2013) GenStat for Windows, 16th Edition. VSN International, Hemel Hempstead.

Whitford, W.G., Van Zee, J., Nash, M.S., Smith, W.E. & Herrick, J.E. (1999) Ants as indicators of exposure to environmental stressors in North American desert grasslands. Environmental Monitoring and Assessment, 54, 143–171.

Yates, M.L., Gibb, H. & Andrew, N.R. (2011) Habitat characteristics may override climatic influences on ant assemblage composition: a study using a 300-km climatic gradient. Australian Journal of Zoology, 59, 332–338.

Yates, C.J. & Hobbs, R.J. (1997) Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. Australian Journal of Botany, 45, 949–973.

Yates, C.J., Norton, D.A. & Hobbs, R.J. (2000) Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecology, 25, 36–47.

Zimmerman, G.M., Goetz, H. & Mielke, P.W. (1985) Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology, 66, 606–611.

Supporting Information

Figure S1. *(a) Our study was located in southeast Australia, (b) with sites located on farms between the towns of Orange and Yass. (c) Sites were 0.8 hectares in size (40m x 200m) with 20x50m quadrats at either end for vegetation surveys. Soil cores were taken from a transect along centre of each site, and bulked into three sub-samples. Multiple soil and vegetation data from each site were averaged to give one measure per site. Ants were collected using four pitfall traps arranged in a square at each end of the site, three traps were randomly selected, sorted, and pooled to give one sample per site. All sites were located in Red gum (Eucalyptus blakelyi) - Yellow box (Eucalyptus melliodora) grassy woodland vegetation, which is characterised by a heterogeneous distribution of trees interspersed with grassland.*

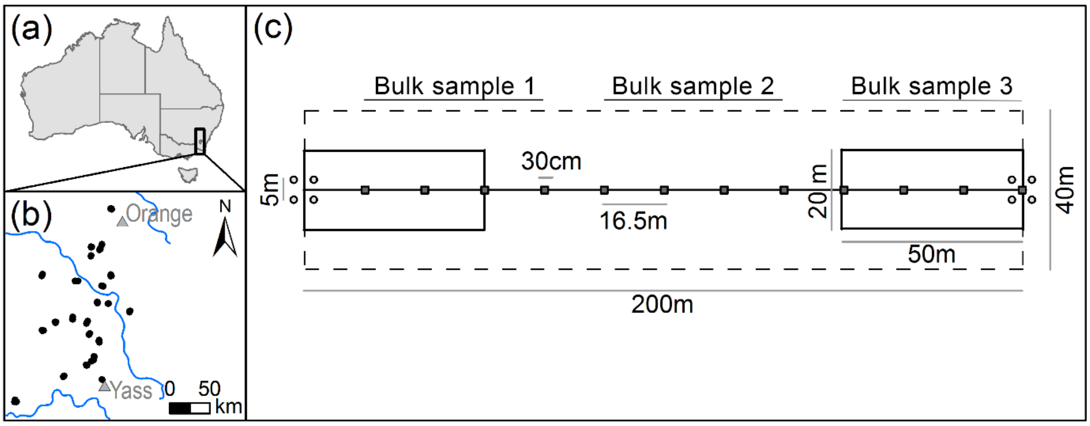


Figure S2. Example of a site from our study area showing the open woodland structure that is typical of the box-gum grassy woodland ecological community. Livestock grazing on some of the sites was by sheep or cattle.

Table S1. *Description of ant functional groups (adapted from Andersen, 1997; Hoffmann & Andersen, 2003; King et al., 1998). *Not analysed in this study.*

Functional Group and major genera	Ecological characteristics
Dominant Dolichoderinae (Iridomyrmex, Anonychomyrma)	Abundant, active, aggressive species that favour hot and open habitats. Strongly competitively dominant over other ants species
Subdominant Camponotini (Camponotus, Polurachis, Opisthopsis)	Co-occurring with, but behaviourally submissive to, Dominant Dolichoderinae. Large body size, nocturnal foraging.
Generalized Myrmecinae (Pheidole, Monomorium, Crematogaster)	Cosmopolitan genera occurring in most habitats. Rapid recruitment and defence of clumped food resources.
Opportunists (Rhytidoponera, Paratrechina, Aphaenogaster, Tetramorium)	Unspecialized ‘weedy’ species characteristic of disturbed sites, or habitat supporting low ant diversity
Hot Climate Specialists (Melophorus, Meranoplus, Monomorium (part))	Arid-adapted species with specializations that reduce interactions with Dominant Dolichoderinae.
Cold Climate Specialists (Prolasius, Notoncus, Monomorium (part))	Distribution in the cool temperate zone,Most abundant where Dominant Dolichderinae are generally not abundant.
Cryptic Species (Solenopsis, Hypoponera, small ponerines and mymecines)	Forage predominantly within soil and litter, little interaction with epigaeic ants.
*Tropical Climate Specialists (Oecophylla, Tetraponera, many other tropical taxa))	Distribution in the humid tropics. Occur in habitat where Dominant Dolichoderinae are not abundant.
*Specialist Predators (Myrmecia, Cerapachys, large ponerines)	Little interaction with other ants due to specialised diet, large body size, small colony size.

Andersen, A.N. (1997) Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography, 24, 433-460.

Hoffmann, B.D. & Andersen, A.N. (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecology, 28, 444-464.

King, J.R., Andersen, A.N., & Cutter, A.D. (1998) Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. Biodiversity and Conservation, 7, 1627-1638.

Table S2. *List of ant species arranged by subfamily and functional group, their total count, and their mean (±SD) count per site (n=78). Ant specimens were counted and identified to species (or assigned to a morphospecies) by a specialist taxonomist, and retained at the Australian Museum, Sydney.*

Subfamily	**Species name**	**Functional group**	**Count**	**Mean**	**SD**
Aenictinae	*Aenictus turneri*	Cryptic species	7	0.09	0.56
Cerapachyinae	*Sphinctomyrmex msp. A*	Cryptic species	7	0.09	0.59
Cerapachyinae	*Cerapachys msp. A*	Specialist predators	1	0.01	0.11
Dolichoderinae	*Anonychomyrma msp. A*	Dominant Dolichoderinae	1	0.01	0.11
Dolichoderinae	*Iridomyrmex bicknelli*	Dominant Dolichoderinae	328	4.21	22.19
Dolichoderinae	*Iridomyrmex discors*	Dominant Dolichoderinae	16	0.21	1.31
Dolichoderinae	*Iridomyrmex msp. A*	Dominant Dolichoderinae	1	0.01	0.11
Dolichoderinae	*Iridomyrmex msp. B*	Dominant Dolichoderinae	33	0.42	1.31
Dolichoderinae	*Iridomyrmex msp. C*	Dominant Dolichoderinae	8	0.10	0.47
Dolichoderinae	*Iridomyrmex msp. D*	Dominant Dolichoderinae	329	4.22	8.13
Dolichoderinae	*Iridomyrmex msp. E*	Dominant Dolichoderinae	21	0.27	1.35
Dolichoderinae	*Iridomyrmex msp. F*	Dominant Dolichoderinae	3714	47.62	298.52
Dolichoderinae	*Iridomyrmex msp. G*	Dominant Dolichoderinae	98	1.26	3.98
Dolichoderinae	*Iridomyrmex msp. H*	Dominant Dolichoderinae	3	0.04	0.34
Dolichoderinae	*Iridomyrmex purpureus*	Dominant Dolichoderinae	1040	13.33	40.41
Dolichoderinae	*Iridomyrmex rufoniger*	Dominant Dolichoderinae	4541	58.22	108.27
Dolichoderinae	*Iridomyrmex spp*	Dominant Dolichoderinae	10	0.13	0.41
Dolichoderinae	*Ochetellus msp. A*	Opportunists	1	0.01	0.11
Dolichoderinae	*Tapinoma msp. A*	Opportunists	150	1.92	3.66
Ectatomminae	*Rhytidoponera metallica*	Opportunists	926	11.87	28.13
Formicinae	*Notoncus capitatus*	Cold climate specialists	15	0.19	1.59
Formicinae	*Notoncus ectatommoides*	Cold climate specialists	267	3.42	7.71
Formicinae	*Prolasius msp. A*	Cold climate specialists	3	0.04	0.25
Formicinae	*Stigmacros msp. A*	Cold climate specialists	6	0.08	0.31
Formicinae	*Stigmacros msp. B*	Cold climate specialists	1	0.01	0.11
Formicinae	*Acropyga msp. A*	Cryptic species	2	0.03	0.23
Formicinae	*Melophorus msp. A*	Hot climate specialists	101	1.29	4.71
Formicinae	*Melophorus msp. B*	Hot climate specialists	20	0.26	1.05
Formicinae	*Melophorus msp. C*	Hot climate specialists	82	1.05	8.05
Formicinae	*Melophorus msp. D*	Hot climate specialists	2	0.03	0.16
Formicinae	*Melophorus msp. E*	Hot climate specialists	33	0.42	1.36
Formicinae	*Melophorus msp. F*	Hot climate specialists	5	0.06	0.29

Subfamily	**Species name**	**Functional group**	**Count**	**Mean**	**SD**
Formicinae	*Melophorus msp. G*	Hot climate specialists	172	2.21	12.15
Formicinae	*Melophorus msp. H*	Hot climate specialists	182	2.33	2.89
Formicinae	*Melophorus msp. J*	Hot climate specialists	36	0.46	2.54
Formicinae	*Melophorus spp*	Hot climate specialists	164	2.10	5.33
Formicinae	*Nylanderia msp. A*	Opportunists	453	5.81	13.83
Formicinae	*Paraparatrechina minutula*	Other	93	1.19	3.61
Formicinae	*Camponotus aeneopilosus*	Subdominant Camponotini	77	0.99	4.11
Formicinae	*Camponotus consobrinus*	Subdominant Camponotini	60	0.77	2.85
Formicinae	*Camponotus ephippium*	Subdominant Camponotini	5	0.06	0.47
Formicinae	*Camponotus msp. A*	Subdominant Camponotini	5	0.06	0.47
Formicinae	*Camponotus msp. B*	Subdominant Camponotini	6	0.08	0.27
Formicinae	*Camponotus msp. C*	Subdominant Camponotini	1	0.01	0.11
Formicinae	*Camponotus msp. D*	Subdominant Camponotini	3	0.04	0.25
Formicinae	*Camponotus nigriceps*	Subdominant Camponotini	18	0.23	0.60
Formicinae	*Camponotus nigroaeneus*	Subdominant Camponotini	5	0.06	0.29
Heteroponerinae	*Heteroponera imbellis*	Cold climate specialists	39	0.50	2.79
Myrmeciinae	*Myrmecia pilosula*	Specialist predators	1	0.01	0.11
Myrmicinae	*Solenopsis msp. A*	Cryptic species	52	0.67	1.22
Myrmicinae	*Strumigenys msp. B*	Cryptic species	1	0.01	0.11
Myrmicinae	*Strumigenys perplexa*	Cryptic species	1	0.01	0.11
Myrmicinae	*Crematogaster msp. A*	Generalist Myrmecinae	150	1.92	6.09
Myrmicinae	*Crematogaster msp. B*	Generalist Myrmecinae	2	0.03	0.16
Myrmicinae	*Monomorium msp. A*	Generalist Myrmecinae	182	2.33	5.28
Myrmicinae	*Monomorium msp. B*	Generalist Myrmecinae	67	0.86	4.31
Myrmicinae	*Monomorium msp. D*	Generalist Myrmecinae	13	0.17	0.84
Myrmicinae	*Monomorium msp. E*	Generalist Myrmecinae	42	0.54	1.66
Myrmicinae	*Monomorium msp. F*	Generalist Myrmecinae	49	0.63	2.37
Myrmicinae	*Monomorium msp. G*	Generalist Myrmecinae	1	0.01	0.11
Myrmicinae	*Monomorium msp. H*	Generalist Myrmecinae	10	0.13	0.63
Myrmicinae	*Monomorium msp. J*	Generalist Myrmecinae	10	0.13	0.93
Myrmicinae	*Monomorium rothsteini*	Generalist Myrmecinae	1454	18.64	64.04
Myrmicinae	*Monomorium sordidum*	Generalist Myrmecinae	2210	28.33	93.64
Myrmicinae	*Monomorium spp.*	Generalist Myrmecinae	2	0.03	0.16
Myrmicinae	*Pheidole msp. A*	Generalist Myrmecinae	281	3.60	11.40
Myrmicinae	*Pheidole msp. B*	Generalist Myrmecinae	2617	33.55	68.92

Subfamily	Species name	Functional group	Count	Mean	SD
Myrmicinae	*Pheidole msp. C*	Generalist Myrmecinae	75	0.96	6.85
Myrmicinae	*Pheidole msp. D*	Generalist Myrmecinae	432	5.54	18.02
Myrmicinae	*Pheidole msp. E*	Generalist Myrmecinae	47	0.60	4.23
Myrmicinae	*Pheidole msp. F*	Generalist Myrmecinae	290	3.72	18.51
Myrmicinae	*Pheidole msp. G*	Generalist Myrmecinae	6	0.08	0.50
Myrmicinae	*Pheidole msp. H*	Generalist Myrmecinae	465	5.96	19.71
Myrmicinae	*Pheidole spp.*	Generalist Myrmecinae	8	0.10	0.35
Myrmicinae	*Adlerzia froggatti*	Hot climate specialists	12	0.15	0.91
Myrmicinae	*Meranoplus msp. A*	Hot climate specialists	44	0.56	2.92
Myrmicinae	*Meranoplus msp. B*	Hot climate specialists	11	0.14	0.42
Myrmicinae	*Aphaenogaster longiceps*	Opportunists	123	1.58	8.10
Myrmicinae	*Cardiocondyla msp. A*	Opportunists	23	0.29	1.42
Myrmicinae	*Tetramorium msp. A*	Opportunists	34	0.44	1.20
Myrmicinae	*Tetramorium msp. B*	Opportunists	13	0.17	0.97
Myrmicinae	*Anillomyrma msp.*	Other	1	0.01	0.11
Myrmicinae	*Mayriella msp. A*	Tropical climate specialists	2	0.03	0.23
Ponerinae	*Hypoponera msp. A*	Cryptic species	1	0.01	0.11
Ponerinae	*Pachycondyla lutea*	Other	235	3.01	26.61
Ponerinae	*Pachycondyla msp. A*	Other	1	0.01	0.11
Ponerinae	*Anochetus armstrongi*	Specialist predators	2	0.03	0.16

Table S3. *Summary of models of abundance and species richness of ant functional groups identified using all-subsets generalised linear regression. Models shown are within two SIC. Significance of variables was determined using deviance ratios.*

Functional Group	**Measure**	**SIC**	**R^2**	**d.f.**	**GH**	**BG**	**LL**	**TS**	**SCN**	**SO**	**SD**	**NPG**	**EPG**	**ASR**	**DGY**
Whole assemblage	Abundance	81.12	8.61	2	-	-	-	-	-	-	-	-	0.011	-	-
		82.28	12.57	3	-	-	-	-	-	-	-	-	0.008	0.077	-
		83.00	11.66	3	-	-	-	-	-	-	-	-	0.007	-	0.122
	Species richness	88.31	11.55	2	-	-	-	-	-	-	-	-	0.003	-	-
		88.88	15.70	3	-	-	-	-	-	-	-	0.066	0.002	-	-
		90.28	14.15	3	-	-	-	-	-	-	-	-	0.002	0.147	-
		90.57	13.82	3	-	0.176	-	-	-	-	-	-	0.003	-	-
		89.67	19.59	4	-	0.070	-	-	-	-	-	0.028	0.002	-	-
		90.66	18.49	4	-	-	-	-	-	-	-	0.057	0.001	0.126	-
Subdominant Camponotini	Abundance	79.52	9.31	2	-	-	-	-	0.008	-	-	-	-	-	-
		81.57	6.69	2	-	-	0.026	-	-	-	-	-	-	-	-
		81.27	12.57	3	-	-	-	-	0.013	-	-	-	-	-	0.108
	Species richness	87.59	17.70	3	-	-	-	-	0.001	-	-	-	-	0.039	-
		88.49	16.72	3	-	-	-	-	0.008	-	-	-	0.064	-	-
		86.54	23.61	4	-	-	-	-	0.000	-	-	-	-	0.005	0.023
		88.04	21.96	4	-	-	-	-	0.006	-	-	-	0.055	0.034	-
		88.13	26.59	5	-	-	-	-	0.002	-	-	-	0.099	0.006	0.041
Opportunists	Abundance	93.45	39.86	4	-	-	-	0.000	-	-	0.000	0.009	-	-	-
		94.29	42.59	5	-	-	-	0.000	-	0.074	0.000	0.002	-	-	-
		94.56	42.38	5	-	-	-	0.007	0.087	-	0.000	0.022	-	-	-
		95.28	41.81	5	-	-	-	0.000	-	-	0.000	0.008	-	-	0.133
		95.38	41.73	5	-	-	-	0.000	-	-	0.000	0.011	0.141	-	-
		95.78	41.42	5	-	-	-	0.000	-	-	0.000	0.006	-	0.180	-
		95.14	45.32	6	-	-	-	0.000	-	0.038	0.000	0.002	0.070	-	-
		95.61	44.95	6	-	-	-	0.004	0.093	0.080	0.000	0.006	-	-	-
	Species richness	84.24	31.28	3	-	-	-	-	0.000	-	-	-	0.000	-	-
		87.66	32.13	4	-	-	-	-	0.000	-	-	-	0.000	0.352	-
		87.87	31.93	4	-	-	-	-	0.000	-	-	0.418	0.000	-	-
		87.96	31.84	4	-	-	0.451	-	0.004	-	-	-	0.000	-	-
		87.99	31.81	4	-	-	-	-	0.000	0.462	-	-	0.000	-	-

