Perry, Justin James (2016) ***Fire management and biodiversity in Northern Australia*****. PhD thesis, James Cook University.**

Fire management and biodiversity in Northern Australia

Thesis submitted by

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2016

For the degree of Doctor of Philosophy

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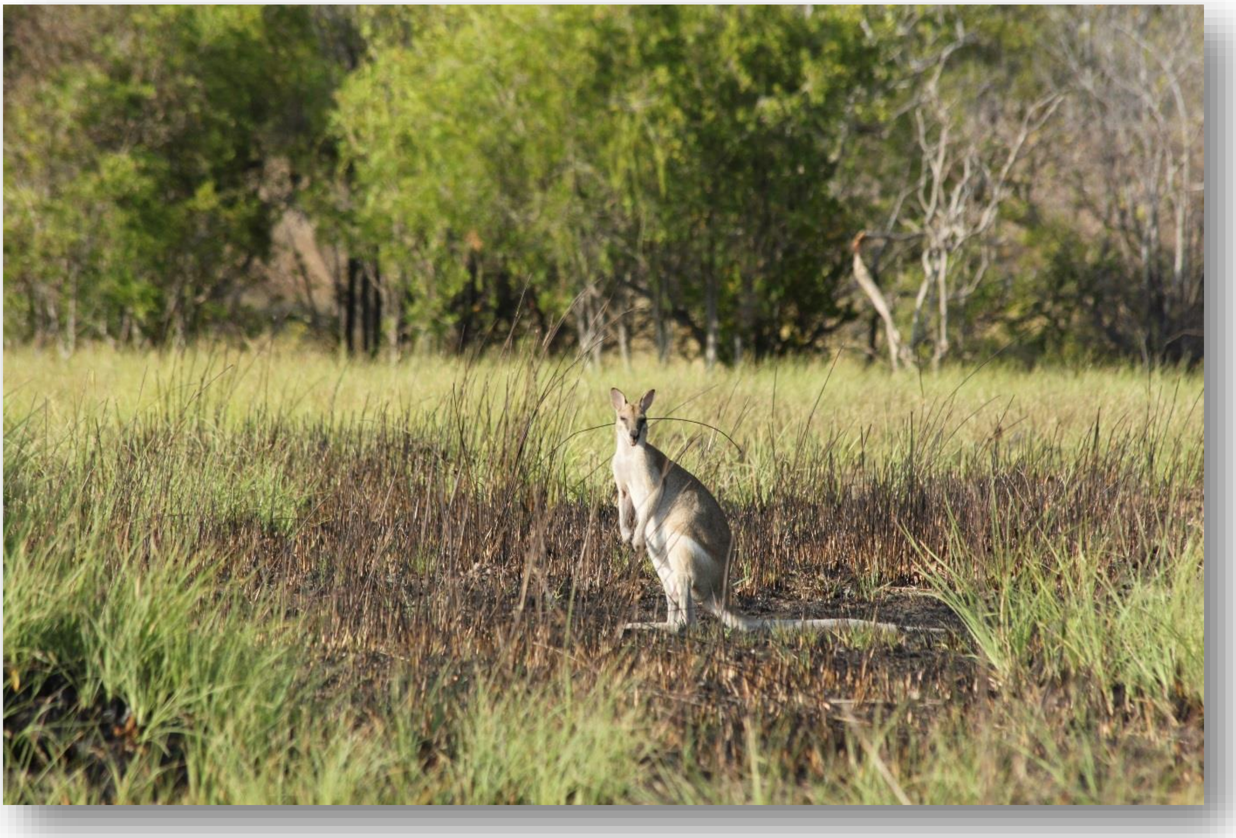

Agile Wallaby (*Macropus agilis*) standing in recently burnt grass on Cape York Peninsula.

(photo: Anders Zimny).

Acknowledgments

Each part of this research was conducted with individuals that are acknowledged at the end of each chapter. This research would not have been possible without the skills and professionalism of the CSIRO biodiversity team (Alex Kutt, Eric Vanderduys, Anders Zimny, Gen Perkins and Nic Coleman). I would particularly like to thank Eric Vanderduys and Anders Zimny who between them have been on every Cape York trip since 2009 and stand alone with their knowledge and passion for wildlife in northern QLD. As well as offering unwavering support both in the technical and scientific elements they have also been exceptional friends that have always made difficult situations easy to deal with. I would also like to thank the crack team of volunteers and sometimes casuals, George Madani, Richard (Twitchy Ritchy) Chamberlain and Brooke Bateman. Matt Vickers has been another fantastic source of support, his out of the box thinking has been a source of inspiration for me and has allowed me to explore analytical techniques and theoretical frameworks that I would have never have discovered on my own. Helen Murphy has provided ongoing and essential input both as a co-author but also during the editing process for other papers that has been critical for preparing papers for publication. These guys are remarkable naturalists, have super intellects and are amazing company to boot. I feel privileged to have worked alongside all of the people listed above.

My supervisors have been exceptional and have all given me substantial support over the last six years. Lin Schwarzkopf provided critical input to help plan the theoretical framework that set up the PhD. She has consistently provided detailed input when I've asked for it which has got me the over line at critical times particularly in the concluding months of this PhD. At other times Lin has let me follow my own path which is a critical part of personal and professional growth that needs to occur when completing a PhD. Jeremy VanDerWal has been constant mentor and friend for the past 8 years, providing the critical support when I needed it and at other times pushing me to work it out on my own which has ultimately been the most rewarding and professionally important aspect of completing this PhD. Jeremy has pushed me to produce high impact science which has necessitated the development of technical and analytical skills. This has provided me with an exceptional skill base which has already led me into high level collaborations with leading research groups working on globally significant analysis. Alex Kutt has supported me in all aspects of this PhD. This has included securing the funding that paid my salary to collect the data, digging the holes and doing the surveys, keeping me focused on key outputs, and finally working with me on the painful and rewarding process of never ending revisions associated with peer review. Without Alex's support and friendship I would never have been able to finish the PhD and retain my sanity.

The people of Cape York have been exceptional, generous with their knowledge and time and patient with my lack of understanding. None of this work would be possible without the help of traditional owners and Aboriginal rangers across Cape York Peninsula. My experience working with Aak Puul Gnangtam (APN) and Kalan has been personally and professionally transformational and provided a unique insight into the way fire should be used. Learning how little we know is often the first step for searching for answers. My work with APN, Kalan and the extended network of long-term Cape York land managers exposed the mountain that still needs to be climbed before we will understand the best way to manage fire for multiple purposes in a rapidly changing world. They always brought me back from the theoretical to the practical, at some stage we have to emerge from theory, light or fight a fire and measure the impact before we will understand what's going on.

I would also like to thank the long-term northern Australia researchers who are referenced throughout this thesis and have shaped the basis of what I know about fire and biodiversity in this region. Without the commitment and tireless work of key individuals (Woinarski, Russel-smith, Williams, Anderson, Parr, Felderhoff, Kutt, Vanderduys to name a few) there wouldn't be a place to start or a story to tell about change. The future of northern Australia's unique biodiversity is largely in the hands of these people and it has been privilege to work alongside them and to be led by their hard work.

Finally my wife Rhonda and kids Nicola and Olivia have suffered through six years of me having two very demanding jobs. They have always supported me and given me the space and time that I need and forgiven my tired grumpiness. Now I owe them some stolen time!

Statement of contribution of others

Research funding

- Commonwealth Government, Caring for my Country
- Commonwealth Government, National Environmental Research Program
- CSIRO Land and Water

Supervision

- Professor Lin Schwarzkopf (Primary)
- Associate Professor Jeremy VanDerWal, Centre for Tropical Biodiversity and Climate Change, JCU
- Associate Professor Alex Kutt, Melbourne University.

- Dr Helen Murphy, CSIRO Land and Water, Atherton.

Statistical, data management, analytical and modelling support

- Jeremy VanDerWal
- Alex Kutt
- Eric Vanderduys
- Nick Coleman
- Gen Perkins
- Matthew Vickers

Editorial assistance

- Chris Pavey
- Alex Kutt
- Helen Murphy
- Eric Vanderduys
- David Westcott

Specific contributions for each chapter.

Chapter 2

Justin Perry and Jeremy VanDerWal developed the concepts for the paper, developed the analytical framework, conducted the analysis and produced the figures and tables. Justin Perry and Helen Murphy conceptualised and planned the paper, wrote and edited the paper and conducted the literature review. Alex Kutt contributed to the conceptual framework of the paper and contributed to editing and writing.

Chapter 3

Justin Perry and M. Sinclair developed the concepts for the paper. H. Wikmunea and S. Wolmby provided the contemporary traditional knowledge and the historical perspective. Dave Martin and Bruce Martin provided historical perspective, the overview of Wik culture and insights into the implications of contemporary fire and land management practices.

Chapter 4

Justin Perry and Alex Kutt conceived the paper, Justin Perry conducted the analysis and wrote the paper. Justin Perry, Alex Kutt and Eric Vanderduys provided editorial input and collected the data used in the paper.

Chapter 5

Justin Perry and Alex Kutt developed the idea, conducted the analysis, and wrote the manuscript, all authors collected data and edited the manuscript.

Chapter 6

Justin Perry, Lin Schwartzkopf and Matthew Vickers devised the study. Eric Vanderduys, Alex Kutt Justin Perry and Anders ZImny conducted the surveys. Justin Perry and Mathew Vickers managed the data and conducted the analysis. Justin Perry wrote the paper. All authors edited the paper.

Chapter 7

Justin Perry, Alex Kutt, Stephen Garnett, and Gay Crowley devised the study. Eric Vanderduys, Genevieve Perkins, Alex Kutt and Justin Perry conducted the surveys. Justin Perry managed the data, conducted the analysis and wrote the paper. All authors edited the paper.

Publications associated with this thesis

Co-authorship of published manuscripts included development of concepts, study design, development of analytical methods, editing manuscripts and collection if data. Details of contributions are included at the end of each chapter and above.

Peer-reviewed publications

Chapter 3.

Perry, J.J., Sinclair, M., Wikmunea, H., Wolmby, S. Martin, D., Martin, B. (2016). The divergence of traditional Aboriginal and contemporary fire management practices on Wik traditional lands, Cape York Peninsula, northern Australia. *Ecological Management and Restoration* (Accepted with revision October 2016).

Chapter 4.

Perry, J., Vanderduys, E.P, Kutt, A.S. (2016). Shifting fire regimes from late to early dry-season fires to abate greenhouse emissions does not completely equate with terrestrial vertebrate biodiversity co-benefits on Cape York Peninsula, Australia. *International Journal of Wildland Fire* (Accepted March 8, 2016).

Chapter 5.

Perry, J., Vanderduys, E.P, Kutt, A.S. (2015). More Famine than feast: pattern and variation in a potentially degenerating mammal fauna on Cape York Peninsula. *Wildlife Research* (Accepted September 6, 2015).

Chapter 7.

Perry, J.J., Kutt A.S., Garnett S.T., Crowley G.M., Vanderduys E.P., and Perkins G.C. (2011). Changes in the avifauna of Cape York Peninsula over a period of 9 years: the relative effects of fire, vegetation type and climate. *Emu* **111**: 120-131. doi: doi:10.1071/MU10009.

Manuscripts in review

Chapter 2.

Perry, J.J., VanDerWal, J., Murphy, H., Kutt, A.S (2016). Hind-casting 60 years of fire weather conditions in the Australian savanna: evidence for a rapidly expanding fire maximum front. Nature Climate Change (Submitted February, 2016).

Chapter 6.

Perry, J.J., Kutt, A.S., Vickers, M., Vanderduys, E., Schwarzkopf, L., Zimny, A. (2016). The Goldilocks effect: Intermediate heterogeneity in vegetation structure maximises diversity of reptiles in savanna. *Biological Conservation* (Submitted April 2016).

Appendices

Relevant manuscripts published during PhD candidature

Appendix 1.

Perry, J.J., Kutt, A., Perkins, G., Vanderduys, E., Colman, N. (2012). A bird survey method for Australian tropical savannas. *Emu*, **112:** 261 – 266.

Appendix 2.

Perry, J.J., Fisher, A., Palmer, C. (2011). Status and habitat of the Carpentarian Grasswren (*Amytornis dorotheae*) in the Northern Territory. *Emu*, **111**: 155-161.

Conference presentations

Ferrier, S., Harwood, T., Hoskins, A., Williams, K., **Perry, J.,** Ota, N., and Ware, C. (2014a). Ecological representativeness of terrestrial protected areas and the future of global biodiversity under climate and land use change. In 'IUCN World Parks Congress - Parks, People, Planet:Inspiriing Solutions' pp. 1. (IUCN, http://worldparkscongress.org/: Sydney Olympic Park, Sydney, Australia.)

Ferrier, S., Harwood, T., Hoskins, A., Williams, K., **Perry, J.,** Ota, N., and Ware, C. (2014b). Ecological representativeness of terrestrial protected areas: sharpening the resolution of global assessment through macroecological modelling. In 'IUCN World Parks Congress - Parks, People, Planet:Inspiriing Solutions' pp. 1. (IUCN, http://worldparkscongress.org/), Sydney Olympic Park, Sydney, Australia.)

Sinclair, M., **Perry, J.,** Creek, D., and Austin, E. (2014). Co-creating solutions and ways to assess their effectiveness. In 'World Parks Congress' pp. 1. (World Parks Congress: Sydney.)

Perry, J. J. (2013) Patterns of fire and biodiversity in Australian tropical savanna: A critical analysis of the relationships between satellites derive fire histories and terrestrial fauna. ATBC conference, San Jose, Costa Rica.

Martin, B. Jaffer, T., Creek, D, Martin, D., Austin, E., **Perry, J.J.,** Sinclair, M (2013) How do I know if I are achieving my vision – Two mobs, one river. World Indigenous Network congress, Darwin, Australia.

Perry, J., VanDerWal, J., Kutt, A., and Perkins, G. (2010). Using species distribution modelling to examine spatio-temporal variation in fire pattern. In 'Sustaining Biodiversity – The next 50 years. Ecological Society of Australia Conference.' pp. 1. (Ecological Society of Australia: Australian National University.)

Williams, K., Prober, S., Harwood, T., Ferrier, S., Manion, G., Rosauer, D., Raisbeck-Brown, N., **Perry, J.**, Jeanneret, T., Lim-Camacho, L., and Doerr, V. (2014). Using community-level ecological models to inform climate adaptation planning for biodiversity: a primer. In 'Climate Adaptation 2014: Future Challenges' pp. 35. (National Climate Change Adaptation Research Facility, http://www.nccarf.edu.au/conference2014: http://www.nccarf.edu.au/event

Gold Coast Convention & Exhibition Centre, Gold Coast, Queensland, Australia.)

Perry, J.J. VanDerWal, J., Kutt, 2011. Using species distribution modelling to examine spatio-temporal variation in fire pattern in Australian tropical savannas. ATBC conference, Arusha, Tanzania.

Perry, J.J. VanderWal, J (2012). Fire in Australia: Color-coding and measuring intuition. Next generation tools for managing and predicting fire risk in Australia. North Australian Fire Managers Forum.

Perry, J.J. VanDerWal, J., Kutt, A.S. and Perkins, G.C., 2010. Using species distribution modelling to examine spatio-temporal variation in fire pattern. Sustaining Biodiversity – The next 50 years. Ecological Society of Australia Conference. December 6th-10th 2010, Australian National University, Canberra.

Perry, J.J., Moore, D. 2010 Using bioacoustics and wireless sensor networks for long-term monitoring and conservation of birds in Northern Australia. Birds Australia Congress, Townsville.

Perkins, G.C., VanDerWal, J., Kutt, A.S. and **Perry, J.J**. 2010. Using weather-based models of species distribution to predict refugia in Australia's tropical savannas. Sustaining Biodiversity – The next 50 years. Ecological Society of Australia Conference. December 6th-10th 2010, Australian National University, Canberra.

Kutt, A.S., VanDerWal, J., Perkins, G.C., **Perry, J.J**. 2010. Spatial and temporal pattern in potential refugia for Australia's tropical savanna birds. Sustaining Biodiversity – The next 50 years. Ecological Society of Australia Conference. December 6th-10th 2010, Australian National University, Canberra

Perkins, G.C., VanDerWal, J., Kutt, A.S. and **Perry, J.J**. 2011. Climate Refugia: A case study of an Australian tropical savanna bird. Ecological Society of Australia Conference. November 21th-25th 2011, Hobart, Tasmania (poster presentation)

Froese, J.G, Murray, J.V., **Perry, J.J.,** van Klinken, R.D (2015) Spatial modelling to estimate the risk of feral pigs to pig farm biosecurity in south-eastern Australia. Manipulating Pig Production XV

Other co-authored peer-reviewed publications relevant to northern Australia biodiversity completed during my candidature

Kutt, A. S., Vanderduys, E. P., Perry, J. J., Mathieson, M. T., and Eyre, T. J. (2016). Yellow-throated miners Manorina flavigula homogenize bird communities across intact and fragmented landscapes. Austral Ecology 41, 316-327. doi: 10.1111/aec.12314.

Kutt, A. S., Vanderduys, E. P., Perry, J. J., and Perkins, G. C. (2012a). Do miners (Manorina spp.) affect bird assemblages in continuous savanna woodlands in north-eastern Australia? Austral Ecology 37, 779-788. doi: 10.1111/j.1442-9993.2011.02338.x.

Kutt, A. S., Vanderduys, E. P., Perry, J. J., Perkins, G. C., Kemp, J. E., Bateman, B. L., Kanowski, J., and Jensen, R. (2012b). Signals of change in tropical savanna woodland vertebrate fauna 5 years after cessation of livestock grazing. Wildlife Research 39, 386-396. doi: http://dx.doi.org/10.1071/WR11137.

Mac Nally, R., Kutt, A. S., Eyre, T. J., Perry, J. J., Vanderduys, E. P., Mathieson, M., Ferguson, D. J., and Thomson, J. R. (2014). The hegemony of the ‘despots’: the control of avifaunas over vast continental areas. Diversity and Distributions 20, 1071-1083. doi: 10.1111/ddi.12211.

Perkins, G. C., Kutt, A. S., Vanderduys, E. P., and Perry, J. J. (2013). Evaluating the costs and sampling adequacy of a vertebrate monitoring program. Australian Zoologist 36, 373-380. doi: doi:10.7882/AZ.2013.003.

Perry, J., Fisher, A., and Palmer, C. (2011). Status and habitat of the Carpentarian Grasswren (Amytornis dorotheae) in the Northern Territory. Emu 111, 155-161. doi: doi:10.1071/MU10013.

Perry, J. J., Kutt, A. S., Perkins, G. C., Vanderduys, E. P., and Colman, N. J. (2012). A bird survey method for Australian tropical savannas. Emu 112, 261-266. doi: http://dx.doi.org/10.1071/MU12007.

Vanderduys, E., Kutt, A., and Perry, J. (2011). Range extensions of two frogs, Cyclorana cryptotis, Litoria electrica and a reptile, Rhynchoedura ornata in Queensland. Australian Zoologist 35, 569-575.

Vanderduys, E. P., Kutt, A. S., Perry, J. J., and Perkins, G. C. (2012). The composition of mixed-species bird flocks in northern Australian savannas. Emu 112, 218-226. doi: http://dx.doi.org/10.1071/MU11041.

VanDerWal, J., Murphy, H. T., Kutt, A. S., Perkins, G. C., Bateman, B., Perry, J. J., and Reside, A. E. (2012). Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nature Climate Change 2. doi: doi:10.1038/nclimate1688

Ziembicki, M. R., Woinarski, J. C. Z., Webb, J. K., Vanderduys, E. P., Tuft, K., Smith, J., Ritchie, E. G., Reardon, T., Radford, I. J., Preece, N., Perry, J. J., Murphy, B., McGregor, H., Legge, S., Leahy, L., Lawes, M. J., Kanowski, J., Johnson, C., James, A. J., Griffiths, A. D., Gillespie, G., Frank, A. S., Fisher, A., and Burbidge, A. (2014). Stemming the tide: progress towards resolving the causes of decline and implementing management responses for the disappearing mammal fauna of northern Australia. THERYA 6, 169-225.

Reports

Justin **Perry**, Gen Perkins, Eric Vanderduys, Anders Zimny (2013) Monitoring the impact of feral pigs (Sus scrofa) in the Archer River Basin, Report to Balkanu.

Williams, K., Harwood, T., **Perry, J**., Perkins, G., Yang, L., Ferrier, S. (2013) Using community-level modelling to map levels of biodiversity significance in the Pilbara bioregion. A report to BHP Pilbara.

Justin **Perry**, Gen Perkins, Eric Vanderduys, Alex Kutt, Bruce Martin, Rob Morris, David Claudie, Lenny Ned, Shane Edwards and George Conrad. 2012. Fire and biodiversity on Cape York Peninsula. Report to Cape York Sustainable Futures.

G. Perkins, E. Vanderduys, A. Kutt, J. **Perry** and N. Colman (2010). Conservation and management of the terrestrial vertebrate fauna of the Xstrata mining lease 8058, Mount Isa.

Animal ethics statement

Animal ethics approval was granted by the CSIRO animal ethics committee and research was conducted under Queensland Scientific Purposes Permit (WISP11870412) and Take, Use, Keep or Interfere with Cultural or Natural Resources (Scientific Purpose) permit number (WITK11870512).

Human ethics statement

The Charles Darwin University Human Research Ethics Committee (EC00154) approved the application for “Research to support Indigenous NRM and Livelihoods: Negotiating and co-creating monitoring, evaluation and reporting plans for Indigenous caring for country and sustainable livelihoods in the Archer Basin with Aak Puul Ngantam and Kalan Enterprises”.

Abstract

Fire is a significant ecological determinant of patterns of plant and animal distributions across the globe. This is especially so for the tropical savanna biome as fire is intrinsically linked with a dynamic weather-driven interplay between C4 grasses and other vegetation types. We know that climate change will dramatically alter global ecosystems in the future, but the implications for savanna ecosystems are less clear. The potential changes are often discussed in terms of how things may alter up to 100 years into the future. In most cases these forecasts are too abstract to translate for land managers who need practical advice that will allow them to adapt in real time and that acknowledges the considerable challenges they face now.

For this thesis I have sampled fire and vertebrate fauna in the dominant vegetation type in northern Australia, open savanna woodland, and used these data to test several hypotheses that will help decision makers and land managers better understand fire management both now and into the future. To adapt to future change and to make better decisions about the current conditions we need to understand the determinants of fire, how these are linked to climate, the impact of human intervention through various fire management strategies, and what the likely implications for biodiversity are.

In this thesis I examine fire and biodiversity at a variety of scales, ranging from pyro-diversity models derived for all of northern Australia to a set of representative sites surveyed on Cape York Peninsula for the three dominant vertebrate taxa (birds, mammals and reptiles). The thesis includes six chapters that begin at the broadest scale (all of northern Australia) and then drill down in scale for the various vertebrate fauna responses.

Chapter 1 introduces fire as a disturbance regime and a ubiquitous part of northern Australia land management. It outlines the structure of the thesis and describes the connectivity of chapters.

Chapter 2 sets the scene for the distribution of fire in northern Australia from a climatic perspective and explicitly links weather and vegetation to fire distribution in recent history. This places the contemporary distribution of fire in a broader temporal perspective and outlines the implications of fire on carbon emissions and describes the variance in annual and inter-annual fire distributions.
Chapter 3 compares contemporary fire management strategies with traditional Aboriginal burning

and discusses the challenges of supporting traditional burning with modern requirements such as infrastructure protection and financial incentives for reducing greenhouse gas emissions.

In **chapter 4** I explore the links between burning for greenhouse gas abatement and vertebrate fauna in savanna ecosystems of Cape York Peninsula. Carbon farming initiatives have rapidly developed in recent years creating incentives for broad scale changes to land management regimes. In the open carbon market a premium can be secured if additional benefits, such as biodiversity conservation or social advancement, can be quantified. In Australia, there is an accepted method for carbon abatement that requires shifting fire frequency from predominantly late to early dry season fires. There is an assumption and some evidence that this might accrue co-benefits for biodiversity. We tested this assumption by comparing terrestrial vertebrate biodiversity patterns (richness and abundance of reptiles, birds and mammals) against increasing fire frequency in the early dry season at the same spatial resolution as the savanna burning methodology.

Chapter 5 examines the contemporary distribution of mammals on Cape York Peninsula (data collected for this thesis) in comparison with limited historical data and changes in mammal fauna across northern Australia. I contextualise the changes in mammal populations with the historical disturbances present in the study area which includes changes to fire regimes.

Chapter 6 focusses on reptiles, one of the most abundant and diverse taxa in savanna ecosystems. Theoretically, if fire changes vegetation patterns then reptiles, as a heliothermic organism should be a good indicator of the impact of altered fire regimes.

Chapter 7 looks at changes in bird distributions across time in the study area. A systematic survey of the avifauna of Cape York Peninsula was conducted in the late 1990s and early 2000s providing an ideal basal dataset for measuring change in the avifauna. A subset (n > 600) of these sites, primarily within savanna landscapes, was selected for re-survey in 2008 to investigate changes in bird communities on Cape York Peninsula. Long-term monitoring can describe important patterns of species change over time, though in the case of large, highly seasonal environments like the tropical savannas, signals of change may manifest over decades rather than annually.

Chapter 8 discusses the broad implications of this research and describes how each chapter has collectively increased the understanding of the impact of fire on biodiversity in northern Australia.

This thesis provides the first major assessment of fire and biodiversity in the savanna ecosystems of Cape York Peninsula and uses novel analytical methods to demonstrate significant shifts in fire frequency in recent history. This dataset and the associated analysis and interpretation has provided a substantial improvement to the collective knowledge of fire and terrestrial vertebrate fauna across northern Australia.

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Chapter 1. Introduction

Fire in a global and Australian savanna context

Global landscapes and vegetation structure and distribution have been formed by a combination of geological processes over millions of years and millennial variance in broad climatic patterns (Bowman 2002; Mackey et al. 2002). Fire plays a critical role in regulating the biophysical structure and composition of ecosystems (Paolo D'Odorico et al. 2006), global and local carbon balances, and global climate through atmospheric CO_2 emissions from biomass burning (van der Werf et al. 2010). Temperature and precipitation drive biomass fuel production, moisture availability, fuel drying cycles and suitable fire weather conditions, which in turn drive fire dynamics and fire return intervals (Bradstock 2010).

Tropical savanna woodlands dominate the northern Australian landscape covering about 2 million km^2 and are the most fire prone ecosystem in the most fire prone continent on earth (Parr and Andersen 2006; Russell-Smith and Whitehead 2015). Unsurprisingly, in this vast and connected pyrophytic ecosystem one of the primary land management tools is prescribed fire. For many thousands of years the primary human influence on the ecosystem was via Aboriginal fire management (Hill et al. 1999). Aboriginal people managed fire for many reasons but it is thought that in northern Australia burning was dominated by widespread but small scale early dry season fires (Bliege Bird et al. 2008). In the past two centuries, fire management has changed and there is ample evidence that this has led to the dominance of high intensity late dry season fires which have been implicated in altered vegetation structure and terrestrial vertebrate declines (Bradstock et al. 2005; Woinarski et al. 1999b).

Fire and climate change in the Australian savanna

Broad scale changes to contemporary fire regimes have been predicted in the next 100 years under future climate change scenarios (Bradstock 2010; Krawchuk et al. 2009; Liu et al. 2010; Pechony and Shindel 2010). Understanding the rates of change and spatial configuration of fire distributions under future climate scenarios is important as fire is a significant driver of biodiversity change (Andersen et al. 2005; Franklin 1999) and is a source of greenhouse gas emissions (Russell-Smith et al. 2009) (Russell-Smith *et al.* 2009).

The broad trajectory of climate change is overwhelmingly accepted by the international scientific community but the spectrum of future predictions (e.g. changes to rainfall) under climate change is highly variable due to the range of alternative climate scenarios (Rogelj et al. 2012). Predictions of changes to fire regimes are therefore limited by this uncertainty. Krawchuck *et al* (2009) suggests that the tropical woodlands of northern Australia will generally become less fire prone due to predicted decreases in vegetation productivity. A reduction in fire probability is also supported by Cary *et al* (2012) who suggest that increased dryness and elevated CO_2 may lengthen fire return intervals and that tropical woodlands have reached the limit of their fire potential and therefore can only decrease in fire probability under future scenarios. There is strong evidence that, in tropical savanna, fire and climate are intrinsically linked (Lehmann *et al*. 2011) and that both are temporally dynamic, meaning climatic envelope modelling that utilises long-term means to derive fire probabilities will smooth the potential impacts and underestimate the extent of change (VanDerWal *et al*. 2012). Given the strong relationship between weather patterns and fire frequency and extent (Alencar *et al*. 2006; Chen et al. 2011; Golding & Betts 2008; Lehmann et al. 2011) I predict that changes to fire distribution will be observed at a finer temporal scale then has been previously investigated and these changes will not be consistent across the area defined as savanna in Australia.

In the context of environmental niche modelling, fire can be placed in the usual theoretical frame work of species environmental requirements (Nix and Kalma 1972) and geographic variation of key environmental factors (Guisan and Thuiller 2005). To adequately predict the distribution of fire in this dynamic ecological system the geographic variation of environmental factors needs to match the fine scale temporal variation that occurs inter and intra-annually. Rapid temporal fluctuations in the geographic distribution of fire in savanna biomes are analogous to pulses in abundance and distribution of r-selected species following favourable climatic conditions (Letnic et al. 2004; Meserve et al. 2003). These pulse events occur when factors that limit population growth change and allow populations to rapidly fill the new resource rich environmental space.

Weather driven changes in fire regimes in northern Australia are analogous to an ideal ‘species’ for correlative modelling, having well established published ecological frameworks (Bradstock 2010; Parisien et al. 2012) coupled with accurate and comprehensive temporal presence and absence records via freely available satellite derived fire histories (http://www.firenorth.org.au/nafi2/). Despite the presence of these historical data, much of the current and historical literature relating to fire and climate emanates from longitudinal field studies, sub-samples of weather stations, or satellite derived fire histories. These studies are limited by sample size and geographic location (one or two geographic locations which are not broadly representative of the study area) or short time frames (10 – 30 year satellite history) which has led to a level of ambiguity about the extent and potential for change. This is especially so for the broad savanna of northern Australia where such longitudinal studies are limited to the far north of the region, and thus do not adequately sample the entire climatic envelope ranging from mesic tropical savanna with mean annual rainfall >1500mm to semi-arid rangelands with rainfall <400mm (Williams et al. 2003; Woinarski et al. 2004a).

Predictive models in dynamic weather driven systems

Species distribution models (SDMs) have been used to hind-cast species distributions to investigate gene flow across millennia (Moritz et al. 2009; Vega et al. 2010) and to forecast the potential for distributional shifts, species vulnerability and compositional change under future climate change scenarios (Ferrier et al. 2007; Reside et al. 2011). SDMs have also been used to provide accurate models of contemporary fire regimes (Parisien et al. 2012), although these studies were done in areas with stable climates when compared with the savanna. The recent development of novel methods for hind-casting species distributions at a fine spatial scale using accurate spatial weather data (Bateman et al. 2011; Reside et al. 2010; VanDerWal et al. 2012) provides an opportunity to extend these methods to predict fire distributions in unstable climatic systems and to develop a better understanding of the historical context of the contemporary data in relation to climate across the breadth of the region. This context will enable future predictions to be put into a theoretical framework that acknowledges the dynamic annual weather patterns that are variably predictable across continental-scale climatic gradients.

Fire management in northern Australia

Fire is managed for various reasons in northern Australia such as biodiversity conservation, carbon abatement, infrastructure protection and to maintain Aboriginal cultural sites and traditional fire management practices. Fire management for biodiversity conservation is often conducted in the early dry season and aims to develop a mosaic of fire scar ages (Legge et al. 2008). Australian Aboriginal people have been using fire to manage the Australian landscape for millennia (Bowman et al. 2011; Russell-Smith et al. 1997; Vigilante 2001). This traditional burning has been changed, adapted and in some cases oppressed across the continent, particularly in the past century. In the vast monsoonal tropics, fire is a critical natural part of ecosystem function due to the annual cycle of wet and dry seasons which promotes rapid vegetation growth and curing every year (Felderhof and Gillieson 2006). Despite the ubiquitous presence of fire and intact Aboriginal knowledge there is still significant debate about the best way to manage fire in this region, particularly in the context of biodiversity conservation (Andersen et al. 2005; Andersen et al. 2006; Driscoll et al. 2010; Parr and Brockett 1999; Whitehead et al. 2005; Ziembicki et al. 2014). A common thread across fire management paradigms is to develop a system that most closely relates to the predominant system instated by Aboriginal people over thousands of years (Bliege Bird et al. 2008; Garde et al. 2009; Horton 1980; Russell-Smith et al. 2013; Russell-Smith et al. 2009; Vigilante and Bowman 2004; Yibarbuk et al. 2001). From a biodiversity perspective, Aboriginal burning presumably most closely replicates the evolutionary processes underlying niche selection by plants and animals that have co-evolved with this particular disturbance regime (Bliege Bird et al. 2008; Hill and Baird 2003).

There has been a general acceptance by land managers in the Australian monsoonal tropics that patchy, early dry season burning is the best proxy for traditional burning practices and this has been the dominant ecological burning regime for several decades (Burrows 1991; Parr and Andersen 2006). More recently, the emergence of a carbon market in Australia has seen the introduction of broad scale prescribed burning with the aim of shifting the predominant fire regime from the late dry season (defined as after August 1) to the early dry season with quantifiable greenhouse gas emission benefits (Russell-Smith et al. 2013). This methodology evolved through collaboration with Aboriginal fire managers in north east Arnhem Land where significant emphasis was placed on participatory approaches to planning and implementation of fire regimes (Russell-Smith et al. 2009).

However, while random patch mosaic burning and increasing early dry season burning frequency has been shown to reduce greenhouse gas emissions the biodiversity benefits are less clear (Parr and Andersen 2006; Perry et al. 2016). Although there have been demonstrated benefits for no burning (Andersen et al. 2005; Woinarski et al. 2004b) the benefits of frequent early burning and patchy burning have not been universally quantified although the theory is intuitively sound (Murphy and Bowman 2007). There is ample evidence that frequent fire alters aspects of biodiversity such as reducing tree biomass (Murphy et al. 2015) and reducing reptile and small mammal abundance and richness (Andersen et al. 2005). On the other hand there is evidence that a reduction in fire frequency has caused woody thickening in unique natural grasslands on Cape York Peninsula (Neldner et al. 1997).

On Cape York Peninsula, which is the focus of the terrestrial vertebrate fauna study presented in this thesis, Crowley and Garnett (2009) described the predominance of “storm burning” on pastoral leases in the region. This method is applied with the aim of reducing woody cover and favour more open grassy woodlands. Additionally, altered fire frequency and fire exclusion in closed forest communities has been shown to promote expansion of these communities in some areas whilst other sensitive forest communities have been negatively impacted on the margins by too frequent and intense fire (Russell-Smith and Stanton 2002).

Fire and terrestrial fauna in northern Australia

Animals in northern Australia have evolved within climatic and geological partitions formed over time to utilise the available resources. Within the range of niches available there are always extremes, i.e. species that utilise a niche that is relict and disconnected or species that are non-selective generalists that can utilise a broad range of environmental and climate conditions. Finely balanced ecological interactions maintain the niche separation and continue to provide the resources required for the maintenance of viable populations. In these cases a disruption of the prevailing system, i.e. human-induced alterations to vegetation and water availability via changed fire regimes, agriculture or horticulture, can have dire consequences for specialist species. Depending on the range of the disruption even generalists can experience significant declines.

In the past 200 years most Australian ecosystems have been dramatically altered directly and indirectly by changes in land use and management associated with the intensification of agriculture, leading to unprecedented declines across all vertebrate taxa (Ford et al. 2001; Johnson 2006; Kutt and Fisher 2011). Northern Australia has not been immune to changes although the rate of change has been slower and less conspicuous and therefore more difficult to record (Lewis 2002). It is often purported that Australian tropical savannas are largely intact and relative to other global savanna regions this is true (Woinarski et al. 2007). However, in the past century significant disruptions to indigenous burning regimes (Russell-Smith et al. 2009) coupled with an intensification of the pastoral industry (Dyer 1997; Fisher et al. 2004; Woinarski et al. 2011) has, in many cases, led to significant structural and floristic vegetation changes via tree clearing, the proliferation of exotic pests (both plants and animals) and degradation of wetlands and rivers.

The coincident changes in fire management and intensified herbivory by domestic stock have had significant cumulative impacts on grass and other ground cover species both by selective grazing and excessively frequent burning which can eliminate fire prone species (ie. *Triodia*) or alter the tree-grass balance by promoting the dominance of trees and shrubs over grasses. This is particularly evident in the displacement of highly nutritious species such as *Alloteropsis semipalmata, Themeda triandra* and perennial sorghums (*Sorghum plumosum*) by less productive species such as *Aristida spp.* and *Heteropogon contortus* (Crowley and Garnett 1998, 2001). This shift in species composition is considered one of the key factors contributing to significant declines in gravinorous birds and mammals across northern Australia (Franklin 1999; Woinarski et al. 2011). More problematic to interpret is the decline of non-gravinorous birds such as black-faced woodswallows (Garnett and Crowley 2000), Carpentarian grasswrens (Appendix 1. Perry et al. 2011a) and treecreepers (Garnett and Crowley 1995a) although these declines are strongly linked to structural changes in habitat; i.e. loss of cover from predators and removal of nesting sites; or a disruption of other food sources, i.e. a reduction in invertebrates. For other taxa there is little knowledge or at least a high level of uncertainty as to the impact of fire on reptiles across the savanna regions (Mott et al. 2010; Woinarski et al. 2004b), though it has been illustrated that shifts in vegetation structure can alter the thermal environment for heliothermic species, thus increasing the susceptibility to change in climate and weather patterns (Huey et al. 2009; Sinervo et al. 2010).

Study aims and hypothesis

The principal aims of this study were to investigate the impact of climate change on fire in northern Australia and to examine the relationship between fire and biodiversity in a region that is particularly fire-prone, and to examine a range of integrated factors relevant to fire (i.e., current and traditional knowledge, predictive models, the fire ecology of species) at scales that are applicable for informing land management decisions.

I explore the aims above by testing three areas of interest that represent common assumptions in fire management and biodiversity conservation in this region that have not been adequately addressed in the available literature.

Hypothesis 1.

Hypothesis one is related to how climate change may have impacted on fire frequency in northern Australia and the propensity for change under future climate scenarios. In this thesis we did not specifically test the relationship between climate change (past or future) and fire and instead we simply test changes in fire weather to demonstrate the propensity for change across climatic gradients. I test how susceptible northern is to Australia to climate change by using weather variables that could change under future climate scenarios. For example, rainfall, temperature, timing and reliability of the northern monsoon all impact fire frequency and are used to model fire in this thesis.

Two main hypothesis are tested using the fire weather model in this thesis;

H_o. (i)

The probability of fire weather that can alter fire frequency in northern Australia has changed (led to conditions that support more frequent fire or less frequent fire) in recent history (the past 60 years).

H_1. (i)

The probability of fire weather that can alter fire frequency has remained the same in recent history.

H_o. (ii)

The probability of fire weather that reduces fire return intervals has changed unequally across the rainfall and temperature gradient in northern Australia which currently has a large range of fire return intervals which are determined by vegetation type and weather.

H_1. (ii)

The probability of fire weather that supports increased fire frequency in northern Australia has not increased because it is at its maximum, across the gradient of rainfall, temperature and vegetation.

Hypothesis 2.

Hypothesis two assesses contemporary fire management on indigenous land in the context of an assumption that modern methods compliment and support traditional Aboriginal burning and the maintenance of traditional practices on Aboriginal land. These modern approaches use tools such as aerial incendiary from helicopter and plane to overcome significant issues with access and timing and are integrated with government policy that seeks to alter the timing and frequency of fire such as the savanna burning methodology for greenhouse gas abatement and early dry season burning for biodiversity conservation.

H_o

Contemporary fire management strategies applied by Aboriginal land managers, such as early dry season burning done from a helicopter using incendiary, do not closely replicate traditional Aboriginal burning across northern Australia.

H_1.

Contemporary fire management strategies closely replicate traditional Aboriginal burning across northern Australia and support the maintenance and transfer of traditional knowledge.

Hypothesis 3.