Functional Group	Measure	SIC	R^2	d.f.	GH	BG	LL	TS	SCN	SO	SD	NPG	EPG	ASR	DGY
Cryptic species	Abundance	81.41	11.20	2	-	-	0.004	-	-	-	-	-	-	-	-
		82.52	9.86	2	-	0.006	-	-	-	-	-	-	-	-	-
		83.30	14.15	3	-	-	0.002	-	-	-	-	-	-	-	0.123
		83.59	13.80	3	-	0.002	-	-	-	-	-	-	-	-	0.076
		83.80	13.54	3	-	-	0.009	-	-	-	0.170	-	-	-	-
	Species richness	76.91	4.77	2	-	-	-	-	-	-	0.062	-	-	-	-
		77.14	4.46	2	-	-	0.071	-	-	-	-	-	-	-	-
		77.42	4.06	2	-	-	-	-	0.085	-	-	-	-	-	-
		77.59	3.82	2	-	0.095	-	-	-	-	-	-	-	-	-
		77.79	3.55	2	-	-	-	0.108	-	-	-	-	-	-	-
Dominant Dolichoderinae	Abundance	93.76	4.88	2	-	-	-	-	-	-	-	-	0.059	-	-
		91.84	21.44	5	0.004	-	-	-	0.012	-	0.006	-	-	-	-
		93.63	19.44	5	0.017	-	-	-	-	-	0.012	-	0.032	-	-
		93.24	24.68	6	0.007	-	-	-	-	-	0.006	-	0.010	-	0.033
		93.64	24.23	6	0.006	-	-	-	0.042	-	0.004	-	0.118	-	-
		93.84	24.01	6	0.002	-	-	-	0.014	-	0.005	-	-	-	0.134
	Species richness	84.55	4.89	2	-	-	-	-	-	-	-	-	-	-	0.058
		85.10	4.20	2	-	0.080	-	-	-	-	-	-	-	-	-
		83.25	11.91	3	-	0.020	-	-	-	-	-	-	-	-	0.015
		85.06	15.03	4	0.015	0.016	-	-	-	-	-	-	-	-	-
		83.43	17.07	4	-	0.006	-	-	-	-	-	0.040	-	-	0.006
Generalist Myrmicinae	Abundance	90.66	24.24	3	-	-	-	-	-	-	-	-	0.021	0.000	-
		90.58	28.51	4	-	-	0.026	-	-	0.019	-	-	-	0.001	-
		88.60	34.64	5	-	-	0.001	-	0.013	0.003	-	-	-	0.001	-
		90.86	32.43	5	-	-	0.006	-	0.023	-	-	-	0.010	0.000	-
		90.15	37.33	6	-	-	0.002	-	0.008	0.024	-	-	0.092	0.001	-
	Species richness	85.58	6.68	2	-	-	-	-	-	-	-	0.026	-	-	-
		86.62	5.42	2	-	-	-	0.046	-	-	-	-	-	-	-
		87.17	4.75	2	-	-	-	-	-	-	-	-	0.062	-	-
		85.64	11.83	3	-	-	-	0.045	-	-	-	0.026	-	-	-
		85.65	11.82	3	-	-	-	-	0.046	-	-	0.010	-	-	-
		85.68	11.78	3	-	-	-	-	-	-	-	0.020	0.047	-	-

		86.97	10.21	3	-	0.099	-	-	-	-	-	0.012	-	-	-
		87.90	9.08	3	-	-	-	-	-	-	0.175	0.023	-	-	-
		87.95	9.02	3	-	-	-	-	-	-	-	0.025	-	0.181	-
		86.65	15.82	4	-	-	-	0.071	-	-	-	0.018	0.073	-	-
		87.07	15.30	4	-	0.092	-	-	-	-	-	0.009	0.044	-	-
		87.12	15.25	4	-	-	-	-	0.095	-	-	0.009	0.097	-	-
		87.24	15.10	4	-	-	-	-	-	-	-	0.017	0.028	0.103	-
		87.89	14.31	4	-	-	-	-	0.041	-	-	0.009	-	0.158	-
Hot climate specialists	Abundance	88.90	5.73	2	-	-	-	-	-	-	-	-	-	-	0.040
		86.49	13.61	3	-	0.013	-	-	-	-	-	-	-	-	0.007
		87.21	17.82	4	-	0.002	-	0.063	-	-	-	-	-	-	0.008
		88.29	16.55	4	-	0.006	-	-	-	-	-	0.121	-	-	0.004
		88.55	16.25	4	-	0.004	-	-	0.143	-	-	-	-	-	0.006
		88.70	16.08	4	-	0.017	-	-	-	-	-	-	0.156	-	0.012
		88.93	15.80	4	-	0.010	-	-	-	0.182	-	-	-	-	0.009
		87.49	22.55	5	-	0.001	-	0.019	-	-	-	-	0.044	-	0.011
		88.39	21.49	5	-	0.001	-	0.041	-	-	-	0.077	-	-	0.004
		88.93	20.86	5	-	0.001	-	0.039	-	0.108	-	-	-	-	0.011
	Species richness	80.65	5.35	2	-	-	-	-	-	-	-	0.047	-	-	-
		81.64	4.04	2	-	-	-	-	-	-	-	-	0.086	-	-
		81.64	9.70	3	-	-	-	-	-	-	-	0.039	0.069	-	-
Cold climate specialists	Abundance	75.10	8.34	2	-	-	-	-	-	-	-	-	-	0.013	-
		77.15	5.51	2	-	-	-	-	-	-	-	-	-	-	0.044
	Species richness	75.17	5.22	2	-	-	-	-	-	0.050	-	-	-	-	-
		75.52	4.72	2	-	-	-	-	-	-	-	0.063	-	-	-
		77.71	1.60	2	-	-	-	-	-	-	-	-	-	0.283	-
		77.41	8.16	3	-	-	-	-	-	0.027	-	-	-	0.136	-
		77.97	7.36	3	-	-	-	-	-	0.159	-	0.204	-	-	-

^GH=Grazing history, GB=Grass biomass, LL=Leaf litter cover, TS=Tree stem count, SCN=Soil C:N ratio, SO=Soil organic fragments > 2mm, SD=Soil bulk density, NPG=Native perennial grass cove, EPG=Exotic perennial grasscover, ASR=Annual stocking rate, DGY=Days grazed per year

Table S4. *Summary of models of individual ant species identified using all-subsets generalised linear regression. Models shown are within two SIC. Significance of variables was determined using deviance ratios.*

Ant species	SIC	R^2	d.f.	GH	BG	LL	TS	SCN	SO	SD	NPG	EPG	ASR	DGY
Rhytidoponera metallica	102.79	54.67	7	0.002	-	-	0.000	-	0.012	0.000	0.000	-	-	-
	103.30	57.04	8	0.001	-	-	0.001	0.061	0.012	0.000	0.000	-	-	-
	104.27	56.43	8	0.002	-	-	0.000	-	0.013	0.000	0.000	-	0.107	-
Iridomyrmex rufoniger	89.45	35.22	6	-	0.001	0.000	-	0.011	-	-	-	0.012	-	0.007
	91.37	28.88	5	-	0.003	0.000	-	0.010	-	-	-	-	-	0.003
	91.54	28.71	5	-	0.001	0.001	-	-	-	-	-	0.011	-	0.006
Iridomyrmex purpureus	92.19	45.74	5	0.001	-	0.000	-	-	-	-	0.017	-	-	-
	93.97	41.07	4	0.000	-	0.000	-	-	-	-	-	-	-	-
	94.10	44.28	5	0.000	-	0.000	-	-	-	-	-	0.050	-	-
	94.58	43.91	5	0.001	-	-	-	0.000	0.003	-	-	-	-	-
	94.94	46.94	6	0.001	-	0.000	-	-	-	-	0.069	0.221	-	-
Monomorium rothsteini	98.84	54.04	6	-	0.001	0.002	-	-	-	0.016	-	-	0.008	0.027
	98.88	56.73	7	0.002	0.000	0.001	-	-	-	-	-	0.032	0.000	-
	99.41	59.10	8	0.014	0.000	0.000	-	-	-	0.054	-	0.032	0.032	-
	99.50	53.63	6	0.002	0.000	0.006	-	-	-	-	-	-	0.000	-
	99.61	58.98	8	0.001	0.001	0.000	0.061	-	-	-	-	0.040	0.000	-
	99.63	56.26	7	0.001	0.002	0.001	0.049	-	-	-	-	-	0.000	-
	99.66	50.82	5	-	0.000	0.000	-	-	-	0.000	-	0.026	-	-
	99.80	56.15	7	0.022	0.000	0.000	-	-	-	0.000	-	0.013	-	-
	99.82	56.14	7	0.019	0.001	0.002	-	-	-	0.054	-	-	0.013	-
	99.83	53.42	6	-	0.001	0.000	-	-	-	0.007	-	0.046	0.056	-
Monomorium sordidum	100.54	65.04	8	0.000	-	0.000	-	0.000	0.000	-	0.001	-	0.021	-
	101.88	62.05	7	0.000	-	0.000	-	0.000	0.000	-	0.002	-	-	-
	101.61	64.47	8	0.000	-	0.000	0.038	0.000	0.000	-	0.000	-	-	-
	102.72	63.89	8	0.000	-	0.000	-	0.000	0.000	-	0.001	-	-	0.072
Pheidole spB	96.45	36.97	7	0.002	-	-	-	0.005	-	-	0.023	0.004	0.001	-
	96.59	36.84	7	0.000	-	-	-	0.002	0.025	-	-	0.026	0.001	-
	97.43	31.96	6	0.001	-	-	-	0.009	0.015	-	-	-	0.003	-
	97.48	31.90	6	0.003	-	-	-	0.003	-	-	-	0.015	0.001	-
	98.13	39.47	8	0.001	-	-	-	0.004	0.104	-	0.095	0.009	0.001	-
	98.38	39.23	8	0.000	-	-	-	0.001	0.006	0.112	-	0.008	0.000	-
Nylanderia spA	83.38	23.70	3	-	-	-	0.000	-	-	0.015	-	-	-	-
	85.27	16.98	2	-	-	-	0.000	-	-	-	-	-	-	-
Notoncus ectatommoides	82.46	13.35	3	-	0.009	-	-	-	-	-	-	-	-	0.011
	83.03	12.65	3	-	0.021	-	-	-	-	-	-	-	0.016	-
	84.27	5.74	2	-	-	-	-	-	-	-	-	-	0.040	-
	84.77	5.12	2	-	0.053	-	-	-	-	-	-	-	-	-
Camponotus consobrinus	95.29	53.32	6	0.000	0.000	0.000	-	-	-	-	0.002	-	-	-
	96.98	55.08	7	0.000	0.000	0.000	-	-	0.110	-	0.009	-	-	-
	97.11	54.99	7	0.000	0.000	0.000	-	-	-	0.120	0.005	-	-	-
	97.37	54.82	7	0.000	0.000	0.000	-	0.141	-	-	0.001	-	-	-

^GH=Grazing history, GB=Grass biomass, LL=Leaf litter cover, TS=Tree stem count, SCN=Soil C:N ratio, SO=Soil organic fragments > 2mm, SD=Soil bulk density, NPG=Native perennial grass cove, EPG=Exotic perennial grass cover, ASR=Annual stocking rate, DGY=Days grazed per year

APPENDIX III. USING EMPIRICAL MODELS OF SPECIES COLONIZATION UNDER MULTIPLE THREATENING PROCESSES TO IDENTIFY COMPLEMENTARY THREAT-MITIGATION STRATEGIES.

Livestock grazing is recognised as a key management tool for the enhancement of biodiversity conservation value in private-protected areas. However, as highlighted in Paper IV in this thesis, little empirical evidence exists to support the ecological impacts of grazing.

As with the above paper (Appendix II), we again explore the impacts of livestock grazing on alternative taxonomic groups to better understand the role of livestock grazing on broader biodiversity of production landscapes; this time birds.

Tulloch, A.I.T., Mortelliti, A., Kay, G.M., Florance, D., Lindenmayer, D., 2016. Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies. Conserv. Biol. 4, 867-882. doi:10.1111/cobi.12672.

Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies.

Abstract

Approaches to prioritize conservation actions are gaining popularity. However, limited empirical evidence exists on which species might benefit most from threat mitigation and on what combination of threats, if mitigated simultaneously, would result in the best outcomes for biodiversity. We devised a way to prioritize threat mitigation at a regional scale with empirical evidence based on predicted changes to population dynamics-information that is lacking in most threat-management prioritization frameworks that rely on expert elicitation. We used dynamic occupancy models to investigate the effects of multiple threats (tree cover, grazing, and presence of an hyperaggressive competitor, the Noisy Miner (*Manorina melanocephala*) on bird-population dynamics in an endangered woodland community in southeastern Australia. The 3 threatening processes had different effects on different species. We used predicted patch-colonization probabilities to estimate the benefit to each species of removing one or more threats. We then determined the complementary set of threat-mitigation strategies that maximized colonization of all species while ensuring that redundant actions with little benefit were avoided. The single action that resulted in the highest colonization was increasing tree cover, which increased patch colonization by 5% and 11% on average across all species and for declining species, respectively. Combining Noisy Miner control with increasing tree cover increased species colonization by 10% and 19% on average for all species and for declining species respectively, and was a higher priority than changing grazing regimes. Guidance for prioritizing threat mitigation is critical in the face of cumulative threatening processes. By

incorporating population dynamics in prioritization of threat management, our approach helps ensure funding is not wasted on ineffective management programs that target the wrong threats or species.

Introduction

Understanding the impacts of threatening processes on native species is the first step toward clarifying choices among conservation actions (Burgman et al. 2007). Allocation of conservation effort should then depend on which strategies most efficiently mitigate the multiple threats acting in a landscape. The effectiveness of such allocation is influenced by how difficult threats are to abate, how each species might respond, and how many species might benefit (Evans et al. 2011). Much progress has been made in developing prioritization frameworks to answer the question of which threat or threats, if abated, would result in the best outcomes for multiple species (e.g., Visconti et al. 2010; Auerbach etal. 2014; Cattarino et al. 2015; Chadès et al. 2015). However, there is still little guidance for practitioners about how best to quantify the impacts of threats and their mitigating actions in a way that reflects real responses in ecological processes over time (but see Santika et al. 2015; Tulloch et al. 2015). Ecological processes such as colonization, extinction, and dispersal are fundamental for maintaining and generating biodiversity (Balmford et al. 1999). These processes are dynamic (i.e., they vary across time and space depending on a range of factors such as resource availability, mortality, and dispersal ability). We used empirical, models to predict the likely effects on bird colonization and extinction rates of reducing single and multiple threats to demonstrate how dynamic ecological processes can be incorporated into prioritizing multispecies threat management.

Traditional multispecies prioritizations rely on systematic conservation-planning tools to allocate effort across space and unrealistically assume a single threat-mitigation action (i.e., designation of a protected area) is sufficient to conserve biodiversity (Margules & Pressey 2000; Visconti et al. 2010). Prioritizations that address multiple actions use simple threat categorizations that tend to assume incorrectly that each threat affects all species equally (Wilson et al. 2011) and that the impact of multiple threats is proportional to the number of threats affecting a species (Auerbach et al. 2014; Cattarino et al. 2015). Prioritizations that quantify differences in the impacts of threats generally focus on a single species (e.g., Santika et al. 2015), which ignores the fact that threat mitigation benefitting one species may be detrimental to another. New multispecies, multithreat prioritization approaches are paving the way for more informed and effective decisions, driven by consideration of how alternative threat mitigation actions may benefit different species of conservation concern and how much actions may cost (Chadès et al. 2015). However, because of a paucity of empirical data on the impacts of threats, multispecies threat-prioritization frameworks typically rely on expert evaluation of the probability of a species' response to a given action (e.g., Chadès et al. 2015; Firn et al. 2015). Expert-elicited information is generally static (i.e., it refers to impacts of actions at a single point in time or in a single location). By failing to account for dynamic ecological processes, the likelihood is reduced of expert-elicited threat prioritization frameworks resulting in long-term biodiversity benefits (Visconti et al. 2010).

The fundamental ecological processes determining site-occupancy dynamics of any species are local extinction and colonization (MacKenzie et al. 2003). Predictions of the responses of these dynamic processes to different intensities and combinations of threats can be coupled with optimization techniques to identify priorities for recovery actions (Santika et al. 2015). Increasingly, researchers are applying models of population dynamics to explore how colonization and extinction rates of different taxa may be affected by changes in ecological conditions brought about, for example, by establishment of plantations of non-native invasive species (Mortelliti & Lindenmayer 2015) or climate change (Ponce-Reyes et al. 2013). This research has improved understanding of the impacts of threatening processes on ecological processes, but how ecological processes may change if one or more threats are reduced remains unclear (but see Santika et al. 2015). Furthermore, models of population dynamics have not been used to incorporate ecological dynamics into prioritizing threat mitigation for multiple species.

We sought to improve conservation outcomes by incorporating ecological dynamics into a multispecies threat-management prioritization framework that identifies the best set of actions for restoring biodiversity. We used empirical evidence to predict changes to patch colonization when the intensity of different threatening processes was reduced. We quantified the effects of multiple threatening processes on bird ecological dynamics (patch occupancy, colonization, and extinction) in an endangered ecological community in eastern Australia. The study was a large-scale natural experiment of incentive mechanisms used to alter the duration, frequency, and intensity of grazing. We uniquely combined socioeconomic information on the history of grazing on farms with repeated sampling of birds to investigate cumulative effects of historical and current threatening processes such as grazing practices and loss of tree cover (Lindenmayer et al. 2012).