The final set of hypotheses are in the context of the impact of fire frequency on terrestrial vertebrate fauna. Fire management strategies for biodiversity conservation in northern Australia are driven by policies that support a reduction in fire frequency and changes in fire timing from late dry season (defined as fires occurring after August 1) to early dry season. In this thesis I test the impact of fire frequency and timing on three vertebrate taxa (birds, mammals and reptiles).

Study Area

In this thesis I conduct research at multiple spatial scales including fire modelling at the continental scale and ecological studies at the regional scale focused predominantly on the tropical savanna woodlands of Cape York Peninsula, Queensland, Australia.

Fire modelling study area

To model the interaction between fire and weather I developed spatio-temporal models at the continental scale but clipped to the northern Australian rangelands boundary. Northern Australia offers an interesting backdrop for completing this research, being the most fire prone place on earth (Parr and Andersen 2006), having a variable climate (Agarwala et al. 2010), having continuing presence and active fire management conducted by indigenous people and supporting unique and diverse fauna of which recent declines have been linked to fire (Woinarski et al. 2011).

Fire and vertebrate fauna study area

The vertebrate fauna data were collected on Cape York Peninsula, Queensland, Australia and mainly focused on the dominant vegetation type, tropical savanna woodlands (Figure 1.1). The Cape York Peninsula bioregion is the northernmost part of Queensland, and encompasses >13 million ha (Figure 1.2). Mean annual rainfall of the peninsula varies from just over 1000 mm at Palmerville on southern Cape York Peninsula (16°00’S, 144°02’E) to >2000 mm at Lockhart River (12°28’S, 143°12’E) on the central eastern coast. Rainfall is primarily orographic and monsoonal in the east and monsoonal in the west (http://www.bom.gov.au/climate/averages/tables/ca_qld_names.shtml Oct 2010). The study area encompasses a broad range of vegetation types, predominantly open eucalypt and Melaleuca woodlands and grasslands (Neldner and Clarkson 1995).

Vertebrate fauna surveys were conducted from 2009-2013 during the dry season (June to November). A total of 208 sites were established in seven property clusters (Figure 1.2). Sites within each property were surveyed over a 4 night, 5 day interval.

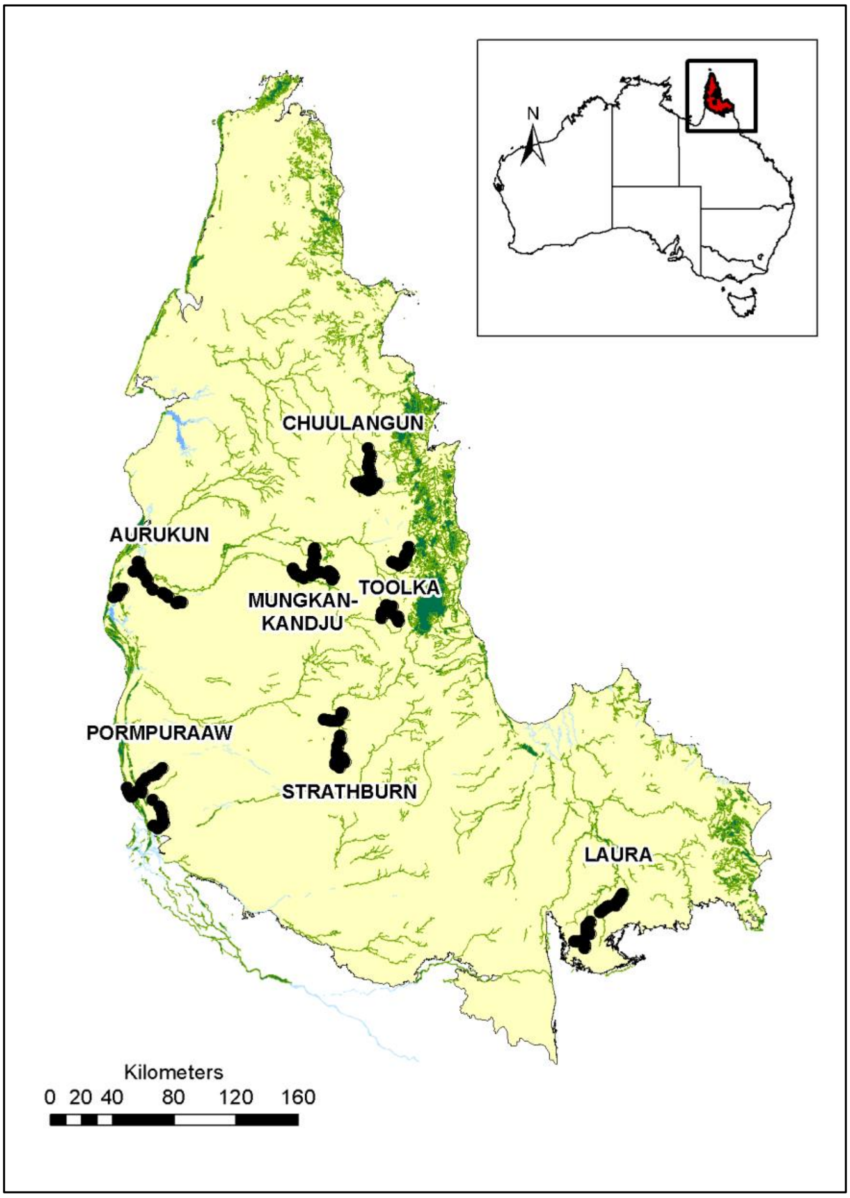


Figure 1.1 Cape York Peninsula with study sites (black points).

Thesis Structure

This thesis combines terrestrial vertebrate data, historical fire and weather data, and Aboriginal traditional knowledge to explore the implications of policy frameworks and current fire management paradigms on terrestrial vertebrate fauna and greenhouse gas emissions. To adequately address these key themes I split the thesis into nested and supportive chapters that focused firstly on the patterns and processes of fire and then on vertebrate fauna response (Figure 1.2).

The broad themes of this thesis are tackled in six data chapters summarised below. Each of these data chapters has been submitted for publication and is in review or is published already. The thesis is tied together with a general introduction and discussion of the implications of this research. Conducting a thesis by papers allows the work to be presented to a much broader audience. The papers have been modified slightly to adhere to copyright law and for consistency.

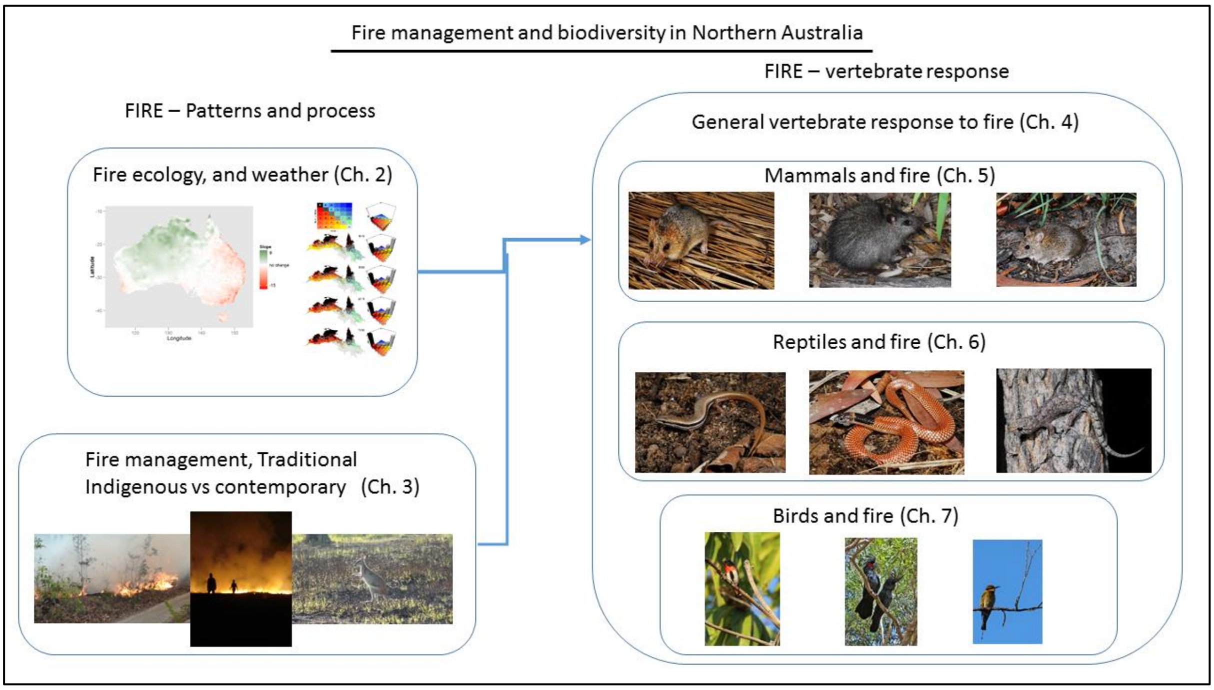


Figure 1.2 Diagram of thesis structure.

Chapter 1 provides a general introduction to fire as an ecological disturbance and its role in shaping vegetation and fauna in Australia. The next two chapters take a broader view of fire and look at the primary influences on its distribution from the climatic, environmental and human perspectives.

Chapter 2 sets the scene for the distribution of fire in northern Australia from a climatic perspective and explicitly links weather and vegetation to fire distribution in recent history. This places the contemporary distribution of fire in a broader temporal perspective and outlines the implications of fire on carbon emissions and describes the variance in annual and inter-annual fire distributions.

Current debate on the extent of change to global fire regimes under altered climate is embedded in the deep past (past 150k), recent past (the past 10-20 years) and the future (climate change projections). I explore the relationship between recent distributions of fire in northern Australia, vegetation type and antecedent observed weather data, and hind-cast potential fire likelihood distributions using spatial monthly weather data (1950 – 2011). The spatio-temporal shifts in relative fire proneness are assessed by quantifying the area, latitude and longitude of predicted fire distributions over that period. In particular I explore how predicted fire distributions have changed across the climatic envelope of northern Australia and test if the predictions are consistent across the gradients. I use this to define areas that are potentially at a fire maximum (as fire prone as they can get) in northern Australia. I found that the potential impact of recent climate change on fire has not been equal across the savanna and that there have been consistent increases in the area suitable for fire for all but the wettest areas (> 1100mm annual average rainfall). This has significant implications for assessing the effect of future climate change on fire in regions with large intra-annual variation in weather.

Chapter 3 explores the human dimension to fire and acknowledges the role of Aboriginal people in shaping the ecology of northern Australia. This chapter also contextualises Aboriginal knowledge and its importance for designing successful contemporary and future fire management. Fire has been a critical component of Aboriginal culture and natural resource management in Australia for millennia. For large parts of Australia, Aboriginal burning has been absent for at least a century following rapid European settlement. In contrast, Aboriginal fire management in northern Australia is widespread and, in some more remote areas, has continued relatively undisrupted despite widespread changes in tenure and land use. For the Wik people of Western Cape York there has been a continued connection to their culture and traditional lands and they have retained a very clear understanding of cultural boundaries, rights and responsibilities. Recently, Wik traditional owners have formed a ranger program which has secured funding to manage contemporary land management issues including the landscape scale management of fire for biodiversity conservation and greenhouse gas abatement. There is an assumption that because the work is being conducted by Aboriginal people, with consent from traditional owners, and on their traditional lands, that the activities are compatible with historic traditional land management and cultural practices. In this chapter I compare contemporary fire management with traditional Aboriginal fire management to objectively assess the compatibility of these two paradigms. I do this by combining the experience and understanding of traditional owners with anthropological and ecological perspectives.

Chapter 4 shifts the focus onto terrestrial biodiversity and fire management on Cape York Peninsula, Queensland, the region that forms the basis of the terrestrial ecology component of this thesis. This chapter contextualises the complexity of fire management and biodiversity patterns by examining the broad relationships between the three main vertebrate taxa (birds, reptiles and mammals) and fire management. In this chapter the savanna burning for greenhouse gas abatement methodology is introduced and critically examined in the context of its influence on biodiversity patterns. Carbon farming initiatives have rapidly developed in recent years influencing broad scale changes to land management regimes. In the open carbon market a premium can be secured if additional benefits, such as biodiversity conservation or social advancement, can be quantified. In Australia, there is an accepted method for carbon abatement that requires shifting fire frequency from predominantly late (defined as fires occurring after August 1) to early dry season fires or by reducing overall fire frequency. There is an assumption and some evidence that this might accrue co-benefits for biodiversity. I tested this assumption by comparing terrestrial vertebrate biodiversity patterns (richness and abundance of reptiles, birds and mammals) against increasing fire frequency in the early and late dry season dry season at the same spatial resolution as the fire management for emission abatement methodology. I systematically sampled 202 sites on Cape York Peninsula, and examined the relationship between vertebrate fauna, fire and environmental metrics. I found that within the approved vegetation type, open woodlands in tropical savanna woodland, early and late dry season fire frequency had the same weak linear relationship with only some elements of the observed fauna. Additionally, the response of each taxa to fire frequency were different across broad vegetation structural categories suggesting that a more nuanced species-specific monitoring approach is required to expose links between savanna burning for carbon abatement and burning for biodiversity benefit.

Chapters 5-7 take the more general terrestrial fauna patterns exposed in chapter 4 and explore the patterns of fire and its influence on each of the taxa in more detail.

Chapter 5 looks at the contemporary distribution of mammals on Cape York Peninsula in comparison with limited historical data and changes in mammal fauna across northern Australia. I contextualise the changes in mammal populations with the historical disturbances present in the study area which includes changes to fire regimes. Global mammal populations continue to be threatened by environmental change, and recent decadal monitoring in northern Australia suggests a collapse in mammal abundance in key locations. Cape York Peninsula has globally significant natural values but there is very little published about the status and distribution of mammals in this region. Following an extensive field survey I investigated two key questions: (i) what is the composition, spatial variation and change from previous regional surveys in the mid to late 1900s in the native terrestrial and arboreal mammal fauna recorded?; and (ii) which landscape and site factors best predict mammal richness and abundance? As part of a team I sampled 202 one-hectare sites across seven locations from 2009 to 2012 in woodlands, closed forest and dune scrub and tussock grasslands. I collected landscape and site-based environmental data for each location, representing fire, weather and vegetation factors. I used generalised linear mixed models to examine the relationship between mammals and these factors. Mammals were generally scarce across the sites and were more abundant and species rich in wet coastal grasslands or closed forests than tropical savanna woodlands. Fire frequency data and the surrounding vegetation complexity were consistent landscape scale predictors for mammals; ground cover and woody complexity were significant at the site-scale. Notwithstanding interpretational constraints related to the limited evidence base of historic sampling, the mammal fauna recorded in this study for Cape York Peninsula was similar in composition to the mammal fauna described from 1948–1980 and surveys in 1985, with some species seemingly declining (e.g. *Melomys burtoni, Dasyurus hallucatus, Sminthopsis virginiae*) and others stable (e.g. *Rattus sordidus*) or more common (e.g. *Rattus tunneyi*); however, across all sites abundance was low, and many sites had few or no mammals. In the absence of consistent long-term systematic monitoring it is difficult to determine if this survey and historical surveys represent pre-European patterns for mammals. The absence or low abundance of mammals in most sites suggests that contemporary patterns may not represent an intact mammal fauna. Due to the equivocal nature of these findings a critical next step is to establish robust monitoring and experimental work to reveal the response of mammals to management interventions.

Chapter 6 focuses on reptiles, one of the most abundant and diverse taxa in savanna ecosystems. Theoretically, if fire changes vegetation patterns, then reptiles as a heliothermic organism, should be a good indicator of the impact of altered fire regimes. Fire is a fundamental driver of vegetation structure in tropical savanna systems and a very widely used management intervention. Understanding the faunal response to disturbances, such as fire, across environmental gradients is important for designing effective fire management in the context of other influences on faunal patterns. In this study I focus on reptiles, a highly diverse and abundant taxon within savanna woodland ecosystems. As part of a team I surveyed reptiles in 202 unique sites (one hectare each) that were dominated by woodland with representative samples of closed forest and open grassland on Cape York Peninsula. I found some effect of remotely sensed fire frequency on vegetation structure in the most and least fire prone habitats, but in the largely undifferentiated and most extensive habitat – open Eucalypt woodlands – an intermediate and less conclusive effect. Reptile assemblages were partitioned along an environmental gradient within broad vegetation groups from least complex (grassland) to most complex (closed forest). Reptile diversity was highest at intermediate to low tree cover and density and low in sites with very low or very high tree cover (though these areas contained unique or specialised species). The implication of this result is that vegetation types with intermediate to low cover, are most suitable for heliothermic species (neither too exposed nor too covered) and fire frequency measured by remote sensing is a poor surrogate for predicting reptile patterns except at the extremes (high or low). This study suggests that fire management that aims to reduce fire frequency at a landscape scale may not lead to changes in reptile diversity unless the intervention is extreme (burning every year or not burning at all).

Chapter 7 looks at changes in bird distributions across time in the study area. An essential component of conservation science is repeated surveys over time to monitor species that might be responding to local factors, such as land management, or more broadly to global change. A systematic survey of the avifauna of Cape York Peninsula was conducted in the late 1990s and early 2000s providing an ideal basal dataset for measuring change in the avifauna. A subset (n > 600) of these sites, primarily within savanna landscapes, was selected for re-survey in 2008 to investigate changes in bird communities on Cape York Peninsula. Changes in mean species richness varied across the study area (decreases in 59 grid cells and increases in 43) with no apparent pattern. Significant change in reporting rates was recorded in 30 species. Four sedentary and highly detectable species declined (Bar-shouldered Dove, *Geopelia humeralis*, Brown Treecreeper *Climacteris picumnus*, Pale-headed Rosella, *Platycercus adscitus* and Sulphur-crested Cockatoo, *Cacatua galerita*) and five increased (Peaceful Dove, *G. striata*, Pheasant Coucal, *Centropus phasianinus,* Weebill, *Smicrornis brevirostris,* White-throated Honeyeater, *Melithreptus albogularis* and Yellow Oriole, *Oriolus flavocinctus*). Habitat preference for the species that showed change remained relatively stable between the two survey periods. Some species that were recorded in very low numbers in the original survey and are considered to be threatened (Brown Treecreeper *C. picumnu* and Black-faced Woodswallow, *Artamus cinereus*) remained in very low numbers or decreased in my survey suggesting that there has been no regional recovery of these species. Long-term monitoring can describe important patterns of species change over time, though in the case of large, highly seasonal environments like the tropical savannas, signals of change may manifest over decades rather than annually.

Finally **chapter 8** discusses the broad implications of this research and describes how each chapter has collectively increased the understanding of the impact of fire on biodiversity in northern Australia. In this chapter I also suggest future research direction for fire ecology in northern Australia.

Chapter 2. Hind-casting 60 years of fire weather conditions in the Australian savanna: evidence for a rapidly expanding fire maximum front

Introduction

Tropical savanna systems cover ~20% of the surface of the earth, have the highest fire frequencies of any biome and contribute the most of any vegetation type to global carbon emissions from burning (Mouillot and Field 2005; van der Werf et al. 2010). Annual temperature and precipitation cycles determine fire frequencies which range from areas consistently at 'fire maximum', i.e. conditions suitable for burning occur every year, to much less frequent fire. The vast northern Australian savannas have experienced a similar velocity of change in temperature and precipitation over the past 60 years (VanDerWal et al. 2013) to that expected under future climate scenarios (Loarie et al. 2009). Given the close control of annual weather on fire activity, we should already be seeing a fingerprint of change on fire frequencies. I used spatially explicit pyrogeography models to hind-cast changes in suitable fire weather and the location of the fire maximum front across northern Australia over the past 60 years. I found that the frequency of suitable fire weather has increased by over 50% in the savannas and that the area under fire maximum conditions in this region increased by 78% from 1950 to 2012. The expanding fire maximum front and the increase in suitable fire weather has potentially resulted in a 50% increase in $C0_2$ emissions and had serious implications for fire management, biodiversity, the carbon balance and livelihoods across the Australian savanna.

Methods

Historical fire data

Over 4.5 million fire occurrence records were derived from MODIS satellite imagery (http://www.firenorth.org.au/nafi2/) by converting monthly satellite derived fire scars into unique records of fire occurrence (month, year, latitude and longitude). As there was a spatial resolution mis-match between fire scar data (~250 m) and the climate data (~5 km) I rounded the fire scar location data up to the climate data resolution and included unique temporal and spatial records. This study focused on fire in Australian savanna so fire records where clipped to this extent to avoid weather patterns in temperate Australia influencing the model.

Weather data

Daily precipitation and temperature minima and maxima from 1950 until 2012 at a 0.05 degree grid scale were accessed from the Australian Water Availability Project (AWAP) (Jones et al. 2009). My weather data were created by calculating mean temperature, temperature seasonality, precipitation and precipitation seasonality for three, six and twelve months previous to each month that a fire was recorded within the period 2004 to 2012. Twelve months was selected as the maximum temporal slice as this has been shown in the literature to be sufficient time to produce enough fuel for fire in the study region (Bradstock 2010). Although the temporal weather variables (three, six and twelve months) exhibited a degree of correlation, the species distribution modelling (SDM) algorithm can handle such correlation (Elith et al. 2006) and I thought it important to explore the detail within the models at a variety of temporal scales.

Species distribution modelling

Here I recognise that fire distribution is limited by physical and stochastic environmental variables in the same way that vagile vertebrate and invertebrate species are. I utilise the moderate resolution satellite fire history data to apply a novel use of well-developed species distribution modelling methods. Species distribution models were run using the presence-only modelling program Maxent (Phillips and Dudík 2008). Maxent uses species presence records to statistically relate species occurrence to environmental variables on the principle of maximum entropy. The weather data files consisted of each unique combination of month, year, latitude and longitude of fire event, and the corresponding weather or climate variables for each relevant time period (antecedent three, six and twelve months, depending on the variable). As distributions are limited by physical as well as the stochastic variables, I used a static broad vegetation type grid to provide a more realistic prediction of limits to dispersal in the region (see Appendix Table 2.2). All default settings were used except for background point allocation. Background points (pseudo-absences) can be selected in a number of ways; here I used all of northern Australia to derive pseudo-absence records as the satellite derived fire scars accurately represent the location of fires in this region so sampling bias was not an issue as is the case with many other examples (VanDerWal et al. 2009). The models were projected onto spatial surfaces consisting of the model variables across Australia for each calendar month between 1950 and 2012.

Direction and extent of change

Binary species distributions were generated using a threshold based on balancing the training omission rate, predicted area and logistic threshold value. This threshold was chosen as the predictions most closely approximated historical fire. 732 predictions were created representing potential changes in fire distribution each month between 1950-2012. The distribution area for each of the 732 monthly predictions was calculated using the R package SDMTools (VanDerWal et al. 2008).

I acknowledge that there are some limitations to the models. Climate grids are interpolated from limited meteorological stations in northern Australia. At the continental scale at which I assessed the changes in weather I were more interested in broad geographic changes to the regional weather patterns across the climate gradient rather than the subtle differences in local weather at finer resolutions. The weather data has been rigorously downscaled and accurately reflects the variability in climate from 1950 to 2012 thus is suitable for these analyses. A clear limitation to the model is the inability to assess time since last fire as these data are not available consistently across the study region prior to the year 2000. In addition the broad vegetation groups used to limit models do not account for land management effects which can dramatically change biomass.

Despite these limitations I have shown that fire weather is relatively predictable (see Appendix - Figure 2.4, -Table 2.1). The key variables that drive fire regimes in northern Australia are low temperature seasonality, high mean temperature across 12 months, relatively high annual rainfall centred around areas receiving around 1200 mm, very low rainfall 3 months leading up to fire and high minimum temperatures in the coldest month in open homogenous vegetation types (see Appendix- -Figure 2.2:2.3, -Table 2.1). The accuracy of these relatively coarse models indicate that with the addition of fine scale local variables and time since last fire a very accurate fire model could be produced for the use of local fire managers and refinement of the greenhouse gas emission calculations.

Results and discussion

Fire plays a critical role in regulating the biophysical structure and composition of ecosystems (Paolo D'Odorico et al. 2006), global and local carbon balances, and global climate through atmospheric CO_2 emissions from biomass burning (van der Werf et al. 2010). Temperature and precipitation drive biomass fuel production, moisture availability, fuel drying cycles and suitable fire weather conditions, which in turn drive fire dynamics and fire return intervals (Bradstock 2010). Widespread changes in pyrogeography are expected under future climate scenarios (Krawchuk et al. 2009; Liu et al. 2010; Pechony and Shindel 2010). Most researchers predict a net increase in fire frequencies worldwide driven by increasing temperatures and biomass drying (Pechony and Shindel 2010). Savannas are usually cited as the exception; they are expected to become less fire prone or show little change in fire frequency under future climate scenarios (Krawchuk et al. 2009; Moritz et al. 2012), in part due to a perception that large parts of savanna systems are already at, or close to, fire maximum and therefore fire activity can only remain static or decrease (Cary et al. 2012). Australia's savannas, which cover about 2 million km^2, are the most fire prone ecosystem in the most fire prone continent on earth (Russell-Smith and Whitehead 2015). We now know that the velocity at which the climatic drivers of fire have changed over the past 60 years in the Australian savannas has been very high and spatially variable, with increases in both temperature and precipitation occurring across much of the biome (VanDerWal et al. 2013). Fire-interval distributions can be expected to have already shifted in response to recent past climate change, in much the same way that species distributions are expected to shift, or have shifted (VanDerWal et al. 2012). A robust understanding of past trajectories of climate change on the spatio-temporal dynamics of suitable fire weather conditions and resulting fire frequencies in savannas will inform better predictions about future trends and the implications for carbon, biodiversity, human societies and economies.

The Australian savannas are characterised climatically by a monsoonal summer wet season, extending from November/December to March/April, and a warm, dry winter. The northern mesic regions, with mean annual rainfall >1500 mm, have traditionally been considered to fall into the fire maximum zone (Russell-Smith et al. 2007) with fire-intervals increasing as mean annual rainfall decreases toward the drier southern areas. The fire season in the savanna begins in the early dry season (April/May) after the vegetation cures, and extends through to the beginning of the next wet season (Sullivan et al. 2012). The length of the fire return interval is key in determining the carbon balance in fire prone savanna ecosystems (Beringer et al. 2007; Enright et al. 2015). Aboveground carbon stocks in savannas globally vary widely according to the extent of tree cover, from 1.8 t C ha^{-1} where trees are absent, to above 30 t C ha^{-1} where there is substantial tree cover (Grace et al. 2006). Modification of fire frequencies influences the tree/grass balance; increasing fire frequency tends to favour the grassy component of savanna systems by suppressing tree establishment and growth, while decreasing frequencies favour tree recruitment and increasing carbon storage in woody components (Beringer et al. 2007; Paolo D'Odorico et al. 2006). Thus, the location of the fire maximum front is critically important in driving carbon dynamics in savanna vegetation, and any change in fire frequencies will have significant effects on carbon emissions and sequestration.

The recent development of novel methods for hind-casting species distributions at a fine spatial and temporal scale using accurate weather data (VanDerWal et al. 2013), when combined with the rapidly improving resolution and accessibility of fire scar (or occurrence) data, lends itself to robust analysis of the effect of recent climate change on pyrogeography. I create temporally explicit pyrogeography models based on weather patterns and broad vegetation types associated with recent (2000-2012) fire events and hind-cast fire conditions conducive to burning over the preceding 60 years in monthly intervals. I use these distribution models to map changes in fire return intervals and the location of the fire maximum front across northern Australia over the past 60 years. For each of the 65835, 0.05 degree grid cells across the Australian savannas, a five year moving window centred on each year from 1952 to 2010 was used to determine the number of times a grid-cell was exposed to suitable fire conditions during the five year period. A cell is considered to be at 'fire maximum' if it experiences two or more consecutive months of weather conducive to burning in every year of the five year moving window.

I found clear evidence for an expanding fire maximum front across the savannas of northern Australia (Figure 2.1). The average area of land now (2012) experiencing suitable fire weather conditions every year has increased by 972,774 km^2 since 1950 with 27 % of the savanna biome now at fire maximum compared to 15% in the 1950's. Another 118,215 km^2 has seen suitable fire conditions on a trajectory toward achieving fire maximum within the next 20 years; even beyond 2030, the fire maximum front retains the momentum for expansion (Figure 2.1). Between 1950 and 1990 the area classified as increasing to fire maximum (during a 5 year moving window) grew, but showed considerable variation, that is, large parts of the landscape experienced fire maximum conditions for short intervals but intermittently experienced years that were less conducive to burning (falling out of the fire maximum category) (Figure 2.2). Post 1990, variation decreased markedly indicating that large parts of the landscape achieved fire maximum conditions and stayed there for the remainder of the 60 year period (Figure 2.2).

Fire weather conditions are relatively stable in the mesic savannas; most of the area in the 'always at fire maximum' category occurs in this region, reflecting the location of the fire maximum front in 1950. Fire weather patterns seasonally also appear relatively stable in the fire maximum region. I have not detected any lengthening of the number of months during the dry season when weather conducive to burning is experienced in this region (see Appendix Figure 2.1). However, the mean first month of fire suitable conditions has marginally decreased shifting from mid-June to early-June suggesting a trend toward earlier drying of fuel with increasing temperatures (see Appendix Figure 2.1). In the western savannas the fire maximum front has shifted south nearly 2 degrees of latitude over the past 60 years. The most dramatic expansions occurred in the 1970's and in the 2000's which were wetter than average. Rainfall has increased during the northern wet season since 1970 and is now well above average across much of the north-west savanna (CSIRO 2014); seasonal rainfall has been shown to be a key driver of fire regimes in savannas globally due to its influence on fuel availability (Nelson et al. 2012).

Fire maximum conditions occur in areas with very reliable seasonal extremes of rainfall and temperature; very wet summers followed by very dry winters, every year. Fire is limited at the climate extremes, i.e where conditions are consistently too wet or too dry to support frequent fire (see Appendix Figure 2.3). In these areas it is only during abnormal conditions (those that reflect the nearly annual cycle in the mesic savanna) that these areas are suitable for fire. Other areas that limit suitable fire conditions are closed forest communities embedded within the fire prone areas (see Appendix Table 2.2). These areas are associated with subtle topographic characteristics that naturally exclude fire, such as drainage lines, rockiness and topographic complexity (Price et al. 2005) or substrates that don't favour biomass production such as saltpans. The landscapes where suitable fire conditions are becoming less frequent (i.e. category 'not increasing') occur primarily in the south-eastern savanna regions which have experienced increasingly drier conditions in the past 60 years (Figure 2.1). In addition, this region is more intensively managed, fires are generally suppressed and cattle grazing may reduce fuel loads.

An increase in suitable fire weather conditions across the northern savannas has potentially increased carbon emissions from burning by 50% in the past 60 years (Figure 2.2) as well as affecting carbon sequestration potential. Woody plant species are likely to suffer 'interval squeeze' resulting in conversion of savannas to grass-dominated systems (Enright et al. 2015). Any stabilizing feedback may be compensated for by high-biomass non-native grasses which are increasing their prevalence across the Australian savannas (Setterfield et al. 2010). The annual and inter-annual variation in the distribution of fire described in this study provides a theoretical base from which to develop more accurate CO_2^e emission calculations.

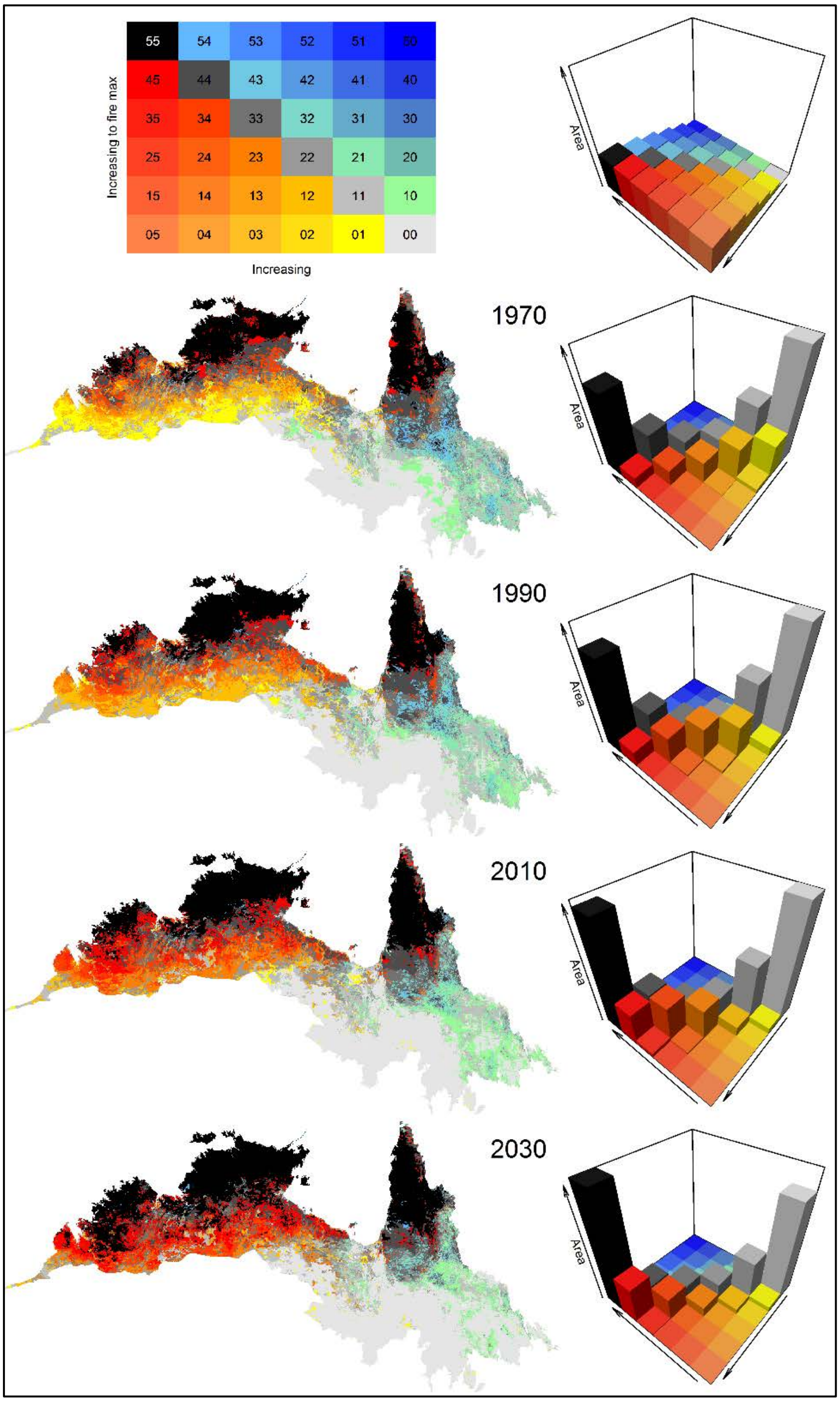


Figure 2.1 Changes in average 5 year moving window fire frequency categories in 20 year time slices from 1950 to 2030. Where 0 is no fire in the five year moving average and 5 is annual fire. The colour chart (top left) represents the change from the previous time slice. For example, if from 1970 to 1990 a pixel went from burning 4 out of 5 years to 5 out of 5 years, or fire max, the pixel value will be 45. Areas at fire maximum in each time slice are coloured black. The perspective plot on the right illustrates the relative change in area across the four time slices. These plots clearly demonstrate fire frequency categories are increasingly trending toward fire maximum. I also use extend the linear model to 2030 to illustrate the potential for further expansion.

The magnitude and extent of changes in fire weather conditions across the Australian savannas over the past 60 years have likely already had a significant impact on biodiversity and ecosystem function. Of great concern currently is the rapid range contraction and severe population declines of small to medium-range native and endemic mammals across northern Australia (Woinarski et al. 2010; Woinarski et al. 2015). Researchers highlight the primary role of feral animals (particularly cats and foxes) and altered fire regimes in these declines (Andersen et al. 2012). There is strong consensus that smaller mammals are highly sensitive to increases in fire frequency, particularly where these changes act synergistically with other threatening processes such as invasive species (Andersen et al. 2012). However, altered fire regimes are generally discussed in terms of disruptions to traditional Aboriginal burning practices following European settlement of northern Australia in the 19th century (Andersen et al. 2012; Russell-Smith et al. 2013). It is widely believed that this has led to an increase in the frequency and extent of high intensity fires occurring late in the dry season (Andersen et al. 2012). I suggest the rapid velocity of climate change over the past 60 years is a major factor in increasing fire frequencies, particularly in the historically more arid areas.

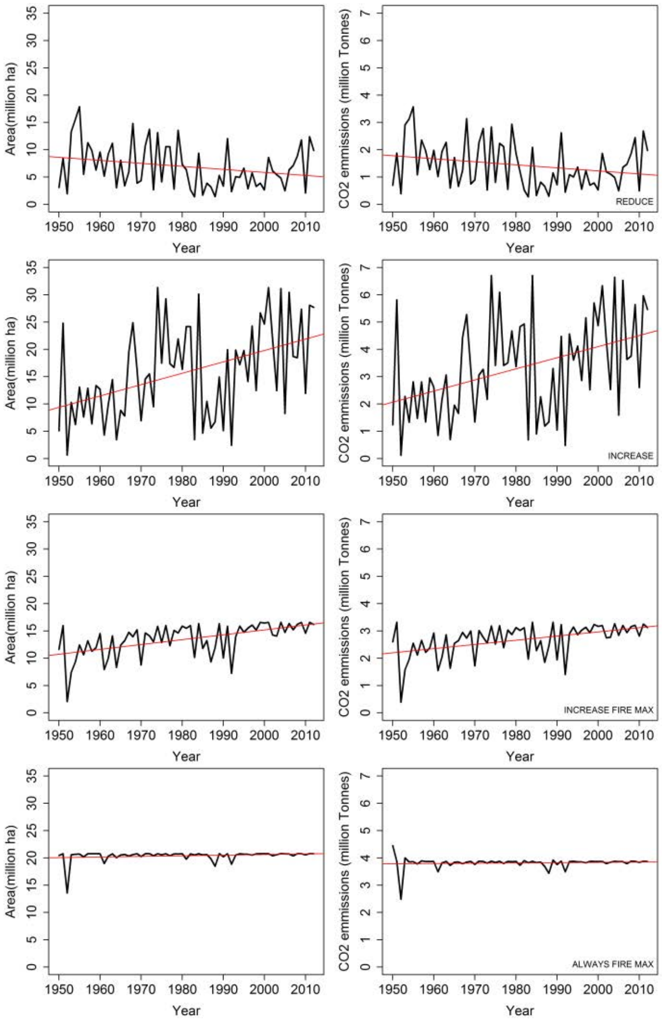


Figure 2.2 Temporal annual variation in predicted area suitable for fire (million hectares - left panels) and potential carbon dioxide equivalent emissions associated with these distributions (millions tonnes – right panels). From top to bottom the panels represent areas that have reduced in fire, increased in fire, increased to fire maximum and those that are always at fire maximum.

Global and continental analyses of fire distributions usually treat savannas as a homogenous entity and often take a temporally static view of fire frequency (Lehmann et al. 2014; Murphy et al. 2013). It is clear from my work that weather conditions conducive to burning are spatially variable across the vast savannas of Australia, ranging from fire maximum to areas that rarely experience suitable fire conditions (see Appendix Figure 2.5). Furthermore, fire weather conditions have been dynamic over the past 60 years exhibiting increasing, decreasing and stable trends (Figure 2.2). Several authors have suggested that fire-intervals in the tropical savannas of northern Australia will likely increase in the future (i.e. become less fire prone) due to predicted decreases in vegetation productivity as a result of declining moisture availability (Cary et al. 2012; Krawchuk et al. 2009). Over the past 60 years we have seen an increase in rainfall over much of Australia's savanna (VanDerWal et al. 2013) (Figure 2.1) and it is clear that warmer and wetter conditions have driven increases in suitable fire conditions by increasing productivity during the wet season (Figure 2.3). Future climate change scenarios for the Australian savannas predict continued warming and most global climate models predict further increases in wet season rainfall, although there is high between model variability (Reside et al. 2011). Given the trajectory of increasing frequency of suitable fire conditions over the past 60 years and predictions for future climate change in the Australian savanna, I expect the fire maximum front to continue expanding as evidenced in the trajectory of current fire conditions (Figure 2.1). Ongoing, large-scale changes in ecosystem structure, biodiversity and the carbon balance should be expected with changing fire regimes. Planning for intensification of land use in the savannas, currently a political imperative in Australia, will need to consider the implications for fire mitigation and fire-fighting readiness. In the near future, methodologies for assessing greenhouse gas abatement for savanna fire (Australian.Government 2015) will need to be modified to account for the dynamic inter-annual variability in monthly fire probability exposed in this study.

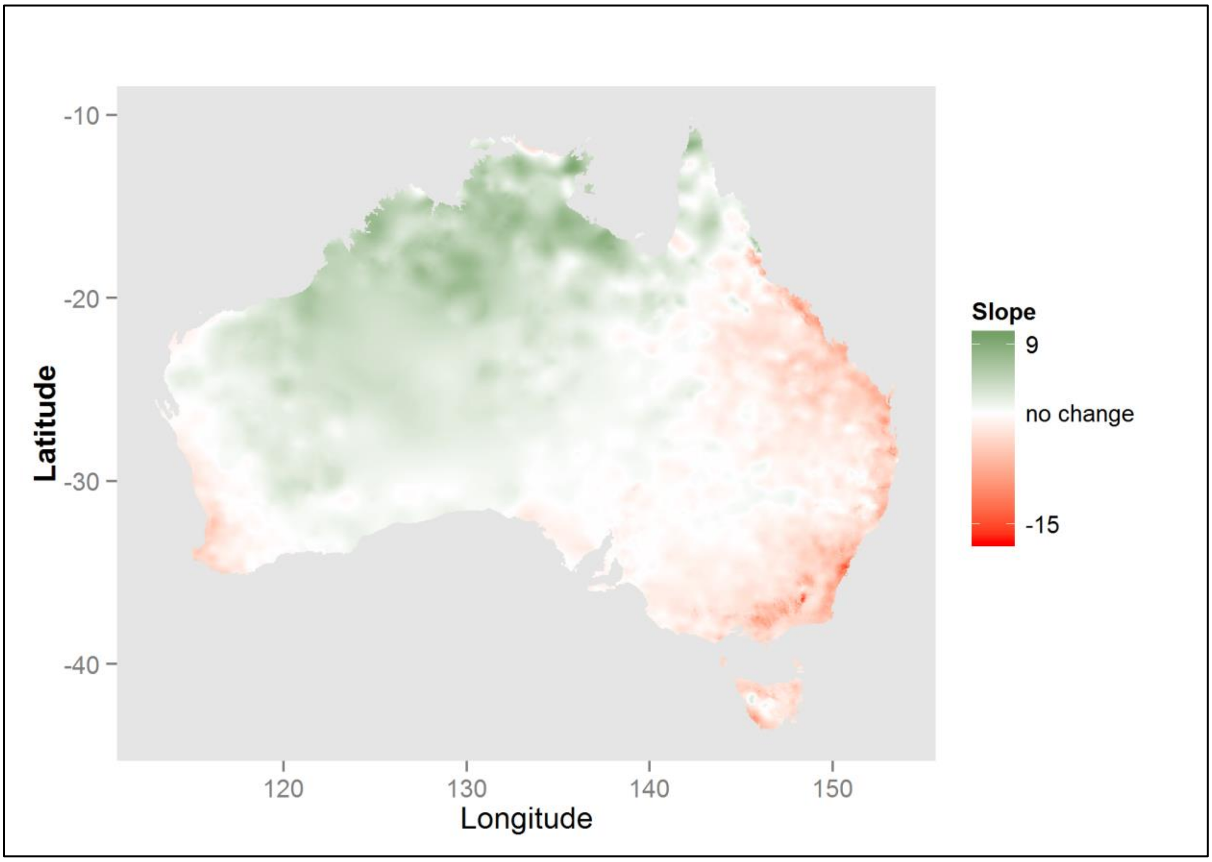
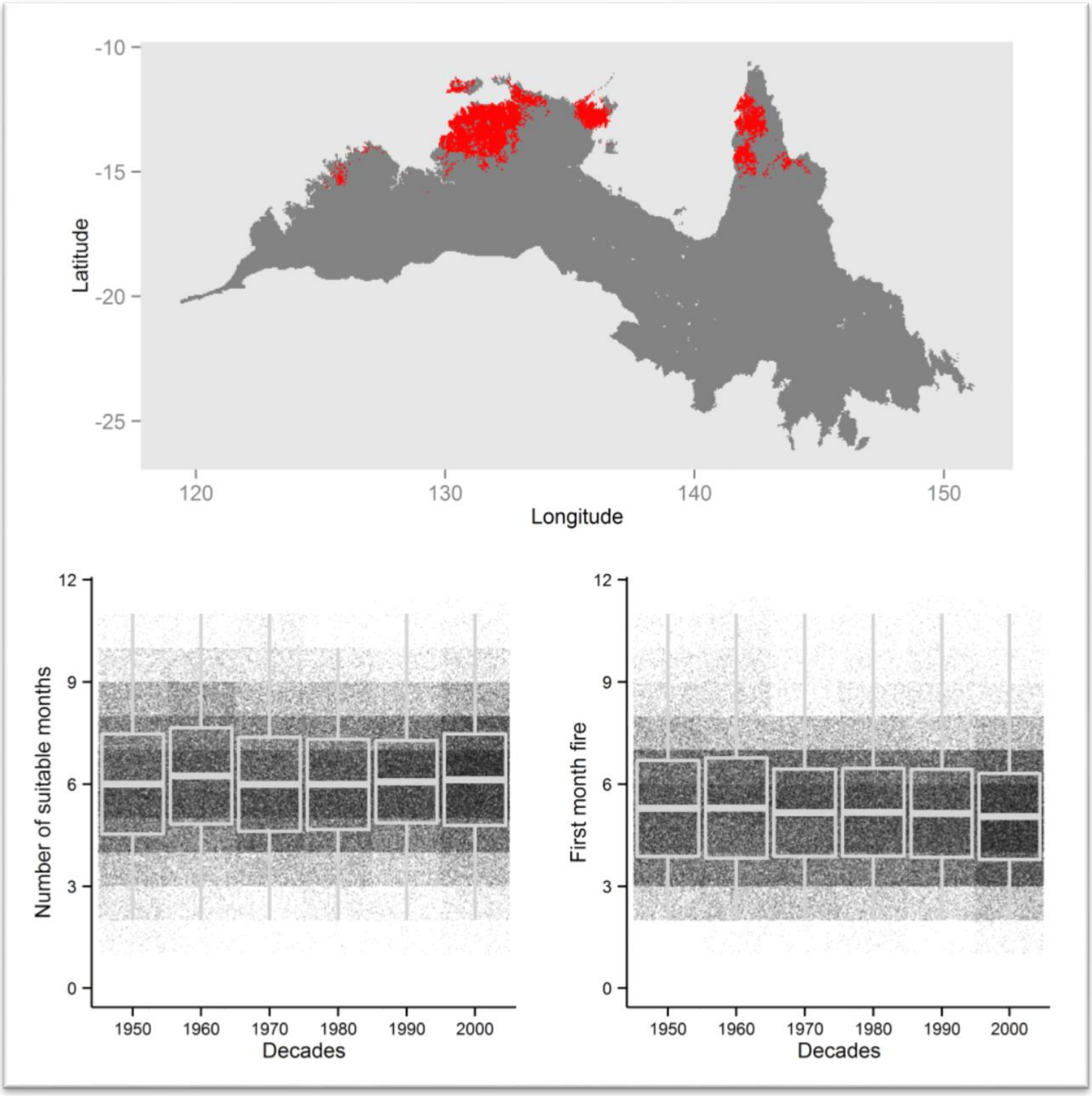


Figure 2.3 Linear model of rainfall change over the study period (1950-2012). Areas where precipitation has not changed are coloured white, increasing precipitation (white to dark green), and decreasing precipitation (white to dark red). Although most of northern Australia has experienced an increase in precipitation the most important areas in the context of fire are those that have shifted closer to the optimal fire conditions (~1200mm annual rainfall). These are generally areas that have historically been characterised by aridity and have become more mesic in past 60 years.

Author contributions

Justin Perry and Jeremy VanDerWal developed the concepts for the paper, developed the analytical framework, conducted the analysis and produced the figures and tables. Justin Perry and Helen Murphy conceptualised and planned the paper, wrote and edited the paper and conducted the literature review. Alex Kutt contributed to the conceptual framework of the paper and contributed to editing and writing.



Appendix Figure 2.1 For areas always at fire maximum (red fill – representing pixels that had at least two consecutive months predicted for fire in every year between 1950 and 2012) decadal mean (plus and minus standard deviations) number of months predicted to be suitable for fire (left bottom) and the first month suitable for fire after the wet season which I have defined as February to February (bottom right). Grey dots illustrating the spread of data and outliers for each decade.

Appendix Table 2.1. Model accuracy (AUC), percentage contributions of environmental variables to individual species distribution models of fire in each month. The suffixes .12m and .3m refers to the weather 12 months and 3 months preceding a fire event. Bc01.12m, Bc01.3m – mean temperature, bc04.12m – temperature seasonality, bc05.12m, bc05.3m – maximum temperature of the warmest month, bc06.12m, bc06.3m – minimum temperature of coldest month, bc12.12m, bc12.3m,– total precipitation, bc15.12m – precipitation seasonality, bc16.12m, precipitation of wettest quarter, bc17.12m, precipitation of driest quarter, Vegetation – broad vegetation type.

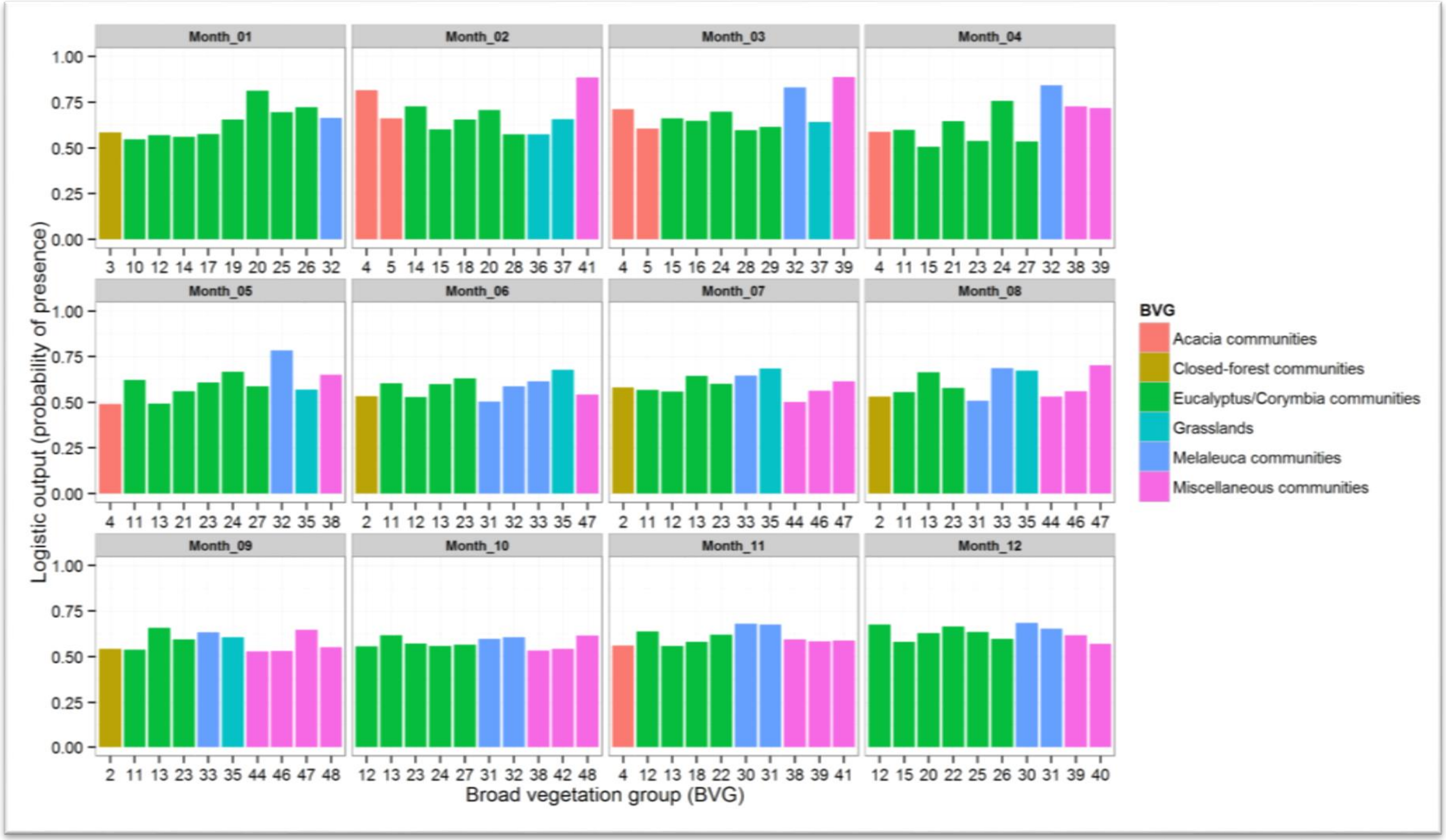
Month	training samples	AUC	Bkgd Points	bc01.12m	bc01.3m	bc04.12m	bc05.12m	bc05.3m	bc06.12m	bc06.3m	bc12.12m	bc12.3m	bc15.12m	bc16.12m	bc17.12m	Vegetation
Jan	5786	0.90	855855	**25.39**	7.22	3.24	3.21	1.70	4.53	1.29	1.90	**19.12**	2.12	**18.31**	2.12	**9.86**
Feb	2026	0.94	855855	3.43	6.31	**8.64**	3.46	1.08	**14.91**	2.77	**10.62**	**18.01**	4.35	5.11	**8.44**	**12.86**
Mar	4590	0.89	855855	**10.76**	**8.89**	**10.76**	3.97	5.60	6.40	**13.54**	6.84	**8.51**	0.95	7.47	**8.15**	**8.16**
Apr	32969	0.87	855855	**11.91**	2.81	4.20	**10.72**	**8.25**	4.94	**8.16**	3.50	5.80	4.24	**21.55**	0.94	**12.98**
May	79549	0.83	855855	**18.57**	2.81	**13.03**	3.91	3.74	1.18	4.08	**15.47**	1.13	3.31	**18.23**	0.75	**13.79**
Jun	71287	0.85	855855	**11.16**	0.86	**49.63**	2.61	2.29	0.41	2.13	**15.12**	2.22	2.05	0.31	3.16	**8.07**
Jul	62240	0.85	855855	0.43	**21.39**	**35.55**	1.79	2.97	0.15	0.31	**21.10**	2.00	1.06	1.70	2.47	**9.08**
Aug	68201	0.83	855855	1.34	**18.46**	**14.54**	2.22	6.99	2.52	3.71	**35.30**	1.05	2.24	0.85	0.44	**10.33**
Sep	77473	0.80	855855	1.45	**19.16**	4.98	2.78	0.94	1.55	0.66	**43.92**	5.25	2.51	7.51	0.68	**8.61**
Oct	86802	0.75	855855	1.28	**17.47**	2.32	1.61	3.38	2.34	0.48	**11.09**	3.06	6.10	**42.09**	0.10	**8.69**
Nov	86271	0.74	855855	**8.16**	1.02	3.39	0.91	7.05	1.18	2.58	**12.87**	**13.85**	2.77	**36.54**	0.15	**9.51**
Dec	39384	0.77	855855	5.69	2.71	**12.08**	0.22	3.81	1.96	7.99	3.54	**26.37**	2.48	**18.85**	0.16	**14.14**

Appendix Table 2.2. Broad vegetation categories used in the model.

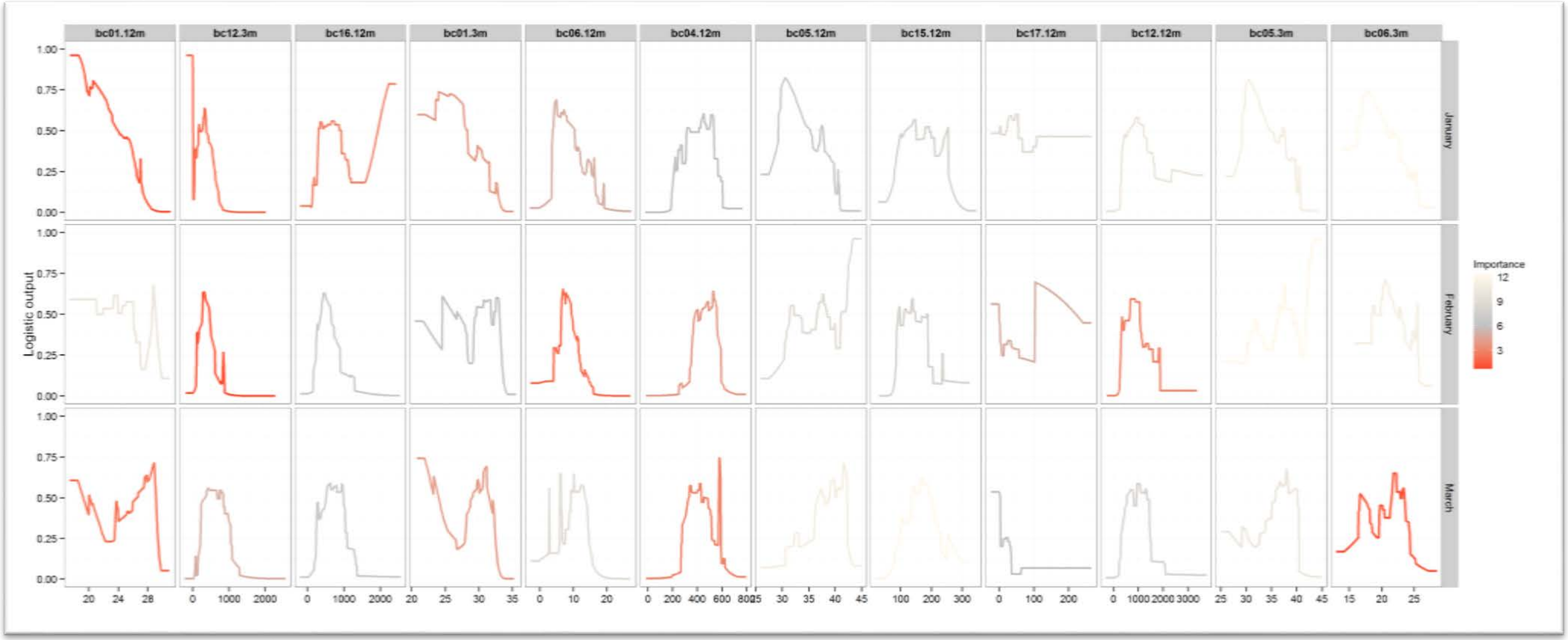
BVG_1M	BVG_1M_DESCRIPTION	BVG	Broad	VegClass
1	Complex closed-forests of the wet tropics, coastal dunes and dunefields	Closed forest communities	1	EOF
2	Deciduous closed-forests and gallery forests on alluvia and low slopes	Closed forest communities	1	EOF
3	Deciduous vine thickets and low woodlands of vine thicket species on depositional plains, basalts, sandstones, metamorphics and volcanics	Closed forest communities	1	EOF
4	Shrublands and tall shrublands dominated by Acacia ancistrocarpa, Acacia eriopoda or Acacia monticola on sandplains	Acacia communities	2	EW
5	Low open woodlands and tall shrublands dominated by Acacia aneura or Archidendropsis basaltica on residual sands	Acacia communities	2	EW
6	Low woodlands and low open woodlands dominated by Acacia cambagei, Acacia tephrina or Acacia georginae on clay plains	Acacia communities	2	EW
7	Woodlands and open woodlands dominated by Acacia harpohpylla, Casuarina cristata, Acacia cambagei or Acacia argyrodendron on clay plains	Acacia communities	2	EW
8	Open forests, woodlands and shrublands of Acacia shirleyi or Acacia spp. on residual hills	Acacia communities	2	EW
9	Woodlands and open forests dominated by Eucalyptus camaldulensis, Eucalyptus microtheca, Corymbia spp. or Eucalyptus spp. on drainage lines and alluvial plains	Eucalyptus/Corymbia communities	3	EW
10	Open forests dominated by Eucalyptus spp. in the wet tropics region	Eucalyptus/Corymbia communities	3	EW
11	Woodlands and low woodlands dominated by Eucalyptus spp. (box), Eucalyptus platyphylla or Eucalyptus melanophloia on alluvium and associated depositional plains	Eucalyptus/Corymbia communities	3	EW
12	Woodlands and open woodlands dominated by Eucalyptus leptophleba on river frontages and undulating plains	Eucalyptus/Corymbia communities	3	EW
13	Open forests and woodlands dominated by Eucalyptus miniata, Eucalyptus tetrodonta on residual sands and erosional surfaces	Eucalyptus/Corymbia communities	3	EW
14	Low open woodlands dominated by Corymbia terminalis or Eucalyptus leucophylla on depositional surfaces	Eucalyptus/Corymbia communities	3	EW
15	Low woodlands of Eucalyptus pruinosa on erosional surfaces and residual sands	Eucalyptus/Corymbia communities	3	EW
16	Low open woodlands dominated by Eucalyptus brevifolia, Corymbia dichromophloia, Eucalyptus leucophloia or Eucalyptus argillacea on erosional surfaces and residual sands	Eucalyptus/Corymbia communities	3	EW
17	Woodlands and open woodlands dominated by Corymbia setosa, Corymbia leichhardtii, Eucalyptus similis or Corymbia lamprophylla on metasediments and erosional surfaces	Eucalyptus/Corymbia communities	3	EW
18	Low open woodlands and woodlands dominated by Corymbia dichromophloia or Corymbia dampieri with Acacia shrubs on erosional surfaces and residual sands	Eucalyptus/Corymbia communities	3	EW

BVG_1M	BVG_1M_DESCRIPTION	BVG	Broad	VegClass
19	Woodlands and open woodlands of Eucalyptus melanophloia, Eucalyptus whitei or Eucalyptus shirleyi on erosional surfaces, metamorphics and acid volcanics	Eucalyptus/Corymbia communities	3	EW
20	Woodlands and open woodlands dominated by Eucalyptus crebra, Eucalyptus cullenii, Eucalyptus leptophleba or Eucalyptus microneura on basalt clay plains	Eucalyptus/Corymbia communities	3	EW
21	Low open woodlands and low woodlands dominated by Eucalyptus orgadophila, Corymbia terminalis or Corymbia grandifolia on clay plains	Eucalyptus/Corymbia communities	3	EW
22	Woodlands dominated by Corymbia grandifolia, Corymbia flavescens or Corymbia polycarpa	Eucalyptus/Corymbia communities	3	EW
23	Woodlands dominated by Eucalyptus tetrodonta on sandstones	Eucalyptus/Corymbia communities	3	SW
24	Low woodlands dominated by Eucalyptus phoenicia on sandstones	Eucalyptus/Corymbia communities	3	SW
25	Woodlands and open woodlands dominated by Eucalyptus spp. (ironbarks), Eucalyptus microneura, Eucalyptus leptophleba or Eucalyptus persistens on shallow soils on undulating to hilly terrain	Eucalyptus/Corymbia communities	3	EW
26	Open-forests and woodlands dominated by Eucalyptus granitica, Lophostemon suaveolens, Eucalyptus fibrosa subsp. (Glen Geddes) on metamorphic and acid volcanic coastal ranges	Eucalyptus/Corymbia communities	3	EW
27	Low woodlands and woodlands dominated by Corymbia dichromophloia or Corymbia capricornia on deeply weathered sandstone plateaus and remnants	Eucalyptus/Corymbia communities	3	SW
28	Low open woodlands dominated by Eucalyptus brevifolia or Eucalyptus leucophloia on deeply weathered sandstone plateaus and remnants, metamorphics and acid volcanics	Eucalyptus/Corymbia communities	3	EW
29	Woodlands dominated by Eucalyptus tectifica or Eucalyptus populnea on sandstone residuals, metamorphics and acid volcanics	Eucalyptus/Corymbia communities	3	EW
30	Tall open shrublands and low open woodlands dominated by Melaleuca citrolens, Melaleuca acacioides or Melaleuca spp. on alluvium and depositional surfaces	Melaleuca communities	4	EW
31	Low woodlands dominated by Melaleuca viridiflora, Melaleuca nervosa or Melaleuca spp. on depositional plains	Melaleuca communities	4	EW
32	Low woodlands and low open woodlands dominated by Melaleuca tamarascina, Melaleuca uncinata or Melaleuca minutifolia	Melaleuca communities	4	EW
33	Open forests and woodlands of Melaleuca spp. associated with rivers, lagoons and swamps	Melaleuca communities	4	EW
34	Closed tussock grasslands and tussock grasslands dominated by Astrebla spp. or Dichanthium spp. with scattered low trees on clay plains	Grasslands	5	EW
35	Tussock grasslands sometimes with Pandanus spp. and palms on marine and alluvial plains	Grasslands	5	EW
36	Sparse tussock grasslands with low woodlands on stony downs	Grasslands	5	EW

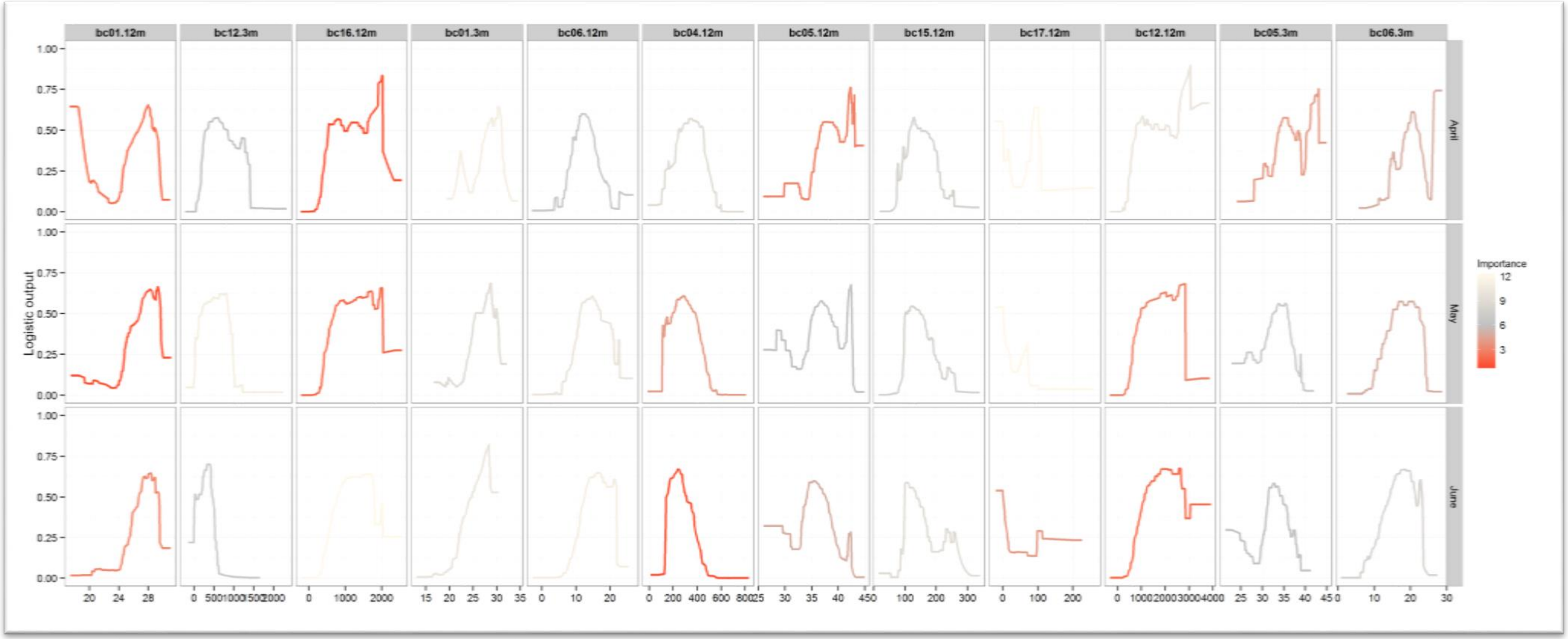
BVG_1M	BVG_1M_DESCRIPTION	BVG	Broad	VegClass
37	Hummock grasslands with scattered trees	Grasslands	5	EW
38	Low open woodlands dominated by Adansonia gregorii	Miscellaneous communities	6	EW
39	Low open woodland dominated by Terminalia spp. on undulating clay plains	Miscellaneous communities	6	EW
40	Low woodlands and low open woodlands dominated by Lysiphyllum cunninghamii	Miscellaneous communities	6	EW
41	Open shrublands and low open woodlands of Grevillea spp. on depositional plains	Miscellaneous communities	6	SH
42	Heathlands and closed shrublands on dunefields, alluvium, plains and volcanic plugs	Miscellaneous communities	6	SH
43	Sedgelands, lakes and lagoons	Miscellaneous communities	7	SH
44	Woodlands, grasslands and herblands on beach ridges and the littoral margin	Miscellaneous communities	7	EW
45	Saline tidal flats and associated grasslands and herblands	Miscellaneous communities	7	SH
46	Closed-forests and low closed-forests dominated by mangroves	Miscellaneous communities	7	EOF
47	Sand blows and rock pavements	Miscellaneous communities	7	SH
48	Miscellaneous vegetation group	Miscellaneous communities	6	SH



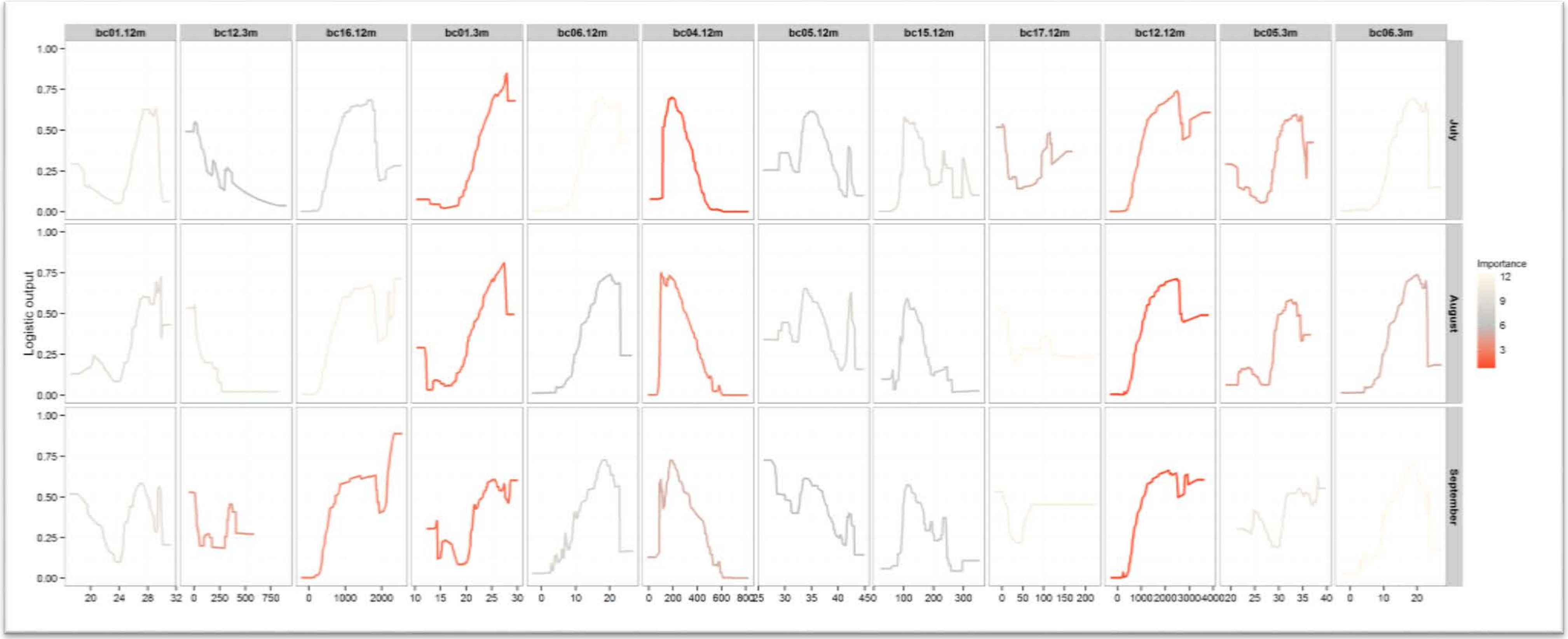
Appendix Figure 2.2 The top ten broad vegetation groups that influenced the model in each month.



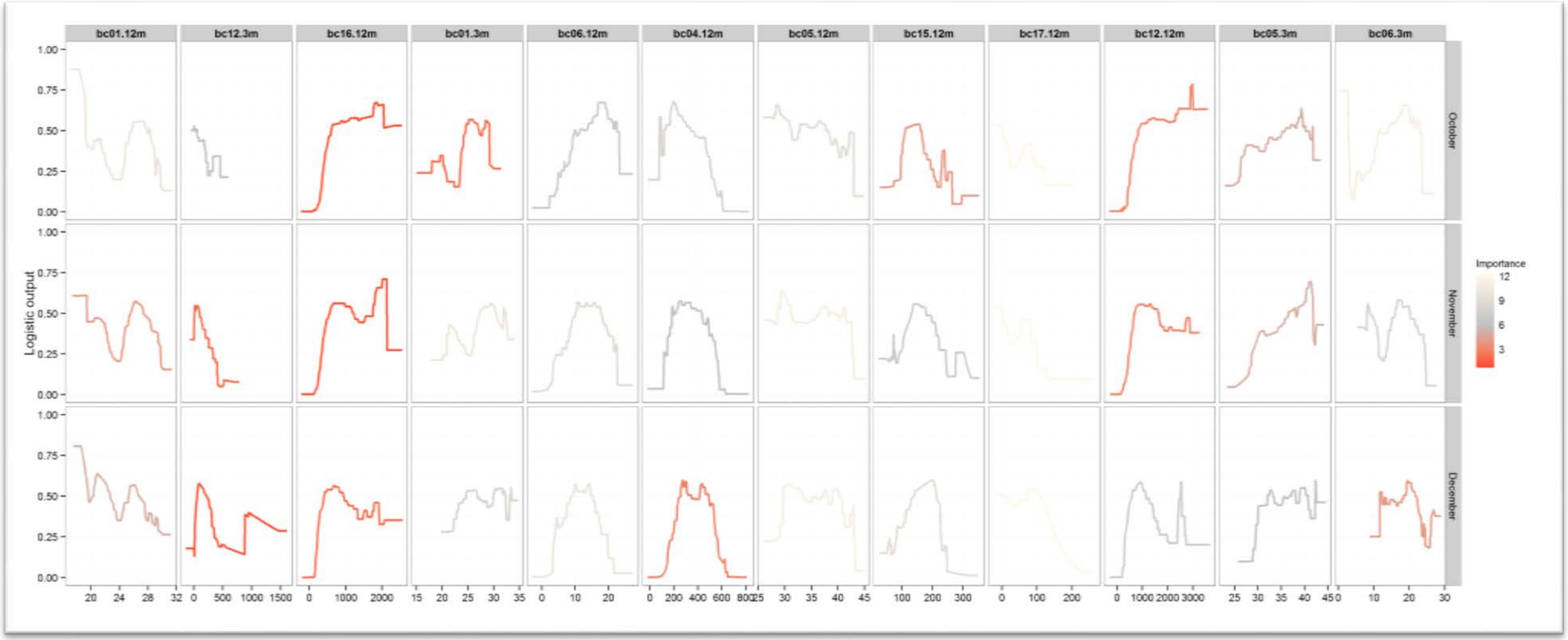
Appendix Figure 2.3. Response variables for monthly fire models (excluding vegetation which is presented in figure S2) across the top presented by month (vertical). Variables coloured in order of model contribution (1 red – highest value to 12 cream - lowest value).



Appendix Figure 2.3. Continued. (April – June).

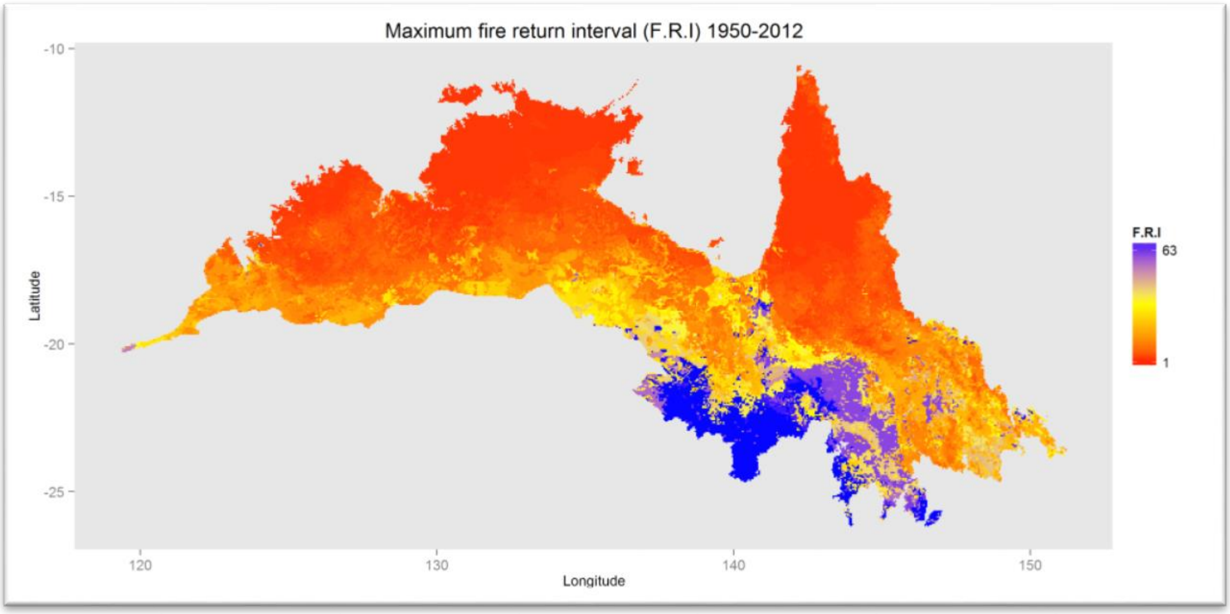


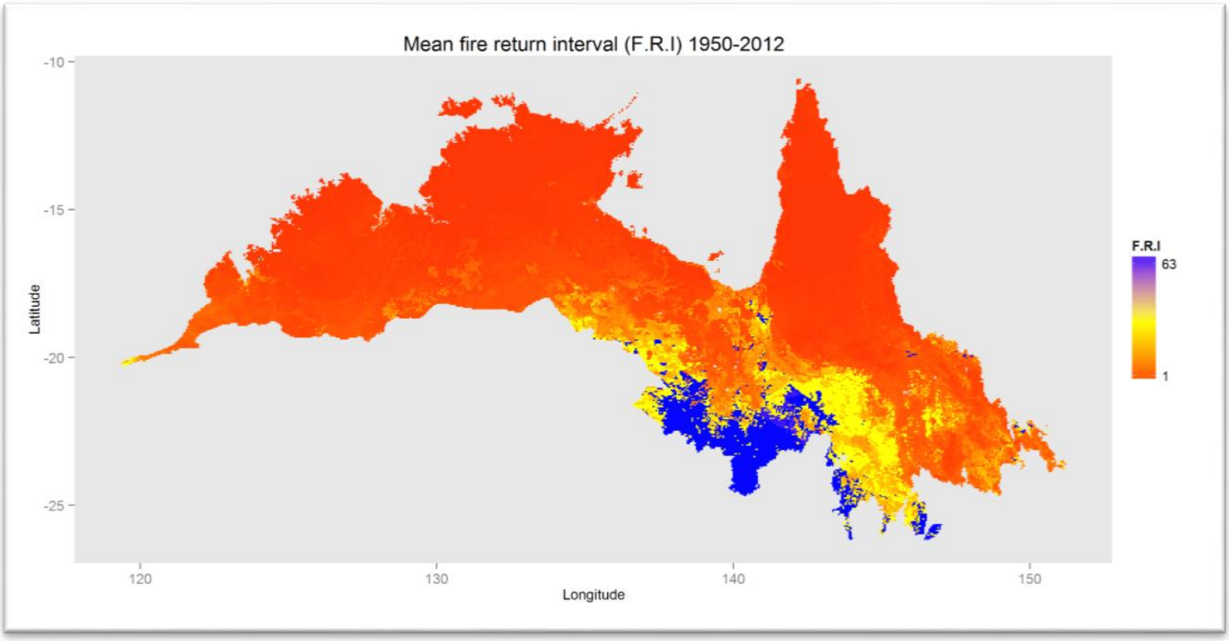
Appendix Figure 2.3. Continued. (July - September).