Understanding the likely effects of threat mitigation is difficult because species responses vary, typically because threats affect different ecological processes in different ways (Isaac

& Cowlishaw 2004; Darling & Côté 2008). We surveyed 37 bird species encompassing a wide range of conservation statuses, ecologies, and life-history traits to ensure that the effects of multiple threats could be assessed across a range of taxa. Previous researchers used static correlative models to demonstrate how grazing effects on birds differed among species, depending on their foraging and nesting requirements (Martin & Possingham 2005; Martin & McIntye 2007). Not all species are likely to decline as a result of a threatening process; thus, resilient species may become threats themselves. For example, in eastern Australia, the abundance of hyperaggressive species (in particular the Noisy Miner [*Manorina melanocephala*]) has increased in degraded areas (Maron et al. 2013). These birds potentially worsen negative impacts of land conversion on susceptible (particularly small-bodied) species through interspecific “despotic” competition (Mac Nally et al. 2012). It is therefore unclear whether taking a single threat-mitigation action in isolation will sufficiently improve population processes or whether combined strategies of managing multiple threats are required (Chadès et al. 2015). The principle of complementarity, a key tenet of systematic conservation planning, can assist with choosing the most effective actions because it ensures prioritization decisions are based on how much new actions complement the benefit to species provided by actions already selected (Moilanen 2008). Adherence to this principle guarantees that all species receive benefits and avoids wasting limited funding on redundant conservation efforts.

We used a complementary threat-management prioritization approach to investigate which combination of 10 threat-mitigation strategies (including reduction of grazing, control of Noisy Miners, or increased tree cover) maximizes patch colonization of multiple species. We explored different benefit scenarios of threat mitigation by increasing realism of expected species responses, from simple categorization of threats to species to complex predictions of likely population dynamics under reduced threats. We examined the relative influence of independent versus multiple threatening processes on bird population dynamics in a degraded agricultural landscape. Finally, we used empirical predictions of bird population dynamics to evaluate the relative benefits of alternative threat mitigation actions and to select complementary action strategies that maximize species colonization.

Methods

Our approach to prioritizing complementary threat-mitigation strategies in multispecies, multithreat contexts had 5 steps: define the problem; identify management objectives; collect empirical data on species responses to different threat intensities; build models to predict ecological processes of colonization and extinction in response to reduced threat intensities; and solve optimization problems.

Study Area, Problem Definition, and Objectives

The Box Gum Grassy Woodland ecological community of eastern Australia is listed as critically endangered under the Environment Protection and Biodiversity Conservation (EPBC) Act 1999. The original continuous coverage of native woodland is highly fragmented (Supporting Information); >85% was cleared for agriculture in the last 230 years (Benson 2008). We included 97 sites in a large-scale experiment established in 2011 across 29 farms (see Supporting Information for details). Our goal was to determine the relative effects on birds of 2 threatening processes: grazing and land clearing. Each site was a remnant woodland patch, selected using a stratification based on topography, past land use (cultivation, grazing, and fertilizer history), and tree cover. Two to 4 sites were selected on 29 farms. Each farm included a fenced grazing-exclusion site (zero grazing intensity by domestic livestock) and 1–3 grazed sites representing rotational (grazed <365 days/year; mean 176 days/rotation) or continuous grazing (Fig. 1). We added a third threat, the Noisy Miner, which was recently listed as a “key threatening process” to biodiversity in Australia (Mac Nally et al. 2012; Maron et al. 2013). Replication of sites with and without Noisy Miners within the grazing and clearing intensification gradient was sufficient to ensure statistical analysis of the effects of Noisy Miners.

We evaluated which of the independent threats, or combination of threats, was best targeted to achieve an objective of maximizing expected patch colonization. We used 2 groups of target species: all bird species or only declining bird species (listed in New South Wales or Commonwealth threatened species legislation or as declining by BirdLife International [2016]).

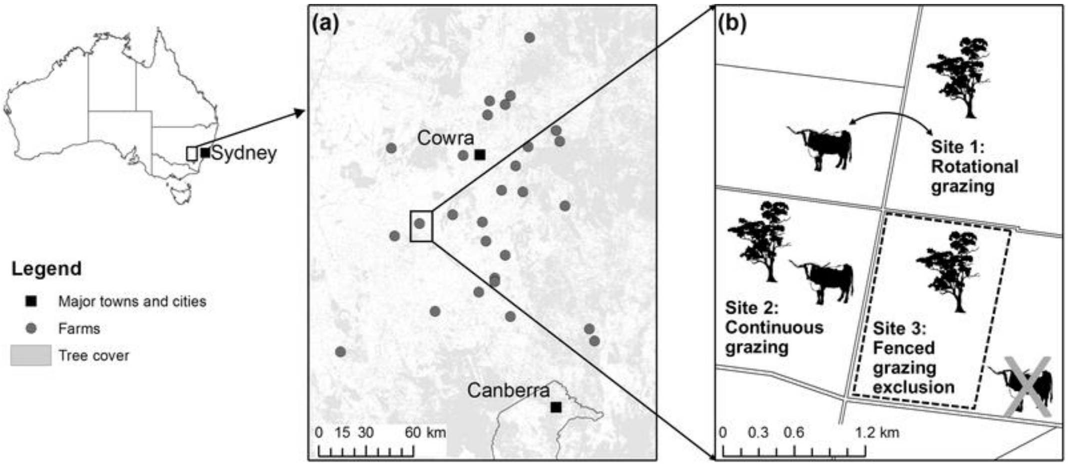


Figure 1. *Hierarchical arrangement of (a) study farms across the landscape and (b) experimental sites with different current grazing regimes on a typical study farm.*

Data Collection on Species and Threats

We surveyed for birds 6 times/year in spring from 2011 to 2013. Each survey comprised repeated 5-min point interval counts at each of 3 points (0, 100, and 200 m) along a 200-m transect within each site. All birds were counted within 50 m of a transect point.

We collected landscape-level data on the underlying environmental conditions: historical grazing regime (a categorical description reflecting continuous or rotational grazing), percent cover of improved pasture or native tree cover surrounding the site, soil phosphorus, elevation, and mean annual temperature and rainfall (climate variables) (Table 1). We also collected site-level data on total ground cover biomass (reflecting food resources for ground foragers).

We surveyed farmers to determine grazing duration per stocking rotation (continuous grazing, grazing 365 days/year; rotational grazing, average grazing across multiple grazing events; grazing exclusion, zero days grazed); grazing frequency; and grazing intensity (i.e., total daily dry sheep equivalent averaged across the entire year [Dorrough et al. 2007] or average daily dry sheep equivalent for grazed days only) (Table 1 & Supporting Information). At each site, we also calculated the abundance of the Noisy Miner (average number of birds recorded in six point counts) (Table 1). Fifteen sites had incomplete data and were removed from analyses, leaving 82 sites. Data were checked for correlations and normality, log transformed if necessary, and standardized for analyses.

Building Occupancy Models

To account for imperfect species detection, we fitted multiseason occupancy models (MacKenzie et al. 2003) to binary detection-history data (i.e., the sequence of detection or

Table 1. *Predictor variables used in bird occupancy models*

Hypothesis	Predictor (abbreviation)	Description	Source	Parameters for prediction[a]
Time	numerical year (yearn)	continuous year accounts for potential trends in the population over time	NA	*p*
	categorical year (year)	categorical year accounts for unmeasured year-specific factors	NA	*p*
Weather at time of sampling	temperature (temp)	categorical estimation of temperature (scale of 0–5 indicating coldest to hottest) during survey	bird surveyors (this study)	*p*
	preceding rainfall (rain)	total site-level rainfall in the 3 months preceding surveys	Australian Bureau of Meteorology	*p*
Historical climate	mean temperature (anntemp)	mean annual temperature 1976–2005; 0.01 degree resolution	derived from long-term average maps (ANUClimate)[b]	Ψ
	mean rainfall (annprec)	mean annual precipitation 1976–2005; 0.01 degree resolution	derived from long-term average maps (ANUClimate)[b]	Ψ
Historical management	regime	grazing regime prior to 2010; categorical: long holistic (high-intensity rotations over a long time frame, for >10 years), short holistic (high intensity rotations over a short time frame, for <5 years, i.e. conversional farming), long rotational (medium intensity over a large proportion but not all of the year) or continuous grazing (i.e., grazed all year)	farmer surveys (this study)	Ψ
	elevation (elev)	elevation in meters	derived from digital elevation model (DEM)	Ψ
	pasture cover (imp250)	proportion of the surrounding landscape (within a 250-m radius from center of site) made up of modified pasture cover in 2010	measured from remotely sensed landuse maps[c]	Ψ, ϒ, ε
	soil nutrients (soilp)	soil phosphorus content (affecting productivity) derived from samples collected once in 2010		Ψ, ϒ, ε
	tree cover (tree)	proportion of the surrounding landscape in a circular buffer (within a 250-m radius from center of site) made up of native woody cover in 2010	measured from remotely sensed Landsat satellite imagery of forest cover (Lymburner et al. 2011)[e]	Ψ, ϒ, ε
Current grazing regime	1. duration(gr.dur)2. frequency (gr.frq)3. intensity(a) dse days	average number of days of each grazing eventnumber of stock resting events per yearaverage	farmer surveys (this study)	ϒ, ε

Hypothesis	Predictor (abbreviation)	Description	Source	Parameters for prediction[a]
	per year (gr.int1)(b) dse days per stock (gr.int2)	annual stocking rateaverage daily grazing intensity across entire year (dry sheep equivalent)daverage daily grazing intensity of each rotation (dry sheep equivalent)		
Current environmental conditions	biomass	mean annual biomass of all groundcover within the woodland patch. Measured in the field and based on 40 20 × 50 m plots along each transect.	biometric surveys (this study)	ϒ, ε
Additional threatening processes	Noisy Miners (minerab)	average abundance of Noisy Miners per site per year (from bird surveys)	bird surveys (this study)	ϒ, ε

[a] Parameters for prediction: detection probability p, probability of a site being occupied during the first survey Ψ; probability of a site being colonized by the target species between sampling sessions ϒ; and probability of the target species becoming locally extinct between sampling sessions ε.

[b] Michael Hutchinson, Jennifer Kesteven, Tingbao Xu, 2014. Daily maximum temperature: ANUClimate 1.0, 0.01 degree, Australian Coverage, 1970-2012. Australian National University, Canberra, Australia.

[c] SCALD (standard classification for attributes of land) classification on 8 April 2011 by New South Wales Office of Environment and Heritage.

[d] The dry sheep equivalent (DSE) is a standard unit frequently used to compare the feed requirements of different classes of stock or to assess the carrying capacity and potential productivity of a given farm or area of grazing land. The feed requirements of livestock vary with their live weight, level of production, physiological state, land topography, and climatic conditions. A single nonlactating ewe is equivalent to one dry sheep.

[e] Lymburner L, Tan P, Mueller N, Thackway R, Lewis A, Thankappan M, Randall L, Islam A, Senarath U, 2011. Dynamic Land Cover Dataset Version 1, Geoscience Australia.

nondetection for each species in each site) with the R package unmarked version 0.10-6 (Fiske & Chandler 2011). The multiple-season framework enabled four dependent parameters to be estimated: detection probability *p* (to account for false absences); probability of a site being occupied during the first survey (Ψ); probability of a site being colonized by the target species between sampling sessions (ϒ); and probability of the target species becoming locally extinct between sampling sessions (ε).

Detection and nondetection were recorded at each site on 6 annual visits (18 visits throughout 3 consecutive years). Prior to occupancy analyses, we selected species with >1% detection rate across the whole landscape (number of detections/number of visits), which resulted in 37 species (including the Noisy Miner). Details on the steps followed for fitting models are in Supporting Information.

To model detectability (*p*), we fitted five models reflecting the effects of time (numerical year [yearn] or categorical [year]) or weather at the time of sampling (total rainfall [rain] in the 3 months preceding surveys or temperature [temp]) on detectability (Field et al. 2002) (Table 1). We used the Akaike information criterion (AIC) to select the best model (Burnham & Anderson 2002).

We then selected the variables that had the greatest influence on site occupancy (Ψ). We restricted these to seven historical landscape-level variables (Table 1) and retained the single best predictor selected based on AIC.

To explore effects of independent versus cumulative impacts of threatening processes, we modeled probabilities of colonization (ϒ) and extinction (ε) as functions of dynamic landscape- and site-level threatening processes: grazing (frequency, duration, and intensity), tree cover, and Noisy Miner abundance (Martin & McIntyer 2007; Maron et al. 2013). We ran models with each process as an independent predictor and with the combination of tree cover plus grazing intensity, tree cover plus Noisy Miners, and Noisy Miners plus grazing intensity. We also fitted 4 models that included other landscape processes (such as productivity) likely to affect colonization and extinction rates: biomass, soil phosphorus, pasture, or the combination of tree cover and soil phosphorus (Watson

2011). To avoid overfitting models, we kept the ratio of the number of parameters to number of sites relatively small, so only additive models were fitted rather than interactions.

We checked that the results of occupancy models relative to the impacts of independent threats corresponded with previous findings in other locations (e.g., Martin & McIntyer 2007). We used model results in two ways to classify species' responses to threats. The first approach was a simple threat categorization based on the results of only the top model (i.e., best-supported according to AIC). Here, species responding negatively to a threat were characterized by decreased occupancy or colonization rate or increased extinction risk in models including that threat. Species responding positively to a threat were characterized by increased occupancy or colonization rate or had a decreased risk of extinction in models including that threat. We classified a species as responding to clearing if the variable tree was included, to grazing if any grazing variables (Gr.dur, Gr.frq, Gr.int1, or Gr.int2) were included, and to Noisy Miners if the variable minerab was included.

Second, we used model predictions based on model averaging and goodness of fit measured through Nagelkerke's R2 (Nagelkerke 1991) to quantify species' probabilistic responses to threats. We used all models within 2 ΔAIC of the top model to determine the average parameter values for colonization and extinction under each threat if the threat was present in the model set (Burnham & Anderson 2002), and considered species to be affected by the threat if the extinction parameter was positive or the colonization parameter was negative.

Complementary Threat-Management Optimization

We used the results of our models to conduct a complementary threat-management prioritization. We evaluated 10 threat-mitigation strategies; each strategy comprised a number of actions required for successful implementation (Firn et al. 2015). The strategies were: restore tree cover; remove Noisy Miners; reduce grazing frequency; reduce grazing duration; reduce grazing intensity; restore trees and reduce grazing intensity; remove Noisy Miners and reduce grazing intensity; remove Noisy Miners and restore trees; remove Noisy Miners and restore trees and reduce grazing intensity; no action (Supporting Information).

We built on the complementary monitoring action prioritization of Tulloch et al. (2013, 2016), who identified the best set of complementary species to maximize the benefits of learning about all species in a network. Instead of prioritizing species, we aimed to find threat-mitigation strategies that maximized species' patch colonization. We defined the benefits (B) of selecting a set of mitigation strategies Z (1 or a combination of the 10 strategies) for a set of target species T (either all 37 species or 16 declining species):

$$B(Z) = \sum_{j \in T} \max_{i \in Z} t_{ij} \text{ with } Z \subseteq S, \qquad (1)$$

where t_{ij} is the benefit of applying threat-mitigation strategy i to expected colonization of target species j and has a value between and including 0 and 1; Z is a subset of S; and S is the fixed set of all potential mitigation strategies. This equation is fundamentally different from the complementarity approaches of systematic conservation planning in which locations that provide low benefits can be selected for action (Margules & Pressey 2000). This is because we sought the mitigation benefits t_{ij} that would contribute the most to restoring species (maximum operator) and summed the values across all target species. Colonization was an explicit objective because we were interested in increasing species patch occupancy. Alternative objectives (e.g., minimizing extinction) are possible to maintain, rather than restore, populations, but were not explored here.

The best complementary set of threat-mitigation strategies *Z** for a set of target species *T* is the set that maximizes *B*(*Z*), the summed benefits t_{ij} for each species, within a given budget (*cmax*), formally:

$$Z^{*} = \mathrm{argmax}_{Z \subseteq S}\{\, B(Z)\ \text{such that}\ \mathrm{cost}(Z) \leq \mathrm{cmax}\},\quad (2)$$

where $\mathrm{argmax}_{Z \subseteq S}$ returns the set of actions *Z** for which *B*(*Z*) is maximized. Complementarity in species responses was included to ensure that redundant threats (i.e., those with no additional impacts on species) were not selected in the best sets of mitigation actions.

We explored three scenarios of how empirical model results might be used to inform t_{ij} (following Auerbach et al. 2015). Each scenario differed in the way the benefits t_{ij} of each threat-mitigation strategy for each species were calculated. Scenarios 1 and 2 simulated expert elicitation, categorizing species' responses according to a basic understanding of the number of threats acting on a species (optimistic scenario) or simply as beneficial or not (pessimistic scenario). Scenario 3 incorporated probabilistic quantification of species responses to multiple threats through process-based prediction of colonization rates (details in Supporting Information).

Scenario 1 represented simple and optimistic management expectations. Benefits under threat reduction were proportional to the number of threats in the top-ranked occupancy model (i.e., the model with the lowest AIC). Using our threat categorization scheme, we assigned each species a t_{ij} from 0 to 1 that was proportional to the number of threats negatively affecting it.

Scenario 2 represented simple and pessimistic management expectations. Species needed all threats that affected them managed to colonize the landscape. Using our threat categorization scheme, we assigned each species a t_{ij} of 0 (no benefit) if the action did not remove all threats and of 1 (complete benefit) only if the action removed all threats.

Scenario 3 was a mechanistic scenario in which empirical occupancy models were used to quantify species colonization under the full range of intensities of each threat. Expected species colonization was predicted using the model-averaged parameters of the best set of models (within 2 ΔAIC), and t_{ij} was the prediction at 25% of the maximum threat level (representing a 75% reduction in the threat, a reasonable assumption given that all threats can rarely be completely removed). Colonization under strategies targeting threats that were not in the best set of models for each species had the same value as no action, calculated as the probability of colonization under high intensities of all 3 threats.

To focus on comparing benefits of alternative mitigation strategies, we set cost(Z) in Eq. (2) as equal to the number of actions chosen. We ran the optimization (Eq. (2)) for each scenario and calculated the benefits $B(Z)$ (in terms of summed and average species colonization) of selecting from 1 to 5 complementary strategies. To do this, we assumed that when multiple strategies were implemented, species' colonization was equal to that provided by the most beneficial strategy (Firn et al. 2015).