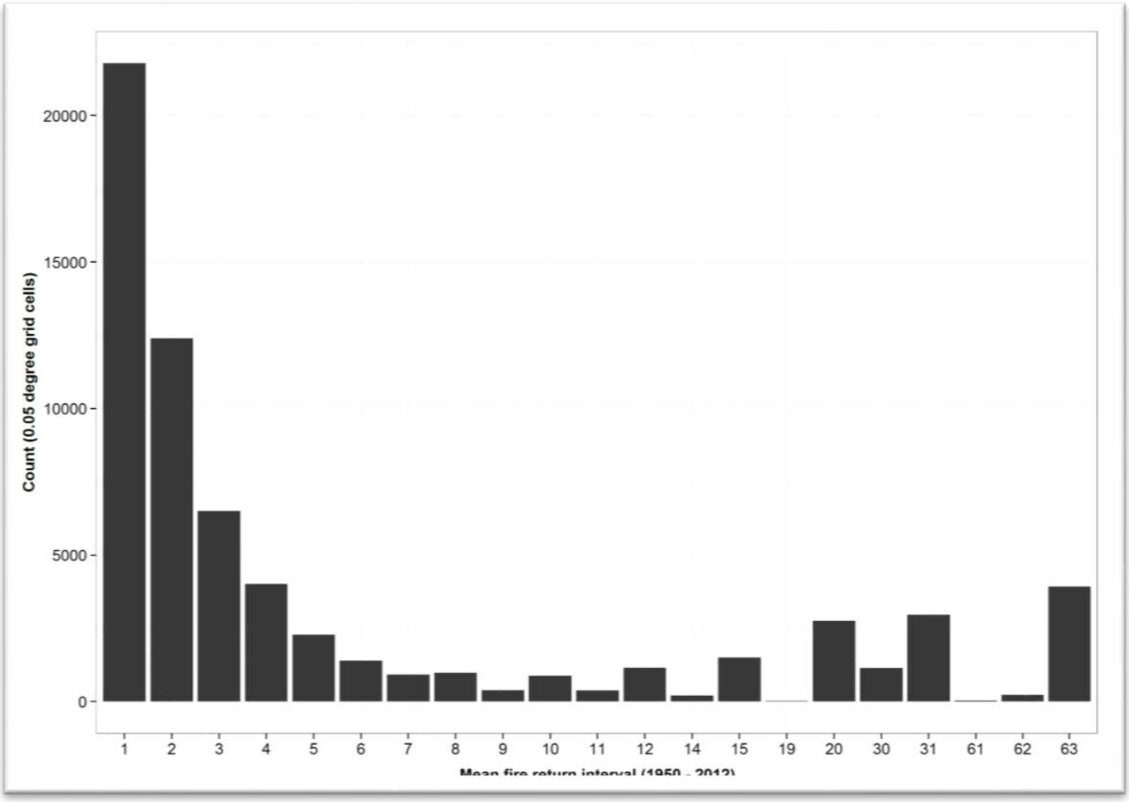
Appendix Figure 2.3. Continued. (October – December).

Appendix Figure 2.4 Real verses modelled relative area predicted (2000 – 2012).





Appendix Figure 2.5. Spatial distribution of fire return intervals. Maximum fire return intervals (top) refer to the longest consecutive time between predicted fire events between 1950 and 2012. Mean fire return intervals is the mean length of time between predicted fire events across the same time period.



Appendix Figure 2.5 Continued. Frequency histogram of mean fire return intervals between 1950 and 2012.

Chapter 3. The divergence of traditional Aboriginal and contemporary fire management practices on Wik traditional lands, Cape York Peninsula, northern Australia.

Introduction

Australian Aboriginal people have been using fire to manage the Australian landscape for millennia (Bowman et al. 2011; Russell-Smith et al. 1997; Vigilante 2001). This traditional burning has been changed, adapted and in some cases oppressed across the continent, particularly in the past century. In the vast monsoonal tropics, fire is a critical natural part of ecosystem function due to the annual cycle of wet and dry seasons which promotes rapid vegetation growth and curing every year (Felderhof and Gillieson 2006). Despite the ubiquitous presence of fire and intact Aboriginal knowledge there is still significant debate about the best way to manage fire in this region, particularly in the context of biodiversity conservation (Andersen et al. 2005; Andersen et al. 2006; Driscoll et al. 2010; Parr and Brockett 1999; Whitehead et al. 2005; Ziembicki et al. 2014). A common thread across fire management paradigms is to develop a system that most closely relates to the predominant system instated by Aboriginal people over thousands of years (Bliege Bird et al. 2008; Horton 1980; Russell-Smith et al. 2013; Russell-Smith et al. 2009; Vigilante and Bowman 2004; Yibarbuk et al. 2001). From a biodiversity perspective, Aboriginal burning presumably most closely replicates the evolutionary processes underlying niche selection by plants and animals that have co-evolved with this particular disturbance regime (Bliege Bird et al. 2008; Hill and Baird 2003).

There has been a general acceptance by land managers in the Australian monsoonal tropics that patchy, early dry season burning is the best proxy for traditional burning practices and this has been the dominant ecological burning regime for several decades (Burrows 1991; Parr and Andersen 2006). More recently, the emergence of a carbon market in Australia has seen the introduction of broad scale prescribed burning with the aim of shifting the predominant fire regime from the late dry season (defined as after August 1) to the early dry season with quantifiable greenhouse gas emission benefits (Russell-Smith et al. 2013). This methodology evolved through collaboration with Aboriginal fire managers in north east Arnhem Land where significant emphasis was placed on participatory approaches to planning and implementation of fire regimes (Russell-Smith et al. 2009).

However, while random patch mosaic burning and increasing early dry season burning frequency has been shown to reduce greenhouse gas emissions the biodiversity benefits are less clear (Parr and Andersen 2006; Perry et al. 2016). Although there have been demonstrated benefits for no burning (Andersen et al. 2005; Woinarski et al. 2004b) the benefits of frequent early burning and patchy burning have not been universally quantified although the theory is intuitively sound (Murphy and

Bowman 2007). There is ample evidence that frequent fire alters aspects of biodiversity such as reducing tree biomass (Murphy et al. 2015) and reducing reptile and small mammal abundance and richness (Andersen et al. 2005).

There is also an assumption that fire management that aims to abate greenhouse gas emissions emulates traditional burning and therefore supports the retention of cultural practices. In reality, the implementation of landscape scale burning that is coherent with the savanna burning determination is usually implemented via the deployment of incendiaries from light plane or helicopter. Burning in this manner reduces the reliance on maintained roads and tracks, which are largely absent in remote northern Australia, but doesn't account for the nuanced traditional burning practices that have shown to positively impact native flora and fauna (Murphy and Bowman 2007; Vigilante and Bowman 2004; Yibarbuk et al. 2001). Understanding the link between the practical implementation of patch burning and its cultural legitimacy is important as cultural co-benefits are increasingly becoming a critical metric for demonstrating triple bottom line outcomes associated with ecosystem service payments and reporting on government funding (Barber 2015). There is also opportunity to leverage substantial financial benefit on open carbon markets if additionality (benefits accrued above the greenhouse gas abatement) can be established (Mason and Plantinga 2013).

Here I explore an example of modern fire management on the West Coast of Cape York Peninsula, comparing the description of traditional burning from authors (HW, SW, DM) with the practical implementation of prescribed burning for carbon abatement and biodiversity. I discuss the issues of practically implementing a traditional burning regime in the complex matrix of decisions and external influences that are associated with modern land management.

The study area

The study area is located in the Archer River Basin (Cape York Peninsula, QLD) which includes the region's largest river (the Archer River). This paper focuses on those traditional lands of the Wik people which lie between the Archer and Kendall Rivers (which include the country of authors BM, HW, and SW) (Figure 3.1). The area is dominated by open savanna woodlands with a heterogeneous matrix of extensive marine plain grasslands, littoral dune forest, riverine gallery forest and open woodlands (Herbarium 2014) (Figure 3.1). The study area has a monsoonal climate with an annual cycle consisting of a long dry season (usually April – December) followed by a short and intense wet season (usually January – March). The average annual rainfall is 1777mm with a high mean annual temperature 26 degrees Celsius (http://www.bom.gov.au/climate/averages/tables/cw_027042.shtml). The combination of high annual temperatures and highly seasonal rainfall makes this area one of the most fire prone ecosystems in the world (Parr and Andersen 2006).

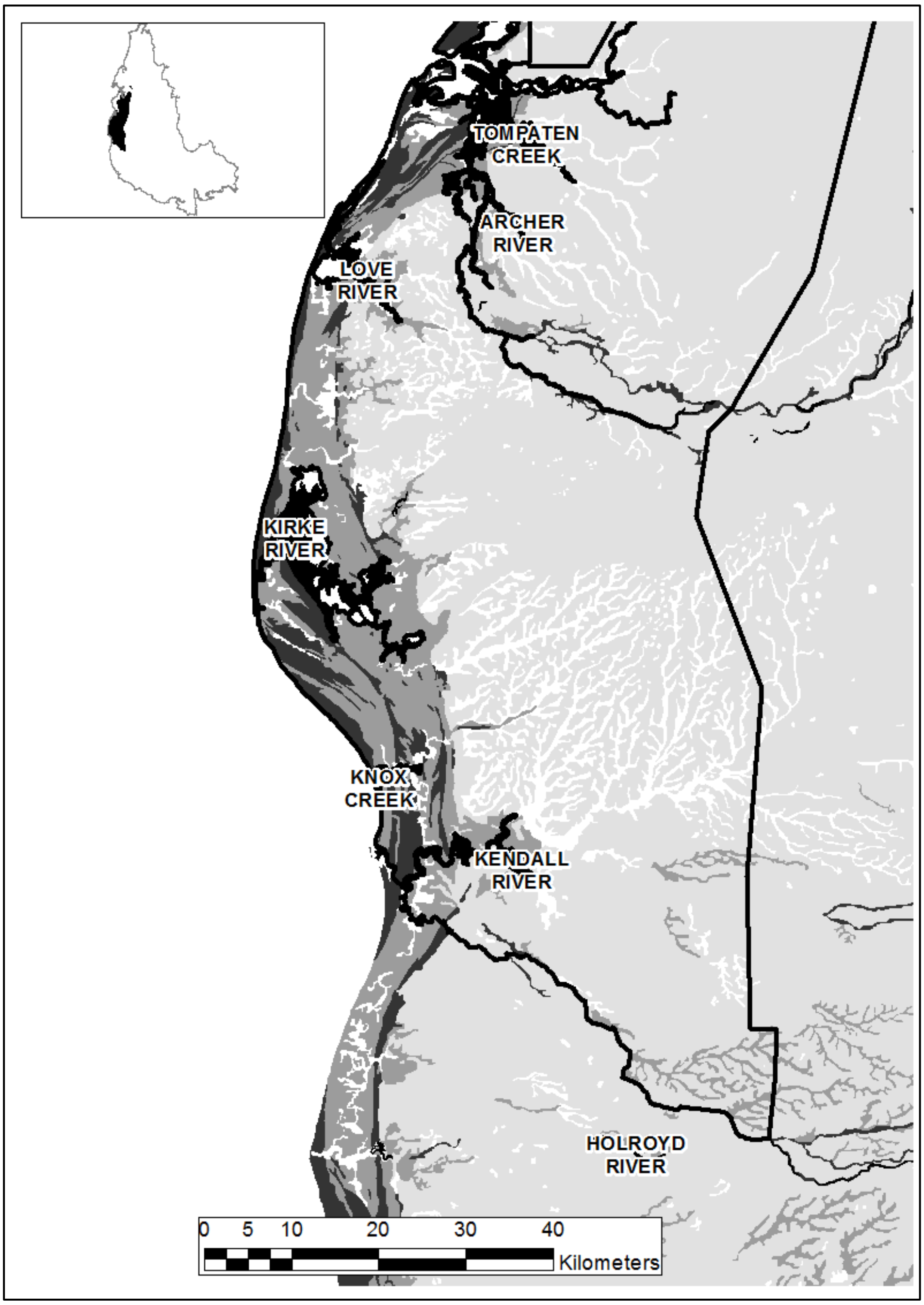


Figure 3.1 The study area and Wik traditional lands located south of the Archer River to the Kendell River and to the Aurukun boundary (dark polygon). The dominant broad vegetation types are displayed (open savanna woodlands - light grey, tropical grasslands - mid-grey and littoral dune scrubs - dark grey).

Wik people and tenures of their lands

The *Mabo* High Court decision in 1992 established the principle that Australian Indigenous peoples could have rights and interests in lands and waters which existed before British sovereignty was asserted by the colonists, and which could be recognised under Australian law. In response, Wik people together with their northern Wik Way kin lodged a native title claim in June 1993 over an extensive area in western Cape York Peninsula, from Weipa south beyond Aurukun almost to Pormpuraaw and inland to near Coen. In a series of determinations by the Federal Court over the intervening years, by October 2012 their native title had been recognised over some 28,000 square kilometres, including the study area (Figure 3.1). In accepting that Wik and Wik Way people had native title, the Court and parties such as the Queensland Government, pastoral station owners in the eastern sectors of the claim, and Rio Tinto with its bauxite mining lease between Aurukun and Weipa, had accepted that evidence of the continuing strength and vitality of Wik and Wik Way cultural connections to their country was of sufficient strength for native title to be recognised. As a result, the formal legal management of Wik and Wik Way people's native title rights and interests is vested in a Prescribed Body Corporate, in this case Ngan Aak Kunch Aboriginal Corporation (NAK), as is required by the Commonwealth *Native Title Act* passed in 1993 in response to the *Mabo* High Court decision. NAK also holds the lands in the Aurukun Shire outside the township itself, including the study area, in a form of inalienable freehold title granted in 2012 under Queensland's *Aboriginal Land Act* (Figure 3.1).

These two complementary forms of recognition of Wik connections to the study area under Australian law intersect with the Wik system itself, under which rights in and responsibilities for country were held primarily at the local level, traditionally by clans whose members traced their connections to country and to sub-regional ceremonial cults through the male line. While each of the clans (whose contemporary manifestations are the recognised Wik families) was traditionally associated with and had responsibilities for a particular estate, clan members did not live solely within their own estates. Resources were exploited seasonally across the multiple environmental niches and zones of this region by bands typically comprised of close kin drawn from several clans. Nonetheless, the movement of other Wik people across clan boundaries, particularly strangers or more distant relations from outside local kin networks, was vigilantly monitored under Wik law and custom (Sutton 1978), and there was a network of named tracks along which those traversing others' country could legitimately do so, designated wells, and specified camping places typically located according to social and geographical distance of the visitors from the land-owning clan.

There were also in the past, and still are in more attenuated form today, a complex of laws and customs concerning the use and sharing of resources among kin and with others. Below, author

(HW) describes (to JP) his understanding of rules around resource use and travel within another clan's lands. HW, whose own country lies at the transition between open savanna woodlands to the east and the coastal plains, dune and estuarine ecosystems to the west, is talking about the movement of an individual from a clan whose country lies in the former zone to hunt in the latter:

(HW)   "See, more food see, he maybe hunt, spear some extra fish they told him to hunt around that area, and how much he gonna get, like maybe five fish or something like that".

(JP) "Yeah, so you come up with a contract. You say you're going to be on my country, you're allowed to take five fish".

(HW) "See you're bringing the traditional owner something, like emu or wallaby to pay them."

(JP) "So I've come off the ridge I've got a wallaby or an emu, come down to the place where you can catch fish and switch it over, here's an emu I'm gonna grab five fish."

(HW) "Yeah that's the way".

HW subsequently told JP that while in contemporary Wik culture there was less of a formal obligation to bring food or other gifts for the traditional owners of country accessed in the course of hunting or fishing visits by other kin, there was still an expectation that permission would be sought from the relevant senior traditional owners.

The process of progressive sedentarisation of Wik people in the Aurukun mission settlement following its establishment early in the 20th century, was to some extent countered by the policies of a strict but (given the historical context of Queensland Aboriginal communities) surprisingly supportive mission regime which facilitated the maintenance of many aspects of Wik people's culture and language, including connections to and use of their traditional lands in the then Aurukun reserve (Martin 1993). A cattle industry in mission times, and its relatively short-lived community-owned successor in the 1980s, along with a Federally-funded outstation support service for a decade from the mid-1970s, helped maintain such knowledge and connections among a set of the families from the study area, and facilitated forms of customary land and resource utilisation and management practices including through burning country. Consequently, while there had been a significant attenuation of traditional knowledge of country and other aspects of culture among younger Wik generations in particular (Martin 1993; Martin and Martin 2016), by the beginning of the 21st century there was still a core of mostly senior individuals who held important elements of traditional Wik environmental and cultural knowledge of the area between the Archer and Kendall Rivers, and had varying degrees of familiarity with their own lands.

With increasing government policy and program focus in recent decades on the township of Aurukun itself and the withdrawal of support for outstations (see contributors in Peterson and Meyers 2016 for discussion of this as a general phenomenon across remote Aboriginal Australia), it has become progressively more difficult for those Wik people whose lands lie south of the Archer River to access their homelands, as the it acts as a significant barrier (Martin and Martin 2016). Currently, the only way to access traditional homelands involves either a helicopter or light plane trip or a 12 hour journey by four wheel drive across the Archer River bridge near Coen and then through three large pastoral stations, or via boat across the Archer River from Aurukun although this relies on a vehicle and equipment being available across the river (Figure 3.2).

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 3.2 The location of the township of Aurukun (black outline -north) demonstrating the challenge Wik people face accessing their traditional estate. The boat route commonly used is displayed (dashed grey line) starting at the Aurukun landing (north) and terminating at the Wik landing (south).

With the lands south of the Archer River largely empty of their traditional owners, contemporary land management is undertaken by the Wik and Kugu Ranger service managed through a Wik-owned company (Aak Puul Ngantam, APN) founded by traditional owner, author (BM). Ranger positions, and the projects they undertake, are largely resourced through Federal and State Government funding and via individual and mostly relatively short-term contracts.

Contemporary fire management on Wik lands

Greenhouse gas abatement through implementation of the savanna burning methodology (Australian.Government 2015) and burning targets set out in national and state funding for land management are the two of the primary reasons for conducting prescribed burning on Wik country, although Wik traditional owners have their own cultural reasons for doing so. The broad but specifically environmental aims of these burning programs are to shift large parts of the landscape from a frequent late dry season to an early dry season dominated regime. This method can earn carbon credits if the savanna burning methodology (Australian.Government 2015) is adhered to but it is also considered to emulate Aboriginal burning regimes and is assumed to have positive biodiversity benefits (Russell-Smith et al. 2013). In the past two years the savanna burning methodology has dominated the fire management strategy due to the significant potential economic benefits associated with it.

Practical implementation of the chosen fire management strategies is rendered all the more difficult by access constraints; for example, direct access to the study area which lies south of the Archer River is restricted by the location of the town of Aurukun on the northern side of its large estuary (Figure 3.2). This severely limits access to the study area, particularly for the majority of Wik traditional owners of these lands who cannot resource their own access to country due to lack of appropriate transport, fuel and equipment. This has caused an imbalance in the way country is accessed and by whom. For example a small team from the Wik and Kugu Rangers discussed above has been tasked with managing the entire estate south of the Archer River for carbon abatement as well as other environmental services. The rangers are resourced to access the region through their employment with APN, but the organisation has neither the capacity nor the resources to support access to country for all traditional owners, since its funding requires that it is necessarily focused on fulfilling external contracts with very specific environmental outcomes. APN does have a long-term goal of developing productive livelihoods for Wik people of the study area, including supporting outstations where possible, but this is dependent upon its establishing commercial enterprises such as a viable cattle business on appropriate areas which eventually can generate funding for these broader social and cultural purposes (Martin and Martin 2016).

Due to access constraints and the requirement of the savanna burning methodology to complete prescribed burning before August 1, fire management in recent times has largely been conducted using aerial incendiaries dropped from a helicopter. The implementation of this strategy has been negotiated directly by APN with the relevant traditional owners through its informed consent processes.

This is not always an unproblematic process from the point of view of APN’s contractual obligations and the environmental values embedded in them. In recent times, there have been some cases where late dry season high intensity wildfires have damaged essential infrastructure (such as outstation buildings, solar arrays, water tanks and water pipes). This has occurred where APN has been unable to conduct prescribed burning for infrastructure protection because the timing for consent from relevant traditional owners has not been in sync with the appropriate timing for these activities or due to closures of some areas by families in accordance with Wik protocols following deaths. Such matters can, unless carefully and respectfully negotiated, compromise environmental values and create tension between traditional owners and Aboriginal rangers. Senior Wik Ranger HW alluded to these factors in a discussion with JP in which he referred to the necessity to consult with and gain the consent of the relevant traditional owners before burning. He was of the view that generally people do not object to the APN rangers managing their country for them, but felt that conflicts can arise when a traditional owner passes away, because then rangers and others are not allowed to access the areas associated with the deceased person until they are ritually opened up by those with the cultural authority to do so. This can delay access for 2–3 months depending on the status of the deceased person and the wishes of the family. Additionally, opening of country can be compromised by the logistics and expense of getting traditional owners out to perform the necessary ritual.

Traditional Wik burning practices

It is a mistake to consider that the contemporary fire management practices outlined above, including the gaining of consent from relevant Wik people for burning country and having the Wik and Kugu Rangers involved, means that such practices can be understood as ‘traditional’ in any unexamined sense. The fact is that Wik burning practices and the responsibilities of individual clans for their own lands have unintentionally been compromised. In most cases the imperatives of external values (typically environmental) and usually negotiated via formal contracts with the State and Federal Governments, or in the case of carbon credits a fixed methodology and associated contract with a private carbon broker, are the primary drivers of fire management, not traditional Aboriginal burning practices. Retaining these traditional practices (and the values that underlie them) is especially difficult under externally contracted land management but requires significant consideration when imposing landscape scale or regional approaches. This is not just the case for Wik lands but is relevant to Cape York Peninsula more generally, since over 60% of Cape York Peninsula is held under Aboriginal freehold (Figure 3.3) and where traditional knowledge and practices remain important.

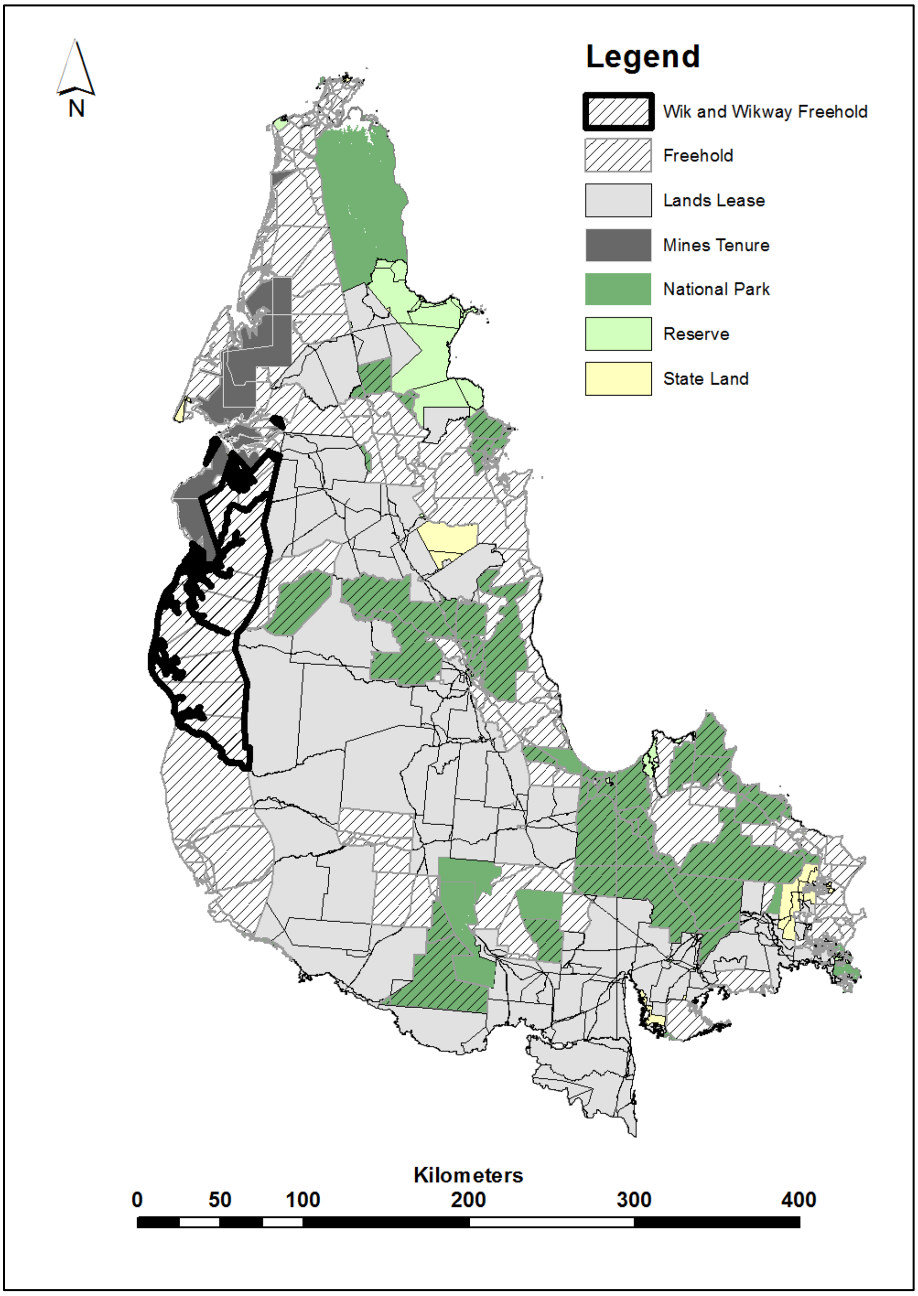


Figure 3.3 Cape York Peninsula bioregion, highlighting Indigenous freehold land (cross hatch) and the total freehold land owned by Wik and Wik Way people (hatch with bold outline).

In contrast to the regional and landscape scale approach to fire management described above, traditionally Wik fire management was undertaken at the local level, in accordance with fine-grained local knowledge of both cultural geography and environmental factors, and was seen as largely the prerogative of those whose country it was (Green and Martin 2016). At this local scale, fire management was undertaken selectively and non-randomly to protect and promote resources (Hill and Baird 2003). Here authors (HW) and (SW) describe a non-random approach to fire management for the protection of resources in coastal dune scrubs to (JP). (HW) is discussing an important yam (*may wathiy*, *Dioscorea transversa*) after finding dried vines during field work:

(JP)

And can you tell us how this may wathiy and other yams relate to fire?

(HW)

"When it starts, when it's ready for harvesting eh, they burn around the areas, around the ridges (HW describing coastal sand dune forest)*, so the fire won't come into the ridge you know and burn the vines and all that. So people can ah, the ladies can come and start digging the yams so they know where the vine goes into the ground, but sometimes when the vine burns they can still see the vines on the trees and they can still dig along way around. But if the vines burn all the way up to the limbs they can't find it".*

(JP)

"So if you were going to try and protect that yam would you burn just around this tree here?"

(HW)

"No no no, burn the whole ridge around, then when the fire starts to come in they put out the fire with leaves. Fighting the fire, whole ridge protected because protect the bush tucker".

(JP)

"Would these ridges ever burn?"

(HW)

"No, maybe today, because a long time when the old people were still alive, … protecting their areas for yams, lighting the fires and fighting the fires around the ridge see. So this can stay the way its stays and vines can show where yams are down to the ground. They keep some yams, They store it in a place, they dig the ground and put their long yams in one ground and cover it up with sand and put the other round yam in another, then they store it that way so people can't find it, stranger people"

"Today the younger people are staying in Aurukun which means the fire can go through the scrub."

(note: 'stranger people' refers to people from other clans visiting without permission).

Above, the authors (HW, SW) described two traditional practices that would have determined the location and timing of fire in these landscapes. Firstly the protection of plants that provide food at particular times of the year and secondly the traditional law that governed travel across clan boundaries and resource utilisation. HW, SW also describe the gender roles in resources management, where men are protecting resources (yams and other bush tucker) and women are harvesting. This is yet another example of active resource management that occurs across seasons which has largely been disrupted due to the centralisation of people into Aurukun. However, it is clear that this management regime (annual burning around resources) would have culminated in a non-random fire regime distributed around the key resources that people were using which reflects fire management practices from other areas in northern Australia (Hill and Baird 2003; Russell-Smith et al. 1997).

Importantly, HW and SW refer to traditional burning in the past tense and make specific reference,

"…… *a long time when the old people were still alive, still doing, protecting their areas for yams*",

"When old people passed away traditional burning stopped",

"Today young people don't know bush foods, they are in Aurukun".

This suggests that traditional burning has been relegated to an historical rather than continuing practice. Although traditional knowledge has been retained, at least by contemporary senior generations, access constraints and external influences have largely removed traditional burning from the landscape in recent history. Acknowledging this as a deficiency in contemporary fire management that aims to approximate traditional burning is an important step to appropriately resourcing the re-implementation of traditional burning alongside fire management for infrastructure management, constraining fire within tenure boundaries and burning for carbon abatement.

Challenges in using traditional burning practices for ecological management

The integration of traditional burning with contemporary land management poses an important philosophical challenge. Traditional burning was done for specific reasons by Aboriginal people who were ranging across their own and others' traditional lands without the need for transport, housing, potable water and electricity, and in the absence of bureaucratic and legal requirements to settle in one location such as school attendance for children. As has been discussed, the contemporary landscape in the study region is largely empty of permanent residents, and furthermore there is a generational gap in the practical implementation of traditional burning (though aspects of the underlying cultural and practical knowledge has been retained by senior people). There are significant financial benefits which can accrue to Aboriginal land owners from burning for carbon abatement and for the protection of biodiversity, and it is more efficient to conduct such activities on a regional or sub-regional scale from a financial and human resourcing perspective. However, undertaking this at a regional scale risks the unintended consequence of eroding the rights and responsibilities of traditional owners for managing their own lands. The issues raised here are symptomatic of a generational shift where Aboriginal decision makers are now required to negotiate the contemporary pressures and responsibilities of contracted land management, but with no leeway within policy and program limitations to seek resourcing of their desire to retain cultural practices and transfer these skills and knowledge to succeeding generations.

Compounding the already complex matrix of decisions for fire management is the emerging imperative and desire for economic independence via enterprise development. In the case of Wik people from the Archer–Kendall River region, this is a key goal of APN who see enterprise development as both a central necessity to create productive livelihoods for upcoming generations, and as an independent source of funding to enable Wik people to re-establish and reproduce meaningful connections to country (Green and Martin 2016; Martin and Martin 2016).

Enterprise development entails additional complexity for environmental and fire management goals, including the protection of infrastructure, the promotion of nutritious grasses for cattle, and protecting key biodiversity assets. The emergence of ecosystem service payments, carbon credits and economic incentives for meeting international and national targets for biodiversity conservation (e.g. Australia's obligations as a signatory to the Convention on Biological Diversity Aichi biodiversity targets) could have perverse impacts on retaining Aboriginal burning practices unless they are given equal value or if the co-benefits are contextualised within an environmental and carbon economy.

Conclusion

The local scale example reported here provides an example of the scale at which fire management was applied traditionally. The successful implementation of a fire management system that more formerly acknowledges the regional complexity of traditional burning could lead to substantial biodiversity conservation and cultural co-benefits. Realistically, a combination of more recent fire management strategies such as broad scale aerial incendiary burning combined with local scale traditional fire management will be required to meet the multiple objectives of contemporary natural resource management. When considering the support of traditional burning, it is important to acknowledge that there are significant differences between traditional Aboriginal burning practices across Australia that are embedded within regionally specific rules and responsibilities.

Author contributions

Justin Perry and M. Sinclair developed the concepts for the paper. H. Wikmunea and S. Wolmby provided the contemporary traditional knowledge and the historical perspective. Dave Martin and

Bruce Martin provided historical perspective, the overview of Wik culture and insights into the implications of contemporary fire and land management practices.

Chapter 4. Shifting fire regimes from late to early dry season fires to abate greenhouse emissions does not completely equate with terrestrial vertebrate biodiversity co-benefits on Cape York Peninsula, Australia.

Introduction

There has been a recent increase in global carbon emission reduction schemes based on changes to land management that are considered to have ancillary "win-win" biodiversity benefits (Phelps et al. 2012). Under the Australian Government's Carbon Farming Initiative (CFI) land managers can earn carbon credits by abating or sequestering carbon through altering natural resource management practices. Carbon credits may be earned from activities such as reducing introduced ruminant density, sequestering carbon via tree planting, reduced deforestation and, more recently, the management of fire to abate the greenhouse gases- methane and nitrous oxide measured in CO_2 equivalence (CO_2e) (Russell-Smith et al. 2009; Russell-Smith et al. 2013). The uptake of such carbon farming initiatives in Australia has rapidly increased in the past decade (Murphy et al. 2015). Fire in the vast Australian tropical savanna is the largest contributor to greenhouse gas emissions in northern Australia. An accepted methodology for reducing these emissions in the savanna region under the *Carbon Credits (Carbon Farming Initiative) Act 2011* is described in the Australian Government determination titled "Carbon Credits (Carbon Farming Initiative – 'Emissions Abatement through Savanna Fire Management') Methodology Determination 2015", henceforth fire management for emission abatement method.

The fire management for emission abatement method aims to reduce emissions through prescribed burning that can demonstrate a reduction in large and intense late dry season wildfires (fires occurring after August 1st , the midpoint of the May to November dry season in the monsoon tropics), to an early dry season fire regime (burning before August 1st). The fire management for emission abatement methodology has evolved within two major paradigms; firstly, in one of the most fire prone places on earth (Parr and Andersen 2006) fire suppression has proven to be impossible and has often led to extreme late dry season fires and secondly fire was traditionally applied more frequently in the early dry season and this offers the most practical approach to managing largely uncontrollable wildfires during the latter part of the dry season (Russell-Smith et al. 2003). Supressing wildfire across vast remote areas with low human populations represents an impossibly expensive task and attempts to apply this management regime have been unsuccessful and led to a dominance of late dry season fire (Russell-Smith et al. 2013). Early dry season fires are considered more benign for wildlife because they are less intense due to the presence of higher moisture in the vegetation and soils and they occur over smaller areas and tend not to burn the canopies of trees (Russell-Smith et al. 2013).

Early dry season fires are also considered to approximate traditional Aboriginal burning (Russell-Smith et al. 2013). Indigenous Australian fire management represents a millennial disturbance regime which is thought to have influenced the patterning of flora and fauna (Flannery 2002). In northern Australia, European disruption of traditional indigenous fire management is very recent so indigenous peoples knowledge of fire management has largely been retained (Russell-Smith et al. 2009). There has been a recent resurgence in traditional burning that had been disrupted (McConchie 2013) while continuous application with limited European influence has continued uninterrupted in some remote parts of northern Australia (Yibarbuk et al. 2001). Re-instating or maintaining traditional burning should theoretically provide greater ancillary benefit for native biodiversity that has co-evolved with this regime (Yibarbuk et al. 2001). The fire management for emission abatement methodology evolved in collaboration with traditional indigenous burning (Russell-Smith et al. 2013) but, as it has expanded beyond the initial project area (in the Northern Territory of Northern Australia), the degree to which it represents traditional burning across the diverse indigenous cultures of northern Australia requires critical assessment which is beyond the scope of this paper. The relationship between traditional burning, the carbon methodology and the consequent impact on terrestrial fauna has not been adequately assessed in the peer reviewed literature.

The legislative requirement for securing carbon credits is to account for CO_2e emission savings by using freely available (NAFI 2014) Moderate Resolution Imaging Spectro-radiometer (MODIS) satellite derived fire scars over a ten year period - broadly calculated by measuring changes in the relative frequency of early compared to late dry season fires and the associated emissions of each regime (Russell-Smith et al. 2013). This methodology only accounts for greenhouse gas abatement not carbon sequestration through fire exclusion which would be more likely to lead to significant vegetation structural changes.

In this paper I explore the relationship between patterns of fire and vertebrate fauna at the spatio-temporal scale at which CO_2e is accounted for using the fire management for emission abatement method. To claim a biodiversity co-benefit in relation to vertebrate fauna using this method, a positive response needs to be demonstrated when comparing the richness and abundance of fauna in early verses late dry season fire frequency. There is ample evidence of the negative relationships between high fire frequency, extent and intensity and terrestrial fauna richness and abundance in tropical ecosystems in Australia (Andersen et al. 2005; Murphy et al. 2010; Woinarski et al. 2010; Woinarski et al. 2004b; Ziembicki et al. 2014). This suggests that a change in fire frequency from late to early season fires, might accrue co-benefits for biodiversity (Murray et al. 2007). However, an explicit link between the fire management for emission abatement method and vertebrate fauna response has not been made. Biodiversity response to disturbance is difficult and expensive to measure in short time frames and across landscapes, regions and bioregional areas (McDonald et al. 2015). Because of the cost and challenges of monitoring biodiversity in vast, difficult to access, remote areas, the use of landscape surrogates such as fire frequency, are conceptually attractive for government and land management agencies, to account for investment, condition trends, and biodiversity benefits (Rocchini et al. 2010).

Although there are axiomatic relationships between fire and biodiversity that should be consistent across particular ecosystems, they are rarely only influenced by fire and the response from fauna is often non-linear and highly variable (Kutt and Woinarski 2007). In northern Australia fire frequency has been shown to be a key determinant of native fauna patterns (Andersen et al. 2005) and the most dramatic response from vertebrate fauna has been associated with long periods of fire exclusion (Andersen et al. 2005; Woinarski et al. 2004b) .

If there is a positive relationship between fire regimes that are dominated by frequent early dry season fires and metrics of vertebrate fauna (richness, abundance and composition) then the fire frequency assessment used to derive carbon credits could claim a biodiversity co-benefit. However, if the biodiversity relationships are more nuanced, and operate at different temporal and spatial scales for different taxa, a more explicit biodiversity accounting system will be required to tease apart the differences that can be ascribed to the fire management action and those that are driven by stochastic variables (climate variability), natural heterogeneity in the landscape (Ferrier and Drielsma 2010) and other disturbances.

Here I investigate the relative influence of early dry season and late dry season fires and other landscape scale factors on vertebrate fauna using three years of systematically collected terrestrial fauna survey data (2009-2013) from 185 woodland sites on Cape York Peninsula. I undertake the comparisons at the same spatial resolution as the fire management for emission abatement methodology (Russell-Smith et al. 2013) and use these data to explore two key questions: (i) Is there a direct relationship between frequency of early dry season fires (EDS) and richness and abundance of terrestrial vertebrate fauna that is significantly different to late dry season fires(LDS)?, and; (ii) if not, what other landscape variables might predict fauna richness and abundance at this scale?

Methods

Study region

The Cape York Peninsula bioregion (CYP) represents the northernmost section of the state of Queensland, Australia, and spans an area of ~13 million ha (Figure 4.1). Mean annual rainfall in this region varies from >2000 mm at Lockhart River (12º 28’ S; 143º 12’ E) on the central east coast down to approximately 1000 mm at Palmerville (16º 00’S; 144º 02’ E) falling within the rainfall range of the mesic fire management for emission abatement methodology (>1000 mm mean annual rainfall in woodlands). Rainfall is primarily orographic and monsoonal on the eastern peninsula and monsoonal in the west (Perry et al. 2011b).

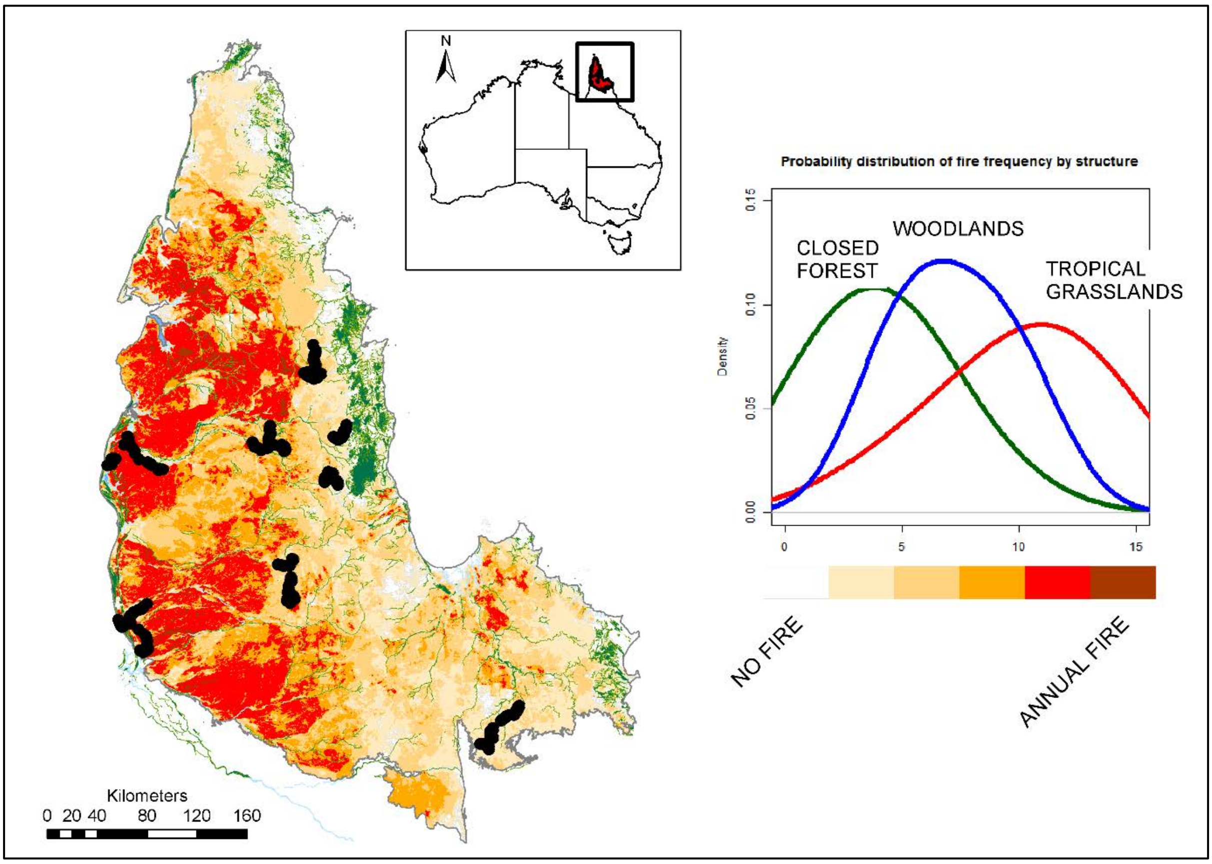


Figure 4.1 The Cape York Peninsula bioregion (study area) overlaid with MODIS-derived fire frequency 2000 – 2013 (beige - no fire to dark red - annual fire) and extent of closed forest (green). Survey sites (n= 202) depicted with black dots. Frequency distribution curves of fire frequency by vegetation structural group within sites are depicted on the right, with green (closed forest), blue (woodland) and red (grassland) lines.

Fire frequency in different broad vegetation types

Fire frequency distribution in three major vegetation structural categories- where vertebrate fauna sampling occurred- (open woodland, tropical grassland and closed forest) was derived using a kernel density estimation with a smoothing parameter (h = 1.9) applied in R (R Development Core Team 2014)

Survey methods

Vertebrate fauna surveys were conducted from 2009-2013 during the dry season (June to November). A total of 202 sites were established in seven property clusters (Figure 4.1). Sites within each property were surveyed once over a 4 night, 5 day interval.

Fauna sampling at each site was conducted within a one-ha quadrat (Kutt et al. 2012c). Nested in each one-ha quadrat was a 50 x 50 m trap array of twenty Elliott box traps (Elliott Scientific Equipment, Upwey), two larger metal cage traps, four pitfalls (60 cm deep and 25 cm diameter) with 30 m and 20 m of drift fence, and six funnel traps on the drift fence. Trapping was supplemented with three diurnal and two 20 minute nocturnal timed searches conducted within the one-ha quadrat. Each of the one-ha quadrat sites were surveyed eight times for birds over the course of five days. Each survey consisted of one experienced observer undertaking a ten-minute count of all birds heard and seen within the plot and at different times of the day. Birds detected outside of the plot were excluded, as were birds flying overhead. Repeated census is considered the most appropriate for tropical savanna woodlands, where bird activity is spatially and temporally dispersed (Perry et al. 2012). I did not correct for detectability because the statistical biases introduced by those corrections are at least as large as those resulting from not accounting for detectability (Royle and Link 2006).

Abundance of each taxa was the total abundance summed over all survey activities at the one-ha sites, and was an index of relative abundance rather than a measure of density (Kutt et al. 2012b). A number of studies have demonstrated that measures of relative abundance provide patterns of population trends proportional to those derived from estimates of absolute abundance (Hopkins and Kennedy 2004; Slade and Blair 2000).

Predictor variables

I investigated six remotely sensed fire, landscape and climate variables as predictors of fauna abundance and species richness. Fire variables were selected in the context of the fire management for emission abatement methodology and the climate and vegetation variables were selected as recognised determinants of faunal patterns in northern Australia. The fire variables were derived from MODIS fire scars and included mean fire size (ha) (mean ha over a 12 year period – connected pixels intersected with site location) and fire frequency in the early dry and late dry season (number of fire scars prior to or after August 1st over a 12 year period). Vegetation heterogeneity was measured as the number of different regional ecosystems in a one kilometre radius (Veg Types 1 km) around the survey site giving an indication of habitat diversity (Queensland Herbarium 2014). Mean annual rainfall (30 year mean, 1990 centred) was derived using daily precipitation grids (0.05 degree grid scale) from the Australian Water Availability Project (Grant et al. 2008; Jones et al. 2007). Foliage projection cover (FPC) was calculated as mean FPC in a one kilometre radius (DSITIA 2015). FPC is derived using Landsat imagery (~30 m resolution) and quantifies the percentage of ground area occupied by the vertical projection of foliage. This provides a continuous variable that more accurately represents subtle variance in structure within the categorical broad vegetation groups (Queensland Herbarium 2014). For example within the vegetation type I are focusing on in this study, open woodlands, there is a natural heterogeneity influenced by landscape features, such as geology, soil and topographic position (Price et al. 2005), where some areas more closely resemble closed forest and others are more like grasslands. Mean values in a 1km moving window were derived using ArcMap 10.2.2 (ESRI 2014) to account for spatial heterogeneity in foliage projection and habitat diversity at a resolution that is meaningful to the species I were examining.

Analysis

Each survey site was stratified by fire frequency and broad vegetation groups – closed forest, woodland and grassland. I mapped the distribution of fire frequency (Figure 4.1) in order to characterise the relative fire proneness of each broad vegetation type. I also examined the variation in mean reptile, mammal and bird richness and abundance recorded in each site across three vegetation types (Figure 4.2) in order to examine how this corresponded to the fire frequency. In the regression analyses I only consider the woodland vegetation sites (n = 185), as these are the dominant vegetation type sampled and is the only vegetation type considered in the fire management for emission abatement methodology (Russell-Smith et al. 2013).

The bird, mammal and reptile community composition, defined as the relative abundance of each species per site, was compared between seven factors; survey location (property, n=7), mean fire size per hectare (n=3), fire frequency in the early dry (n=3), late dry season (n=3), vegetation types within 1 km (n=3), mean annual rainfall (n=3) and foliage projection cover within 1 km (n=3). Then each factor alone, along with the interaction with property was examined using a two-way crossed design using PERMANOVA in the PRIMER 6 / PERMANOVA+ program (Anderson et al. 2008). PERMANOVA is a distance-based, non-parametric, multivariate analysis of variance that calculates a pseudo *F*-statistic and associated *P*-value by means of permutations, rather than relying on normaltheory tables (Anderson 2001). I used the Bray-Curtis dissimilarity measure and 9999 permutations on square-root transformed data for birds, mammals and reptiles.

I examined the relationship between my six environmental factors and fauna richness and abundance via generalised linear mixed (multi-level) models using the lme4 package (Bates et al. 2010) in conjunction with lme4test package (Kuznetsova et al. 2014). All analyses were undertaken using the R program (R Development Core Team 2014). Mixed models combine both fixed and random terms and estimate the variance within a group against the variance of the whole dataset. In this case I used property (n=7) location as the random effect given the site survey locations were spatially clustered (Figure 4.1). I fitted non-linear models (Poisson model with a logarithmic link function), and estimated the size and direction of each fixed effect. In this analysis I scaled the environmental variables between zero and one so the estimates were directly comparable and tested the significance of each independent variable, rather than multi-variable models. I acknowledge that there will be interactions between variables but I chose to explore univariate responses as the remotely sensed and site measured variables were correlated and this would confound the interpretation of multivariate outputs. I fitted generalised linear models (GLM – Poisson) on the most predictive landscape variable (ie. FPC) and provide comparative regressions of early and late dry season fire frequency for each taxa using the ggplots2 (Whickam 2009) package also using the R program (R Development Core Team 2014).

Results

Fire frequency at the landscape scale is distributed unequally across the closed forest, woodland and grassland vegetation types I sampled (Figure 4.1). Closed forests are the least fire prone, woodlands have a wide distribution centred on moderate fire frequency and fire frequency distributions within tropical grasslands are broadly distributed but the mean is skewed toward high fire frequency (Figure 4.1). Between these broad vegetation types, the bird, mammal and reptile abundance and species richness was also variable (Figure 4.2). Mean mammal abundance and richness was low in the woodlands and higher in grasslands and closed forest (the two fire frequency extremes); mean bird abundance and richness was high in the least fire prone environment (closed forest) and declined in a linear fashion to the most fire prone (grasslands); and mean reptile abundance and richness is high in closed forest and woodlands, and declined dramatically in grasslands (Figure 4.2) with reptile richness highest in tropical woodlands.

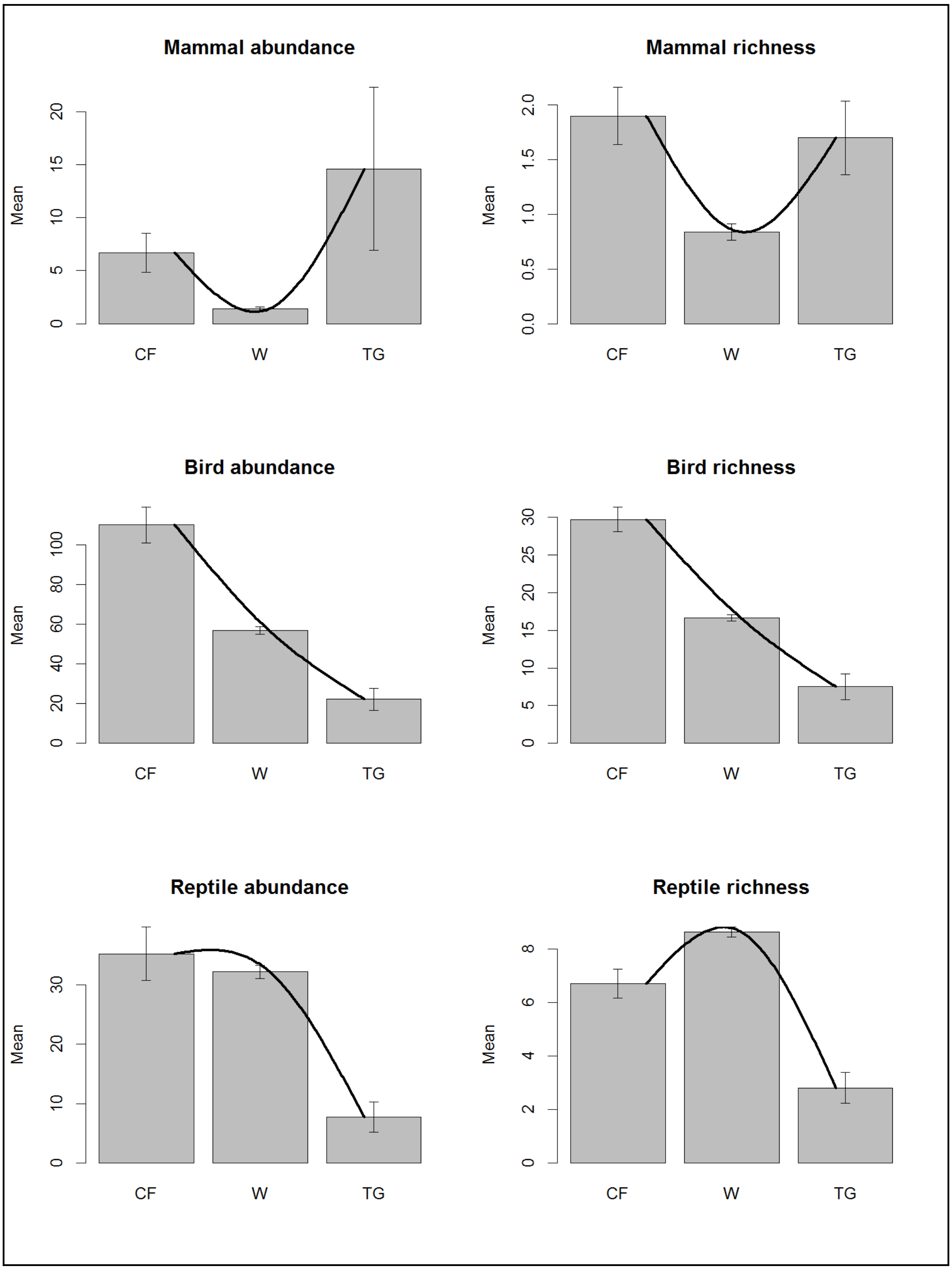


Figure 4.2 The mean (and standard error) of mammal, bird and reptile species richness and abundance across the three habitat types. W = Eucalyptus and other (*Melaleuca* and *Lophostemon* dominated) woodlands, CF = closed forest/dune scrub and TG = tussock grasslands.

The PERMANOVA results confirmed a strong property effect on the composition of birds, mammals and reptiles. There was a significant effect for early dry season fire frequency and late dry season fire frequency and bird composition as well as foliage projective cover and reptile composition (Table 4.1). However, there were a number of significant interactions between property and factors such as fire frequency (mammals, reptiles), fire size (mammals, reptiles), foliage projective cover (mammals, reptiles) and rainfall (reptiles) (Table 4.1). This suggests that composition is influenced by variation in fire, vegetation and rainfall factors, but at a property or location scale (ie. clusters of properties) rather than across the landscape.

The regression models of the six main fire and environmental factors for the woodland vegetation types indicated that all were predictive of bird abundance; all except for mean rainfall were predictive of mammal abundance; and all except FPC were predictive of reptile abundance. Using the estimate as a broad indicator of the strength of the effect (given the variables were normalised) FPC, Mean rainfall and Veg Types were the larger (positive) effect for birds, for mammals FPC (positive) and Mean fire size (ha) and Early Dry Season FF (negative) were larger, and for reptiles, Mean fire size (ha) and Early Dry Season FF (negative) and Mean rainfall (positive) were the largest (Table 4.2). For species richness there were fewer significant relationships. For birds there were only three, and FPC and Veg Types had the larger effect, for mammals there were also three, but FPC clearly was the strongest effect and for reptiles, only FPC was significant (Table 4.2).

Table 4.1. The results of the two-way PERMANOVA, based on Bray-Curtis dissimilarities of bird, reptile and mammal assemblages across the survey sites. Seven factors and the interaction with property location were tested. Ns is not significant, * = P <0.05, ** = P < 0.01, *** = P = 0.001. ns = not significant.

Factors	**Birds**				**Mammals**			**Reptiles**		
	d.f.	**M.S.**	**Pseudo-*F***	***P***	**M.S.**	**Pseudo-*F***	***P***	**M.S.**	**Pseudo-*F***	***P***
Property	7	36.3	1.31	*	4630	3.17	***	12956	6.65	***
Early Dry Season FF	2	5368	2.03	*	2094	0.84	ns	4824	1.82	ns
Early Dry Season FF x Property	8	2629	0.98	ns	2951	2.05	***	2982	1.58	**
Late Dry Season FF	2	6366	2.62	**	1540	1.09	ns	3706	1.73	ns
Late Dry Season FF x Property	8	2372	0.88	ns	1382	0.92	ns	2178	1.12	ns
Mean fire size	2	2656	0.86	ns	1373	0.70	ns	2716	0.92	ns
Mean fire size x Property	8	3160	1.18	ns	2063	1.41	*	3210	1.69	**
FPC	2	2350	0.77	ns	2950	0.92	ns	6730	2.02	*
FPC x Property		3082	1.15	ns	3491	2.62	**	3575	2.01	***
Vegetation Types 1km	2	2627	1.12	ns	2443	1.42	ns	2580	1.25	ns
Vegetation Types 1km x Property	8	2290	0.83	ns	1737	1.18	ns	2067	1.06	ns
Mean rainfall	2	2496	0.749	ns	4896	2.41	ns	8001	0.96	ns
Mean rainfall x Property	8	3348	1.24	ns	1926	1.33	ns	7851	4.30	***

Table 4.2. The results of the generalised linear mixed modelling for bird, mammal and reptile abundance and species richness. The estimate is the direction of the effect, the Wald statistic is an equivalent to the F statistic and *P* is the significance level. Ns is not significant, * = P <0.05, ** = P < 0.01, *** = P < 0.001.

	Birds				**Mammals**				**Reptiles**			
Factors	**Est**	**SE**	**Wald**	**p**	**Est**	**SE**	**Wald**	**p**	**Est**	**SE**	**Wald**	**p**
Abundance												
Early Dry Season FF	-0.378	0.052	-7.197	***	-1.760	0.315	-5.586	***	-0.170	0.075	-2.254	*
Late Dry Season FF	-0.259	0.063	-4.099	***	-0.608	0.299	-2.032	*	-0.497	0.088	-5.657	***
Mean fire size (ha)	-0.644	0.085	-7.584	***	-1.836	0.429	-4.278	***	-0.403	0.117	-3.441	**
FPC	0.831	0.079	10.585	***	2.697	0.359	7.503	***	0.005	0.111	0.043	ns
Veg Types 1 km	0.732	0.050	14.628	***	1.488	0.253	5.878	***	0.301	0.069	4.348	***
Mean rainfall	0.823	0.214	3.850	***	0.559	0.593	0.943	ns	0.377	0.178	2.119	*
Richness												
Early Dry Season FF	-0.141	0.094	-1.493	ns	-1.004	0.374	-2.682	*	0.136	0.127	1.069	ns
Late Dry Season FF	-0.059	0.110	-0.542	ns	-0.523	0.440	-1.188	ns	0.048	0.153	0.313	ns
Mean fire size (ha)	-0.399	0.149	-2.673	**	-0.917	0.564	-1.626	ns	0.033	0.201	0.164	ns
FPC	0.633	0.126	5.022	***	1.683	0.464	3.628	***	-0.588	0.192	-3.068	**
Veg Types 1 km	0.518	0.094	5.506	***	0.822	0.357	2.306	*	0.013	0.135	0.098	ns
Mean rainfall	0.187	0.144	1.300	ns	0.143	0.418	0.343	ns	0.054	0.156	0.346	ns

Within woodland vegetation types, increasing foliage projection was positively associated bird and mammal abundance and richness and negatively associated with reptile abundance and richness though the linear relationship was weak (Figure 4.3). Early dry season and late dry season fire frequency had very little influence across the taxa (Figure 4.4).

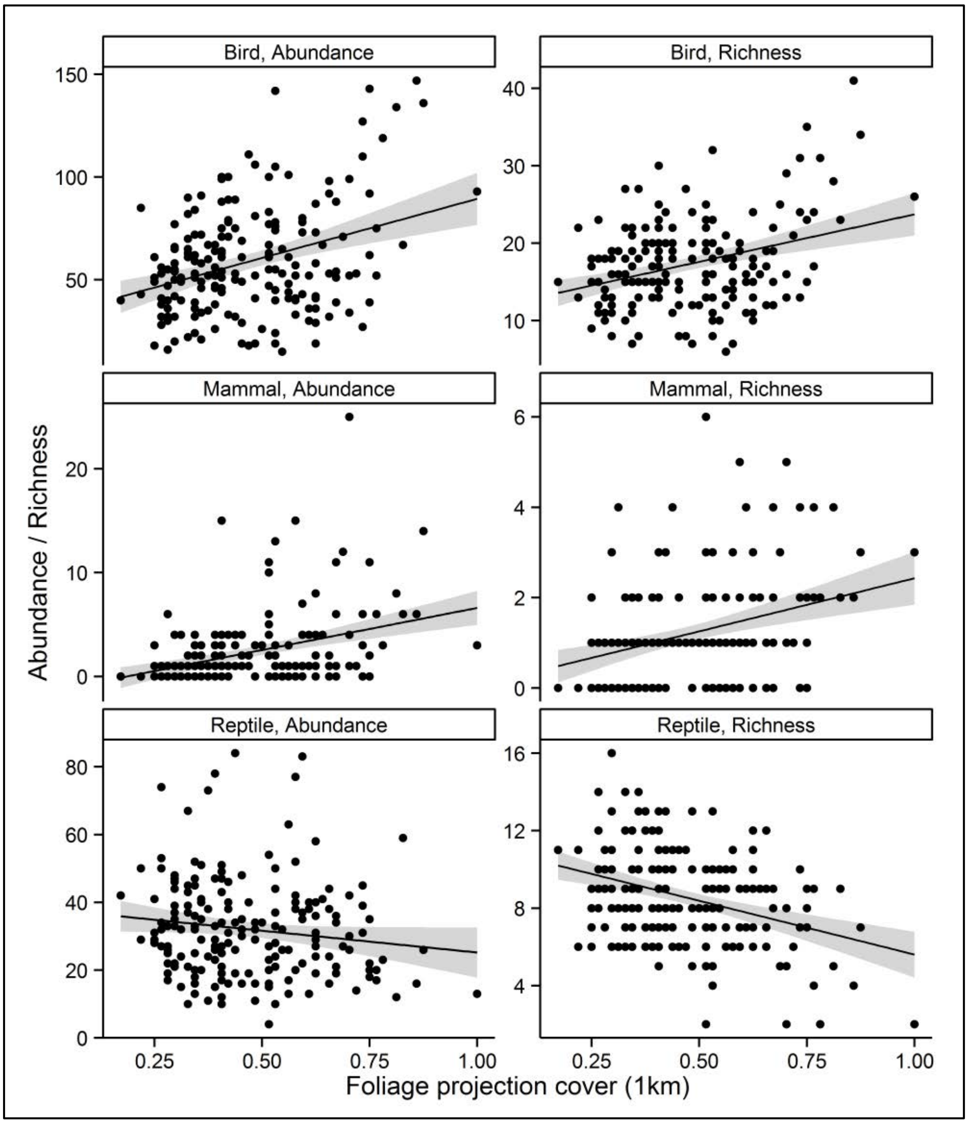


Figure 4.3 The relationship between mammal, bird and reptile species richness and abundance and foliage projection cover within a 1 km radius.

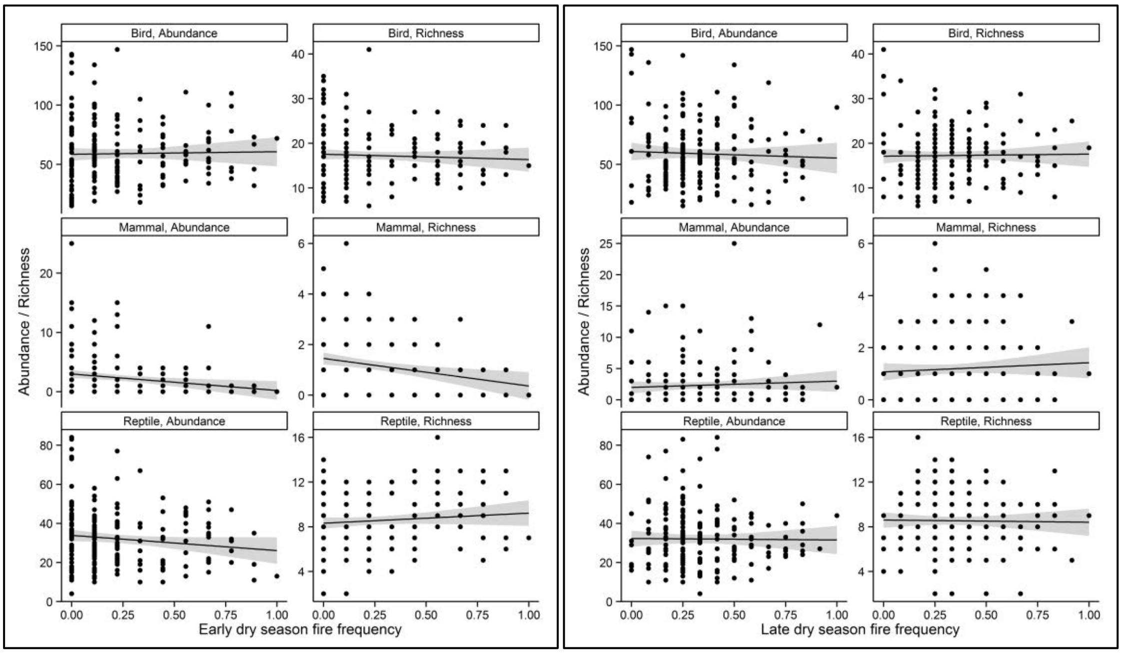


Figure 4.4 The relationship between mammal, bird and reptile species richness and abundance and early and late dry season fire frequency.

Discussion

There are two notable outcomes of my study that have relevance for fire management and carbon accounting in northern Australia. Firstly the patterns of abundance and species richness across the woodland vegetation types was highly variable, with mammals depleted, birds intermediate and reptiles with high abundance and species richness relative to closed forest and grassland communities. This suggests that measurement of biodiversity benefits following prescribed burning in woodlands, requires an understanding of the inherent ecology of different components of the savanna fauna (Kutt et al. 2012c). Secondly there were few consistent relationships between the abundance and diversity of vertebrate fauna and fire metrics, landscape scale vegetation or climate measures. In particular, compositional patterns did not change greatly and there were better relationships between abundance of taxa and my six factors and species richness was primarily influenced by vegetation associations. Although it might seem impractical to expect any single environmental factor to forecast biodiversity pattern at such a coarse grain, there are national imperatives to account for continental scale biodiversity trends (Beeton et al. 2006) and to directly measure or benchmark biodiversity responses as a component of carbon accounting methods (Fitzsimons 2012).

I recognise some limitations in my study, namely; my site data was a snapshot of what would be a more dynamic annual fauna pattern; my analysis of only univariate models when multivariate responses of fauna are more likely; and the influence of local and site-scale factors on what is recorded at any one time (Price et al. 2013); my fire metrics express existing fire regimes rather than following a change from late to early dry season fire frequency. However the focus of this study was to test the broad relationships between early and late dry season fire frequency at the scale at which the savanna burning methodology is applied (Walsh et al. 2014) and to assess transparently the advantages and weakness in the use of remotely sensed metrics to characterise biodiversity pattern (Oliver et al. 2014). For the future, the data set analysed here provides an ideal baseline for measuring change as the fire management for emission abatement methodology is applied across the study area.

There have been strong arguments that fire management for biological conservation should be more prescriptive (Driscoll et al. 2010). In the case of fire management for greenhouse gas abatement the primary goal is to reduce greenhouse gas emissions, not to promote aspects of biodiversity. My results suggest that richness and abundance of vertebrate fauna of woodlands is equally well predicted by landscape heterogeneity, foliage projective cover and the number of vegetation types in the surrounding landscape- and that fire frequency, early or late, elicits similar responses. This does not unequivocally suggest that early dry season fire frequency is not exerting some control on vegetation and fauna patterns, however, I suggest that more subtle metrics are required to account for biodiversity hysteresis. For example (Murphy et al. 2015) model vegetation dynamics that manifest over multiple decades suggesting that extant woodland patterns are the product of processes that are operating over much longer time periods than the abatement method reporting period (10 years). Changes to terrestrial fauna have occurred over many decades post European settlement which have been linked to the cessation of indigenous burning and the introduction then intensification of cattle ranching. Notably, changes in mammal populations in key sites in northern Australia, though rapid, have manifest over decades (Woinarski et al. 2010). Therefore the interplay of geographical location, history, and extreme changes (i.e. full exclusion of fire) all influence vegetation and therefore biodiversity pattern (Woinarski et al. 2004b). Even then, savanna woodland structure can remain relatively unchanged in the presence of frequent fire regardless of its timing and only exclusion has unequivocally demonstrated the return of previously absent fire sensitive species (Woinarski et al. 2004b).

My study suggests that remotely sensed fire frequency in the early and late dry season influences only some components of terrestrial fauna in woodlands. In savannas, heterogeneity at different scales (Price et al. 2010), including spatial and temporal variation (Price et al. 2013), influence bird, reptile and mammal species composition, richness and abundance. Therefore fire management that aims to maximise biodiversity should account for the differential effects within and between taxa (e.g. granivorous birds, Crowley and Garnett 1998). For example, predominantly heliothermic reptiles occur in open woodland communities, and they rely on thermal heterogeneity in the landscape, which can be favoured by intermediate fire frequencies (Huey et al. 2009). Fire regimes that promote multiple vegetation strata in less complex vegetation types theoretically provides greater niche diversity and available shelter for behavioural thermoregulation (Vickers et al. 2011). Although an exact fire recipe to sustain all species seems an improbable management goal, knowledge of taxa- or species-oriented goals for fire management have improved substantially (Woinarski and Legge 2013).

For fire management in northern Australia, a common aim is to return fire regimes to a pre-European state by aiming to replicate an abstraction of traditional indigenous fire management practices, often overly simplified to the mosaic burning paradigm (Parr and Andersen 2006). Australia’s fire and carbon methodology evolved in this paradigm (Russell-Smith et al. 2013). However, in all but a few cases, where the implications of prescribed fire have been explicitly measured (Legge et al. 2008; Parr and Andersen 2006), this approach ignores individual species responses, and assumes that by emulating a traditional regime, biodiversity will enter a more desirable “natural state” (Bradstock et al. 2005). In many cases indigenous burning involved protecting key resources that sustained populations and the use of fire varied in timing and extent to develop a non-random fire regime. In this sense whether fires were applied before or after August 1 was of little consequence, and the frequency of fire was based on the utility of fire for access and asset protection. Clearly the rigidity of the binary definition of early and late dry season used in the abatement method leaves little room for the application of traditional indigenous burning. My data suggest that, more pragmatically, fire management for biodiversity conservation may benefit from accepting that vertebrate diversity and abundance is promoted by a natural heterogeneity within the more broadly defined savanna ecosystem. To adequately account for this heterogeneity in the context of fire, it is necessary to first stratify the data to reflect the underlying differences in patterns due to evolutionary processes that have led to niche separation (Pepper et al. 2008) and natural species distributions and the natural distribution of fire (Pausas and Keeley 2009).

Fire frequency in Australian tropical savannas is mediated by landscape pattern, antecedent weather and land use (Whitehead et al. 2005). Vegetation structure is determined by a similar combination of physical and stochastic variables (Banfai and Bowman 2006; Fensham and Butler 2004; Fensham et al. 2003). However, the human manipulation of fire regimes within the natural vegetation gradient can produce anomalous vegetation structure such as the presence of dry rainforest in savanna woodlands (Fensham and Butler 2004) or woody growth in grasslands (Crowley and Garnett 1998). My results indicated that landscapes that had many different vegetation types (as measured by the count of vegetation types within 1km) and high foliage projection cover (denser canopies) support higher mammal and bird richness and abundance. This accepted relationship between vegetation complexity and species diversity suggests that management for the exclusion of fire in tropical savanna in areas adjacent to vegetation where fire is naturally excluded, representing a small percentage of the region, may lead to significant benefit for birds and mammals (Andersen et al. 2005; Andersen et al. 2012).

Although fire reduction strategies could provide tangible benefits for vertebrate fauna in savanna woodlands, it is important to acknowledge the practical challenges of implementing such a strategy. There are very few examples of successful fire exclusion in savanna woodlands (Russell-Smith et al. 2003) and the successful examples are at small scales and associated with abnormal circumstances (Woinarski et al. 2004b). Additionally, long-term fire exclusion in naturally fire prone vegetation types does not necessarily offer permanent changes for biodiversity. For example, following the transformation of savanna woodland to closed forest following ~20 years of fire exclusion, in a vegetation type that typically burns biennially, it was returned to its original state soon after fire was re-introduced (Scott et al. 2012). Concentrating on areas that are naturally protected from fire (Andersen et al. 2012; Price et al. 2005) could alleviate some of the practical challenges associated with exclusion. Legislative instruments or market incentives that promote carbon sequestration, as opposed to the current greenhouse gas abatement method, could provide the significant resources required for conducting successful targeted fire frequency reduction. Furthermore, recent research has demonstrated that landscape scale fire reduction can be achieved through non-random targeted patch burning (Trauernicht et al. 2015). However, it should be noted that in the absence of significant and ongoing financial and technical support fire exclusion is unlikely to succeed and could lead to the resumption of large late dry season fires.

Conclusion

Overall, I find the assumption that fire regimes that are aimed at reducing greenhouse gas emissions will have a measureable ancillary biodiversity benefit lacks support at the scale of the fire management for emission abatement methodology. This does not discount the use of the methodology for achieving co-benefits to biodiversity at the scale of tropical woodlands in northern

Australia. However, I cannot expect a predictable response from fauna across all landscapes at moderate spatial and temporal scales, and I argue that assessment of a biodiversity benefit from a particular fire management strategy requires on-ground measurement of responses from each taxa in different locations, different scales and over long time periods.

Fire is an important management tool for biodiversity conservation in savanna ecosystems and my study suggests that (i) management strategies need to be attuned to the local patterns in species and landscape; (ii) have a clear understanding of the different and variable responses of many components of the wildlife in the landscape, and (iii) moderate resolution remotely sensed fire histories on their own are too coarse to adequately capture the subtlety and rapid change that can occur in taxa across vast heterogeneous landscapes. There is evidence that reduction and exclusion of fire, and the resulting increase in woodland structural complexity, more directly benefits biodiversity than a fire frequency based regime to minimise emissions. However, exclusion is feasible only in special circumstances and reduction is likely to increase the risk of intense and large scale late dry season fires.

Author contributions.

Justin Perry and Alex Kutt conceived the paper, Justin Perry conducted the analysis and wrote the paper. Justin Perry, Alex Kutt and Eric Vanderduys provided editorial input and collected the data used in the paper.

Chapter 5. More famine than feast: pattern and variation in a potentially degenerating mammal fauna on Cape York Peninsula

Introduction

Globally, mammal populations continue to be threatened by environmental change, and many species are suffering severe declines (Cardillo et al. 2005). Species are at risk because of the interplay between environmental change and intrinsic life history traits (i.e. breeding biology and dispersal), though the relative effect of each varies between taxa and geographic region (Collen et al. 2011). There are a multitude of known threats to species ranging from habitat modification via clearing, fire and grazing (Kutt and Woinarski 2007), climate change (Rowe et al. 2011), introduced species (Johnson and Isaac 2009), direct human intervention via hunting for food or killing native apex predators (Colman et al. 2014) and synergistic effects between threats (Ziembicki et al. 2014). The effects are not necessarily restricted to a particular mammal size across different continents, or to land tenure, as declines are occurring in both conservation reserves as well as in unprotected areas (Craigie et al. 2010; Kutt and Gordon 2012).

The mammal fauna of northern Australia is also seemingly crumbling (Fisher et al. 2014). Long-term monitoring in key sites in tropical savannas has revealed that over a decade or more the small mammal fauna has collapsed and remained in depleted numbers (Woinarski et al. 2010). Though the mammal assemblages in some areas seem able to recover quickly with intervention (Legge et al. 2011), others have not (Kutt et al. 2012c). Mammal decline has been well documented in the Top End of the Northern Territory and the Kimberley in recent decades (Radford et al. 2014), but in Queensland, systematic fauna monitoring has been spatially ad hoc and is largely a recent phenomenon (Eyre et al. 2011; Perry et al. 2011b), meaning any declines that may have occurred would be largely undocumented. A long-term program of surveys was commenced in the 1970s, but the data were not collected using systematic methods, and are unpublished or unavailable for further analysis (Kirkpatrick and Lavery 1979). Retrospective analysis in one Queensland region using components of these data indicates small changes in the mammal fauna, but the low number of records overall (data originally collected in 1973 and resampled in 2002) ambiguously suggests an already diminished fauna (Woinarski et al. 2006). This limited information base and the lack of adequate historical information on mammal patterns can cause distorted views of the biodiversity condition of many ecosystems (Bilney 2014). There is fossil and subfossil evidence of the presence across parts of Queensland of some mammal species that have now disappeared and are currently restricted to small areas and specialised habitat in the Northern Territory and Western Australia (Cramb and Hocknull 2010; Sobbe and Price 2014).

Fire is considered a key determinant of biodiversity patterns in many biomes and changed regimes are known to have a critical negative effect on mammals (Kelly et al. 2013). A key prediction under projected climate change in northern Australia is that fire frequency and intensity may increase into the future and that this will have significant negative implications for the composition, structure and distribution of vegetation communities (Murphy et al. 2013). This may, in turn, adversely affect the fauna in these changing ecosystems. The magnitude of effect of fire on species and communities is deeply interactive with other environmental factors such as domestic livestock grazing, vegetation type, topographic complexity and landscape position (Clarke et al. 2010; Price et al. 2013). Understanding how landscape scale and more localised spatial and temporal heterogeneity affect fauna patterns is important in predicting responses to ecosystem change, particularly for species that are under threat and declining (Andersen et al. 2012).

Cape York Peninsula is a significant biogeographic, cultural and conservation landscape in northern Australia that has been considered frequently for World Heritage listing (Skilton et al. 2014). The fauna is considered unique, of biogeographic significance and diverse with Australo-Papuan influences (Schodde and Calaby 1972). There is some evidence of past and contemporary patterns of fauna change and loss (Kutt et al. 2005; Winter and Allison 1980), and there is also some evidence of population fluctuations in some mammal species (Winter 2007) and limited evidence of change when considered at the resolution of biogeographic regions (McKenzie et al. 2007). The limited historical evidence reduces the certainty about the extent or timing of any contemporary mammal declines.

In this study I examined four years of systematically collected mammal survey data (2009–12) from 202 sites on Cape York Peninsula, northern Australia, stratified by fire frequency (NAFI, 2014). I use these data to investigate the relationships between mammal richness, abundance and species patterns and both landscape and site-scale predictive variables. I investigate two key questions: (i) what is the general composition and pattern in the native terrestrial and arboreal mammal fauna recorded; and (ii) what is the relative effect of landscape and site factors on the richness and abundance recorded. In this study I fitted only additive models and examined site and landscape effects separately, as I was interested in the key factors that might predict mammal patterns, rather than more complex interactive effects at different scales. Though my survey methods and effort differed, I also review and compare the frequency of mammal species recorded in two previous mammal surveys on Cape York Peninsula (Winter and Allison 1980; Winter and Atherton 1985) to tease out evidence of any major changes. Finally, with an emphasis on fire management, I discuss the implications of my results in the context of mammal community change in northern Australia and the management and conservation implications for Cape York Peninsula.

Methods

Study region

The Cape York Peninsula bioregion represents the northernmost section of the state of Queensland, Australia, and includes an area ~13 million ha (Figure 5.1). The area has a very low permanent human population (~8000) dominated by Indigenous people (67%) (Moorcroft et al. 2012). Access is via a sparse locally managed road network, accessible only during the dry season, with most of the land mass accessible only via unmaintained cattle station tracks. Mean annual rainfall in this region varies from >2000 mm at Lockhart River (12°28′S, 143°12′E) on the central east coast down to ~1000 mm at Palmerville (16°00′S, 144°02′E). Rainfall is primarily orographic and monsoonal on the eastern peninsula and monsoonal in the west (Perry et al. 2011b). Cape York Peninsula shares many elements of fauna with the rest of monsoonal northern Australia, but also supports its own distinct fauna associated with unique and extensive rainforest and the region's proximity to Papua New Guinea (Hitchcock et al. 2013; Ziembicki et al. 2014). The mammal fauna recorded in this study is also typical of the general composition of Australian mammal fauna with a high diversity of marsupials, rodents and bats (Ziembicki et al. 2014).