Results

Species Population Processes

Accounting for only the top model in our simple threat categorization indicated that 26 species (70%) were negatively affected by at least 1 threatening process (Table 2); 13 of these were affected negatively by cumulative impacts of at least 2 threats. Loss of tree cover and grazing intensity were equally ranked as affecting the most species (Fig. 2a). Effects of Noisy Miners on colonization or extinction were usually associated with another threat (Table 2 & Fig. 2b). Accounting for all processes in the top set of models increased the number of species affected by at least 1 threatening process to 30 (Table 2), and tree cover loss became the most influential independent threat on patch colonization (Fig. 2b).

Depending on how threats were categorized, 5–11 species responded positively (increased colonization or decreased extinction) to at least one threatening process (Figs. 2a & 3a), including an introduced species, the Common Starling (*Sturnus vulgaris*), which increased as grazing intensity increased.

Complementary Threat Management

A mechanistic process-based approach to prioritizing threat management always outperformed simple optimistic and pessimistic threat categorizations (Fig. 4). Increasing tree cover was the best single strategy for maximizing patch colonization (Table 2). Relative to no action it resulted in an average increase in colonization of 5% and 11% for all and for declining species only respectively (Fig. 2b). Using a categorical approach to describe species' responses to threats always resulted in grazing intensity being the optimal threat mitigation action, regardless of whether categorization was pessimistic or optimistic (Fig. 4). A combined strategy of removing Noisy Miners and increasing tree cover was of higher priority under the process-based approach than any strategies changing grazing regimes. Average patch colonization increased by 10% and 19% for all species and declining species only, respectively, under increased tree cover and reduced Noisy Miner abundance (Figs. 3f and 4).

Table 2. *Top-ranked occupancy models for all 37 modeled bird species that occur in the endangered Box Gum Grassy Woodland and the results of classifying each species' threat response on basis of either the parameters in the single best-supported model or the model-averaged parameters for the entire top-model set*

Species	R^2	**ΔAIC**	**Model[a]**	**Top model response (simple threat categorization approach)[b]**	**Model-averaged negative colonization or positive extinction responses to threats in top model set (probabilistic approach)**
Australian Magpie	0.19	0	Ψ(annprec)γ(.)ε(tree)p(YN)	c1	0[c]
	0.19	1.47	Ψ(annprec)γ(.)ε(soilP+tree)p(YN)		
	0.19	1.91	Ψ(annprec)γ(.)ε(minerab+tree)p(YN)		
	0.19	2.00	Ψ(annprec)γ(tree)ε(tree)p(YN)		
Black-faced Cuckoo-shrike[d]	0.19	0	Ψ(tree)γ(Gr.int2+tree)ε(.)p(.)	c0g0	3
	0.20	0.76	Ψ(tree)γ(Gr.int2+Gr.dur)ε(.)p(.)		
	0.22	0.80	Ψ(.)γ(Gr.int2+tree)ε(.)p(.)		
	0.18	0.85	Ψ(tree)γ(Gr.dur)ε(.)p(.)		
	0.20	1.02	Ψ(.)γ(minerab+tree)ε(.)p(.)		
Brown Treecreeper[e]	0.22	0	Ψ(regime)γ(Gr.int1)ε(.)p(temp)	g0	1
	0.24	0.34	Ψ(regime)γ(Gr.int2)ε(Gr.int2)p(temp)		
	0.23	1.19	Ψ(regime)γ(.)ε(Gr.int2+tree)p(temp)		
	0.21	1.43	Ψ(regime)γ(Gr.int2)ε(.)p(temp)		
	0.20	1.94	Ψ(regime)γ(.)ε(Gr.int2)p(temp)		
Buff-rumped Thornbill[d]	0.36	0	Ψ(tree)γ(minerab+tree)ε(.)p(Y)	c0m0	2
Common Starling[f]	0.57	0	Ψ(tree)γ(Gr.int2+tree)ε(Gr.int2+tree)p(rain)	c1g1	0[c]
	0.57	1.17	Ψ(tree)γ(soilP+tree)ε(soilP+tree)p(rain)		
Eastern Rosella	0.29	0	Ψ(tree)γ(.)ε(Gr.int2+minerab)p(rain)	c1g0m1	0[c]
	0.27	0.75	Ψ(tree)γ(.)ε(minerab)p(rain)		

Species	R^2	ΔAIC	Model[a]	Top model response (simple threat categorization approach)[b]	Model-averaged negative colonization or positive extinction responses to threats in top model set (probabilistic approach)
	0.28	1.19	Ψ(tree)γ(minerab)ε(minerab)p(rain)		
Grey Butcherbird	0.15	0	Ψ(soilP)γ(minerab)ε(minerab)p(.)	m1	0 [c]
	0.10	1.08	Ψ(soilP)γ(minerab)ε(.)p(.)		
	0.13	0.08	Ψ(soilP)γ(.)ε(minerab)p(.)		
	0.10	1.15	Ψ(soilP)γ(.)ε(biomass)p(.)		
	0.12	1.47	Ψ(soilP)γ(biomass)ε(biomass)p(.)		
	0.09	1.50	Ψ(soilP)γ(.)ε(Gr.dur)p(.)		
Grey Fantail	0.35	0	Ψ(anntemp)γ(minerab+tree)ε(.)p(Y)	c0m0	2
Grey Shrike-Thrush	0.25	0	Ψ(soilP)γ(.)ε(Gr.frq)p(rain)	g0	2
	0.29	0.81	Ψ(soilP)γ(Gr.int2+minerab)ε(.)p(rain)		
	0.25	1.50	Ψ(soilP)γ(Gr.frq)ε(.)p(rain)		
	0.25	2.00	Ψ(soilP)γ(Gr.frq)ε(Gr.frq)p(rain)		
Jacky Winter[d]	0.18	0	Ψ(elev)γ(tree)ε(.)p(YN)	c0	2
	0.16	0.21	Ψ(.)γ(tree)ε(.)p(YN)		
	0.20	0.63	Ψ(elev)γ(Gr.int2+tree)ε(.)p(YN)		
	0.17	0.86	Ψ(.)γ(Gr.int2+tree)ε(.)p(YN)		
Little Friarbird	0.39	0	Ψ(soilP)γ(soilP+tree)ε(soilP+tree)p(.)	c0	2
	0.36	0.74	Ψ(soilP)γ(.)ε(soilP+tree)p(.)		
	0.35	1.01	Ψ(soilP)γ(.)ε(Gr.int2+tree)p(.)		
	0.35	1.41	Ψ(soilP)γ(Gr.int2+Gr.frq)ε(Gr.int2+Gr.frq)p(.)		
	0.38	1.86	Ψ(soilP)γ(Gr.int2+Gr.dur)ε(Gr.int2+Gr.dur)p(.)		
Magpie-lark	0.20	0	Ψ(soilP)γ(.)ε(biomass)p(temp)	N	0 [c]
	0.17	0.59	Ψ(soilP)γ(Gr.int1)ε(.)p(temp)		
	0.19	0.68	Ψ(soilP)γ(Gr.int2+dur)ε(.)p(temp)		
	0.19	0.74	Ψ(soilP)γ(Gr.int1)ε(Gr.int1)p(temp)		
	0.19	0.99	Ψ(soilP)γ(.)ε(minerab)p(temp)		
Mistletoebird[d]	0.35	0	Ψ(regime)γ(minerab+tree)ε(.)p(rain)	c0g0m0	2
Noisy Friarbird	0.30	0	Ψ(tree)γ(.)ε(tree)p(temp)	c0	3
	0.31	0.41	Ψ(tree)γ(tree)ε(tree)p(temp)		
	0.30	1.36	Ψ(tree)γ(.)ε(minerab+tree)p(temp)		
	0.30	1.55	Ψ(tree)γ(.)ε(soilP+tree)p(temp)		

Species	R^2	ΔAIC	Model[a]	Top model response (simple threat categorization approach)[b]	Model-averaged negative colonization or positive extinction responses to threats in top model set (probabilistic approach)
	0.30	1.92	Ψ(tree)γ(.)ε(Gr.int2+tree)p(temp)		
Noisy Miner[g]	0.23	0	Ψ(annprec)γ(soilP+tree)ε(.)p(temp)	c1	0 [c]
	0.21	0.16	Ψ(annprec)γ(Gr.dur)ε(.)p(temp)		
Red-rumped Parrot	0.31	0	Ψ(tree)γ(tree)ε(tree)p(Y)	c1	1 [c]
	0.29	0.15	Ψ(tree)γ(tree)ε(.)p(Y)		
	0.31	0.32	Ψ(tree)γ(soilP+tree)ε(.)p(Y)		
	0.31	0.59	Ψ(tree)γ(.)ε(minerab+tree)p(Y)		
	0.29	0.88	Ψ(tree)γ(soilP)ε(.)p(Y)		
	0.28	1.08	Ψ(tree)γ(.)ε(tree)p(Y)		
	0.30	1.11	Ψ(tree)γ(Gr.int2+tree)ε(.)p(Y)		
	0.30	1.22	Ψ(tree)γ(Gr.int2+minerab)ε(.)p(Y)		
	0.30	1.47	Ψ(tree)γ(Gr.frq)ε(Gr.frq)p(Y)		
Red Wattlebird	0.37	0	Ψ(tree)γ(soilP+tree)ε(.)p(Y)	c0	1
	0.37	0.15	Ψ(tree)γ(soilP)ε(soilP)p(Y)		
	0.37	1.63	Ψ(tree)γ(soilP)ε(.)p(Y)		
Restless Flycatcher [d]	0.21	0	Ψ(soilP)γ(Gr.int2+Gr.dur)ε(.)p(.)	g0	1
Rufous Songlark	0.18	0	Ψ(elev)γ(.)ε(soilP)p(rain)	N	0 [c]
	0.18	0.03	Ψ(elev)γ(.)ε(Gr.frq)p(rain)		
	0.17	1.28	Ψ(elev)γ(soilP)ε(.)p(rain)		
	0.18	1.43	Ψ(elev)γ(.)ε(soilP+tree)p(rain)		
	0.18	1.89	Ψ(elev)γ(Gr.frq)ε(Gr.frq)p(rain)		
Rufous Whistler [d]	0.38	0	Ψ(soilP)γ(Gr.int2+minerab)ε(.)p(rain)	g0m0	2
Sacred Kingfisher	0.26	0	Ψ(elev)γ(Gr.int2+minerab)ε(.)p(temp)	g0m0	3
	0.23	0.15	Ψ(elev)γ(minerab)ε(.)p(temp)		
	0.25	0.27	Ψ(elev)γ(minerab+tree)ε(.)p(temp)		
	0.24	0.31	Ψ(elev)γ(biomass)ε(biomass)p(temp)		
	0.24	0.35	Ψ(elev)γ(Gr.int2)ε(Gr.int2)p(temp)		
	0.21	0.40	Ψ(elev)γ(biomass)ε(.)p(temp)		
	0.21	0.44	Ψ(elev)γ(.)ε(Gr.int2)p(temp)		
	0.24	0.52	Ψ(elev)γ(Gr.int2+Gr.dur)ε(.)p(temp)		
	0.23	0.60	Ψ(elev)γ(minerab)ε(minerab)p(temp)		
Silvereye	0.19	0	Ψ(elev)γ(Gr.int2+minerab)ε(.)p(YN)	g0m0	2
	0.16	0.55	Ψ(elev)γ(.)ε(minerab)p(YN)		

Species	R^2	ΔAIC	Model[a]	Top model response (simple threat categorization approach)[b]	Model-averaged negative colonization or positive extinction responses to threats in top model set (probabilistic approach)
	0.15	0.81	Ψ(elev)γ(minerab)ε(.)p(YN)		
	0.12	1.10	Ψ(.)γ(.)ε(minerab)p(YN)		
	0.14	1.70	Ψ(elev)γ(.)ε(Gr.int2+minerab)p(YN)		
	0.17	1.77	Ψ(elev)γ(minerab+tree)ε(.)p(YN)		
Spotted Pardalote [d]	0.28	0	Ψ(tree)γ(soilP)ε(.)p(Y)	c0	3
	0.28	0.34	Ψ(tree)γ(.)ε(soilP)p(Y)		
	0.28	0.40	Ψ(tree)γ(tree)ε(.)p(Y)		
	0.30	0.58	Ψ(tree)γ(soilP)ε(soilP)p(Y)		
	0.27	0.68	Ψ(tree)γ(Gr.int2)ε(.)p(Y)		
	0.29	1.22	Ψ(tree)γ(soilP+tree)ε(.)p(Y)		
	0.27	1.26	Ψ(tree)γ(.)ε(minerab)p(Y)		
	0.27	1.35	Ψ(tree)γ(biomass)ε(.)p(Y)		
	0.27	1.78	Ψ(tree)γ(.)ε(tree)p(Y)		
Striated Pardalote [d]	0.26	0	Ψ(tree)γ(tree)ε(.)p(Y)	c1	2 [c]
	0.27	0.10	Ψ(tree)γ(Gr.int2+tree)ε(.)p(Y)		
	0.27	0.64	Ψ(tree)γ(minerab+tree)ε(.)p(Y)		
	0.26	1.17	Ψ(tree)γ(soilP+tree)ε(.)p(Y)		
	0.26	1.28	Ψ(tree)γ(tree)ε(tree)p(Y)		
Striated Thornbill [d]	0.36	0	Ψ(anntemp)γ(.)ε(tree)p(temp)	c0	3
	0.36	0.23	Ψ(anntemp)γ(tree)ε(tree)p(temp)		
	0.35	0.74	Ψ(anntemp)γ(.)ε(Gr.int2+tree)p(temp)		
	0.33	1.44	Ψ(anntemp)γ(.)ε(minerab+tree)p(temp)		
	0.34	1.77	Ψ(anntemp)γ(.)ε(soilP+tree)p(temp)		
Superb Fairy-wren	0.10	0	Ψ(annprec)γ(.)ε(Gr.dur)p(.)	N	3
	0.07	0.44	Ψ(annprec)γ(minerab)ε(.)p(.)		
	0.04	0.65	Ψ(.)γ(.)ε(Gr.dur)p(.)		
	0.06	0.90	Ψ(annprec)γ(.)ε(tree)p(.)		
	0.06	1.00	Ψ(annprec)γ(minerab)ε(minerab)p(.)		
	0.06	1.09	Ψ(annprec)γ(minerab+tree)ε(.)p(.)		
	0.08	1.27	Ψ(annprec)γ(.)ε(Gr.int2+Gr.dur)p(.)		
	0.08	1.35	Ψ(.)γ(minerab)ε(minerab)p(.)		
	0.07	1.82	Ψ(annprec)γ(Gr.dur)ε(Gr.dur)p(.)		
	0.05	1.84	Ψ(annprec)γ(.)ε(minerab)p(.)		
Superb Parrot [h]	0.33	0	Ψ(tree)γ(Gr.int2+minerab)ε(.)p(.)	c1g0m1	1

Species	R^2	ΔAIC	Model[a]	Top model response (simple threat categorization approach)[b]	Model-averaged negative colonization or positive extinction responses to threats in top model set (probabilistic approach)
	0.31	0.50	Ψ(tree)γ(minerab)ε(.)p(.)		
	0.32	1.21	Ψ(tree)γ(minerab)ε(minerab)p(.)		
Weebill [d]	0.33	0	Ψ(tree)γ(.)ε(Gr.int2+Gr.dur)p(Y)	c0g0	2
	0.32	0.89	Ψ(tree)γ(Gr.int2+minerab)ε(.)p(Y)		
	0.32	1.04	Ψ(tree)γ(.)ε(Gr.int2+minerab)p(Y)		
	0.30	1.24	Ψ(tree)γ(.)ε(Gr.int2)p(Y)		
	0.31	1.88	Ψ(tree)γ(Gr.int2)ε(Gr.int2)p(Y)		
White-plumed Honeyeater	0.20	0	Ψ(soilP)γ(.)ε(soilP)p(rain)	N	1
	0.22	0.18	Ψ(soilP)γ(.)ε(soilP+tree)p(rain)		
	0.22	0.40	Ψ(soilP)γ (soilP)ε(soilP)p(rain)		
	0.19	1.07	Ψ(soilP)γ(Gr.dur)ε(.)p(rain)		
White-throated Gerygone [d]	0.30	0	Ψ(tree)γ(minerab+tree)ε(.)p(.)	c0m0	2
White-throated Treecreeper	0.23	0	Ψ(regime)γ(tree)ε(.)p(rain)	c0g0	2
White-winged Chough	0.25	0	Ψ(soilP)γ(.)ε(soilP)p(temp)	N	1
	0.25	0.16	Ψ(soilP)γ(.)ε(biomass)p(temp)		
	0.30	0.25	Ψ(soilP)γ(Gr.int2+Gr.dur)ε(.)p(temp)		
	0.27	1.00	Ψ(soilP)γ(soilP)ε(soilP)p(temp)		
White-winged Triller	0.28	0	Ψ(tree)γ(minerab)ε(.)p(Y)	c1m0	1
	0.28	0.10	Ψ(tree)γ(.)ε(tree)p(Y)		
	0.25	1.24	Ψ(.)γ(minerab)ε(.)p(Y)		
	0.27	1.44	Ψ(tree)γ(tree)ε(.)p(Y)		
Willie Wagtail	0.15	0	Ψ(tree)γ(.)ε(minerab+tree)p(Y)	c0m0	3
	0.15	0.10	Ψ(tree)γ(.)ε(soilP+tree)p(Y)		
	0.13	0.49	Ψ(.)γ(.)ε(minerab+tree)p(Y)		
	0.13	0.50	Ψ(tree)γ(.)ε(tree)p(Y)		
	0.12	0.83	Ψ(.)γ(.)ε(soilP+tree)p(Y)		
	0.10	1.01	Ψ(.)γ(.)ε(tree)p(Y)		
	0.14	1.17	Ψ(tree)γ(.)ε(Gr.int2+tree)p(Y)		
	0.11	1.76	Ψ(.)γ(.)ε(Gr.int2+tree)p(Y)		

Species	R^2	ΔAIC	Model[a]	Top model response (simple threat categorization approach)[b]	Model-averaged negative colonization or positive extinction responses to threats in top model set (probabilistic approach)
Yellow-faced Honeyeater [d]	0.41	0	Ψ(temp)γ(Gr.int2+minerab)ε(.)p(rain)	g0m0	3
	0.40	0.35	Ψ(temp)γ(tree)ε(tree)p(rain)		
	0.40	0.65	Ψ(temp)γ(minerab+tree)ε(.)p(rain)		
	0.43	1.24	Ψ(temp)γ(Gr.int2+tree)ε(.)p(rain)		
	0.39	1.49	Ψ(temp)γ(Gr.int2+Gr.frq)ε(.)p(rain)		
Yellow-rumped Thornbill [d]	0.21	0	Ψ(elev)γ(minerab)ε(minerab)p(.)	m0	1
Yellow Thornbill [d]	0.17	0	Ψ(tree)γ(Gr.int2+tree)ε(.)p(.)	c0g0	2
	0.17	0.07	Ψ(tree)γ(Gr.frq)ε(.)p(.)		
	0.19	0.45	Ψ(tree)γ(.)ε(soilP+tree)p(.)		
	0.17	1.47	Ψ(tree)γ(tree)ε(tree)p(.)		
	0.12	1.84	Ψ(tree)γ(soilP)ε(.)p(.)		

a Model ranking according to ΔAIC (change in Akaike information criterion from top model) Only models with ΔAIC<2 are shown. All models shown were used to derive model-averaged parameters for estimating colonization rates under alternative threat-mitigation strategies.

b Response (to cumulative threats of grazing, Noisy Miners, and vegetation clearing): c0, clearing negative response (i.e., a positive response to tree cover); c1, clearing positive response (indicated by a negative response to increasing tree cover); g1, grazing positive response; g0, grazing negative response; m0, miner negative response; m1, miner positive response; N, neither grazing nor clearing nor miner effects in top model (or no clear response, i.e. top model had a coefficient of determination of R2 < 0.15).

c For at least one threatening process (grazing, tree clearing, or noisy miners, or a combination of these 3 processes), model-averaged (models within ΔAIC < 2 of top model) patch colonization is positive, or patch extinction is negative.

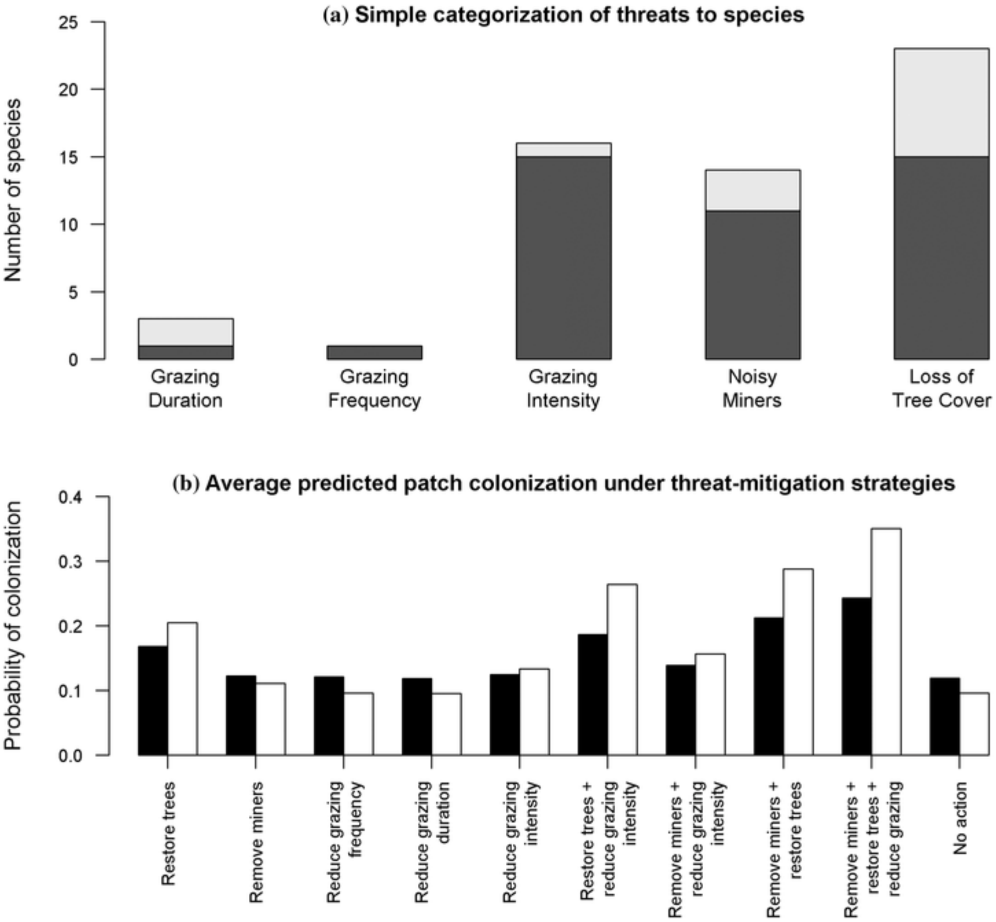
d Listed as declining by BirdLife International (2016).

e Listed at a State level as vulnerable under the New South Wales Threatened Species Conservation Act 1995.

f Invasive species.

g Listed as a Key Threatening Process under the Australian Government Environment Protection and Biodiversity Conservation Act 1999.

h Listed nationally as vulnerable under the Australian Government Environment Protection and Biodiversity Conservation Act 1999.


(a) Simple categorization of threats to species

(b) Average predicted patch colonization under threat-mitigation strategies

Figure 2. *Effects of grazing, Noisy Miners (an aggressive competitor), and tree loss on 37 bird species in the endangered Box Gum Grassy Woodland of Australia, calculated using different approaches for determining responses to threatening processes: (a) simple threat categorization based on the best-supported occupancy model (lowest Akaike information criterion) of negatively (dark grey, increase or decrease, respectively, in extinction or colonization) or not adversely (light grey, decrease or increase, respectively, in extinction or colonization or no response) affected by threat and (b) average process-based patch colonization benefits under various threat-mitigation strategies (see Eq. (1); summed benefits* $\mathrm{B}(Z)$ *produced similar patterns) (black, all species; white, declining species).*

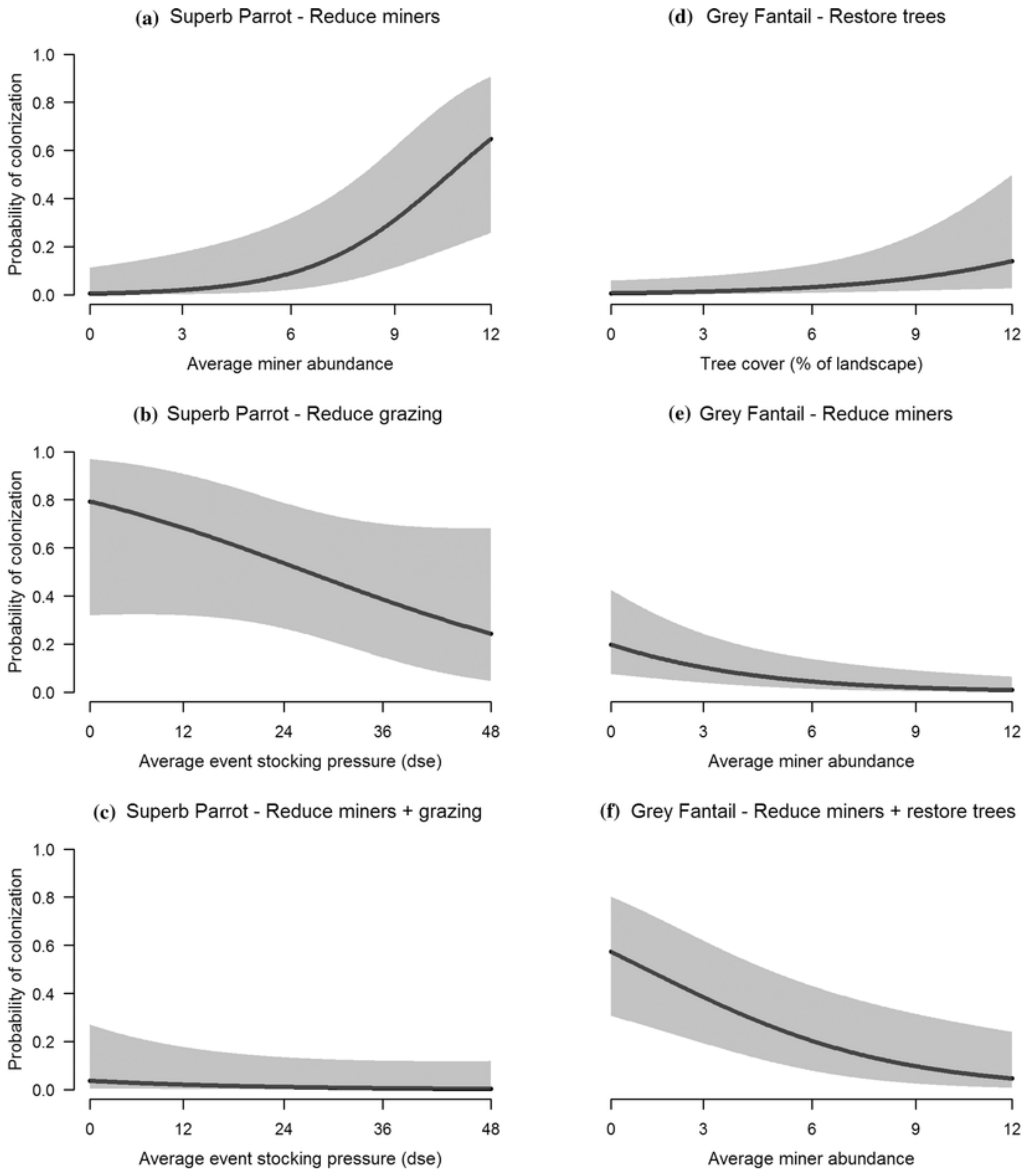


Figure 3. *Predicted colonization probabilities (and 95% CI) for the (a–c) vulnerable Superb Parrot and (d–f) Grey Fantail in the endangered Box Gum Grassy Woodland of Australia under various threat-mitigation strategies: (a) reduced only Noisy Miner abundance (tree cover low and grazing intensity high), (b) reduced grazing intensity (tree cover low and Noisy Miner abundance high), (c) combined grazing intensity and Noisy Miner reduction, (d) tree restoration only (Noisy Miner abundance and grazing intensity high), (e) reduced Noisy Miner abundance only (grazing intensity high and tree cover low), and (f) restoration of tree cover and reduced Noisy Miner abundance (grazing intensity high).*

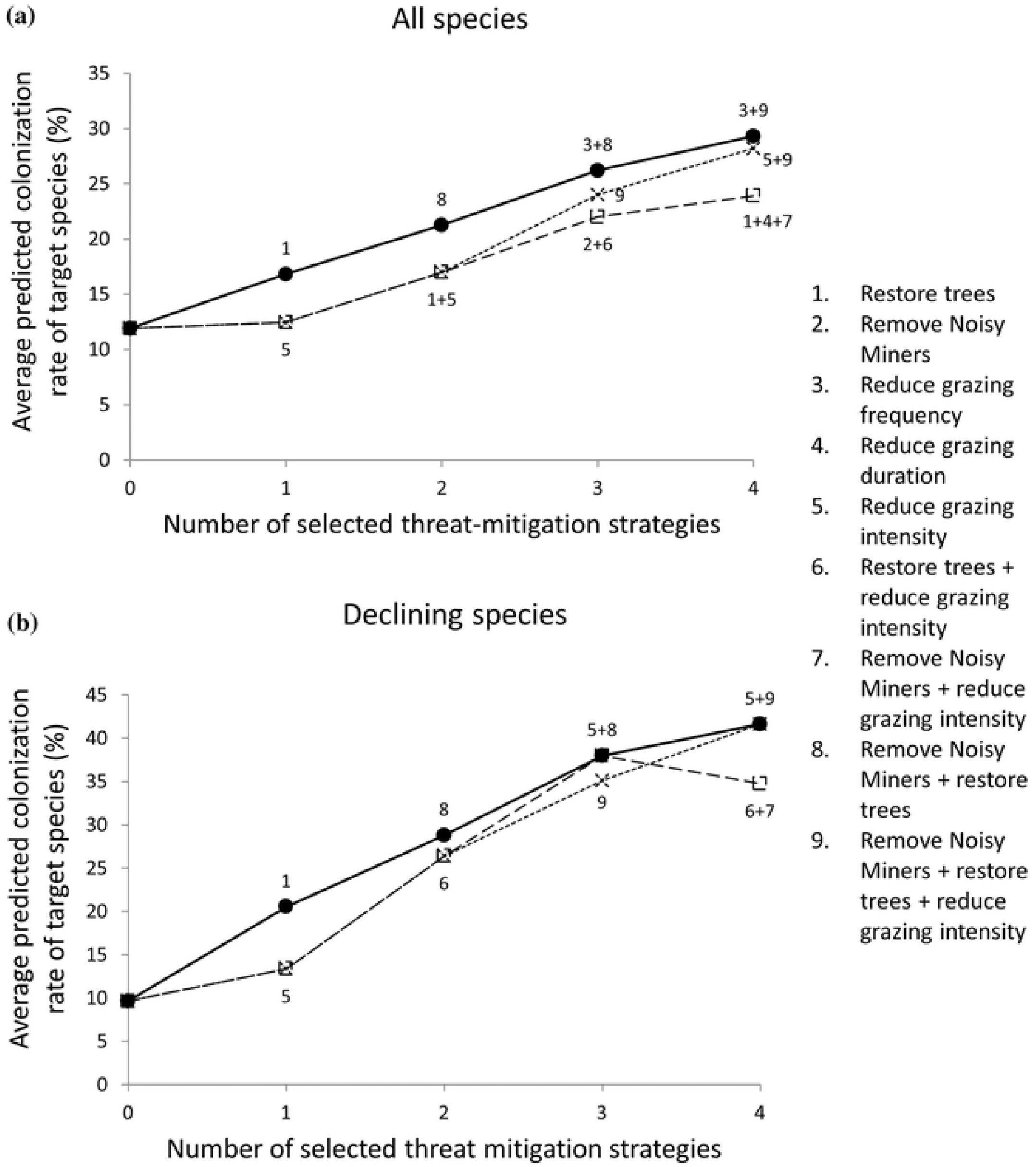


Figure 4. *Average predicted colonization of (a) all 37 bird species and (b) 17 declining bird species under selected threat-mitigation strategies in the endangered Box Gum Grassy Woodland of Australia (solid line, process-based mechanistic scenario informed by predicted colonization rates; dashed line open squares, simple threat-categorization approach simulating an optimistic expert; dashed line crosses, simple threat-categorization approach simulating a pessimistic expert; summed colonization rates produced similar curves). Results are for budgets that accommodate up to 4 actions (see Supporting Information for results with higher budgets).*

In some cases, intervention was predicted to disadvantage species. For nine species, predicted colonization declined when one or more threats were mitigated compared with no action (Supporting Information). The Striated Pardalote (*Pardalotus striatus*) had the largest expected decline in patch colonization, from 84% under no action to 18% under restoration of tree cover. The nationally vulnerable Superb Parrot was the only threatened species likely to experience reduced colonization under mitigation of a threatening process (strategies controlling Noisy Miners [Fig. 3a]), but colonization was predicted to increase if grazing intensity was reduced (Figs. 3b-c).

Discussion

Species responses to threats and threat-mitigation actions differ; thus, a fundamental understanding of ecological processes is needed before landscapes can be managed and species restored. Our results show that processes of colonization and extinction for woodland bird species in an endangered ecosystem were affected by multiple threatening processes of grazing intensity, tree clearing, and Noisy Miners (Table 2). Only 7 species were not negatively affected by at least one threat. We found that different combinations of threat-mitigation strategies would likely result in improved colonization of different sets of species. Combined threat-mitigation strategies were more effective than independent actions at restoring bird populations. Our process-based approach to quantifying threat-mitigation benefits always resulted in higher colonization outcomes than our threat-categorization approaches based on current frameworks that do not account for dynamic ecological processes (e.g., Auerbach et al. 2014; Chadès et al. 2015).

Prioritizing Single Versus Multiple Threats

Because 57% of the bird species were negatively affected by more than one threat (multiple threatening processes were present in the top set of colonization models for 21 species [Table 2]), multiple-threat strategies were more effective for restoring populations than single-threat strategies (e.g., Fig. 2b and 3f). For example, independently controlling Noisy Miners had little effect on patch colonization compared with no action (Fig. 2b) and was therefore always lower priority compared with reducing Noisy Miners plus increasing tree cover (Fig. 4). However, many conservation prioritizations focus only on mitigating a single threat (e.g., designating protected areas to prevent further habitat loss [Visconti et al. 2010]). These prioritizations fail to explore whether actions might benefit more species if they were combined or whether two complementary independent strategies conducted in different parts of the landscape might be better at restoring populations than managing only one threat. By ignoring multiple threats, these prioritizations underpredict the benefits of mitigating threats that are best reduced in concert, thereby missing opportunities for managing sensitive species that are declining due to multiple threats (Foster et al. 2015).

Our complementary threat-management prioritization showed that both independent and combined threat-mitigation strategies may be useful for improving colonization within a single landscape. This suggests that targeting different patches with different strategies may result in higher benefits to all species than applying one strategy across the whole landscape (Fig. 4). For example, reducing grazing intensity in woodland patches was only selected as an action to restore declining species when the threats of tree loss plus Noisy Miners were being mitigated simultaneously in others (Fig. 4b). Choosing to restore tree cover (e.g., by preventing clearing and active revegetation) or to passively restore ground cover (e.g., by reducing grazing) or both depends on which species are targeted for recovery. Although most species in our study benefitted from at least one threat-mitigation action, 13 species may not respond at all or may even decline under some threat-mitigation actions (including a species listed as vulnerable at the national level [Fig. 2a]). Some of these species, such as the Striated Pardalote, take advantage of the greater number of insects in unhealthy trees in fragmented landscapes (Watson 2011). However, several bird species identified as invasive or influencing the abundance of other birds (e.g. Common Starlings, Noisy Miners, Grey Butcherbirds [Mac Nally et al. 2012]) also were predicted to decline under actions, such as reducing grazing intensity or increasing tree cover, that did not include direct control (e.g., culling).