Surveys

Vertebrate fauna surveys were conducted from 2009 to 2012 during the dry season (June to November). In total, 202 sites were established on seven properties (Figure 5.1). Sites on each property were surveyed over a 4-night, 5-day interval. Sites were stratified by fire frequency within broad vegetation groups (Neldner and Clarkson 1995) to reflect the relative dominance of each vegetation group on Cape York Peninsula: Eucalyptus woodland (n = 141), other woodland (Melaleuca- and Lophostemon dominated communities) (n = 31), closed forest and dune scrub (n = 20) and tussock grasslands (n = 10). Closed forest in this circumstance includes closed vegetation types of a similar structure and floristic composition including rainforest, littoral forest on coastal dunes and gallery forest on riparian and alluvial sites. Elevation at the sites ranged from 5 to 644 m above sea level based on the nine-second digital elevation model (Pascoe et al. 2012).

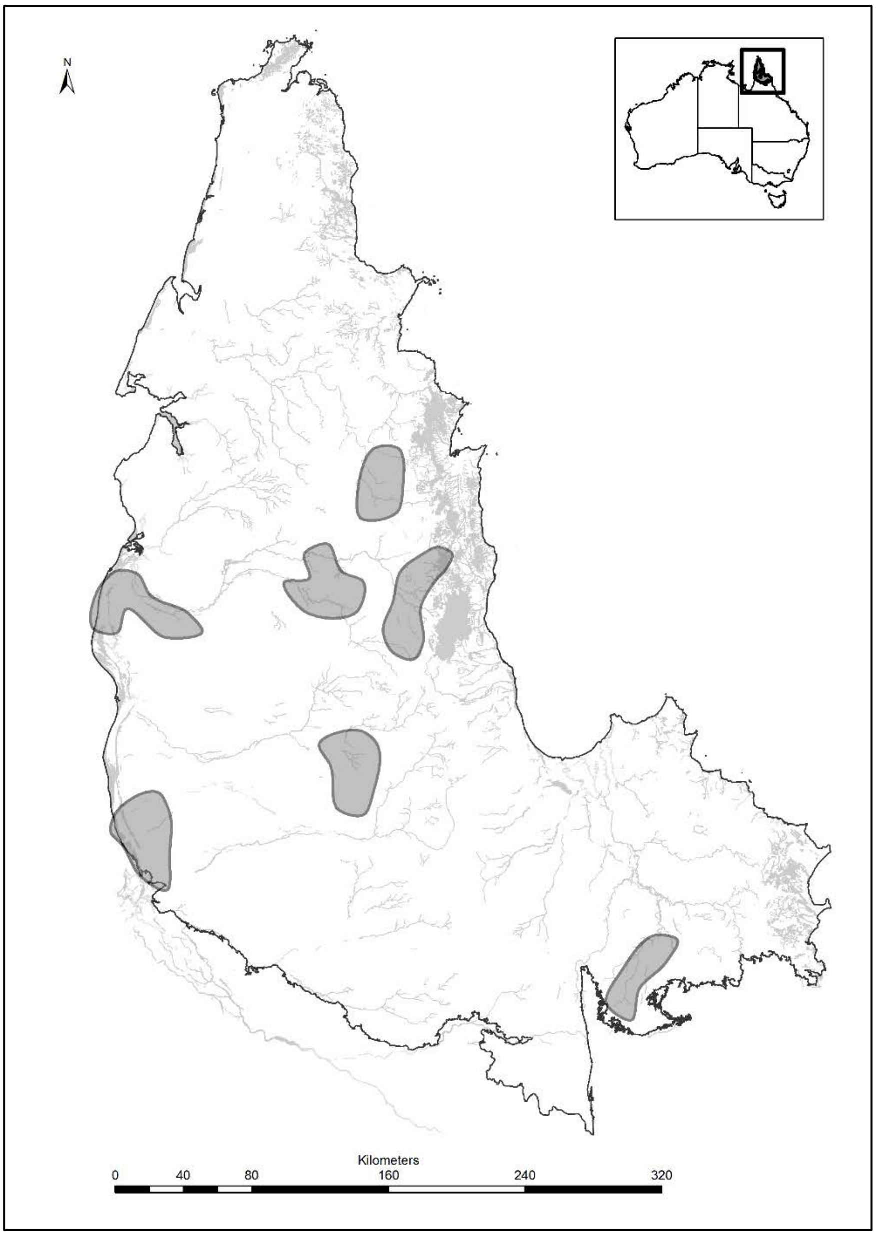


Figure 5.1 The location of the seven survey areas on Cape York Peninsula.

Mammal sampling at each site used a standardised approach, conducted in a 1-ha quadrat (Kutt et al. 2012c). Nested in each 1-ha quadrat was a 50 × 50 m trap array of 20 Elliott box traps (Elliott Scientific Equipment, Upwey, Victoria) placed 10 m apart along the perimeter, two larger metal cage traps placed at opposing corners, and four pitfalls (60 cm deep and 30 cm diameter) 10 m apart and arranged in a ‘T’ configuration (with 20 m and 10 m of drift fence) and six funnel traps (one on either side of the drift fence, at the ends of the ‘T’ configuration). Elliott and cage traps were baited with peanut butter, honey, oats and vanilla, and additionally with dry mixed cereal and meat ‘dog biscuits’ in each alternative trap; raw chicken offcuts were placed in cage traps. Traps were checked in the morning and afternoon and opened for a 96-h period. Trapping was supplemented by timed searches: three diurnal and two nocturnal searches each of 20 search-minutes duration conducted in the 1-ha quadrat. Nocturnal and diurnal counts included active (log rolling, litter raking) and passive (looking for eye shine, listening for nocturnal calls) searches.

For each quadrat and survey I calculated an index of abundance for each species, a standard method for tropical savanna surveys (Kutt and Fisher 2011). This index was a cumulative total of all captures and observations, and is hereafter referred to as 'abundance'. Several studies have demonstrated that variation in trap success rates for an individual species between sites or time periods provides a generally good measure of variation underlying density of that species between sites or time periods (Hopkins and Kennedy 2004; Slade and Blair 2000).

Environmental variables

I investigated site-based (quantitative measurements collected in a 1-ha area surrounding the trap array) and remotely sensed fire, climate and habitat variables as predictors of fauna composition, abundance and species richness. The variables were chosen due to being recognised and published determinants of fauna pattern in northern Queensland tropical savanna, namely, fire (Perry et al. 2011b), weather patterns (Reside et al. 2010), vegetation type (Kutt et al. 2012c), landscape context (Price et al. 2013), elevation (Kutt et al. 2011), woody vegetation structure (Tassicker et al. 2006) and ground cover (Ward and Kutt 2009). Site-based variables were those collected in the 1-ha study sites, and landscape scale variables were those derived from remotely sensed data.

The landscape level variables were: fire frequency (number of years burnt in the 10 years before the survey date), derived by overlaying the location of site and date of survey on the historical MODIS satellite derived monthly fire scar data obtained from the northern Australian fire information site (NAFI 2014); vegetation complexity, measured as the number of different regional ecosystem types (Queensland Herbarium 2014) in a 1-km2 grid-cell centred on the survey site; nine-second digital elevation (Pascoe et al. 2012); and average annual rainfall (30 year mean, 1990 centred), derived using daily precipitation and temperature grids (0.05 degree grid scale) from the Australian Water Availability Project (Grant et al. 2008). The site-based variables were: estimated time since fire, recorded via visual inspection of the survey site and scored as 0 (≤1 year since last burn), 1 (1–5 years since last burn), 2 (5–10 years since last burn) and 3 (>10 years since last burn); total woody (tree and shrub) vegetation cover, measured as crown cover intersecting a 100-m line transect down the centre of the 1-ha site; strata, as the total number of canopy, sub-canopy, recruiting trees, shrub, ground cover layers in the 1-ha area; and ground cover (plant cover) as measured in five 1 × 1 m plots along the 100-m transect line. I recognise the importance of grazing pressure and weed invasion for fauna conservation in northern Australia (Kutt and Kemp 2012; Kutt et al. 2012b), and grazing impact and weed extent at each site were assessed in four categories ranging from none (0) to very high (4). However, as almost all the sites were scored as zero for both variables I did not include them in the analysis.

Four variables – mean annual temperature, time since last fire, bare ground and litter cover – were highly correlated (Spearman pairwise correlation coefficients >0.5) to mean annual rainfall, fire frequency and ground cover respectively and excluded from analysis. High co-linearity among explanatory variables can lead to high standard errors and difficulties in interpreting parameter estimates in generalised linear models (Graham 2003).

Analysis

I used regression to examine the variation in abundance and richness of all mammals, three mammal functional groups (small terrestrial, macropod, arboreal), and abundance of all species with respect to landscape and site measures. I examined two predictive models: a landscape model comprising MODIS-derived fire frequency, landscape complexity, rainfall and elevation; and a site model comprising the wildfire measure, the number of vegetation strata, the cover of woody vegetation and the ground cover. As there was potential for spatial autocorrelation within the properties I accounted for this by using generalised linear mixed (multi-level) models (GLMMs) via REML in GenStat 8 8 (Payne et al. 2010) and tested spatial autocorrelation with Mantel tests (Borcard and Legendre 2012). Mixed models combine both fixed and random terms and can account for multiple sources of variation between sites (i.e. 1-ha site) within locations (i.e. properties)) (Payne et al. 2010). As the data are nested and the spatial scale of nesting coincides with the spatial scale of autocorrelation, the use of GLMMs, and the use of property as a random term, take account of dependencies within sites (Zuur et al. 2009). However, as a further test of spatial autocorrelation, I applied a multivariate Mantel's test and created a Mantel correlogram. I constructed a site by species distance matrix (Euclidian) and a geographic distance matrix using the latitude and longitude. The extent of spatial autocorrelation was then examined by pairwise permutation tests (n = 999) across ten equal distance classes. All analyses were performed using the program PASSaGE v. 2 (Rosenberg and Anderson 2011). The significance level for a correlation was Bonferroni-corrected by dividing by the number of distance classes (Legendre and Legendre 1998).

I fitted log-linear models (i.e. a Poisson model with a logarithmic link), and estimated the size and direction of each fixed effect. As the output does not identify minimal adequate models, but instead builds models sequentially, I tested the significance of each independent variable, recognising that if two or more factors were significant there would be a degree of interaction. Variance components were estimated using maximum likelihood for the fixed effects and dispersion components, and approximate empirical Bayes estimates of the random effects and significance of the fixed effect was assessed via the Wald statistic (Payne et al. 2010). For individual species analysis I only examined species recorded in more than five sites. Many of my site data had absences, and GLMMs are also an appropriate method for count data that is highly skewed and has many zeros (Zuur et al. 2009). To account for any over-dispersion, the GLMM regressions in GenStat estimate the dispersion parameter, and adjust the standard errors of the parameter estimates to take this into account (Payne et al. 2010).

I present the mean and standard error of species richness and abundance for each functional group (small terrestrial, macropod, arboreal) and the mean and quartiles for fire frequency for each of the habitat types investigated. I also present exemplar fitted log-linear regressions (small mammal richness and abundance, *Isoodon macrourus, Rattus sordidus* and *R. tunneyi*) using the ggplots2 (Whickam 2009) package (GLM, family = Poisson) using the R program (R Development Core Team 2014).

Results

I obtained a total of 492 mammal records across seven properties on Cape York Peninsula during four years of surveying (2009–12) (Figure 5.1). I recorded 24 native mammal species including four macropods, five arboreal mammals, three terrestrial dasyurids and 11 rodents. The most abundantly recorded mammals were *Rattus sordidus, R. tunneyi, Macropus agilis* and *Melomys capensis*, and these were also the most frequently recorded species. Nine species were only recorded as a total of five or fewer individuals, and 13 were recorded in five or fewer sites. The most species rich sites contained only four or five species, and 80 of the 202 sites recorded no mammals. The mean site richness and abundance for small mammals was very low in Eucalyptus and other woodlands, and higher in closed forest/and dune scrub to tropical grasslands (Figure 5.2).

The proportion of sites that recorded no mammals varied across the habitat types: 0.5% for closed forests, 10% for tussock grasslands, 35.4% for *Melaleuca* woodlands and 47.5% for *Eucalyptus* woodlands (see Appendix Table 5.1). However, the tussock grasslands only recorded four species, the closed forest and *Melaleuca* woodlands 12 species, and the *Eucalyptus* woodlands 20 species. The mean abundance for species in each habitat type ranged from 1.4 to 11.2 in tussock grasslands (e.g. *Planigale ingrami* to *Rattus sordidus*), 0.3 to 0.45 in *Melaleuca* woodlands (*Melomys burtoni* to *Rattus tunneyi*), 0.01 to 0.26 in *Eucalyptus* woodlands (e.g. *Mesembriomys gouldii* to *Macropus agilis*) and 0.1 to 2.95 in closed forests (e.g. *Uromys caudimaculatus* to *Rattus tunneyi*) (see Appendix Table 5.1).

The mean fire frequency for each of the habitat types indicated that closed forest had the lowest (two in every 10 years), Melaleuca and Eucalyptus woodlands intermediate (four or five in every 10 years), and tussock grasslands the highest (7.5 in every 10 years) (Figure 5.3). However, the ranges of fire frequencies for each habitat were 0–6, 0–9, 0–7 and 2–10 for those vegetation types respectively (Figure 5.3).

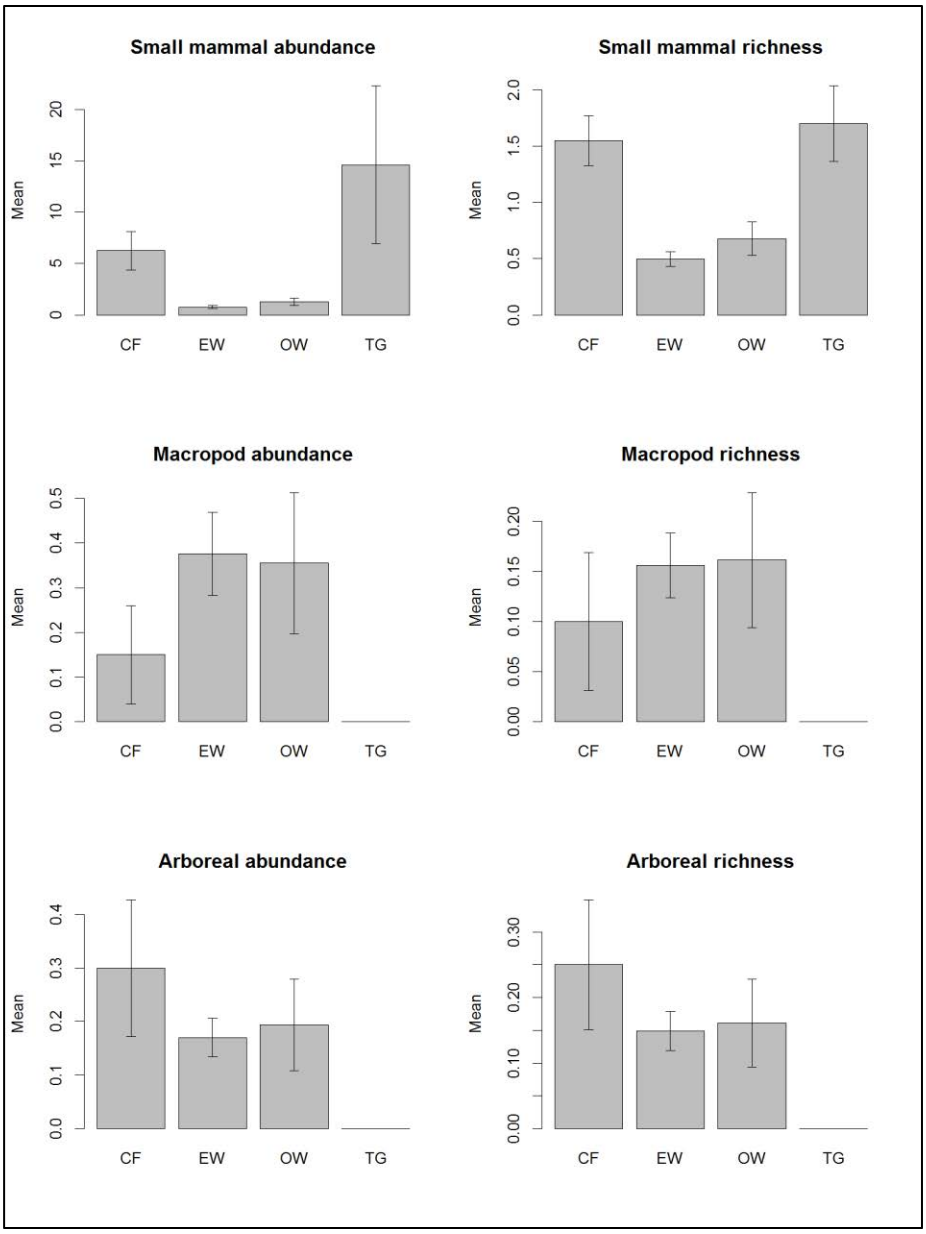


Figure 5.2 The mean (and standard error) of small mammal, arboreal mammal and macropod species richness and abundance across the four habitat types sampled. EW = Eucalyptus woodland, OW = other woodland (*Melaleuca* and Lophostemon dominated communities), CF = closed forest/dune scrub and TG = tussock grasslands.

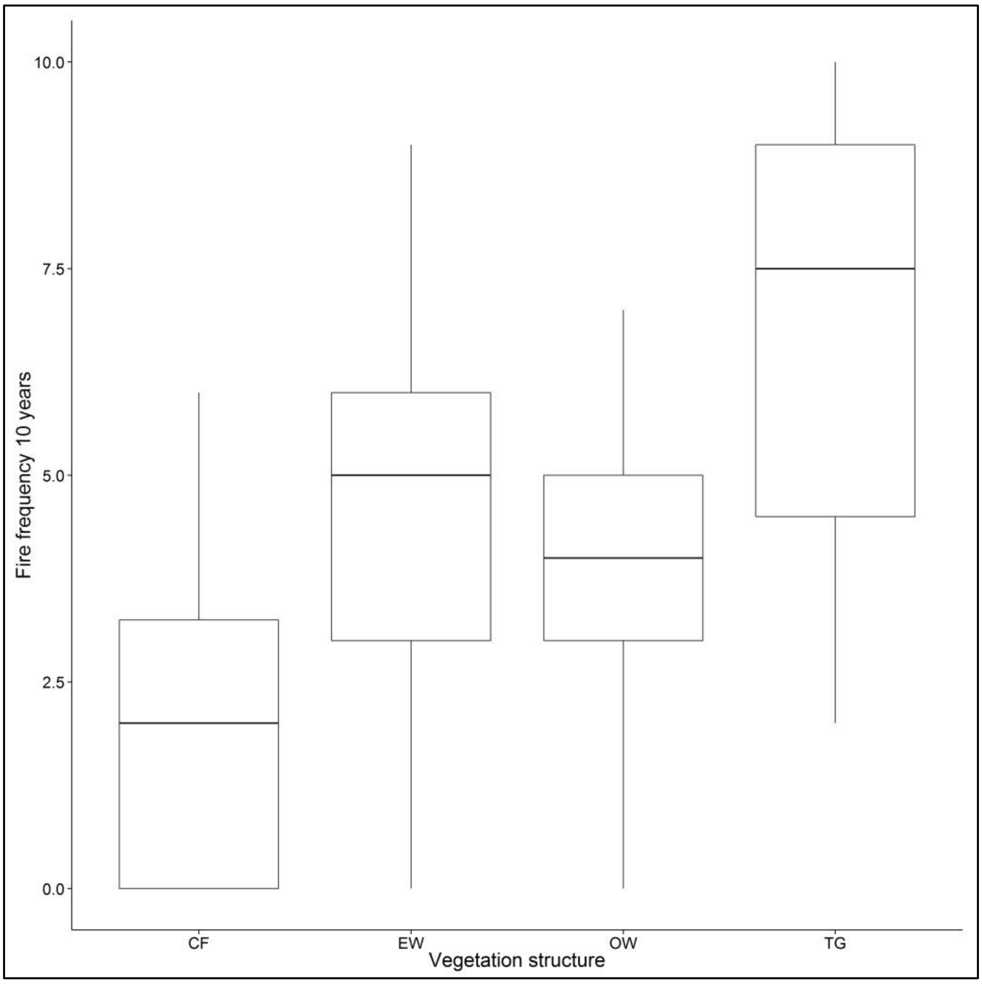


Figure 5.3. The mean and quartiles for fire frequency for the ten prior years for each of my survey sites. The vertical lines represent the entire range. CF = closed forest / dune scrub, OW = other / Melaleuca woodlands, EW = Eucalyptus woodlands, TG = tussock grasslands

Coarse comparisons can be made between my surveys and past surveys (Table 5.1). I did not record Dasyurus hallucatus, Sminthopsis archeri, Acrobates pygmaeus, Pseudocheirus peregrinus and four macropods that were recorded by Winter and Atherton (1985), while they did not record Dactylopsila trivirgata, Macropus giganteus, Mesembriomys gouldii and Zyzomys argurus and I did. Two species, Planigale ingrami and Petaurus norfolcensis, were not previously recorded for Cape York Peninsula. (Winter and Atherton 1985) presented their results as species present or absent in 73 × 5 degree grid squares and included an assessment of whether the species was abundant, common, uncommon or scarce. In comparison, my results can be assessed as the total frequency of occurrence per site (n = 202) (Table 5.1). Using these frequencies for sites (my surveys) and grids (Winter and Atherton), Sminthopsis virginiae, Trichosurus vulpecula, Petaurus breviceps, Macropus agilis, Macropus antilopinus, Hydromys chrysogaster, Melomys burtoni, Pseudomys delicatulus, Rattus sordidus and Uromys caudimaculatus were less frequently recorded in the present survey, and Planigale maculata, Isoodon macrourus, Melomys capensis and Rattus tunneyi more frequently (Table 5.1).

The use of property as a random term in my GLMMs did account for any spatial autocorrelation that may have existed in the seven properties. However, examination of the Mantel test indicated that the correlation between the mammal composition and geographic distance matrices was non-significant and weak (R = 0.03) and the correlogram presented very low and non-significant Mantel correlations in 10 distance categories, including the first one or two distance categories that represent the properties.

The landscape models identified eight groups or species with a single main effect, two with two terms, and two with three terms (Table 5.2). Arboreal mammal abundance and richness decreased with increasing fire frequency as did *Petaurus norfolcensis*, *Melomys capensis* and *Rattus tunneyi* abundance. *P. norfolcensis* abundance declined with increasing elevation and landscape vegetation complexity. Macropod abundance and richness increased with landscape vegetation complexity as did *Macropus agilis* and *Isoodon macrourus* abundance. Small mammal abundance and richness increased with increasing rainfall, and small mammal richness increased with increasing landscape vegetation complexity. *Planigale maculata* decreased in abundance with increasing rainfall but was more abundant with increasing fire frequency. The two *Rattus* species had contrasting relationships: *R. sordidus* increasing in abundance with increasing fire frequency, but decreasing with increasing landscape vegetation complexity; and *R. tunneyi* decreasing in abundance with increasing fire frequency, but increasing with landscape vegetation complexity (Table 5.2).

The site models were more complex than the landscape models, and identified five groups or species with a single main effect, five with two terms, and two with three terms (Table 5.3). There was an increasing abundance of arboreal mammals, macropod abundance and *P. norfolcensis* with increasing time since fire. This was also the case with five other species, but there were other significant terms associated with these species: small mammal abundance (negative relationship with strata, positive with ground cover); small mammal richness (positive relationship with ground cover); *M. capensis* (positive with woody cover); and *R. tunneyi* (positive relationship with strata and ground cover) (Table 5.3). The remaining significant models linked changes in vegetation structure with different species: *I. macrourus* increasing abundance with increasing ground cover; *M. agilis* abundance increasing with both increasing woody vegetation and ground cover; *M. antilopinus* abundance increasing with decreasing woody cover; and *R. sordidus* abundance increasing with increasing ground cover, but decreasing with increasing woody vegetation cover (Table 5.3).

The exemplar relationships plotted indicated the nature of some of the regressions (Figure 5.4). Small mammal richness and abundance increased with increasing rainfall, though for abundance there were a small number of super-abundant sites that influenced the relationship. *R. sordidus* and *I. macrourus* increased in abundance at sites with increasing ground cover, but again there were prominent outliers (Figure 5.4). Finally, *R. sordidus* declined with increasing woody cover whereas *R. tunneyi* increased in abundance (Figure 5.4).

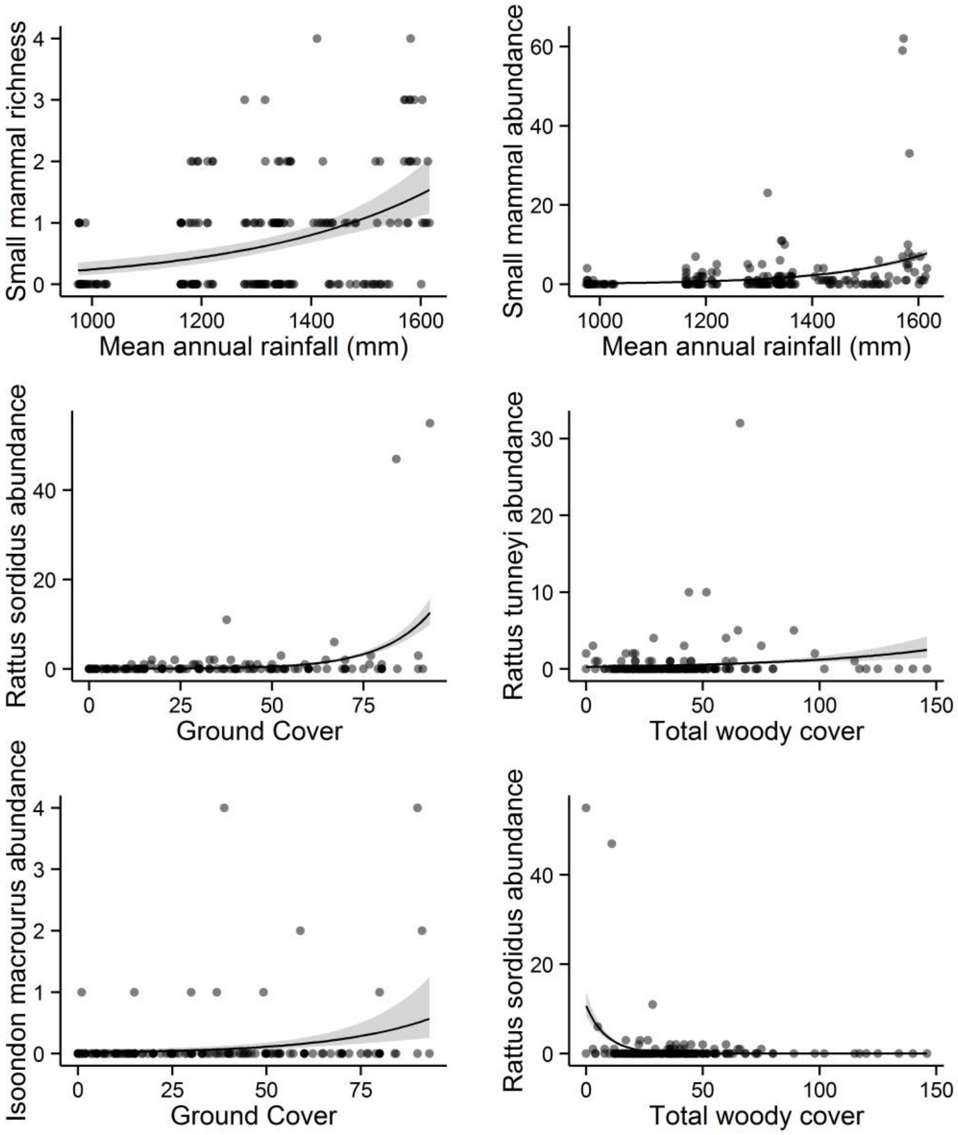


Figure 5.4 Generalised linear model regression of small mammal richness and abundance and mean annual rainfall, Isoodon macrurous and Rattus sordidus and ground cover and R. tunneyi and R. sordidus and total woody cover.

Discussion

In this study I systematically assessed patterns of mammal richness and abundance on Cape York Peninsula for the first time in 30 years. The timing of this research is important in the context of evidence of small mammal decline in similar latitudes and ecosystems in the Northern Territory and Western Australia that has occurred during this period (Ziembicki et al. 2014). Mammal richness recorded by this study was moderately high (22 of 32 previously recorded species plus two species not previously recorded) (Winter and Allison 1980; Winter and Atherton 1985). Grasslands were characterised by few species in relatively high mean abundance and ubiquity (i.e. most sites). Eucalyptus woodlands were more species rich but the mean abundances were very low. Although gamma diversity was high only 15 species were recorded more than five times. In part, this reflects species that are restricted to specialised habitats (e.g. *Zyzomys argurus, Spilocuscus maculatus, Dactylopsila trivirgata*), but those with a more catholic distribution and affinity to tropical savannas (the most extensive landscape by area in Cape York Peninsula) were sparse as well (e.g. *Planigale, Rattus, Pseudomys, Sminthopsis*). Patterns of low mammal diversity in tropical savanna woodlands are in keeping with some other locations in northern Queensland (Kutt et al. 2012c) and the more recently depleting fauna of monsoon tropical woodlands in the Northern Territory (Woinarski et al. 2010), though there are some areas (tropical savannas ~1000 m in altitude in the Einasleigh Uplands) where the mammal fauna is abundant and largely intact (Vanderduys et al. 2012).

Comparison between this survey and previous surveys (Winter and Allison 1980; Winter and Atherton 1985) in many of the areas I sampled suggests equivocal or unequal changes between different elements of the mammal fauna: dramatic for some groups or species (e.g. decline in Dasyurus hallucatus), and little change in others (e.g. Muridae rodents on the whole). Although infrequently recorded, my records of Isoodon macrourus are significant (and equivalent to Winter and Atherton 1985) because it has been suggested that they are disappearing in northern Australia because of increasing fire frequency and extent (Pardon et al. 2003). Though the comparison between my survey and past surveys is confounded by different survey methods (i.e. my use of pitfall traps; their use of break back traps) and, more than likely, total survey effort, there are three general outcomes that can be noted: (i) some mammals are likely to have suffered a decline in the past 30 years (Dasyurus hallucatus, Sminthopsis virginiae, Sminthopsis archeri, Trichosurus vulpecula, Pseudocheirus peregrinus, Melomys burtoni, Pseudomys delicatulus), whereas other species were recorded at similar frequencies; (ii) some species in this survey, and in Winter and Atherton (1985), are spatially clustered in particular locations or habitats such as grasslands or more complex forests (e.g. Planigale maculata, Melomys capensis); and (iii) many of the common elements of the mammal fauna may occur naturally in low abundance, are uncommon or irruptive (e.g. Rattus spp.). Despite an ambiguous signal of change over time, my results hint that there has been a reduction in the richness, abundance and distribution of some elements of the mammal fauna on Cape York Peninsula, at least in some locations, that may be shifting to a depleted state (Radford et al. 2014), and this change may have commenced in recent decades (Winter and Allison 1980).

There are two facets of my survey data and analysis that need discussion. First, I examined landscape and site factors separately via additive models that identified the key subset of factors at each scale that were predictive of mammal functional group or species richness and abundance. The rationale for this is that this is the first time there has been a detailed quantitative analysis of the determinants of mammal pattern on Cape York Peninsula and I wanted to identify the dominant predictors at each scale that could then inform more detailed survey and experimental programs to define and prioritise future management (McDonald et al. 2015). Second, it is clear from the data that a few sites recorded outlier populations of mammals at very high abundance, and there were many others with zeros. My analysis, using mixed models, is appropriate for this skewed data (Bolker et al. 2009), and I did not want to remove these outliers in the data as they demonstrate that distribution is very patchy and interspersed with a small number of apogees that may represent natural refuges or foci for conservation (Reside et al. 2014).

There was a clear division in the abundance of some species across the different habitat types that links to the geographical location, the vegetation structure and type, and the resilience or response of the species to fire. The exemplar species in this regard are R. sordidus and R. tunneyi, the former an irruptive grassland species widely distributed across central and northern Queensland and the latter a species considered to have historically declined in Queensland and a marker for current mammal changes in the north and west of Australia (Frank et al. 2014). The interpretation of the pattern recorded in this study is that R. tunneyi are more abundant in closed forest (complex woody structure and low ground cover) and grasslands, and R. sordidus are mainly associated with wet coastal grasslands. The persistence of both species in coastal grasslands, even though they are subject to intense annual fires, is possibly associated with the high annual productivity and rapid regrowth after fire in this vegetation type (Felderhof and Gillieson 2006). Rattus sordidus, Planigale ingrami and Sminthopsis virginiae may seek shelter in soil cracks. Rattus tunneyi were abundant in coastal dune forest as well, where they were observed climbing along vines and in the complex mid-storey. The low abundance and frequency of both Rattus species (and other genera such as Sminthopsis and Planigale) in the Eucalyptus woodlands could be associated with the interaction between high fire frequency and low ground cover, and this is linked to increased predation success by feral cats (Fisher et al. 2014). The exclusion of fire in mesic tropical savanna woodlands has been shown to promote increased richness of fire sensitive species and more complex vegetation structure which may favour declining species (Woinarski et al. 2004b). It is likely that the natural distribution of these mammal species would have been influenced by the relative fire proneness of each broad vegetation type, and under the fire regimes in which these animals evolved, tropical savanna woodland would have had high variance in fire frequency over time (Barbour and Schlesinger 2012). Woodland structure can be influenced by topography, landscape position and soil type, and combinations of these elements can offer natural protection from frequent fire (Price et al. 2007). These areas may provide the most stability in the structural complexity favoured by many woodland mammal species.

From a landscape perspective, both the MODIS-derived fire frequency data and the surrounding vegetation complexity were the more consistent predictors of mammal pattern. In highly seasonal environments such as tropical savannas, temporal changes in habitat and resources both in the local context and surrounding landscape matrix are significant determinants of the spatial distribution of terrestrial species (Price et al. 2007). Environmental heterogeneity, as a general rule, is a key determinant of patterns in species richness (Stein et al. 2014). Five mammal species or functional groups showed a negative response to fire frequency and two species showed a positive response. This is consistent with Woinarski *et al*. (2010) who established a relationship between high fire frequency and mammal loss. However, the different responses to fire among species that I recorded are by no means unusual or unexpected (Levin et al. 2012). For example, the composition of vegetation communities within the adjacent area (i.e. fire prone or fire sensitive) will influence which species persist in the landscape, hence the importance of vegetation complexity within 1 km reported in this study. Rainfall was significantly and positively related to small mammal abundance and richness, and the link between productivity, rainfall and mammal abundance is well established (Byrom et al. 2014). The highest mammal abundance recorded during my four-year period of survey, Aurukun 2010, was associated with above average antecedent rainfall from Aurukun (2008–09 wet season 2230 mm), and significant dry season rainfall (BOM 2015).

The site models suggest that ground cover, woody complexity and the local measure of time since fire are important determinants of mammal patterns. Self-evidently, woody vegetation structure is linked to arboreal mammal presence or abundance (Smith and Murray 2003), but time since fire was also important, suggesting that areas that are subject to frequent fire are not favourable to possum or glider persistence (Isaac et al. 2008). The negative relationship between fire frequency and arboreal mammal presence has been recorded previously for Cape York Peninsula in Eucalyptus woodlands (Winter 2007). Fire exclusion also supports other scansorial species such as M. capensis, which are more abundant in complex woodland and closed forest (Leung 1999). The relationship between ground cover and small mammals (and species such as Isoodon macrourus) is significant, as the link between frequent fire, loss of shelter and, by association, increased feral predation on exposed animals is considered a core determinant of mammal decline (Pardon et al. 2003; Price et al. 2010). Management actions that promote the persistence of adequate native ground cover in an appropriate configuration, either as shelter for smaller species or food for large grazing herbivores is a critically important conservation measure (Kutt and Gordon 2012).

Conclusion

The mammal fauna recorded in this study for Cape York Peninsula was moderately diverse despite the survey site bias toward Eucalyptus woodland sites. The composition of species recorded in the survey has not changed markedly from recent historical surveys (Winter and Atherton 1985), but there was a lack of abundance in many species (compared with Winter and Atherton 1985). The most abundant species I recorded was Rattus (new world rodents), and a sparse dasyurid fauna was recorded (three of six savanna species). Given the historical data in this region are only partially comparable with my survey, and many species were typically recorded in low numbers then and now, it is difficult to grasp whether the mammals have recently dissipated on Cape York Peninsula, changed in diversity in the distant past (1900–50), are naturally dispersed and of low abundance (Kutt et al. 2005), or have changed slowly over recent decades unnoticed. Unequivocally, we know some species, such as Dasyurus hallucatus, did have their populations destroyed by cane toads Rhinella marinus (Burnett 1997), but comparisons of the inventory of species from 1948 to 1979 described very little change in the total fauna (Winter and Allison 1980). There is a danger that acceptance of current patterns as near natural can severely underestimate the level of long-term mammal change (Bilney et al. 2010). For example, even though regional composition has remained intact, out of 172 woodland sites surveyed even the most frequently observed and abundant small mammals (Rattus tunneyi and Rattus sordidus) were only found in 19 sites. Three woodland species (Pseudomys delicatulus, 11 sites; Planigale maculata, 10 sites; and Leggadina lakedownensis, 8 sites) had a mean abundance of <0.1 when measured across woodland sites. This presents a degree of emptiness within the woodlands across much of the region, despite this habitat being overall the most species rich. A disturbing facet of this is the relatively low historical disturbance on Cape York Peninsula, but there is evidence that even subtle shifts in management can have substantial impact on woodland species and function (Crowley and Garnett 2001).

In this study there was a clear indication that both landscape and site factors influence the mammal diversity on Cape York Peninsula, and that the combination of broad and site-scale fire and vegetation configuration is most important. The relationship between fire and mammal richness and abundance is complex, interactive with other factors and species-specific. Fire frequency across the region is mediated by landscape heterogeneity, climate and elevation, and is highly dependent on weather and land use (Whitehead et al. 2005). The need for consistent systematic monitoring and experimental work examining the putative management actions is an important next step for reducing the uncertainty that limits my ability to define robust conservation actions for mammals in this region. For example, creation of landscape scale enclosures to test explicitly the effect of the removal of potential threatening processes (i.e. fire and introduced predators) will increase our understanding of the hysteresis of mammal recovery on Cape York Peninsula (Frank et al. 2014).

Author contributions

Justin Perry and Alex Kutt developed the idea, conducted the analysis, and wrote the manuscript, all authors collected data and edited the manuscript.

Table 5.1 The relative number of mammal records per site / location for this survey compared to other large surveys or data reviews on Cape York Peninsula. Rainforest species are excluded.

Scientific name	**Common name**	**This survey 2009-2012**		**Winter and Atherton 1985**		**Winter and Allison 1980**
		sites=202	**%**	**grid squares=73**	**%**	**recorded 1948 -1980**
Dasyuridae						
Dasyurus hallucatus	Northern quoll			5 (abundant)	6.8%	*
Planigale ingrami	long-tailed planigale	5	2.5%			
Planigale maculata	common planigale	10	5.0%	1 (scarce)	1.4%	*
Antechinus flavipes	yellow-footed antechinus					*
Sminthopsis archeri	chestnut dunnart			2 (uncommon)	2.7%	*
Sminthopsis virginiae	red-cheeked dunnart	3	1.5%	5 (common)	6.8%	*
Peramelidae						
Isoodon macrourus	northern brown bandicoot	10	5.0%	1 (scarce)	1.4%	*
Phalangeridae						
Spilocuscus maculatus	common spotted cuscus	3	1.5%	2 (uncommon)	2.7%	*
Trichosurus vulpecula	common brushtail possum	8	4.0%	9 (common)	12.3%	*
Petauridae						
Acrobates pygmaeus	feathertail glider			1 (scarce)	1.4%	*
Dactylopsila trivirgata	striped possum	1	0.5%			*
Petaurus breviceps	sugar glider	10	5.0%	9 (common)	12.3%	*
Petaurus norfolcensis	squirrel glider	10	5.0%			
Pseudocheirus peregrinus	common ringtail possum			1 (uncommon)	1.4%	*
Macropodidae						
Onychogalea ungifera	northern nailtail wallaby					*
Macropus agilis	agile wallaby	22	10.9%	44 (abundant)	60.3%	*
Macropus antilopinus	antilopine wallaroo	5	2.5%	15 (abundant)	20.5%	*
Macropus giganteus	eastern grey kangaroo	1	0.5%			*
Macropus parryi	whiptail wallaby					*

Scientific name	**Common name**	**This survey 2009-2012**		**Winter and Atherton 1985**		**Winter and Allison 1980**
		sites=202	**%**	**grid squares=73**	**%**	**recorded 1948 -1980**
Macropus robustus	common walleroo					*
Petrogale coenensis	Cape York rock-wallaby	1	0.5%			*
Thyloglae stigmata	red-legged pademelon			1 (uncommon)	1.4%	*
Wallabia bicolor	swamp wallaby					*
Muridae						
Hydromys chrysogaster	water rat	3	1.5%	6 (common)	8.2%	*
Leggadina lakedownensis	Lakeland Downs mouse	8	4.0%	3 (uncommon)	4.1%	*
Melomys burtoni	grassland melomys	2	1.0%	16 (abundant)	21.9%	*
Melomys capensis	Cape York melomys	15	7.4%	3 (common)	4.1%	*
Mesembriomys gouldii	black-footed tree-rat	1	0.5%			*
Pseudomys delicatulus	delicate mouse	13	6.4%	7 (abundant)	9.6%	*
Rattus leucopus	Cape York rat	5	2.5%	2 (scarce)	2.7%	*
Rattus sordidus	canefield rat	28	13.9%	16 (abundant)	21.9%	*
Rattus tunneyi	pale field-rat	35	17.3%	5 (scarce)	6.8%	*
Uromys caudimaculatus	giant white-tailed rat	4	2.0%	5 (common)	6.8%	*
Zyzomys argurus	common rock-rat	1	0.5%			*

Table 5.2 The results of the generalised linear mixed modelling for abundance and species richness of three functional groups and abundance of seven species (the species presented here are those that were abundant enough to warrant analysis). For the landscape model there were four fixed effects and property location was the random effect. The estimate is the direction of the effect, the Wald statistic is an equivalent to the F statistic and *P* is the significance level (up to 0.1).