Advantages and Disadvantages of Empirical Modeling

Our results highlight the benefits of understanding population-process responses to threats and the problems with using simple threat categorizations to inform prioritizations of threat mitigation. Threat-mitigation strategies selected using mechanistic predictions always resulted in higher colonization than alternative strategies selected according to threat categorizations (Fig. 4). Mechanistic predictions were modeled probabilities of colonization under reduced intensities of a given threatening process (Fig. 3), rather than actual responses to each threat-mitigation action, which were not possible to quantify because Noisy Miner reduction and tree restoration have not yet been conducted. Using an occupancy modeling approach allowed us to discover population processes under varying threat intensities, but data requirements for this approach (multiple seasons of detections) and three years of data collection meant that models could not be built for 40 rare species (Mackenzie & Royle 2005). When there are rare components in a species community that cannot be modeled, we suggest using a combination of expert elicitation and process-based models to reduce the likelihood of perverse outcomes. (Our pessimistic and optimistic scenarios simulating expert elicitation were reasonably effective if not optimal at increasing colonization rates [Fig. 4].)

Although we did not explore interactions between species, using empirical data ensured that relative expected colonization rates under threat mitigation were predicted from real bird assemblages. In landscapes with strong interspecies interactions, unpredictable cascade effects or interaction destabilization could occur when one species disappears or changes in abundance within a community (such as when a management action leads to competitor or mesopredator release [Ruscoe et al. 2011]). Our predictions provide a first step to understanding how bird populations might be improved in the landscape and are valuable for informing an adaptive-management approach that embraces uncertainty by applying alternative optimal threat-mitigation strategies across different patches.

One assumption was that threatening processes might be reversed by either reducing their intensity, frequency, or duration (for grazing and Noisy Miners) or by restoring the landscape (tree cover). Threat mitigation can have different outcomes depending on the history of the landscape and may include system recovery, but it could also result in novel ecosystems (Lindenmayer et al. 2008). For instance, locations where land condition has been considerably altered due to intensive historical agricultural land-use practices over a long time may respond more slowly (or not at all) to restoration of tree cover or grazing removal than places where the land has been grazed in a less intensive manner or for a shorter time (Duncan & Dorrough 2009). To deal with this, information on land condition or historical land management could be incorporated into spatial allocation of resources to threat mitigation (Fischer et al. 2010). Using our process-based prioritization approach, we found a set of actions that may best mitigate the major threats known to occur across our study landscape. However, other actions are possible, and other factors (e.g., invasive predators and climate change) are likely to affect species either independently or in concert with our threatening processes (Firn et al. 2015).

Implications for Decision Making

Independent threat-mitigation actions may have limited effect if other threatening processes continue to affect species. By conducting a complementary threat-management prioritization, we demonstrated that cumulative impacts of a despotic species, the Noisy Miner, were most effectively mitigated when ongoing threatening processes of tree cover loss and habitat degradation due to grazing were also addressed. The results of empirical process-based studies such as these should inform and validate expert-elicited prioritizations of threat-mitigation actions for multiple species. In doing so, biodiversity outcomes will be improved through an understanding of which complementary threats, if managed independently versus together, will have the greatest impact on ecological processes of native biodiversity in degraded landscapes.

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References

Auerbach NA, Tulloch AIT, Possingham HP. 2014. Informed actions: where to cost effectively manage multiple threats to species to maximize return on investment. Ecological Applications 24:1357–1373.

Auerbach NA, Wilson KA, Tulloch AIT, Rhodes JR, Hanson JO, Possingham HP. 2015. Effects of threat management interactions on conservation priorities. Conservation Biology 29:1626–1635.

Balmford A, Mace GM, Ginsberg JR. 1999. The challenges to conservation in a changing world: putting processes on the map. Pages 1–28 in Mace GM, Balmford A, Ginsberg JR, editors. Conservation in a changing world. Cambridge University Press, Cambridge.

Benson J. 2008. New South Wales vegetation classification and assessment. Part 2: Plant communities of the NSW Southwestern Slopes Bioregion and update of NSW Western Plains plant communities, Version 2 of the NSWVCA database. Cunninghamia 104:599–673.

Burgman MA, Keith D, Hopper SD, Widyatmoko D, Drill C. 2007. Threat syndromes and conservation of the Australian flora. Biological Conservation 134:73–82.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cattarino L, Hermoso V, Carwardine J, Kennard MJ, Linke S. 2015. Multi-Action planning for threat management: a novel approach for the spatial prioritization of conservation actions. PLoS ONE 10: e0128027. DOI: 10.1371/journal.pone.0128027.

Chadès I, Nicol S, van Leeuwen S, Walters B, Firn J, Reeson A, Martin TG, Carwardine J. 2015. Benefits of integrating complementarity into priority threat management. Conservation Biology 29:525–536.

Darling ES, Côté IM. 2008. Quantifying the evidence for ecological synergies. Ecology Letters 11:1278–1286.

Dorrough J, Moll J, Crosthwaite J. 2007. Can intensification of temperate Australian livestock production systems save land for native biodiversity? Agriculture, Ecosystems & Environment 121:222–232.

Duncan DH, Dorrough JW. 2009. Historical and current land use shape landscape restoration options in the Australian wheat and sheep farming zone. Landscape and Urban Planning 91:124–132.

Evans MC, Possingham HP, Wilson KA. 2011. What to do in the face of multiple threats? Incorporating dependencies within a return on investment framework for conservation. Diversity and Distributions 17:437–450.

Field SA, Tyre AJ, Possingham HP. 2002. Estimating bird species richness: How should repeat surveys be organized in time? Austral Ecology 27:624–629.

Firn J, Martin TG, Chades I, Walters B, Hayes J, Nicol S, Carwardine J. 2015. Priority threat management of non-native plants to maintain ecosystem integrity across heterogeneous landscapes. Journal of Applied Ecology 52:1135–1144.

Fischer J, Sherren K, Stott J, Zerger A, Warren G, Stein J. 2010. Toward landscape-wide conservation outcomes in Australia's temperate grazing region. Frontiers in Ecology and the Environment 8:69–74.

Fiske I, Chandler R. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Foster CN, Barton PS, Wood JT, Lindenmayer DB. 2015. Interactive effects of fire and large herbivores on web-building spiders. Oecologia 179:237–248.

Isaac NJB, Cowlishaw G. 2004. How species respond to multiple extinction threats. Proceedings of the Royal Society of London B: Biological Sciences 271:1135–1141.

Lindenmayer DB, Fischer J, Felton A, Crane M, Michael D, Macgregor C, Montague-Drake R, Manning A, Hobbs RJ. 2008. Novel ecosystems resulting from landscape transformation create dilemmas for modern conservation practice. Conservation Letters 1:129–135.

Lindenmayer DB, Zammit C, Attwood SJ, Burns E, Shepherd CL, Kay G, Wood J. 2012. A novel and cost-effective monitoring approach for outcomes in an Australian biodiversity conservation incentive program. PLoS ONE 7:e50872. DOI: 10.1371/journal.pone.0050872.

Mac Nally R, Bowen M, Howes A, McAlpine CA, Maron M. 2012. Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. Ecology 93:668–678.

MacKenzie DI, Nichols JD, Hines JE, Knutson MG, Franklin AB. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Mackenzie DI, Royle JA. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.

Margules CR, Pressey RL. 2000. Systematic conservation planning. Nature 405:243–253.

Maron M, Grey MJ, Catterall CP, Major RE, Oliver DL, Clarke MF, Loyn RH, Mac Nally R, Davidson I, Thomson JR. 2013. Avifaunal disarray due to a single despotic species. Diversity and Distributions 19:1468–1479.

Martin TG, McIntye S. 2007. Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. Conservation Biology 21:504–514.

Martin TG, Possingham HP. 2005. Predicting the impact of livestock grazing on birds using foraging height data. Journal of Applied Ecology 42:400–408.

Moilanen A. 2008. Generalized complementarity and mapping of the concepts of systematic conservation planning. Conservation Biology 22:1655–1658.

Mortelliti A, Lindenmayer DB. 2015. Effects of landscape transformation on bird colonization and extinction patterns in a large-scale, long-term natural experiment. Conservation Biology 29:1314–1326.

Nagelkerke NJ. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Ponce-Reyes R, Nicholson E, Baxter PWJ, Fuller RA, Possingham H. 2013. Extinction risk in cloud forest fragments under climate change and habitat loss. Diversity and Distributions 19:518–529.

Ruscoe WA, et al. 2011. Unexpected consequences of control: competitive vs.predator release in a four-species assemblage of invasive mammals. Ecology Letters 14:1035–1042.

Santika T, McAlpine CA, Lunney D, Wilson KA, Rhodes JR. 2015. Assessing spatio-temporal priorities for species' recovery in broad-scale dynamic landscapes. Journal of Applied Ecology 52:832–840.

Tulloch AIT, Chadès I, Possingham HP. 2013. Accounting for complementarity to maximize monitoring power for species management. Conservation Biology 27:988–999.

Tulloch VJD, et al. 2015. Why do we map threats? Linking threat mapping with actions to make better conservation decisions. Frontiers in Ecology and the Environment 13:91–99.

Tulloch AIT, Chadés I, Dujardin Y, Westgate MJ, Lane PW, Lindenmayer D. 2016. Dynamic species co-occurrence networks require dynamic biodiversity surrogates. Ecography DOI: 10.1111/ecog.02143.

Visconti P, Pressey RL, Segan DB, Wintle BA. 2010. Conservation planning with dynamic threats: the role of spatial design and priority setting for species' persistence. Biological Conservation 143:756–767.

Watson DM. 2011. A productivity-based explanation for woodland bird declines: poorer soils yield less food. EMU 111:10–18.

Wilson KA, Evans MC, Di Marco M, Green DC, Boitani L, Possingham HP, Chiozza F, Rondinini C. 2011. Prioritizing conservation investments for mammal species globally. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 366:2670–2680.

Supporting Information

Appendix S1. Additional methodological details

Study area

Land conversion for agriculture poses one of the greatest threats to terrestrial biodiversity (Foley et al. 2005). It leads to habitat loss and fragmentation, and cascading effects on community composition through habitat and soil degradation and the spread of invasive species (McIntyre & Lavorel 2007). In many parts of the world including Australia, the traditional approach to recover biodiversity in fragmented agricultural landscapes has been to restore tree cover through replanting vegetation, an action that has received millions of dollars of government and private funding (Lindenmayer et al. 2010; Smith et al. 2013; Fischer et al. 2014). An alternative approach gaining prominence is holistic grazing (Mattison & Norris 2005; Mooney et al. 2005), in which intense rotational pulses are followed by resting the land. In doing so, native pastures might recover passively in a way that restores habitat and food resources for native biodiversity, and also improves land condition and the quality of livestock feed.

Over the past several decades, public-supported financial incentives have been employed in conservation programs to encourage changing land use practices to a more holistic approach that includes high-intensity short-duration grazing or cropping. Examples include the Australian Federal Government Box-gum Grassy Woodland project (Kay et al. 2013) and the Washington Sustainable Food & Farming Network's "Beefing Up the Palouse—an Alternative to the Conservation Reserve Program" (http://wsffn.org/our-work/beefing-up-the-palouse-project, Accessed 3 July 2015).

In 2008 the Australian Government began a trial of stewardship payments to landholders on 163 farms spread over a distance of >1000 km from south-western NSW north to Queensland. The program targeted the Lachlan and Murrumbidgee catchments in the eastern Australian sheep–wheat belt (Kay et al. 2013), with objectives of changing grazing intensity to promote biodiversity outcomes in the endangered Box Gum Grassy Woodland ecological community (Lindenmayer et al. 2012).. The native vegetation of this community is dominated by White Box *Eucalyptus albens*, Grey Box *E. microcarpa*, Yellow Box *E. melliodora*, and Blakely's Red Gum *E. blakelyi*, and is highly fragmented (Fig. S1), with >85% having been cleared in the last 230 years for agriculture (Benson 2008). Within this incentive scheme there are 163 farms spread over 7 catchments stretching from south-western NSW north to Queensland – a distance of more than 1000 km (Lindenmayer et al. 2012). Historically (i.e. over the previous 10 years or more), each of these farms had undergone one of four types of management: long holistic (high intensity over a long time frame, for >10yrs), short holistic (high intensity over a short time frame, for <5yrs, i.e. conversional farming), long rotational (medium intensity over a large proportion but not all of the year) or continuous grazing (i.e. grazed all year). We set this as the background 'regime' of management, representing the historical effects of grazing (Table 1, main text).

Sites spanned an intensification gradient from little cleared or grazed, unfertilized and uncultivated woodlands to intensively cleared, grazed, fertilized and sown pastures. The current level of grazing threat within a patch was represented by selecting at least two sites within each farm, with one site ungrazed (fenced off from cattle), and one site undergoing grazing. The majority of farms had three to four sites, with one site ungrazed (fenced off from cattle), one site undergoing low-intensity grazing, and one site undergoing high-intensity grazing, but in some farms this was not possible due to grazing history and economic constraints. Sites were stratified based on levels of tree cover and included sites with both no noisy miners and high levels of noisy miners (Table S1). These sites therefore represented a continuum of the level of impact from three threatening processes, from almost zero impact (sites with no Noisy Miners, no grazing, and high tree cover) to high impact (sites with high numbers of miners, high grazing intensity, and low tree cover; Fig. S1).

Data collection

Landholder surveys were conducted to gather detailed management information for each site at the commencement of the study (2011). This involved semi-structured 2 hour interviews with each landholder. Surveys gathered data regarding (but not limited to): (i) past and present grazing management (as far as possible), including domestic (sheep and cattle) and native (kangaroo) grazing, (ii) fire history, (iii) chemical (fertilizer) history, and (iv) invasive species (cats, foxes, noxious plants) records. Additional surveys were repeated at the end of each year of the study to gather livestock records from each farmer (containing information for every grazing rotation at every site on the type of stock, number of stocking days, and number of resting days between rotations).

Each site was surveyed for birds 6 times per year in spring from 2011 to 2013. In any given year, each site was surveyed by at least two different observers on a different day to limit day and observer effects (Field et al. 2002; Lindenmayer et al. 2009). Surveys were completed within four hours of dawn and were not undertaken on windy or rainy days. This approach generates reliable presence-absence and detection frequency data (Cunningham et al. 1999; Cunningham & Lindenmayer 2005). A total of 77 species were detected more than once, of which 37 species could generate dynamic occupancy models (see Table S2 for species details).

Before fitting models, we tested all variables for correlations using the Pearson's product-moment coefficient. Despite expectations that grazing variables might be correlated, no variables were correlated (Pearson's product-moment correlation coefficient <0.6), most likely due to the variability in grazing regimes across the landscape, and due to the fact that some rotational grazing regimes were high-intensity but low-duration, some high-intensity high-duration, some low-intensity high-duration, and some low-intensity low-duration.

Figure S1. *Endangered Box Gum Grassy Woodland ecological community, showing example sites of (a) low grazing intensity, low clearing, (b) low grazing intensity, high clearing, (c) high grazing intensity, low clearing, and (d) high grazing intensity, high clearing.*

Table S1. *Summary of data for the three threatening processes of tree clearing, alternative grazing regimes and Noisy Miner abundance in the Box Gum Grassy woodlands case study.*

	Tree clearing (% cover: “tree”)	Grazing intensity (DSE rate: “Gr.int”)	Grazing frequency (annual number of resting events: “Gr.frq”)	Grazing duration (average number of days grazed per event: “Gr.dur”)	Noisy Miner average annual abundance per site (“minerab”)
Mean of variable	25.87	Annual: 5.65 Event: 101.32	1.81	176.20	1.1
S.D. of variable	20.09	Annual: 7.77 Event: 177.65	2.17	131.92	1.84
Range of variable	0-88.01	Annual: 0-47.07 Event: 0-1355.45	0-13	0-365	0-13

Table S2. *List of all bird species modelled in the Box Gum Grassy woodlands case study.*

Common name	Scientific name	NSW threat status [a]	Common-wealth threat status [b]
Australian Magpie	*Cracticus tibicen*		
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*		Declining
Brown Treecreeper	*Climacteris picumnus*	Vulnerable (ACT)	Declining
Buff-rumped Thornbill	*Acanthiza reguloides*		Declining
Common Starling	*Sturnus vulgaris*		Invasive
Eastern Rosella	*Platycercus eximius*		
Grey Butcherbird	*Cracticus torquatus*		
Grey Fantail	*Rhipidura albiscapa*		
Grey Shrike-Thrush	*Colluricincla harmonica*		
Jacky Winter	*Microeca fascinans*		Declining
Little Friarbird	*Philemon citreogularis*		
Magpie-lark	*Grallina cyanoleuca*		
Mistletoebird	*Dicaeum hirundinaceum*		Declining
Noisy Friarbird	*Philemon corniculatus*		
Noisy Miner	*Manorina melanocephala*		Threatening Process
Red Wattlebird	*Anthochaera carunculata*		
Red-rumped Parrot	*Psephotus haematonotus*		
Restless Flycatcher	*Myiagra inquieta*		Migratory, declining
Rufous Songlark	*Cincloramphus mathewsi*		
Rufous Whistler	*Pachycephala rufiventris*		Declining
Sacred Kingfisher	*Todiramphus sanctus*		
Silvereye	*Zosterops lateralis*		
Spotted Pardalote	*Pardalotus punctatus*		Declining
Striated Pardalote	*Pardalotus striatus*		Declining
Striated Thornbill	*Acanthiza lineata*		Declining
Superb Fairy-wren	*Malurus cyaneus*		
Superb Parrot	*Polytelis swainsonii*	Vulnerable	Vulnerable
Weebill	*Smicrornis brevirostris*		Declining

Common name	Scientific name	NSW threat status [a]	Common-wealth threat status [b]
White-plumed Honeyeater	*Lichenostomus pencillatus*		
White-throated Gerygone	*Gerygone albogularis*		Declining
White-throated Treecreeper	*Cormobates leucophaea*		
White-winged Chough	*Corcorax melanorhamphos*		
White-winged Triller	*Lalage sueurii*		
Willie Wagtail	*Rhipidura leucophrys*		
Yellow Thornbill	*Acanthiza nana*		Declining
Yellow-faced Honeyeater	*Lichenostomus chrysops*		Declining
Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*		Declining

a. *Listed at a state level as vulnerable under the New South Wales Threatened Species Conservation Act 1995.*

b. *Listed nationally under the Australian Government Environmental Protection and Biodiversity Act 1999 or by BirdLife International (2016)*

Model fitting

We followed a 3 step protocol for fitting the multiple-season occupancy models. Colonization and extinction are estimated from the detection history data as probabilities rather than arbitrarily defined events, after accounting for uncertainty in detection, and therefore are expected to be relatively unbiased (MacKenzie et al. 2003; MacKenzie et al. 2006).