	Fire frequency				**Vegetation complexity**				**Rainfall**				**Elevation**			
	Estimate	**SE**	**Wald**	**P**	**Estimate**	**SE**	**Wald**	**P**	**Estimate**	**SE**	**Wald**	**P**	**Estimate**	**SE**	**Wald**	**P**
Arboreal abundance	-1.441	0.854	2.84	0.092												
Arboreal richness	-1.709	0.817	4.38	0.036												
Macropod abundance					1.772	0.990	3.20	0.075								
Small mammal abundance	1.484	0.670	4.91	0.028					2.500	1.383	3.27	0.099				
Small mammal richness					0.842	0.425	3.91	0.049	1.772	0.644	7.56	0.023				
Planigale maculata	3.680	1.839	4.00	0.047												
Isoodon macrourus					3.123	1.591	3.85	0.051								
Petaurus norfolcensis	-3.728	1.188	9.84	0.002	-4.212	1.602	6.91	0.009					-6.482	2.035	10.14	0.002
Macropus agilis					3.531	0.986	12.82	<0.001								
Melomys capensis	-3.718	1.417	6.88	0.010												
Rattus sordidus	11.29	4.987	5.13	0.025												
Rattus tunneyi	-2.398	0.855	7.86	0.006	1.811	0.755	5.74	0.017					3.431	1.730	3.93	0.052

Table 5.3 The results of the generalised linear mixed modelling for abundance and species richness of three functional groups and abundance of seven species. For the site model there were four fixed effects and property location was the random effect. The estimate is the direction of the effect, the Wald statistic is an equivalent to the F statistic and *P* is the significance level (up to 0.1).

	Time since wildfire				**Strata**				**Woody cover**				**Ground cover**			
	Estimate	**SE**	**Wald**	**P**	**Estimate**	**SE**	**Wald**	**P**	**Estimate**	**SE**	**Wald**	**P**	**Estimate**	**SE**	**Wald**	**P**
Arboreal abundance	0.022	0.007	9.41	0.002												
Arboreal richness					0.485	0.299	3.54	0.060	0.018	0.007	6.95	0.008				
Macropod abundance	0.013	0.007	4.98	0.027												
Small mammal abundance	0.534	0.166	10.31	0.002	-0.344	0.099	12.04	<0.001					0.026	0.004	29.47	<0.001
Small mammal richness	0.258	0.166	4.96	0.027									0.006	0.003	3.19	0.075
Isoodon macrourus													0.031	0.146	9.57	0.002
Petaurus norfolcensis	0.028	0.009	8.39	0.004												
Macropus agilis									0.023	0.009	5.95	0.002	0.028	0.009	5.95	0.016
Macropus antilopinus									-0.071	0.039	3.26	0.073				
Melomys capensis	1.103	0.352	9.77	0.002					0.016	0.006	7.48	0.007				
Rattus sordidus									-0.069	0.022	9.38	0.003	0.044	0.013	11.62	<0.001
Rattus tunneyi	1.379	0.252	29.91	<0.001	0.496	0.258	3.68	0.056					0.014	0.007	3.47	0.064

Appendix Table 5.1. Complete mammal species list for the survey indicating the number of sites recorded in each of the four main habitats surveyed, mean abundance per habitat and number of sites where mammals were present or absent.

Scientific name	**Common name**	**Grassland**		**Melaleuca woodland**		**Eucalyptus woodland**		**Closed forest and Dune scrub**	
		n=10	**Mean**	**n=31**	**Mean**	**n=141**	**Mean**	**n=20**	**Mean**
Sites with mammals absent		1 (10.0%)		11 (35.4%)		67 (47.5%)		1 (0.5%)	
Sites with mammals present		9 (90.0%)		20 (64.6%)		74 (52.5%)		19 (99.5%)	
Arboreal abundance			0.00		0.19		0.17		0.30
Arboreal richness			0.00		0.16		0.15		0.25
Macropod abundance			0.00		0.35		0.38		0.15
Macropod richness			0.00		0.16		0.16		0.10
Small mammal abundance			14.6		1.29		0.77		6.25
Small mammal richness			1.70		0.67		0.49		1.55
Dasyuridae									
Planigale ingrami	long-tailed planigale	5	1.40	0	0.00	0	0.00	0	0.00
Planigale maculata	common planigale	0	0.00	2	0.06	8	0.08	0	0.00
Sminthopsis virginiae	red-cheeked dunnart	2	1.10	0	0.00	0	0.00	1	0.05
Peramelidae									
Isoodon macrourus	northern brown bandicoot	0	0.00	2	0.16	8	0.09	0	0.00
Phalangeridae									
Spilocuscus maculatus	common spotted cuscus	0	0.00	0	0.00	1	0.01	2	0.10
Trichosurus vulpecula	common brushtail possum	0	0.00	1	0.03	5	0.04	2	0.15
Petauridae									
Dactylopsila trivirgata	striped possum	0	0.00	0	0.00	0	0.00	0	0.00
Petaurus breviceps	sugar glider	0	0.00	1	0.03	9	0.08	0	0.00
Petaurus norfolcensis	squirrel glider	0	0.00	3	0.13	6	0.04	1	0.05
Macropodidae									

Scientific name	Common name	Grassland		Melaleuca woodland		Eucalyptus woodland		Closed forest and Dune scrub	
		n=10	Mean	n=31	Mean	n=141	Mean	n=20	Mean
Macropus agilis	agile wallaby	0	0.00	5	0.35	15	0.26	2	0.15
Macropus antilopinus	antilopine wallaroo	0	0.00	0	0.00	5	0.09	0	0.00
Macropus giganteus	eastern grey kangaroo	0	0.00	0	0.00	1	0.01	0	0.00
Petrogale coenensis	Cape York rock-wallaby	0	0.00	0	0.00	1	0.01	0	0.00
Muridae									
Hydromys chrysogaster	water rat	0	0.00	1	0.03	1	0.01	1	0.05
Leggadina lakedownensis	Lakeland Downs mouse	0	0.00	0	0.00	8	0.06	0	0.00
Melomys burtoni	grassland melomys	0	0.00	1	0.03	1	0.01	0	0.00
Melomys capensis	Cape York melomys	0	0.00	1	0.13	5	0.06	9	1.45
Mesembriomys gouldii	black-footed tree-rat	0	0.00	0	0.00	1	0.01	0	0.00
Pseudomys delicatulus	delicate mouse	0	0.00	2	0.10	9	0.08	2	0.25
Rattus leucopus	Cape York rat	0	0.00	0	0.00	0	0.00	5	1.10
Rattus sordidus	canefield rat	5	11.20	6	0.32	13	0.20	4	0.30
Rattus tunneyi	pale field-rat	9	0.90	6	0.45	13	0.16	7	2.95
Uromys caudimaculatus	giant white-tailed rat	0	0.00	0	0.00	2	0.02	2	0.10
Zyzomys argurus	common rock-rat	0	0.00	0	0.00	1	0.01	0	0.00

Chapter 6. The Goldilocks effect: Intermediate heterogeneity in vegetation structure maximises diversity of reptiles in savanna

Introduction

Local- and landscape scale fire, vegetation and climate patterns, and their interactions, are significant ecological determinants of plant and animal distributions across the globe (Bond et al. 2005). Understanding the different responses of species, guilds and taxonomic groups to disturbance (e.g., fire) at different scales is central to effective and appropriate conservation management of species and communities (Diniz et al. 2011; Santos and Cheylan 2013). Assemblage patterns and distribution of large mobile species such as birds and large mammals, are often determined at the landscape level (Price et al. 2010; Ziembicki and Woinarski 2007). For smaller, more sedentary species, like reptiles, local factors such as substrate, habitat structure and the thermal dynamics of their location may have more influence on their abundance and distribution (Price et al. 2010; Valentine and Schwarzkopf 2009), although medium-scale factors, such as habitat condition or extent of clearing at a site, are still relevant (Bruton et al. 2016).

Herpetofauna play a fundamental role in the trophic organisation of tropical and arid natural systems (Read and Scoleri 2015). Despite the widely acknowledged importance of reptiles in ecology, there is very little literature exploring their response to common disturbances (Christoffel and Lepczyk 2012). In the tropical savanna woodlands of northern Australia the influence of imposed disturbance regimes, such as fire, introduced species, tree clearing or grazing pressure, on reptile assemblage patterns has received little attention (c.f., Abom and Schwarzkopf 2016; Abom et al. 2015; Trainor and Woinarski 1994; Valentine and Schwarzkopf 2009).

Around 20% of the earth's surface is categorised as tropical savanna (Mouillot and Field 2005; Russell-Smith et al. 2003; van der Werf et al. 2008). In Australia about one third of the land mass falls into this vegetation category, which is dominated by open woodlands with relatively low topographic complexity (Woinarski et al. 2007). As with much of the Australian continent, savannas support a very diverse reptile fauna that is well adapted to the extremes of climate and very frequent fire (Woinarski et al. 2007). Previous research has demonstrated a link between fire at site scales (~1ha) and reptile community dynamics (Abom and Schwarzkopf 2016; Price et al. 2010; Woinarski et al. 1999a). Thermal heterogeneity is a key factor influencing reptile distributions (Goodman 2009) and is highly correlated with insolation and vegetation structure (Storlie et al. 2014). Consequently, fire management that alters vegetation structure can influence reptile assemblage patterns (Abom et al. 2015; Santos and Cheylan 2013; Valentine and Schwarzkopf 2009). Given the interaction between fire, vegetation structure and insolation, I propose that reptile diversity should respond to subtle changes in vegetation cover and structure, despite perceptions that savanna woodlands are homogenous (Price et al. 2010). The influence of commonly used correlates for vertebrate community structure, such as categorical vegetation types and remotely sensed fire frequency, may be too spatially and temporally imprecise in reflecting the habitat features that shape reptile community structure, because they thermoregulate behaviourally, and have limited dispersal (Vickers and Schwarzkopf 2016). Therefore, I predict that local scale heterogeneity within savanna woodlands (i.e., variation in vegetation cover), and the transition between major vegetation types (i.e., from grassland to woodland to closed forest) will exert more influence on reptile diversity than does landscape vegetation pattern (as assessed by remotely sensed fire frequency).

The ability to predict the likely response of different taxa to varying environmental circumstances, in this case across a gradient of fire and vegetation structure, will allow us to better design prescriptive management interventions. This is particularly important in northern Australia where there are economic incentives to change fire regimes for the abatement of greenhouse gas emissions (Russell-Smith et al. 2013). The link between fire regime and reptile diversity is unclear. Heliothermic and thigmothermic reptiles rely on thermal heterogeneity in the landscape, which can be favoured by intermediate fire frequencies (Huey et al. 2009; Perry et al. 2016). So if one aim of fire management is to increase reptile diversity, then, hypothetically, fire should be managed to maintain or increase structural diversity at fine scales (metres) which aids behavioural thermoregulation (Vickers et al. 2011). To understand the response of any organism to disturbance, I first need to describe the patterns of species distributions along an environmental gradient (Ferrier et al. 2007).

Although there are the well-developed theoretical frame works predicting the likely temperature tolerances of reptiles (Vickers et al. 2011), explicit links between reptile populations in natural systems and factors influencing natural insolation (vegetation structure) have not been well established. In the northern Australian wet tropics there is an established correlation between above-canopy air temperature (Grant et al. 2008) and the much reduced temperatures, experienced by many reptiles, that are provided by canopy and cover (Shoo et al. 2010; Storlie et al. 2014). This suggests there may be a strong relationship between thermal heterogeneity and proxies for vegetation structure such as increasing ground cover, total woody cover, foliage projection and vertical structure (number of different strata). In this study, we examine the relationship between reptile diversity and vegetation structural patterns, and concurrently the relationship between fire frequency at several scales and vegetation structure. I describe the response of reptiles to a gradient of fire and vegetation structure using data collected from 202 sites on Cape York Peninsula, northern Australia. I investigate three important and nested questions: (i) how well do remotely sensed fire frequency reflect measures of vegetation structure in my study sites; (ii) how well do landscape and local site-scale vegetation measures and fire frequency account for reptile diversity and; (iii) can fire frequency be used to predict reptile patterns, or are local habitat factors that reflect the potential thermal features (i.e. total woody cover) more important? I discuss the results in the context of contemporary fire and vegetation management practices in northern Australia.

Methods

Study region

The Cape York Peninsula bioregion (Cape York Peninsula) represents the northern-most section of the state of Queensland, Australia, and includes an area ~13 million ha (Figure 6.1). The mean annual rainfall in this region varies from >2000 mm at Lockhart River (12º 28’ S; 143º 12’ E) on the central east coast down to approximately 1000 mm at Palmerville (16º 00’S; 144º 02’ E). Rainfall is primarily orographic and monsoonal on the eastern peninsula and monsoonal in the west (Perry et al. 2011b).

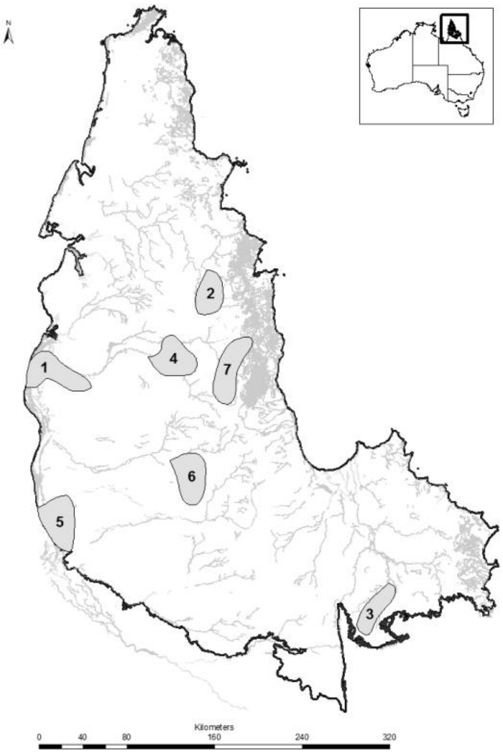


Figure 6.1. The location of the survey areas (grey polygons) and Cape York Peninsula within Australia. Numbers 1 – 7 in the polygons relate to the site numbers in the summary data (Table 6.2).

Survey methods

Vertebrate fauna surveys were conducted in the study area from 2009-2012 during the dry season (June to November). A total of 202 sites were established in seven property clusters (Figure 6.1) and were stratified by fire frequency within broad vegetation groups, defined by Neldner and Clarkson (1995). The number of sites chosen in each broad vegetation group reflected the relative dominance of each type on Cape York Peninsula. Of these 202 sites 185 were categorised as woodland (Queensland Herbarium 2014).

Reptile sampling at each site used a standardised approach, conducted within a one-ha quadrat (Kutt et al. 2012c). In each quadrat I placed four pitfalls (40 cm deep and 30 cm diameter), 10 m apart and arranged in a 'T' configuration (each arm with 10 m of drift fence) and six funnel traps (one on either side of the draft fence, at the ends of the 'T'). Trapping was supplemented with three diurnal and two nocturnal timed searches each of 20 search-minutes duration conducted within the one-ha quadrat. Each quadrat was surveyed over a four-night, five-day interval.

For each quadrat I calculated richness, measures of composition and index of abundance for each species, a standard method for tropical savanna surveys (Kutt et al. 2012c). This index was a cumulative total of all captures and observations, and is hereafter referred to as 'abundance'. Several studies have demonstrated that variation in trap success rates for an individual species among sites or time periods provides a generally good measure of variation underlying density of that species between sites or time periods (Hopkins and Kennedy 2004; Slade and Blair 2000).

Predictor variables

I used both site-based and remotely sensed fire and vegetation variables as predictors of reptile composition, abundance and species richness. The variables were chosen because they are recognised and published determinants of vertebrate patterns in northern Australia (Kutt et al. 2012c; Perry et al. 2011b; Price et al. 2013; Ward and Kutt 2009). The landscape level variables were: fire frequency (defined as years burnt between 2000 and 2013) derived from pre-processed MODIS satellite imagery (NAFI 2014); vegetation complexity measured as the number of different broad vegetation groups (Neldner and Clarkson 1995) within a 1 km radius of the centre of the site (~314 ha area); Foliage projection was calculated as mean foliage projection cover in a one kilometre radius (DSITIA 2015). Foliage projection cover is derived using Landsat imagery (~30 m resolution) and quantifies the percentage of ground area occupied by the vertical projection of foliage. This provides a continuous variable that reflects subtle variance in structure within the categorical broad vegetation groups (Queensland Herbarium 2014). For example within the vegetation type I am focusing on in this study, open woodlands, there is a natural heterogeneity influenced by landscape features, such as geology, soil and topographic position (Price et al. 2005), where some areas more closely resemble closed forest and others are more like grasslands. Mean values in a 1km moving window were derived using ArcMap 10.2.2 (ESRI 2014) to account for spatial heterogeneity in foliage projection and habitat diversity at a resolution that is meaningful to the species I am examining. The site-based variables were: total woody (tree and shrub) vegetation cover (hereafter total woody cover) measured as crown cover intersecting a 100-m line transecting the centre of the one-ha site; Strata, measured as the total number of vegetation strata (i.e., canopy, sub-canopy, recruiting trees, shrub, and ground cover, maximum strata = 5) in the one-ha area; and ground cover measured as live plant cover in five one-by-one metre plots down the central 100-m transect. I recognise that foliage projection cover and total woody cover are somewhat correlated but retain the two variables in the analysis to account for the below-canopy complexity that cannot be detected from the remotely sensed foliage projection cover (see Appendix Figure 6.1).

Data Analysis - Relationship between fire and vegetation structure.

To determine the correlation of predictor variables at site and landscape scales I derived correlation coefficients between the landscape scale and site-scale environmental factors (number of regional ecosystems within 1km of site, number of strata at the site, average foliage projection cover within 1km of site, total woody cover ~1ha, average ground cover ~1ha and fire frequency) *via* the corrplots (Wei 2015) package in R (R Development Core Team 2014). For testing the strength of the relationship between the most commonly used remotely sensed proxy for canopy cover (foliage projection cover) and the site-scale counterpart (total woody cover) I used a least squares regression and produced an R-squared value.

After establishing the relationship between landscape and site-scale woody structure I used quantile regression to test the influence of fire frequency on these variables. Quantile regression was used as the data had unequal variation and this method provides an estimate of the maximum, rather than the mean influence of x on y (Cade and Noon 2003). For the site-based variable (total woody cover) I examined fire frequency with total woody cover at the 202 sites. For the remotely sensed foliage projection cover values I created a regular sample grid for woodland vegetation on Cape York Peninsula of ~60000 points using ArcMap 10 (ESRI 2014). The Cape York Peninsula grid was intersected with fire frequency and foliage projection cover value and used in the quantile regression. To clarify the spread of the data I produced a box and whisker graph (mean, standard deviation and range) using the regional foliage projection cover and fire frequency with R (R Development Core Team 2014) using the ggplots2 package (Whickam 2009).

Data analysis - Diversity of reptiles along an environmental gradient

In nature, species community composition is rarely partitioned by simple, well-defined categorical boundaries; that is, species composition does not turnover entirely when shifting between broad vegetation types. Furthermore, within broad vegetation categories there is a gradient of environmental variables (micro-climate and variance in structure) that influences the composition and abundance of vertebrate communities (Ferrier et al. 2007). The dissimilarity (distance) between environmental variables that forms a gradient of change is often referred to as environmental space and this is often a better predictor of species composition than geographic distance. To examine the changes in reptile diversity when considering changes in environmental space I used a Multinomial Diversity Model (MDM) (De'Ath 2012). The MDM parameterises Shannon diversity and links it to the multinomial linear model. This means I can predict diversity as a function of quantitative or categorical environmental variables. The MDM uses entropy as a measure similar to sum of squares, which I use to explore the relative effects of my predictor variables using additive models. The additive models reflect my aim to determine the most influential predictors of reptile diversity. I first tested the response of entropy to total woody cover on its own then incrementally added the remaining variables and report the changes in entropy, diversity and delta entropy and diversity. The full model was total woody cover + foliage projection cover + strata + fire frequency + ground cover. Diversity and entropy are analogous to each other but I derive diversity (the exponent of entropy), which reflects the effective number of species, to aid in the interpretation of the models. For each model I present the change in mean site entropy and diversity in response to the environmental variables. I also report delta entropy and diversity representing changes in entropy in response to the configuration of proportional abundances with each model which reflects the influence of environment on turnover.

Additionally, I tested the relative influence of a landscape scale model (containing remotely sensed variables) and a site-scale model (containing variables measured in the 1ha sites) and a combined site and landscape model. I report the changes in entropy by model for each species ranked by abundance relative to a constant or gamma diversity model (fits a constant for each species across sites) and a site or alpha diversity model (fits species data exactly) using an entropy plot. I also use the model outputs to visualise the interactions between influential predictor variables and diversity in three dimensions using bi-plots, which provides a means of interpreting the non-linear interactions between environment and diversity in environmental space. All MDM analysis were done in R (R Development Core Team 2014) using the MDM package (Death 2013).

Results

My survey recorded a total of 5905 individual reptiles, comprising 27 species across 202 sites located on seven properties on Cape York Peninsula during four years of surveying (2009 – 2012) (Figure 6.1, Table 6.2).

Fire frequency and woodland structure

Remotely sensed canopy cover (foliage projection cover) had a strong linear relationship with site-based measurement woody structure (total woody cover) ($R^2 = 0.4$, $p = <0.0001$) (see Appendix Figure 6.2). The relationship between vegetation structure and remotely sensed fire frequency wasn't as strong, and was more variable. Fire frequency was negatively correlated with total woody cover ($r = -0.34$) as was foliage projection cover ($r = -0.21$) and local vegetation complexity ($r = -0.22$). Ground cover was positively correlated with fire frequency ($r = 0.19$) and number of vegetation strata (Strata) had a very weak correlation with fire frequency and was most strongly correlated with foliage projection cover and total woody cover ($r = 0.14$). The strongest correlation for all variables was between total woody cover and foliage projection cover ($r = 0.64$) suggesting that the remotely sensed variable foliage projection cover provides a reasonable approximation of the complexity of vegetation structure at site scales.

When considering the sample of woodlands for the entire Cape York Peninsula region, by least squares regression, fire frequency was a poor predictor of foliage projection cover(Figure 6.2a), and at the site-scale for total woody cover (Figure 6.2b) except at the 90% quantile. The effect of fire frequency on the upper limit of foliage projection cover was clear: in all but the most frequently burnt (13-14 years out of 14) and least frequently burnt (1-2 years out of 14) the mean and standard deviation of foliage projection cover were remarkably similar (Figure 6.3). The upper limit of foliage projection cover increased when fire frequency was below 8, accompanied by an increased inter-quartile-range as fire frequency decreased to 1 (Figure 6.3). The upper limit of foliage projection cover decreases with fire frequency above 8 (Figure 6.3). Sites in the 90% quantile for foliage projection cover represent only ~6% of the total sample for Cape York Peninsula woodlands.

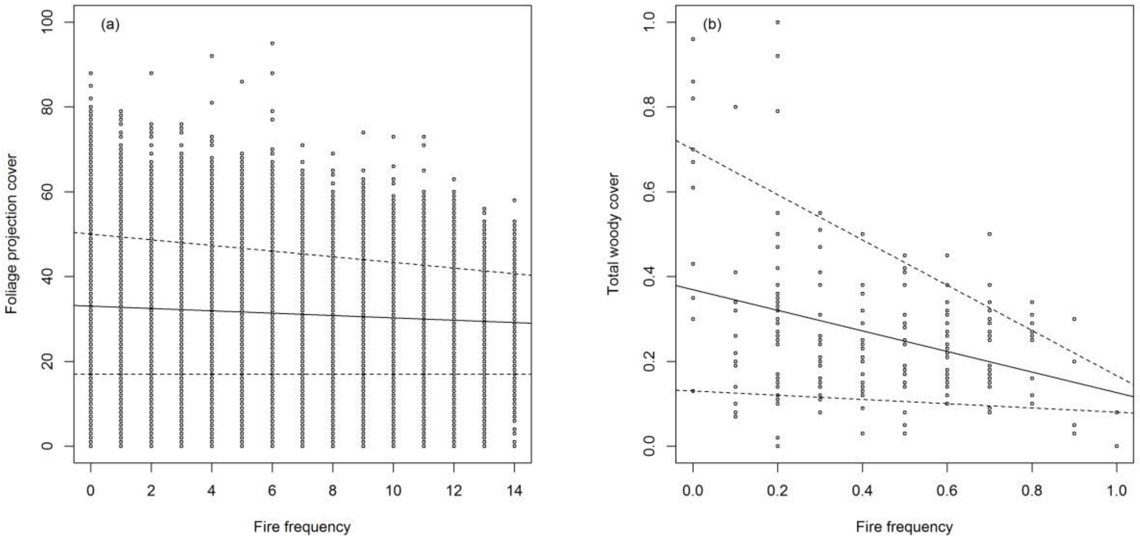


Figure 6.2 Least squares regression demonstrating the linear relationship between fire frequency and foliage projection cover (a) in ~60000 regular sample of woodland sites across Cape York Peninsula and fire frequency and total woody cover at sites (b) using the 10% quantile regression (bottom dashed line), least squares regression (middle solid line) and 90% qunatile regression (top dashed line).

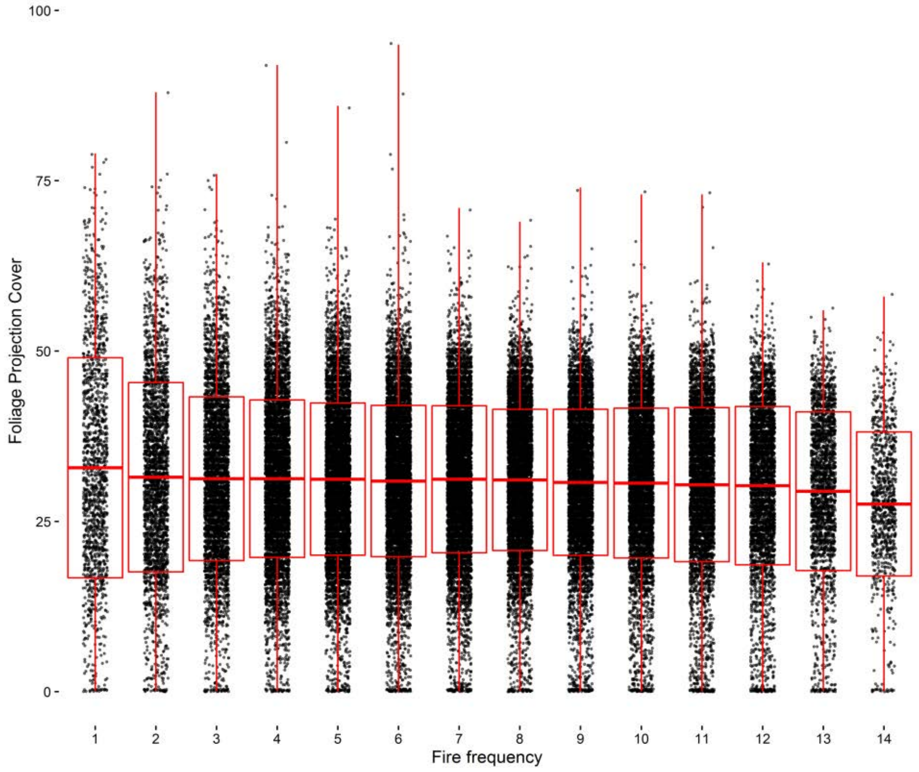


Figure 6.3 Mean, standard deviation and range of foliage projection cover values in each fire frequency category (1-14). Black points in each category are the intersecting fire frequency and foliage projection cover samples.

Reptile diversity and vegetation structural gradients.

Additive MDM models identify total woody cover and foliage projection cover and their interactions as the most influential predictors for reptile diversity in my study area (Table 6.1). Most of the variance is explained by the total woody cover model. The addition of Strata, fire frequency and ground cover provided little further explanatory power (Table 6.1). Entropies accounted for by site and landscape scale models varied across the 26 species (Figure 6.4). Entropy of the most abundant and wide spread litter skinks, *Carlia sexdentata* and *Carlia munda* was most influenced by the landscape model. The same pattern was evident to a lesser degree with the tree skinks *Cryptoblepharus metallicus*, *Cryptoblepharus virgatus,* largely fossorial *Ctenotus brevipes, Eremiascincus pardalis, Glaphyromorphus nigricaudis,* the agamid *Diporiphora bilineata* and the arboreal varanid *Varunus scalaris*. The site-scale model was more influential for *Ctenotus spaldingi, Carlia vivax, Carlia storri, Gehyra baliola, Carlia schmeltzii,* and *Furina ornata.* The combined site and landscape model favoured the litter skink *Carlia jarnoldae*, large bodied skink *Ctenotus robustus* and tree skink *Cryptoblepharus adamsi.* The remaining species were not influenced greatly by any of the models (Figure 6.4).

Table 6.1. Changes in parametric Shannon entropy (^{1}H) and change in entropy ($\Delta\ ^{1}H$) and Shannon diversity (^{1}D) and change in diversity ($\Delta\ ^{1}D$) from the constant model (fits a constant for each species across all sites) in response to predictor variables.

Models	^{1}H	$\Delta\ ^{1}H$	^{1}D	$\Delta\ ^{1}D$
Constant	2.81		16.53	
total woody cover	2.70	0.11	14.81	1.12
total woody cover + foliage projection cover	2.63	0.06	13.88	1.07
total woody cover + foliage projection cover + Strata	2.60	0.03	13.45	1.03
total woody cover + foliage projection cover + Strata + fire frequency	2.57	0.03	13.11	1.03
total woody cover + foliage projection cover + Strata + fire frequency + ground cover	2.54	0.03	12.73	1.03

Table 6.2. Abundance of reptiles, ordered from most abundant to least abundant, across the seven Cape York Peninsula properties. P1 – P7 represent sites (S) clustered within the seven properties (P).

Species	P1 (S28)	P2(S30)	P3(S27)	P4(S28)	P5(S30)	P6(S30)	P7(S30)	Total
Carlia sexdentata	326	271		22	49	16	369	1053
Carlia jarnoldae	1	281	63	149		30	154	678
Gehyra dubia	64	66	83	154	72	84	107	630
Carlia munda	32		71	82	182	191	3	561
Ctenotus spaldingi	60	113	6	165	19	122	15	500
Lygisaurus aeratus	4	56	42	82	44	121	67	416
Diporiphora bilineata	47	86	21	37		11	40	242
Cryptoblepharus metallicus	27	33	21	43	21	65	12	222
Heteronotia binoei	23	17	49	49	10	50	5	203

Oedura castelnaui	31	48	36	13	19	15	22	184
Amalosia rhombifer	12	41	31	29	18	12	28	171
Carlia vivax		21	13	10		68	44	156
Morethia taeniopleura	38	1	19	45		18	8	129
Cryptoblepharus virgatus	13	28		20	25	15	26	127
Carlia storri	6	19					86	111
Ctenotus brevipes	63	15	11	6	6	3	6	110
Eremiascincus pardalis				10	31	51	12	104
Gehyra baliola		19	16				42	77
Nactus eboracensis	8	18		20		5	23	74
Glaphyromorphus nigricaudis	3	13					17	33
Ctenotus robustus				2	7	18		27
Varanus scalaris	1	3	1	3	12	1		21
Cryptoblepharus adamsi			18					18
Carlia schmeltzii		1	8	1		4	4	18
Tropidonophis mairii	3	1				4	9	17
Furina ornata		3	1	5	1	1	2	13
Dendrelaphis punctata	2	2	1	2	2		1	10

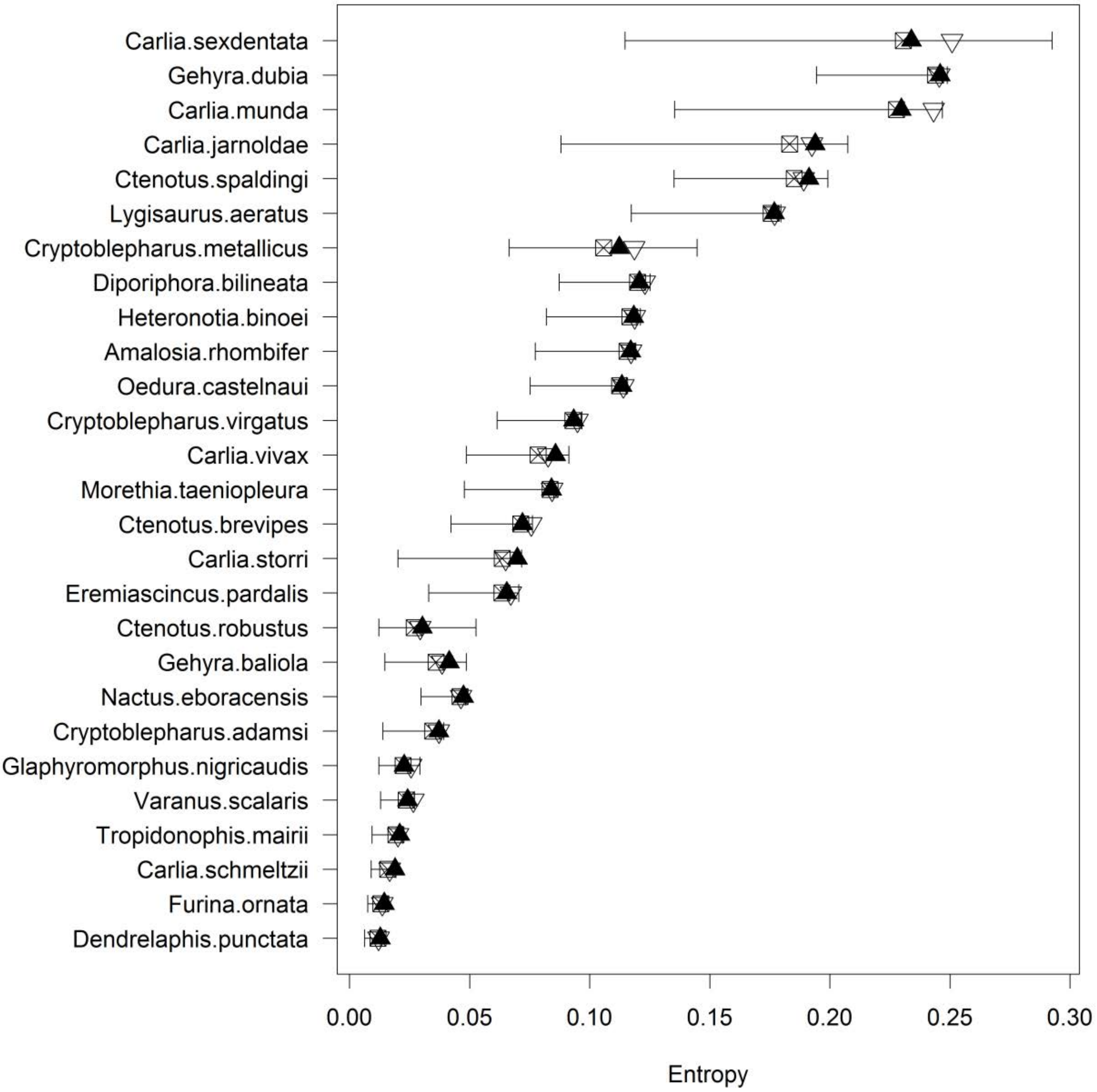


Figure 6.4 Entropy plot of species scaled by abundance across sites. The left hand bar represent the site model, right hand bar represents a constant model, inverted open triangle is total woody cover, solid triangle is total woody cover + foliage projection cover, solid circle total woody cover + foliage projection cover + Strata, open square is total woody cover + foliage projection cover + Strata + fire frequency and crossed circle is total woody cover + foliage projection cover + Strata + fire frequency + ground cover.

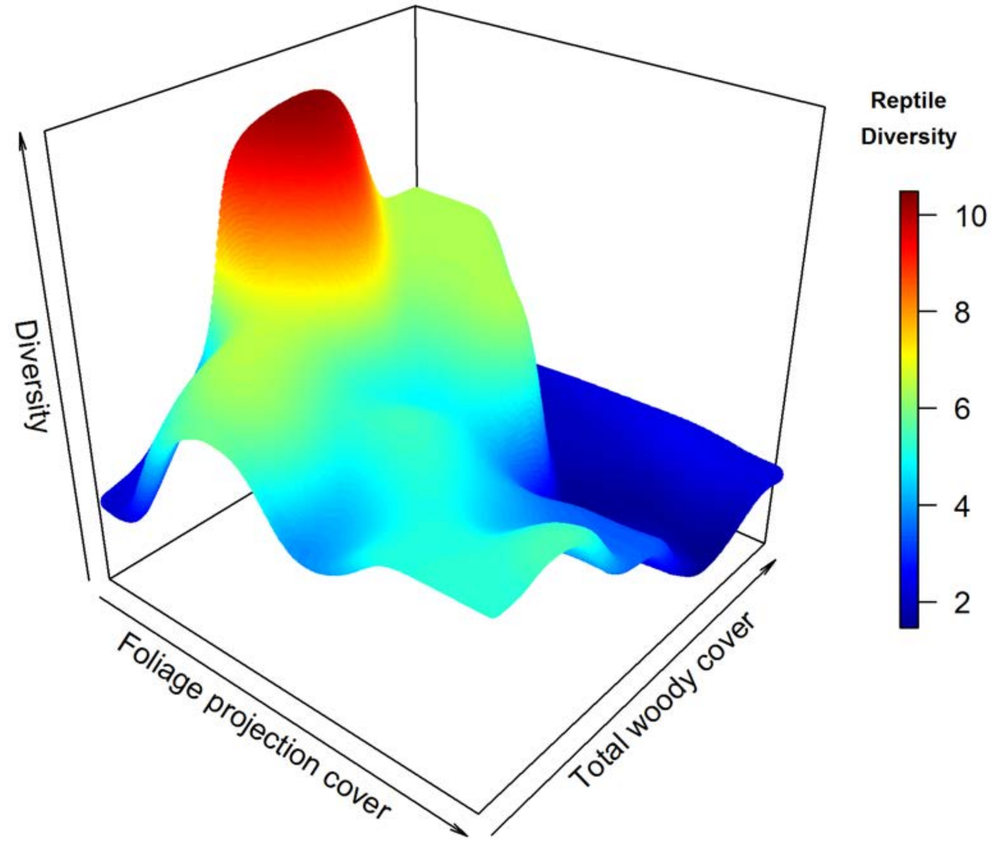


Figure 6.5 The relationship between Reptile diversity with total woody cover and foliage projection cover. Predicted reptile diversity (z) is scaled by the interaction between total woody cover (x) and fire frequency (y).