1) We started by modelling *p* (detection probability). We fitted five detectability models: rain in the previous 3 months (continuous), temperature at the time of the survey (categorical), categorical year (i.e. year specific variation), numerical year (i.e. implying a trend in detectability), and constant across years/sites:

   Model 1: $\Psi(.)\gamma(.)\varepsilon(.)p(.)$
   Model 2: $\Psi(.)\gamma(.)\varepsilon(.)p(Y)$
   Model 3: $\Psi(.)\gamma(.)\varepsilon(.)p(YN)$
   Model 4: $\Psi(.)\gamma(.)\varepsilon(.)p(rain)$
   Model 5: $\Psi(.)\gamma(.)\varepsilon(.)p(temp)$

   The best model was selected through the Akaike Information Criterion (AIC; Burnham & Anderson 2002). The variable included in the top-ranking detection model was retained in all the following steps (e.g. if the top-ranking model included *p* as function of year, all the following models included *p* as function of year).

2) We then selected the most important variables influencing Ψ (the probability of a site being occupied in 2011, the first year of the study). Ψ was modelled as a function of: a) tree cover in the 500-m circle, b) grazing regime, c) environmental variables (see Table 1 in the main text). Here we show an example of a species with detectability modelled using Y:

   Model 6: $\Psi(.)\gamma(.)\varepsilon(.)p(Y)$
   Model 7: $\Psi(regime)\gamma(.)\varepsilon(.)p(Y)$
   Model 8: $\Psi(IMP250)\gamma(.)\varepsilon(.)p(Y)$

Model 9: Ψ(elev)γ(.)ε(.)p(Y)
Model 10: Ψ(soilP)γ(.)ε(.)p(Y)
Model 11: Ψ(tree)γ(.)ε(.)p(Y)
Model 12: Ψ(anntemp)γ(.)ε(.)p(Y)
Model 13: Ψ(annprec)γ(.)ε(.)p(Y)

The variable included in the top ranking occupancy model was retained in the following step.

3) We modelled the probability of colonization (*ϒ*) and the probability of extinction (*ε*) as functions of the following variables: a) site-specific abundance of noisy miners in the given year, b) tree cover in the 500-m circle c) grazing (either frequency, duration, intensity, or a combination), d) soil nutrients, e) biomass, and f) soil nutrients plus tree cover. Additive combinations of a), b) and c) were also evaluated. Here we show an example of a species with detectability modelled using Y and first year occupancy modelled using annual precipitation:

Threats:
Model 14: Ψ(annprec)γ(minerab)ε(minerab)p(Y)
Model 15: Ψ(annprec)γ(minerab)ε(.)p(Y)
Model 16: Ψ(annprec)γ(.)ε(minerab)p(Y)
Model 17: Ψ(annprec)γ(tree)ε(tree)p(Y)
Model 18: Ψ(annprec)γ(tree)ε(.)p(Y)
Model 19: Ψ(annprec)γ(.)ε(tree)p(Y)
Model 20: Ψ(annprec)γ(Gr.int1)ε(Gr.int1)p(Y)
Model 21: Ψ(annprec)γ(Gr.int1)ε(.)p(Y)
Model 22: Ψ(annprec)γ(.)ε(Gr.int1)p(Y)
Model 23: Ψ(annprec)γ(Gr.int2)ε(Gr.int2)p(Y)
Model 24: Ψ(annprec)γ(Gr.int2)ε(.)p(Y)
Model 25: Ψ(annprec)γ(.)ε(Gr.int2)p(Y)
Model 26: Ψ(annprec)γ(Gr.frq)ε(Gr.frq)p(Y)
Model 27: Ψ(annprec)γ(Gr.frq)ε(.)p(Y)
Model 28: Ψ(annprec)γ(.)ε(Gr.frq)p(Y)

Model 29: Ψ(annprec)γ(Gr.dur)ε(Gr.dur)p(Y)

Model 30: Ψ(annprec)γ(Gr.dur)ε(.)p(Y)

Model 31: Ψ(annprec)γ(.)ε(Gr.dur)p(Y)

Model 32: Ψ(annprec)γ(tree+minerab)ε(tree+minerab)p(Y)

Model 33: Ψ(annprec)γ(tree+minerab)ε(.)p(Y)

Model 34: Ψ(annprec)γ(.)ε(tree+minerab)p(Y)

Model 35: Ψ(annprec)γ(tree+Gr.int2)ε(tree+Gr.int2)p(Y)

Model 36: Ψ(annprec)γ(tree+Gr.int2)ε(.)p(Y)

Model 37: Ψ(annprec)γ(.)ε(tree+Gr.int2)p(Y)

Model 38: Ψ(annprec)γ(minerab+Gr.int2)ε(minerab+Gr.int2)p(Y)

Model 39: Ψ(annprec)γ(minerab+Gr.int2)ε(.)p(Y)

Model 40: Ψ(annprec)γ(.)ε(minerab+Gr.int2)p(Y)

Model 41: Ψ(annprec)γ(Gr.int2+Gr.dur)ε(Gr.int2+Gr.dur)p(Y)

Model 42: Ψ(annprec)γ(Gr.int2+Gr.dur)ε(.)p(Y)

Model 43: Ψ(annprec)γ(.)ε(Gr.int2+Gr.dur)p(Y)

Model 44: Ψ(annprec)γ(Gr.int2+Gr.frq)ε(Gr.int2+Gr.frq)p(Y)

Model 45: Ψ(annprec)γ(Gr.int2+Gr.frq)ε(.)p(Y)

Model 46: Ψ(annprec)γ(.)ε(Gr.int2+Gr.frq)p(Y)

Model 47: Ψ(annprec)γ(Gr.frq+Gr.dur)ε(Gr.frq+Gr.dur)p(Y)

Model 48: Ψ(annprec)γ(Gr.frq+Gr.dur)ε(.)p(Y)

Model 49: Ψ(annprec)γ(.)ε(Gr.frq+Gr.dur)p(Y)

Environment:

Model 50: Ψ(annprec)γ(soilP+tree)ε(soilP+tree)p(Y)

Model 51: Ψ(annprec)γ(soilP+tree)ε(.)p(Y)

Model 52: Ψ(annprec)γ(.)ε(soilP+tree)p(Y)

Model 53: Ψ(annprec)γ(soilP)ε(soilP)p(Y)

Model 54: Ψ(annprec)γ(soilP)ε(.)p(Y)

Model 55: Ψ(annprec)γ(.)ε(soilP)p(Y)

Model 56: Ψ(annprec)γ(biomass)ε(biomass)p(Y)

Model 57: Ψ(annprec)γ(biomass)ε(.)p(Y)
Model 58: Ψ(annprec)γ(.)ε(biomass)p(Y)

Because of the nested structure of our design, we checked for spatial autocorrelation in the residuals of the top model (Zuur et al. 2009). We did this by calculating spline correlograms for each of the three time periods and for the average values across years after finding the best set of models for each species. No evidence of spatial autocorrelation was detected.

Optimization scenarios

We evaluated 10 threat mitigation strategies, with each strategy comprising of a number of actions required for successfully implementation (Table S3).

We explored three scenarios of the ways in which empirical model results might be used to inform t_{ij} (following Auerbach et al. 2015). Each scenario differed in the way it calculated the benefits t_{ij} of each threat mitigation strategy for each species. The first two scenarios simulated expert elicitation by categorizing species' responses according to a basic understanding of the number of threats acting on a species (optimistic scenario) or simply as beneficial or not (pessimistic scenario). The third mechanistic scenario incorporated the nuances of species responses to multiple threats through process-based prediction of colonization rates:

(a) Simple optimistic scenario: Using our categorization of whether or not a species is affected by each threat irrespective of whether the threat affected colonization, extinction or occupancy, we assigned each species a benefit that was proportional to the number of threats that affected it. Species affected by 3 threats therefore received a benefit of 1 for the triple action "Remove miners + restore trees + reduce grazing intensity", but also received a benefit of 0.75 if two threats were mitigated, and 0.5 if one threat was mitigated (see Supporting Material for more details). Species affected by no threats received benefits of 0.5 under all actions. The "no action" benefits were set at 0.25 for species affected by at least 1 threat (this assumes "optimistic" baseline colonization rate across the landscape of 0.25 under "no action").

Table S3. *Threat-mitigation strategies and description of actions to restore woodland birds in the study.*

Threat-mitigation strategy	**Brief description of actions[1]**
1. Restore tree cover	weed control and site preparation
	staged planting of native vegetation
	ongoing maintenance (e.g. weed control)
	fencing off revegetation in grazed locations
2. Remove Noisy Miners	monitoring
	nest destruction
	culling of birds (shooting from the ground)
	public engagement
3. Reduce grazing frequency	community engagement and incentive programs
	reduced number of stocking events per year on farms
4. Reduce grazing duration	community engagement and incentive programs
	reduced duration of stocking events on farms
	increased duration of resting periods (between stocking rotations) on farms
5. Reduce grazing intensity	community engagement and incentive programs
	fencing off remnants
	reduced livestock numbers on farms
	switching of livestock type on farms (e.g. from cattle to sheep)
6. Restore trees + reduce grazing intensity	strategies 1 and 5 combined
7. Remove Noisy Miners + reduce grazing intensity	strategies 2 and 5 combined
8. Remove Noisy Miners + restore trees	strategies 1 and 2 combined

9. Remove Noisy Miners + restore trees + reduce grazing intensity	
10. No action	monitoring only

[1] *Strategies were determined based on literature review and consultation with local land managers. Due to the low effectiveness of strategies 3 and 4 in terms of increasing species' colonization rates, these were not considered for any combined strategies.*

(b) Simple pessimistic scenario: Using our categorization of whether or not a species is affected by each threat irrespective of whether the threat affected colonization, extinction or occupancy, we assigned each species a benefit score of 0 (no benefit) if the action did not remove all of its threats, and 1 (complete benefit) if the action removed all of its threats. Species affected by all 3 threats therefore only received a value of 1 for the triple action "Remove miners + restore trees + reduce grazing intensity". Only species unaffected by any threats received a benefit of 1 for "no action", with zero benefit for all other species if there was no action (this assumes "pessimistic" baseline colonization rate across the landscape of zero under "no action").

(c) Mechanistic scenario: Using the predicted probabilities of occupancy, colonization and extinction for each species to derive probabilities of each species responding to one or more threat mitigation actions versus no action (i.e. no change to current state). Here, t_{ij} was calculated directly from the predictions of colonization from the model-averaged parameters of the best set of models (within 2 AIC), i.e.:

$$t_{ij} = P(\text{colonization})|\text{threat mitigation action.}$$

Values for all actions not targeting threats that were listed in the best set of models for each species were set to the same value as the 'no action' probability (i.e. the current probability of occupancy in the landscape). We set a target of achieving 75% reduction in the threat. This means that colonization probabilities for a given threat mitigation action were derived from the 75th quantile of the model for tree cover (for which the aim was to increase the cover), and the 25th quantile for the models for miners and grazing (for which the aim was to reduce the threat), or combinations of these for multiple actions. We believe this is a more realistic portrayal of threat mitigation than taking the highest prediction as is it difficult if not impossible to completely eradicate most threats from landscapes.

We set costs equal to the number of actions chosen (i.e. a single action costs “1”, whereas a combined strategy of mitigating two threats costs “2”). We acknowledge that this is not a realistic representation of management costs, however we were interested in the relative priorities of threats for mitigation based on empirical data on the importance of these threats for species, rather than the costs of doing the management which are site-specific.

For those threatening processes that cannot be mapped and predicted using empirical models of occupancy, colonization and extinction, alternative approaches such as Bayesian models could be explored. These models allow prior information on the likelihood of that threatening process impacting a given species might be used to account for variability in model predictions, or maps and models of the history of invasive species management (based on landholder surveys) might be used as a surrogate for the intensity of that threat (Tulloch et al. 2014).

Supporting References

Auerbach, N. A., K. A. Wilson, A. I. T. Tulloch, J. R. Rhodes, J. O. Hanson, and H. P. Possingham. 2015. Effects of threat management interactions on conservation priorities. Conservation Biology:early online doi:10.1111/cobi.12551.

Benson, J. 2008. New South Wales vegetation classification and assessment: Part 2 plant communities of the NSW Southwestern Slopes Bioregion and update of NSW Western Plains plant communities, Version 2 of the NSWVCA database. Cunninghamia 104:599–673.

BirdLife International. 2016. IUCN Red List for birds, Downloaded from http://www.birdlife.org on 17/01/2016.

Burnham, K. P., and D. R. Anderson 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Cunningham, R. B., and D. B. Lindenmayer. 2005. Modeling count data of rare species: Some statistical issues. Ecology 86:1135-1142.

Cunningham, R. B., D. B. Lindenmayer, H. A. Nix, and B. D. Lindenmayr. 1999. Quantifying observer heterogeneity in bird counts. Australian Journal of Ecology 24:270-277.

Field, S. A., A. J. Tyre, and H. P. Possingham. 2002. Estimating bird species richness: How should repeat surveys be organized in time? Austral Ecology 27:624-629.

Fischer, J., D. J. Abson, V. Butsic, M. J. Chappell, J. Ekroos, J. Hanspach, T. Kuemmerle, H. G. Smith, and H. von Wehrden. 2014. Land Sparing Versus Land Sharing: Moving Forward. Conservation Letters 7:149-157.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global Consequences of Land Use. Science 309:570-574.

Kay, G., D. Florance, J. Wood, and D. B. Lindenmayer. 2013. Environmental Stewardship Box Gum Grassy Woodland Monitoring Project. Final Monitoring Report for the Department of Sustainability, Environment, Water, Population and Communities (SEWPAC). Fenner School of Environment and Society, Australian National University, Canberra, A.C.T.

Lindenmayer, D. B., E. J. Knight, M. J. Crane, R. Montague-Drake, D. R. Michael, and C. I. MacGregor. 2010. What makes an effective restoration planting for woodland birds? Biological Conservation 143:289-301.

Lindenmayer, D. B., J. T. Wood, and C. MacGregor. 2009. Do observer differences in bird detection affect inferences from large-scale ecological studies? Emu 109:100-106.

Lindenmayer, D. B., C. Zammit, S. J. Attwood, E. Burns, C. L. Shepherd, G. Kay, and J. Wood. 2012. A Novel and Cost-Effective Monitoring Approach for Outcomes in an

Australian Biodiversity Conservation Incentive Program. PLoS ONE 7:e50872.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200-2207.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Amsterdam.

Martin, T. G., and H. P. Possingham. 2005. Predicting the impact of livestock grazing on birds using foraging height data. Journal of Applied Ecology 42:400-408.

Mattison, E. H. A., and K. Norris. 2005. Bridging the gaps between agricultural policy, land-use and biodiversity. Trends in Ecology & Evolution 20:610-616.

McIntyre, S., and S. Lavorel. 2007. A conceptual model of land use effects on the structure and function of herbaceous vegetation. Agriculture Ecosystems & Environment 119:11-21.

Mooney, H., A. Cropper, and W. Reid. 2005. Confronting the human dilemma. Nature 434:561-562.

Smith, F. P., S. M. Prober, A. P. N. House, and S. McIntyre. 2013. Maximizing retention of native biodiversity in Australian agricultural landscapes—The 10:20:40:30 guidelines. Agriculture, Ecosystems & Environment 166:35-45.

Tulloch, A. I. T., V. J. D. Tulloch, M. C. Evans, and M. Mills. 2014. The Value of Using Feasibility Models in Systematic Conservation Planning to Predict Landholder Management Uptake. Conservation Biology 28:1462-1473.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Appendix S2: Colonization rates under different threat mitigation strategies

Here we provide the matrices used in optimization of threat mitigation strategies for our 37 bird species under different scenarios of calculating expected benefits, and a summary of additional threat management findings.

Using the results of the occupancy models to quantify likely threat responses instead of classify threat responses (scenarios 1 and 2) changed the number of species affected by alternative threat mitigation strategies, and changed the magnitude of this impact. Although there were no significant differences between average colonization rates under each threat management strategy (Fig. S2), individual species varied greatly between and within scenarios (Tables S4, S5, S6).Historical land management practices influenced the probability of woodland patch occupancy (Ψ) of 70% (26) of the 37 woodland bird species, with 8 species affected most by soil characteristics, 3 species by the past grazing regime, and 15 species by the availability of remnant woody tree cover (Table 2, main text). The probability of occupancy of the remaining 11 species was best predicted using environmental variables (temperature, precipitation, or elevation). The colonization and extinction rates of 32 out of the 37 species were affected by at least one threatening process (Table 2, main text; Tables S4 to S6).

As expected, Noisy Miner colonization rates were predicted to decline under all strategies involving Noisy Miner control under scenarios 1 (optimistic categorization of threats; Table S4) and 2 (pessimistic categorization of threats; Table S5). Under our process-based scenario, colonization rates were >20% lower under all strategies involving noisy miner control (Table S6), compared with a “no action” strategy. The only exception to this was a strategy of reducing grazing duration (shorter grazing events) which was expected to have almost no effect on Noisy Miner colonization rates (Table S6).This is because Noisy Miner colonization was predicted to decline with soil phosphorus and tree cover, and increase with shorter grazing events (Table 2, main text).

The Yellow Thornbill and the Black-faced Cuckoo-Shrike had the highest expected changes in predicted patch colonization between no action and under threat mitigation using our mechanistic approach (Table S6). The Yellow Thornbill was predicted to increase from <1 to 95% and the Black-faced Cuckoo-Shrike from 2 to 97% probability of colonization, both under the three-threat mitigation strategy.

The species most likely to be adversely affected by threat mitigation measures, i.e. predicted to decline in patch colonization (Tables S4 to S6), were the Common Starling (predicted to suffer a reduction in colonization of 42% under a combined action of restoring trees and reducing grazing intensity), Grey Butcherbird (9% to 4% decline in colonization under all noisy miner control strategies), Noisy Miner (decline in colonization under all strategies except for reducing grazing duration), Red-rumped Parrot (3% decline in colonization under combined strategy of reducing miners and restoring tree cover), and White-winged Triller (11% decline in colonization under combined strategy of reducing grazing and miners plus increasing tree cover).

We found that the impact of different grazing practices (e.g. rest period duration and stocking levels) varied for different species (Tables S4 to S6). Most species responded negatively to high grazing intensity and were more likely to colonize woodland patches under reduced-intensity grazing, in particular birds that forage in the shrub layer and nest close to the ground (unpublished manuscript). All three species responding positively to grazing duration responded negatively to grazing intensity (Table 2 in main text). Although grazing intensity was categorized as affecting as many species as loss of tree cover, our threat mitigation optimization showed that changing grazing regimes was lower priority than increasing tree cover and controlling Noisy Miners (Table S7). This implies that grazing influences breeding success as well as foraging as previously demonstrated (Martin & Possingham 2005).

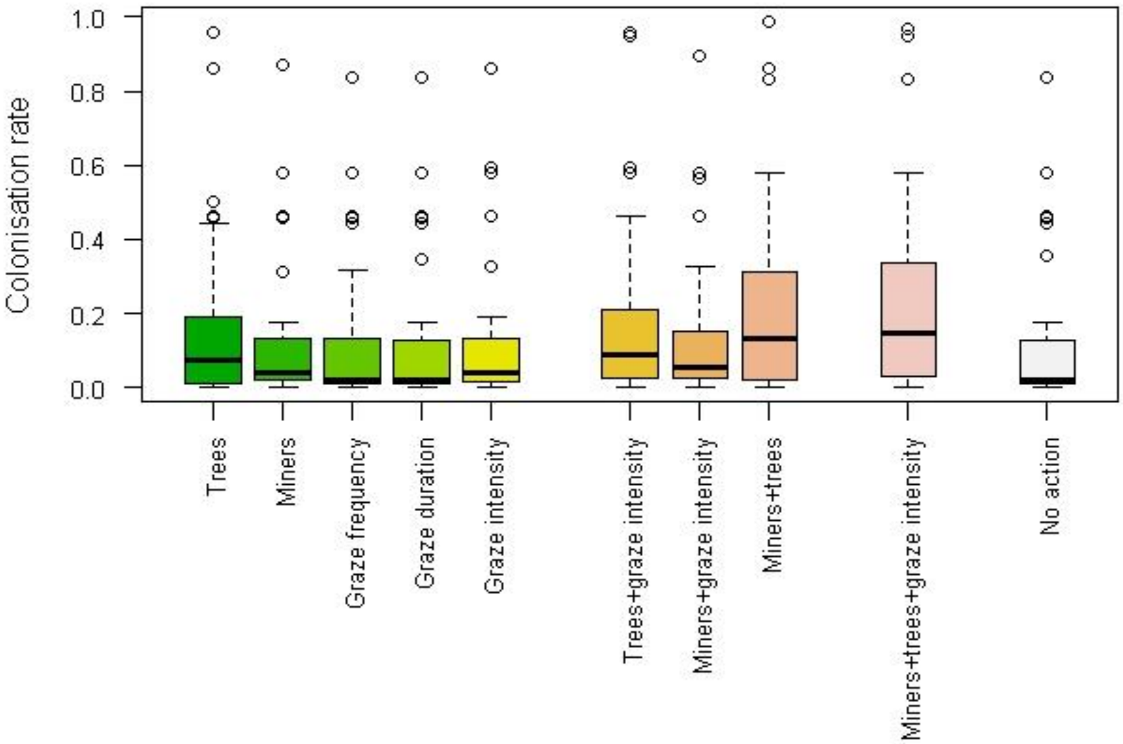

Figure S2. *Predicted colonization rate (from model-averaged parameters of occupancy models) under different threat mitigation strategies for all species.*

Table S4. *Expected benefits of alternative threat mitigation actions determined for scenario 1 (optimistic scenario – species receives partial benefit from threat management proportional to number of threats).*

Species	Increase tree cover	Reduce noisy miners	Reduce grazing freq-uency	Reduce grazing duration	Reduce grazing intensity	Trees + grazing intensity	Miners + grazing intensity	Miners + trees	Miners + trees + grazing intensity	No action
Australian Magpie	0.5	1	1	1	1	0.5	1	0.5	0.5	1
Black-faced Cuckoo-shrike	0.75	0.5	0.5	0.5	0.75	1	0.75	0.75	1	0.5
Brown Treecreeper	0.5	0.5	0.5	0.5	1	1	1	0.5	1	0.5
Buff-rumped Thornbill	0.75	0.75	0.5	0.5	0.5	0.75	0.75	1	1	0.5
Common Starling	0.5	1	1	1	0.5	0.5	0.5	0.5	0.5	1
Eastern Rosella	0.25	0.25	0.5	0.5	0.75	0.5	0.5	0.25	0.25	0.5
Grey Butcherbird	1	0.5	1	1	1	1	0.5	0.5	0.5	1
Grey Fantail	0.75	0.75	0.5	0.5	0.5	0.75	0.75	1	1	0.5
Grey Shrike-Thrush	0.5	0.5	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Jacky Winter	1	0.5	0.5	0.5	0.5	1	0.5	1	0.5	0.5
Little Friarbird	1	0.5	0.5	0.5	0.5	1	0.5	1	0.5	0.5
Magpie-lark	1	1	1	1	1	1	1	1	1	1
Mistletoebird	0.75	0.75	0.75	0.75	0.75	1	1	1	1	0.5
Noisy Friarbird	1	0.5	0.5	0.5	0.5	1	0.5	1	0.5	0.5
Noisy Miner	0.5	1	1	1	1	0.5	1	0.5	0.5	1
Red Wattlebird	1	0.5	0.5	0.5	0.5	1	0.5	1	0.5	0.5
Red-rumped Parrot	0.5	1	1	1	1	0.5	1	0.5	0.5	1
Restless Flycatcher	0.5	0.5	0.25	0.5	1	1	1	0.5	1	0.5
Rufous Songlark	1	1	1	1	1	1	1	1	1	1
Rufous Whistler	0.5	0.75	0.5	0.5	0.75	0.75	1	0.75	1	0.5
Sacred Kingfisher	0.5	0.75	0.5	0.5	0.75	0.75	1	0.75	1	0.5
Silvereye	0.5	0.75	0.5	0.5	0.75	0.75	1	0.75	1	0.5
Spotted Pardalote	1	0.5	0.5	0.5	0.5	1	0.5	1	0.5	0.5
Striated Pardalote	0.5	1	1	1	1	0.5	1	0.5	0.5	1
Striated Thornbill	1	0.5	0.5	0.5	0.5	1	0.5	1	0.5	0.5
Superb Fairy-wren	0.5	0.5	0.5	1	0.5	0.5	0.5	0.5	0.5	0.5
Superb Parrot	0.25	0.25	0.5	0.5	0.75	0.5	0.5	0.25	0.25	0.5

Species	Increase tree cover	Reduce noisy miners	Reduce grazing freq-uency	Reduce grazing duration	Reduce grazing intensity	Trees + grazing intensity	Miners + grazing intensity	Miners + trees	Miners + trees + grazing intensity	No action
Weebill	0.75	0.5	0.25	0.5	0.75	1	0.75	0.75	1	0.5
White-plumed Honeyeater	1	1	1	1	1	1	1	1	1	1
White-throated Gerygone	0.75	0.75	0.5	0.5	0.5	0.75	0.75	1	1	0.5
White-throated Treecreeper	0.75	0.5	0.75	0.75	0.75	1	0.75	0.75	1	0.5
White-winged Chough	1	1	1	1	1	1	1	1	1	1
White-winged Triller	0.25	1	0.5	0.5	0.5	0.25	1	0.5	0.5	0.5
Willie Wagtail	0.75	0.75	0.5	0.5	0.5	0.75	0.75	1	1	0.5
Yellow Thornbill	0.75	0.5	0.5	0.5	0.75	1	0.75	0.75	1	0.5
Yellow-faced Honeyeater	0.5	0.75	0.5	0.5	0.75	0.75	1	0.75	1	0.5
Yellow-rumped Thornbill	0.5	1	0.5	0.5	0.5	0.5	1	1	1	0.5

Table S5. *Expected benefits of alternative threat mitigation actions determined for scenario 2 (pessimistic scenario – species needs all threats managed to receive full benefit).*

Species	Increase tree cover	Reduce noisy miners	Reduce grazing frequency	Reduce grazing duration	Reduce grazing intensity	Trees + grazing intensity	Miners + grazing intensity	Miners + trees	Miners + trees + grazing intensity	No Action
Australian Magpie	0	1	1	1	1	0	0	0	0	1
Black-faced Cuckoo-shrike	0	0	0	0	0	1	0	0	1	0
Brown Treecreeper	0	0	0	0	1	1	1	0	1	0
Buff-rumped Thornbill	0	0	0	0	0	0	0	1	1	0
Common Starling	0	1	1	1	0	0	0	0	0	1
Eastern Rosella	0	0	0	0	1	0	0	0	0	0
Grey Butcherbird	1	0	1	1	1	1	0	0	0	1
Grey Fantail	0	0	0	0	0	0	0	1	1	0
Grey Shrike-Thrush	0	0	1	0	0	0	0	0	0	0
Jacky Winter	1	0	0	0	0	1	0	1	1	0
Little Friarbird	1	0	0	0	0	1	0	1	1	0
Magpie-lark	1	1	1	1	1	1	1	1	1	1
Mistletoebird	0	0	0	0	0	0	0	0	1	0
Noisy Friarbird	1	0	0	0	0	1	0	1	1	0
Noisy Miner	0	0	1	1	1	0	0	0	0	1
Red Wattlebird	1	0	0	0	0	1	0	1	1	0
Red-rumped Parrot	0	1	1	1	1	0	0	0	0	1
Restless Flycatcher	0	0	0	0	1	1	1	0	1	0
Rufous Songlark	1	1	1	1	1	1	1	1	1	1
Rufous Whistler	0	0	0	0	0	0	1	0	1	0

Sacred Kingfisher	0	0	0	0	0	0	1	0	1	0
Silvereye	0	0	0	0	0	0	1	0	1	0
Spotted Pardalote	1	0	0	0	0	1	0	1	1	0
Striated Pardalote	0	1	1	1	1	0	0	0	0	1
Striated Thornbill	1	0	0	0	0	1	0	0	1	0
Superb Fairy-wren	0	0	0	1	0	0	0	0	0	0
Superb Parrot	0	0	0	0	1	0	0	0	0	0
Weebill	0	0	0	0	0	1	0	0	1	0
White-plumed Honeyeater	1	1	1	1	1	1	1	1	1	1
White-throated Gerygone	0	0	0	0	0	0	0	1	1	0
White-throated Treecreeper	0	0	0	0	0	1	0	0	1	0
White-winged Chough	1	1	1	1	1	1	1	1	1	1
White-winged Triller	0	1	0	0	0	0	1	0	0	0
Willie Wagtail	0	0	0	0	0	0	0	1	1	0
Yellow Thornbill	0	0	0	0	0	1	0	0	1	0
Yellow-faced Honeyeater	0	0	0	0	0	0	1	0	1	0
Yellow-rumped Thornbill	0	1	0	0	0	0	1	1	1	0

Table S6. *Expected benefits of alternative threat mitigation actions determined for scenario 3 (mechanistic scenario – realistic colonization rates under different threat intensities).*

Species	Increase tree cover	Reduce noisy miners	Reduce grazing frequency	Reduce grazing duration	Reduce grazing intensity	Trees + grazing intensity	Miners + grazing intensity	Miners + trees	Miners + trees + grazing intensity	No action
Australian Magpie	0.50	0.58	0.58	0.58	0.58	0.58	0.58	0.58	0.58	0.58
Black-faced Cuckoo-shrike	0.96	0.03	0.02	0.00	0.02	0.96	0.03	0.99	0.97	0.02
Brown Treecreeper	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.01
Buff-rumped Thornbill	0.01	0.03	0.00	0.00	0.00	0.01	0.03	0.46	0.46	0.00
Common Starling	0.46	0.46	0.46	0.46	0.19	0.04	0.12	0.15	0.04	0.46
Eastern Rosella	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46
Grey Butcherbird	0.09	0.04	0.09	0.09	0.09	0.09	0.04	0.04	0.04	0.09
Grey Fantail	0.08	0.16	0.01	0.01	0.01	0.08	0.16	0.55	0.55	0.01
Grey Shrike-Thrush	0.01	0.01	0.01	0.01	0.01	0.01	0.03	0.01	0.03	0.01
Jacky Winter	0.31	0.02	0.02	0.02	0.04	0.42	0.04	0.31	0.42	0.02
Little Friarbird	0.03	0.02	0.32	0.02	0.02	0.03	0.02	0.03	0.03	0.02
Magpie-lark	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Mistletoebird	0.34	0.11	0.01	0.01	0.01	0.34	0.11	0.83	0.83	0.01
Noisy Friarbird	0.19	0.15	0.15	0.15	0.15	0.19	0.15	0.19	0.19	0.15
Noisy Miner	0.13	0.13	0.13	0.35	0.13	0.13	0.13	0.13	0.13	0.36
Red Wattlebird	0.06	0.03	0.03	0.03	0.03	0.03	0.03	0.06	0.06	0.03
Red-rumped Parrot	0.07	0.10	0.10	0.13	0.11	0.08	0.11	0.07	0.08	0.10
Restless Flycatcher	0.00	0.00	0.00	0.00	0.33	0.33	0.33	0.00	0.33	0.00
Rufous Songlark	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
Rufous Whistler	0.01	0.13	0.01	0.01	0.09	0.09	0.56	0.13	0.56	0.01
Sacred Kingfisher	0.01	0.08	0.01	0.01	0.03	0.13	0.03	0.15	0.15	0.01
Silvereye	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.02	0.03	0.00
Spotted Pardalote	0.18	0.13	0.13	0.13	0.13	0.18	0.13	0.18	0.18	0.13
Striated Pardalote	0.18	0.87	0.84	0.84	0.86	0.29	0.89	0.22	0.33	0.84
Striated Thornbill	0.09	0.07	0.07	0.07	0.07	0.09	0.07	0.09	0.09	0.07
Superb Fairy-wren	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Superb Parrot	0.45	0.02	0.45	0.45	0.59	0.59	0.01	0.01	0.02	0.45
Weebill	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00

Species	Increase tree cover	Reduce noisy miners	Reduce grazing freq-uency	Reduce grazing duration	Reduce grazing intensity	Trees + grazing intensity	Miners + grazing intensity	Miners + trees	Miners + trees + grazing intensity	No action
White-plumed Honeyeater	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
White-throated Gerygone	0.01	0.07	0.00	0.00	0.00	0.01	0.07	0.34	0.34	0.00
White-throated Treecreeper	0.21	0.04	0.04	0.04	0.04	0.21	0.04	0.21	0.21	0.04
White-winged Chough	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
White-winged Triller	0.09	0.12	0.16	0.16	0.16	0.09	0.12	0.05	0.05	0.16
Willie Wagtail	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
Yellow Thornbill	0.86	0.00	0.00	0.00	0.01	0.95	0.01	0.86	0.95	0.00
Yellow-faced Honeyeater	0.06	0.04	0.01	0.01	0.07	0.12	0.17	0.13	0.27	0.01
Yellow-rumped Thornbill	0.07	0.31	0.07	0.07	0.07	0.07	0.31	0.31	0.31	0.07

Table S7. *Results of priority threat management under different scenarios of data informing likely response to threats, showing (a) result for all species, and (b) results for only declining species, of reducing intensities of 1, 2, 3, 4 or 5 threats. A value of 1 in a column indicates that the strategy was selected under the given budget.*

Threat mitigation strategy	**Mechanistic approach**					**Optimistic approach**					**Pessimistic approach**				
	1	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
(a) All species															
Restore trees	1						1		1	1		1			
Remove miners								1							1
Reduce grazing frequency			1	1	1										
Reduce grazing duration					1				1	1					
Reduce grazing intensity						1	1				1	1		1	1
Restore trees + reduce grazing intensity								1							
Remove miners + reduce grazing intensity									1						
Remove miners + restore trees		1	1												
Remove miners + restore trees + reduce grazing intensity				1	1					1			1	1	1
No action															
(b) Declining species															
Restore trees	1									1					
Remove miners					1										
Reduce grazing frequency															
Reduce grazing duration															
Reduce grazing intensity			1	1	1	1		1		1	1			1	1
Restore trees + reduce grazing intensity							1		1			1			
Remove miners + reduce grazing intensity									1						
Remove miners + restore trees		1	1					1							
Remove miners + restore trees + reduce grazing intensity				1	1					1			1	1	1
No action															