Reptile diversity changed across the vegetation structural gradient and was highest in areas of low- to mid-complexity as defined by total woody cover and foliage projection cover (Figure 6.5). When accounting for both remotely sensed (foliage projection cover) and site-scale measurements of vegetation structure (total woody cover) I found a very strong relationship between reptile diversity and moderately low foliage projection cover and total woody cover demonstrating a relationship between below-canopy complexity and canopy cover (Figure 6.5). Where total woody cover was very high reptile diversity was very low and decreasing foliage projection cover didn't dramatically influence diversity except at the lower end of the foliage projection cover and total woody cover interaction. Conversely, lower total woody cover positively influenced the diversity of reptiles at the higher end of foliage projection cover, suggesting that there was a more complex interplay between site level complexity, expressed by tree density, and the coarser remotely sensed proxy which can only detect canopy cover (see Appendix Figure 6.1).

There was a complex interactive effect between total woody cover and fire frequency on predicted reptile richness, where fire frequency was very high and total woody cover was moderately low, reptile richness was high. There was another peak of reptile richness where total woody cover was very low and fire frequency was moderate. Where fire frequency was very high and total woody cover was very low (i.e., structure was open and homogenous), and also where total woody cover was high but fire frequency low, reptile diversity was lowest. Reptile diversity remained relatively high across the fire frequency gradient where total woody cover was moderately low (Figure 6.6).

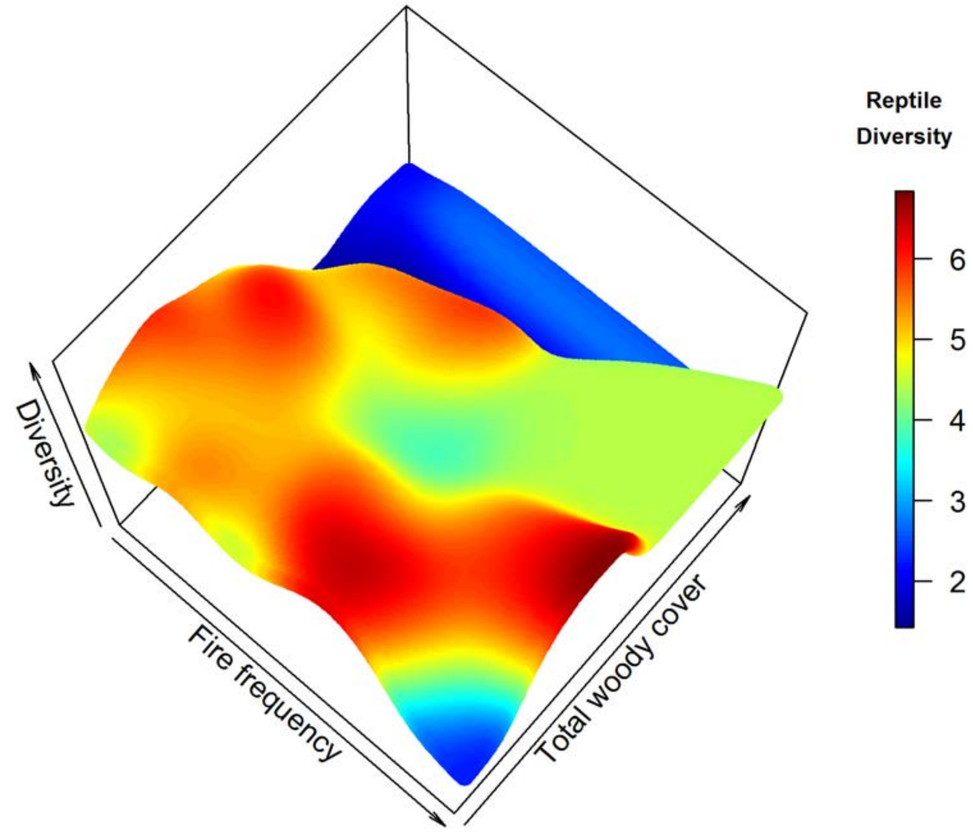


Figure 6.6 The relationship between reptile diversity, fire frequency and total woody cover (total woody cover). The predicted reptiles diversity (z) is scaled by the interaction between foliage projection cover (x) and total woody cover (y).

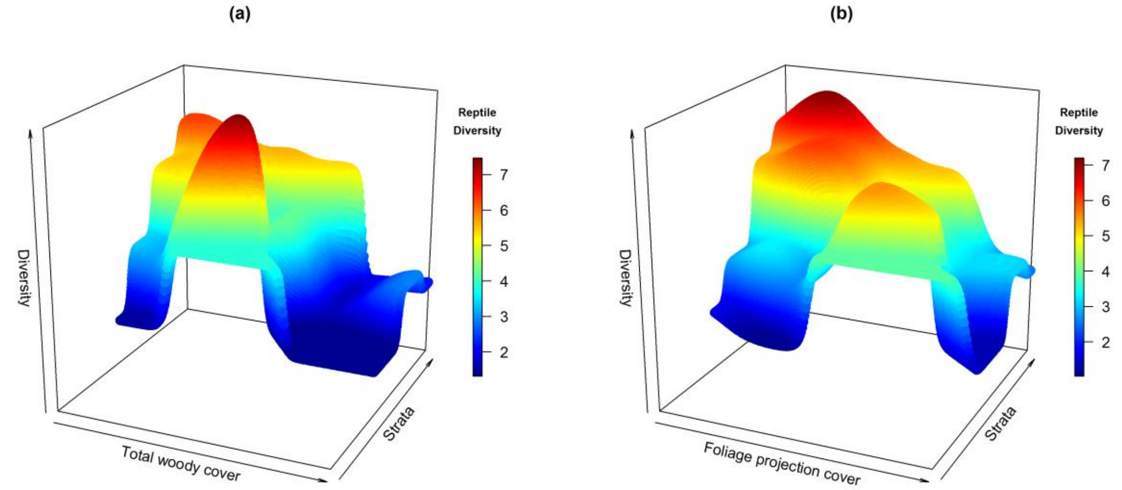


Figure 6.7 The changes in predicted reptile diversity along the gradient of: (a) the interaction between total woody cover and strata, and; (b) the interaction between foliage projection cover and Strata. Predicted diversity (z) scaled by the interaction between a) total woody cover (x) and Strata (y) and b) foliage projection cover (x) and Strata (y) .

Vertical complexity, as measured in this case by the number of vegetation strata, was less influential on reptile diversity yet demonstrated a unique interaction with foliage projection cover and total woody cover (Figure 6.7). Again, the influence on diversity was similar between the landscape scale variable (foliage projection cover, Figure 6.7a) and the site-scale variable (total woody cover, Figure 6.7b). A distinct peak in reptile diversity was evident with intermediate woody cover and moderately complex vertical strata. Where total woody cover was very low and Strata was very high, representing very open, homogenous landscapes where structural complexity was increased through the presence of shrubs and trees, reptile diversity was the highest. Where vertical complexity was low, only areas with medium total woody cover support high reptile diversity, with a sharp decline in diversity observed at high and low total woody cover. The influence of Strata on diversity was negative with increasing total woody cover above ~50%, although there was a small positive, influence on reptile diversity where total woody cover was very high (Fig 6.7a). The patterns of diversity for foliage projection cover and Strata were very similar to those for total woody cover and Strata, although diversity was much higher across the interacting foliage projection cover and Strata gradient (Figure 6.7b).

Discussion

In this study we sought to clarify the relationship between fire frequency, vegetation structure at local and landscape scales and reptile diversity.   I found that remotely sensed fire frequency only influenced vegetation structure at the upper and lower extremes (very dense and very open areas). There was a clear linear relationship between the remotely sensed, landscape scale (foliage projection cover) and site-scale vegetation structure (total woody cover) although the relationship was not perfect particularly at the upper limits of vegetation density and cover. There was also a strong relationship between these two measures of woody vegetation structure and reptile diversity, though it was non-linear, and the reptile community response varied with different environmental factors. Importantly, the site-scale metrics were better at describing subtle differences in the response of some of the more restricted species.

Relationship between remotely sensed fire frequency and vegetation structure.

Fire frequency did not have a consistent effect on vegetation structure, with a strong effect evident at the extremes: those areas that burnt very frequently (every year) or rarely (1 in 14 years). Vegetation patterns, therefore, are not strongly predicted by fire frequency in the median fire frequency zones (i.e., the mean, standard deviation, and range of foliage projective cover were strikingly similar in all but the extreme ends of the fire frequency spectrum) at the temporal scale in which it is commonly measured. Thus, a very significant change in fire frequency is required before structural change will be detectable in most savanna vegetation types. Other studies have found that long unburnt tropical savannas (>20 years) become more closed, with dense, and more jungle-like vegetation (Woinarski et al. 2004b). Also, models of the effect of gamba grass (*Andropogon gayanus*) invasion in savanna woodlands suggest that frequent, hot fires initially do not change woodland structure until a threshold is reached and the woody strata disappear (Rossiter et al. 2003). Therefore, research examining the influence of fire frequency on biodiversity needs to account for temporal thresholds and altered intensity of fire, and should stratify the distribution of fire and vegetation structure to provide a typology of expected responses before generalising among vegetation types. My study provides a basis for assessing the potential impact of altered vegetation structure on reptiles in tropical savanna ecosystems. Additionally, I provide much-needed empirical observations of the responses of reptiles to altered fire regimes, one of the most commonly applied management interventions in tropical savanna ecosystems.

Influence of vegetation structure on reptile diversity

In my study the variables that most influenced reptile diversity were continuous and reflected gradual changes in tree and shrub cover and complexity. At the broadest scale, I found a clear relationship between a coarse proxy for insolation (foliage projection cover) and reptile diversity. As this variable was remotely sensed, it only reflected the total canopy cover as seen from above, and doesn't really describe the complexity that exists below-canopy (see Appendix Figure 6.1). The site level metrics that reflected the below-canopy complexity (vertical structure – Strata and tree density – total woody cover), were strongly related to variance in reptile diversity, and interacted. Clearly, for species influenced by variables at fine scales, below-canopy metrics were required. Pavey et al (2015) argue that the assessment of habitat suitability for homogenous systems requires a deeper understanding of species response to environmental factors. My study suggests that intact savannas would also benefit from this approach.

In tropical savanna woodlands, I found lower reptile diversity in areas with low and high total woody cover and foliage projection cover. Although I found lower diversity at the structural extremes, these areas supported unique species critical to gamma diversity. For example, fossorial species (*Glaphyromorphus nigricaudis, Eremiascincus pardalis and Furina ornata*) occurred only in areas with closed canopies and high ground cover or litter. Conversely, at the other end of the vegetation spectrum, large bodied species with high heat tolerance (*Ctenotus robustus, Diporiphora bilineata* - this study*, Demansia vestigiata, Pseudonaja textilis and Oxyuranus scutellatus* - incidental records) occurred primarily in coastal grasslands that burn very frequently. These unique ecosystems represent ~6% of the study area, generally reflecting the spatial configuration of broad vegetation types in northern Australia. It is likely that the most influential management interventions for maintaining gamma diversity will be focused on the ~6% of the landscape that holds the unique alpha diversity where the vegetation structure is significantly different from the broader landscape. While providing shelter and stability, threats to these areas pose significant contemporary and future threats to their geographically restricted fauna (Woinarski et al. 2011). Such areas have become degraded and less connected to each other in recent history (Whitehead et al. 2005). It is from studies of these unique areas that many of the examples used to illustrate the impact of fire on terrestrial flora (Russell-Smith et al. 2002), and vertebrate fauna, have emanated. Threatened species decline in semi-arid refugial plateaus (Perry et al. 2011a; Trainor 1996; Trainor et al. 2000) and invertebrate declines following changed fire regimes in rugged sandstone landscapes (Lowe 1995) are both examples of negative responses of fauna to fire in specialised communities but are not representative of the responses of the majority of savanna landscape fauna.

Management implications

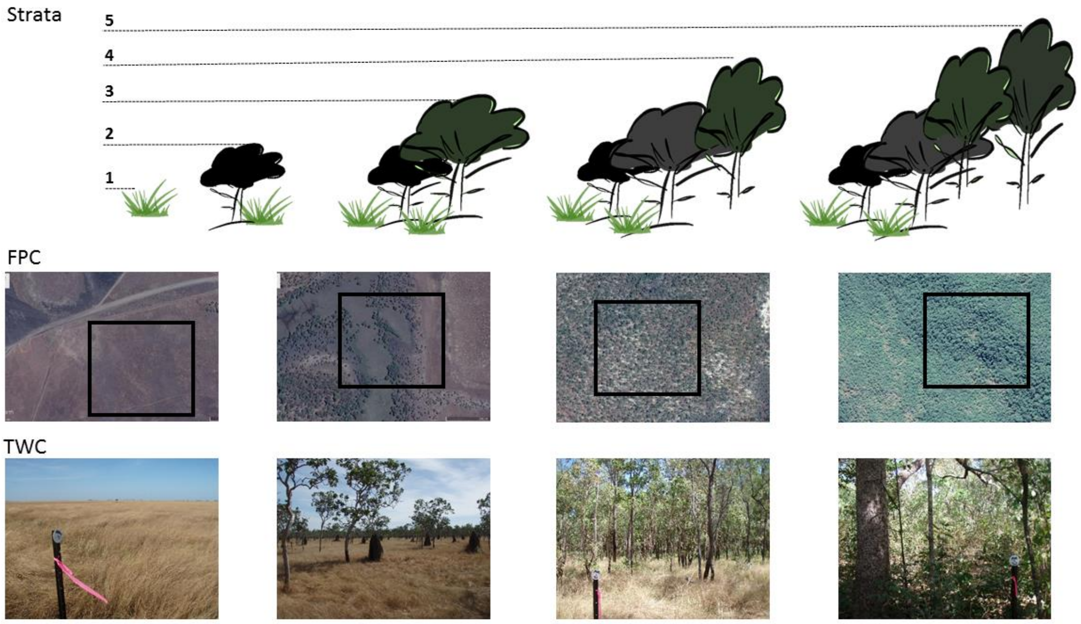
There are three important management implications of this study for reptiles in largely intact tropical savanna biomes. Firstly, in these environments, the landscape and site-scale habitat configurations are less discrete and less consolidated than in fragmented landscapes, where the contrasts between cleared and uncleared areas are distinct. For example, the difference between broad-acre cropping and remanent vegetation provides a relatively unambiguous scenario for testing biodiversity change in a binary landscape and the effect of this disturbance regime on different species and taxa (Bruton et al. 2015). Therefore, managers of intact savanna landscapes need to understand that faunal response to disturbance will be more subtle and will resolve at finer resolutions than the distinct binary responses evident in fragmented landscapes (Price et al. 2010). Though there is evidence that landscape context is important for reptiles in disturbed or regenerating environments, habitat quality is consistently the most influential aspect for herpetofauna both in cleared, partially disturbed and intact vegetation (Bruton et al. 2016; Kutt et al. 2012a).

Secondly, I have provided quantitative evidence that fire frequency at the spatial and temporal scale where data is available for analysis (i.e., 14 years for northern Australia) has only a limited relationship with the vegetation structure and pattern – the factors that is most strongly correlated with reptile diversity in the tropical savanna system I studied. In Australian tropical savannas, prescribed fire management is one of the most commonly applied management tool for biodiversity conservation (Perry et al. 2016), and its effects are usually measured using short-term, moderate resolution satellite imagery with derived summaries such as frequency of fire in the past 10-15 years, season and extent of fire. In Australia, there is government environmental policy that aims to assess and therefore manipulate prescriptive fire management for biodiversity conservation and greenhouse gas abatement using these metrics (Russell-Smith et al. 2013) and there is an assumption that fire regimes that provide quantified reduction in greenhouse gas emissions will have biodiversity co-benefits. The results of my study suggest that to quantify fire management and greenhouse gas abatement co-benefits for reptiles, fire frequency is an insufficient tool on its own, and complimentary quantification of the changes to vegetation structure at smaller scales are required. I conclude from this that the fire frequency, at least as typically reported at a broad landscape scale, is not suitably refined to characterise community composition of reptiles in these savannas, except in the most and least wooded environments.

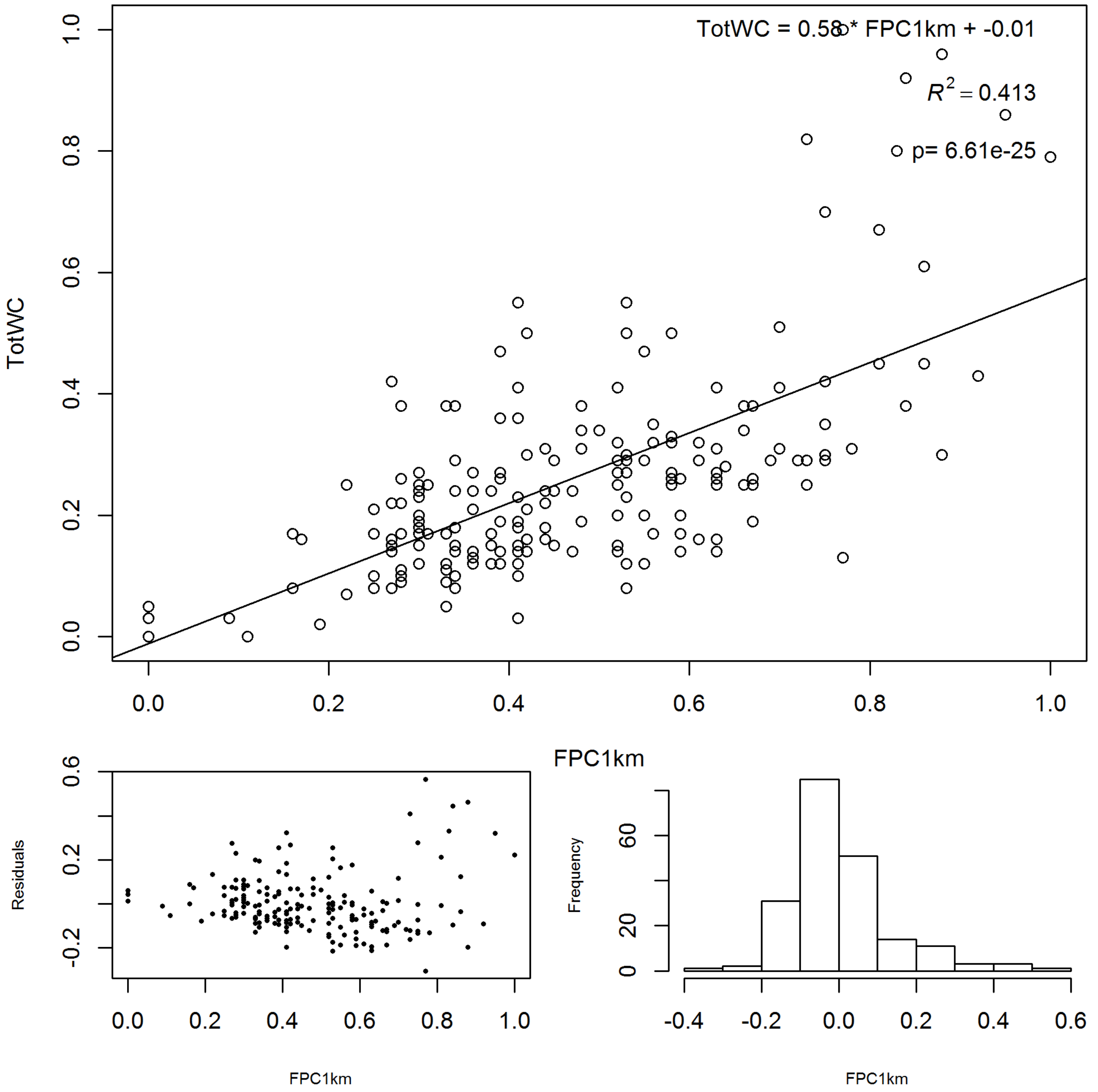
Lastly I found that though a relatively open vegetation structure promotes reptile diversity, in general reptiles prefer some canopy to none. I have demonstrated that fire exclusion may not provide the best outcomes for reptile alpha diversity favoured by open woodlands. However, gamma diversity relies on the unique species that occur in closed forest in the study area, which are rarely found outside of areas that naturally exclude fire (Price et al. 2010; Price et al. 2003; Price et al. 2007). There are two integrated management and policy implications for this. The Australian Commonwealth Government (2015) is providing substantial investment into the develop and agricultural intensification of northern Australia, and this may result in rapid large scale tree clearing and the homogenisation of vegetation through improved pastures or cropping (Kutt et al. 2009). Land clearing, the reduction in habitat quality and the introduction of invasive pasture grasses may change the thermal heterogeneity of landscapes, and this change will unequivocally impact reptile diversity (Bruton et al. 2015; Valentine and Schwarzkopf 2009). In contrast fire management aimed at carbon sequestration requires a reduction of fire frequency or total fire exclusion to promote the growth and permanency of biomass (Murphy et al. 2015). The interplay and co-management of these two potential landscape drivers in these environments will be an important challenge for tropical savanna conservation into the future.

Conclusions

Quantifying the relationship between fire, vegetation structure and biodiversity is particularly important in the Australian savanna context as there is an unresolved debate regarding the potential benefits for biodiversity of burning for the abatement of greenhouse gases (Russell-Smith et al. 2013); a national imperative to develop intact landscapes (Commonwealth.Government 2015); and financial incentives for demonstrating biodiversity benefit could be significant and warrant rigorous attention (Murray et al. 2007). In the largely intact woodlands of northern Australia (Kutt et al. 2012c; Scott et al. 2012) disturbance regimes are more subtle when compared to highly fragmented ecosystems in southern Australia (Lindenmayer and Fischer 2006). My study suggests that management or policy tools that rely on landscape scale or remotely sensed metrics and surrogates to predict biodiversity, must be tested using field data and must take into account the ecology and life history of the target taxa.



Appendix Figure 6.1 Pictorial representation of the difference between three key predictor variables. Strata (top) reflects the below-canopy vertical complexity, total woody cover (middle) reflects the below-canopy complexity and foliage projection cover (bottom) represents the above-canopy cover reflecting how open or closed a site is to sunlight.



Appendix Figure 6.2 Least squares regression demonstrating the linear relationship between total woody cover and foliage projection cover. R^2 and P value reported (top). Residuals (bottom left) and frequency histogram (bottom right).

Contribution of authours

Justin Perry, Lin Schwartzkopf and Matthew Vickers devised the study. Eric Vanderduys, Alex Kutt Justin Perry and Anders ZImny conducted the surveys. Justin Perry and Mathew Vickers managed the data and conducted the analysis. Justin Perry wrote the paper. All authors edited the paper.

Chapter 7. Changes in the avifauna of Cape York Peninsula over a period of 9 years: the relative effects of fire, vegetation type and climate

Introduction

There is increasing concern that populations of many plants and animals of the seemingly intact landscapes of the tropical savannas of northern Australia are declining (Burbidge et al. 2009). In some species the changes have been rapid and with clear causation, such as the decline of the Northern Quoll (*Dasyurus hallucatus*) and the arrival of the poisonous Cane Toad (*Rhinella marina*) (Burnett 1992). In other cases, such as granivorous birds, the reasons for the change are more difficult to grasp (Franklin et al. 2005), though the standard amalgam of fire, grazing by introduced herbivores, and feral predators are pronounced as the main interacting effects (Johnson et al. 2007; Kutt and Woinarski 2007). One of the reasons for this lack of certainty is the absence of longitudinal studies that clearly track changes in vertebrate fauna and associated management and landscape changes. Of the few completed studies, some point to declines of uncertain cause (Woinarski et al. 2001), whereas one study observed a short-term recovery following altered land management practices (Legge et al. 2008).

Bird atlas data are a significant resource for monitoring and identifying species under threat or suffering ongoing decline (Dunn and Weston 2008). These data can also be used to describe patterns of changes in populations or ecology, such as delayed migration and changes in the timing of breeding associated with climate change (Miller-Rushing et al. 2008). Australia has a successful atlassing scheme operated by Birds Australia, with intensive surveying occurring between 1977 and 1981 (Blakers et al. 1984) and between 1998 and 2002 (Barrett et al. 2003), with ongoing collection of atlas data since 2002. In Australia, these data have been used to examine changes in bird populations over time, and have indicated shifts in geographical and migrational range, phenology and shifting food resources (Chambers et al. 2005; La Sorte and Thompson 2007).

Cape York Peninsula is considered one of Australia's most significant biogeographical regions (Woinarski et al. 2007). The allure of the northern tip of Australia for biologists has meant that there is ample historical data with which to compare contemporary data to examine the patterns of change and distribution in many species (see review in Kutt et al. 2005). Up to 11 species of mammal have undergone some change since 1948, but more recently there have been well documented cases of declines of avian populations, the most notable examples being the Brown Treecreeper (*Climacteris picumnus melanotus*), Golden-shouldered Parrot (*Psephotus chrysopterygius*) (Garnett and Crowley 1995a, b; Weaver 1982) and the Black-faced Woodswallow (*Artamus cinereus normani*) (Garnett and Crowley 2000). Altered fire regimes are considered the primary threat to biodiversity on Cape York Peninsula (Felderhof and Gillieson 2006), with a lack of fire leading to loss of grasslands and grassy woodlands and associated fauna, particularly on eastern Cape York Peninsula (Crowley et al. 2009; Crowley and Garnett 1996, 1999), and extensive late dry season fires that remove habitat and refuge areas, particularly on western Cape York Peninsula (Felderhof and Gillieson 2006).

On Cape York Peninsula, a comprehensive dataset of bird occurrence, fire history (2000–08, derived from remotely sensed data) and long-term climate data provided an opportunity to examine whether bird populations have changed and why by re-surveying a subset of the sites. Specifically, I asked two questions: (1) has there been a significant change in occurrence of birds over the period of the two surveys? and (2) can changes in species occurrence be attributed to the effects of changes in climate, habitat (vegetation type) or management (i.e. fire) at a landscape scale? I also assess the value of broad scale multi-observer datasets in supporting decisions and actions on land management and in building more robust monitoring systems.

Methods

Study area

The Cape York Peninsula bioregion is the northernmost part of Queensland, and encompasses >13 million ha (Figure 7.1). Mean annual rainfall of the Peninsula varies from just over 1000 mm at Palmerville on southern Cape York Peninsula (16°00’S, 144°02’E) to >2000 mm at Lockhart River (12°28’S, 143°12’E) on the central eastern coast. Rainfall is primarily orographic and monsoonal in the east and monsoonal in the west (http://www.bom.gov.au/climate/averages/tables/ca_qld_names.shtml Oct 2010). The study area encompasses a broad range of vegetation types, predominantly open eucalypt and Melaleuca woodlands and grasslands (Neldner and Clarkson 1995). Across Cape York Peninsula, the 3 years preceding 2000 were far wetter (mean 1438 ± 663 mm, range 591–4679 mm) than the 3 years to December 2008 (mean 1180 ± 559 mm, range 270–4995mm).

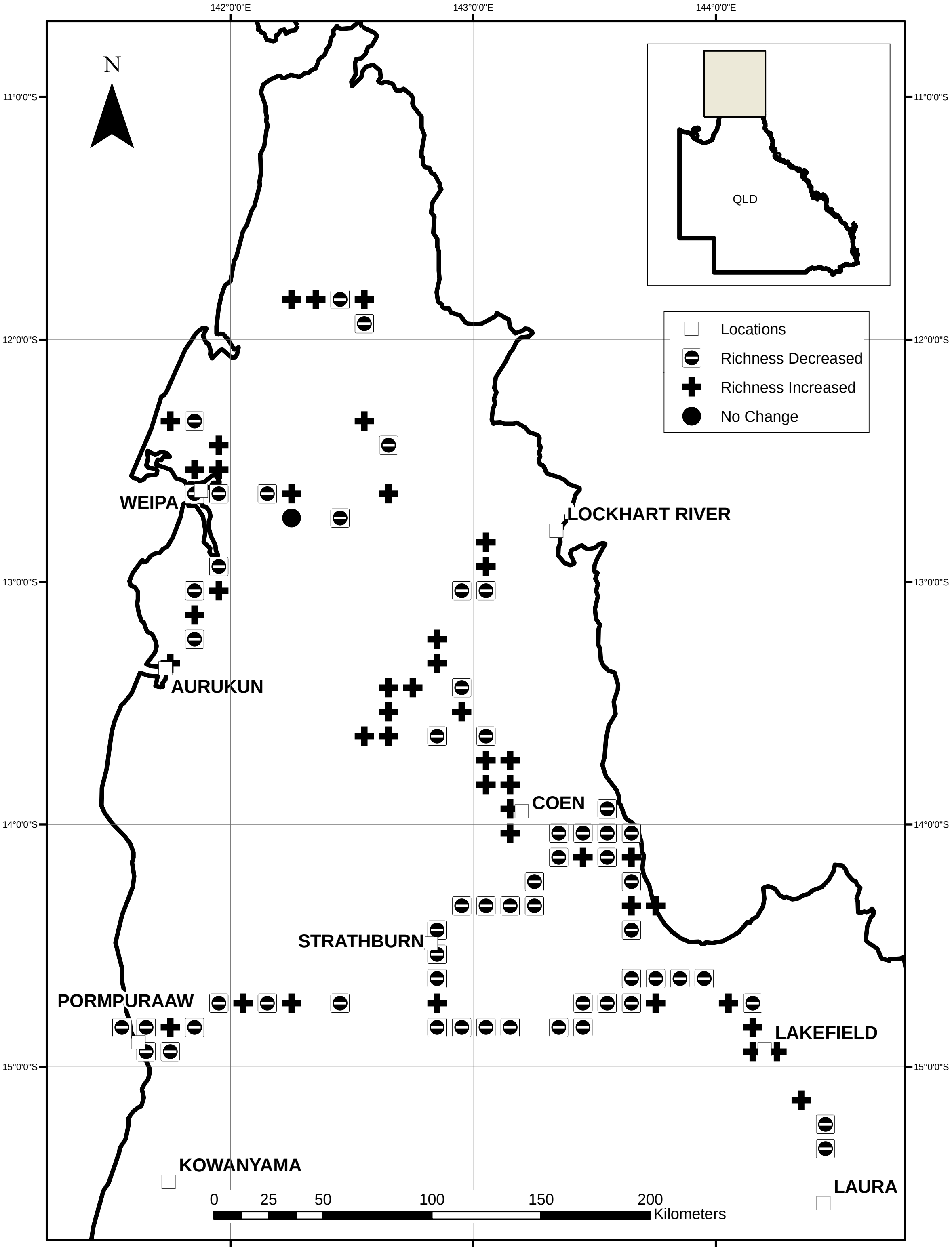


Figure 7.1 Location of sites within the Cape York Peninsula, northern Australia indicating an increase (+) and decrease (-) in species richness (mean species per 10km^2 grid-cell) between the two surveys.

Surveys

Original survey

The original survey was designed and managed by the Queensland Parks and Wildlife Service and completed with the assistance of volunteers from Birds Australia (S. T. Garnett, pers.comm.). Potential survey points were randomly selected using the broad vegetation groups (BVG) of Cape York Peninsula (Neldner and Clarkson 1995). An additional set of points was selected for each BVG but constrained to within 5 km of a gazetted road. Mean distance between survey sites was ~30 km. Overall, 2500 unique sites were surveyed between February 1998 and December 2001 and which I label the '2000 survey' throughout this paper.

Contemporary survey site selection

I used five criteria to select a subset of the original 2500 survey sites that were to be surveyed again.

1. Sites were selected to capture a subset of species on Cape York Peninsula that have been described in the literature as sensitive to fire. These species included Brown Treecreeper, Crimson Finch (Neochmia phaeton evangelinae), Star Finch (Neochmia ruficauda), Black-faced Woodswallow, Red-backed Fairy-wren (Malurus melanocephalus), Pied Butcherbird (Cracticus nigrogularis) and Black-backed Butcherbird (C. quoyi) (Beeton et al. 2006; Garnett et al. 2005; Russell and Rowley 1998; Todd et al. 2003).
2. Sites were selected to represent the range of tropical savanna vegetation types and fire histories across the geographic space on Cape York Peninsula.
3. I restricted sites to woodland communities typically affected by fire unless they included records of the target species.
4. Sites were selected by logistic considerations, such as ease of access and location near groups of other sites (i.e. efficiency of sampling).
5. Finally, in order to reduce the effect of seasonal variation, I identified sites that had originally been surveyed in, or close to, my sampling period (September–January).

Using these criteria, a total of 600 unique sites were chosen, of which 418 were sampled.

Survey methodology

Surveys of birds were undertaken in December 2008 using the standard 20-min area search used by Birds Australia, which was the method used during most of the original survey. These surveys involve searching within a 500-m radius of a geo-coded point, and preferably consisting of the same or similar habitat type for 20 min (Birds Australia, 2009, http://www.birdsaustralia.com.au/). Surveys were undertaken throughout daylight hours, though wherever possible not during the period of least avian activity, between 1100 hours and 1500 hours. All birds seen and heard at each site were recorded; if the survey site comprised a mix of vegetation types or if birds were using a different vegetation type close to the survey site, this was noted. In both survey periods, teams consisted of experienced surveyors who were familiar with the birds of northern Queensland, minimising observer bias, an issue that will be explored in the discussion.

Analysis

A 10-km^2 grid was chosen to represent the species richness of a particular area while taking into account clusters of survey points. The change in species richness between the two survey periods (2000 survey to 2008) was examined by comparing the mean species richness determined for each grid-cell. To do this, the species richness of all surveys within each grid-cell was summed and then divided by the number of surveys. All analyses were undertaken using the packages adehabitat and maptools in R version 2.8.0 (R Development Core Team 2009). The mean number of species recorded for each grid-cell is graphically presented in Figure 7.1, as having increased, decreased or not having changed between the two survey periods.

I tested the change in frequency of records of species between the first and second survey using a sign test, which is a presence–absence data equivalent of a non-parametric Wilcoxon signed rank test. This test does not make any assumptions about the form of the distribution (Byrkit 1987) and operates under the null hypothesis that there is an equal probability of each species being present (x+) or absent (x–) at each site. In order to increase the strength of the analysis, only species with more than five records in the first survey period were included. I examined whether changes in reporting rate were associated with the patterns of movement of species. For this, each species was assigned to one of five residency status categories: waterbird, resident, nomad, migrant and partial migrant after Woinarski and Catterall (2004).

Finally I used presence–absence ecological niche modelling to investigate the relative effect of a range of landscape scale biophysical (climate, vegetation) and land management (fire) variables (Table 7.1) on the frequency of records of key avian species for both the original and current survey. I selected species on the basis of the following criteria: there was a significant change in reporting between the two survey periods; the species was cited in the literature as declining or increasing on Cape York Peninsula (Garnett et al. 2005; Russell and Rowley 1998; Todd et al. 2003); it was highly detectable (visually or aurally); and it was sedentary or locally nomadic. Assessment of ‘highly detectable’ was made from existing unpublished data collected during systematic bird surveys conducted in the northern Gulf of Carpentaria in similar tropical savanna vegetation (J. J. Perry, A. S. Kutt, E. P. Vanderduys and G. C. Perkins, unpubl. data).

Table 7.1. List of landscape variables used in distribution modelling, including data source and coding.

Variable	**Source**	**Range**
Fire frequency 00 - 08	250m pixel resolution derived from MODIS between 2000 and 2008 (Thompson and Gobius 2008) Ranging between 0 – no fire in eight years to 9 - annual fire.	Early Fire Frequency 0 – 7 (January to August) Storm Fire Frequency 0 – 5 (November to January) All Fire Frequency 0 – 9
Mean annual rainfall	Derived using Anuclim 5.1 software (McMahon et al. 1995) and a ~250 m resolution DEM (GEODATA 9 second DEM Version 2: Geoscience Australia, http://www.ga.gov.au/).	969 – 2756 mm
Mean annual temperature	As above	20.1 – 26.8
Three year Foley's index for 2000 and 2008	Derived in R using interpolated rainfall grids ranging from 1960 to 2008 for Australia at a 5km pixel resolution and following the methods of (Fensham and Holman 1999; Foley 1957; Maher 1973).	2000 = -0.22 – 3.72 2008 = -0.55 – 2.89
Vegetation categories	Dominant vegetation split into broad vegetation groups following the categorisation in (Neldner and Clarkson 1995)	Miscellaneous = 0, Beach Scrub= 1, Eucalyptus Woodland - Flats = 2, Eucalyptus Woodland - Hills = 3, Eucalyptus Woodland – Wet = 4, Closed Forest = 5, Grassland = 6, Acacia = 7, Mangrove = 8, Ti Tree = 9, Bare and Rock = 10, Dry Scrub = 11, Heath = 12 Wetland = 13, Eucalyptus Forest = 14.
Foilage Projective Cover (FPC)	On a continuous scale ranging from 100 – no foliage project (grassland) to 200 – 100% foliage projection (closed forest). (FPC) is the percentage of ground area occupied by the vertical projection of foliage (Armston et al. 2004). Rescaled to 0 – 100.	1 – 86

Ecological niche modelling was done on the two survey datasets using maximum entropy (MAXENT) species habitat modelling with the program MAXENT version 3.3.0 (Phillips et al. 2006). MAXENT is a presence-only probabilistic model that uses selected environmental variables to determine the most likely theoretic niche for each species. MAXENT creates a uniform layer (x) that represents a probability distribution of entropy based on the set of environmental variables selected as the background for the model. The presence records for each species are then compared to the background values to determine which variables are most likely to be driving species distributions using a logistic approach. Model accuracy was determined by comparing how distant the presence records are from the random background as measured by the area under the receiver operator curve (AUC). A model that is no better than random will have an AUC of ~0.5 whereas a very accurate model will have an AUC approaching 1 (Phillips et al. 2006). MAXENT is particularly useful for studies such as this where some species are recorded infrequently (i.e. as little as five data points). MAXENT outperforms a range of modelling methods under these conditions and has equal performance when using more robust datasets (Guisan et al. 2007).

Environmental variables

Frequency of fire, vegetation type, 3-year Foley's drought index, rainfall and temperature were used to inform the model (Table 7.1). Grids of fire frequency at a 250-m pixel resolution between 2000 and 2008 were derived by Cape York Sustainable Futures - then Cape York Development Association; Thompson and Gobius (2008). For the period 1999 to 2003, Landsat 7 ETM+ Quicklook jpeg scenes where used to identify manually and digitise fire scars. After this point MODIS imagery was used with semi-automated classification of visually identified fire scars using ERDAS IMAGINE (www.erdas.com). Fire scars after 2006 were derived using segmentation and classification of difference images in Definiens eCognition (http://earth.definiens.com/products Nov 2010). A 3-year Foley's drought index was derived for each survey site; this measures the deviation of rainfall from the 1960–2008 mean annual rainfall for the 3 years before each survey period (Fensham and Holman 1999).

Because high co-linearity among explanatory variables can lead to high standard errors and difficulties in interpreting parameter estimates (Graham 2003), I did not include pairs of explanatory variables with Spearman pairwise correlation coefficients >0.5 in the same model. There were significant correlations between all of the base climatic variables. As a result, only mean annual temperature and mean annual precipitation were used. In addition, there were significant correlations between elevation and climatic variables and therefore elevation was not used in this analysis.

Taxonomy

Avian nomenclature follows Christidis and Boles (2008); for a full listing of species recorded in the 2000 and 2008 surveys, see Appendix Table 7.1.

Results

The changes in species richness between the two surveys, 2000 and 2008, varied and an almost even split of increase and decrease was recorded (Figure 7.1). Overall, 59 grid-cells recorded a decrease in mean species richness when compared to the original survey. There were marginally fewer grid cells (n = 43) where mean species richness was greater than in the original surveys. The greatest decrease in mean number of species per grid was found in the southern Cape York Peninsula between Pormpuraaw and Lakefield National Park, where almost every grid-cell recorded a decrease. The inverse of this trend was recorded in the sites located between Coen and Rokeby National Park on central Cape York Peninsula (Figure 7.1).

Table 7.2. Species recorded at five or more sites and parameters describing their positive or negative change from baseline (time 0 = 2000) to subsequent (time 1 = 2008) sampling. Changes are tested via a sign test. Probability levels: *, P < 0.05, **, P < 0.01, ***, P < 0.001. Only birds with significant change are tabulated. Direction of change indicated by – or + in the % change column. Residency status derived from (Chan 2001), (Higgins et al. 2001) and (Barrett et al. 2003). N = Nomad, P = partial migrant, M = Migrant, S = Sedentary. The additional code 'W' denotes wetland species. Detection status is coded as H = High, M = Moderate and L = Low.

Species	**Residency status**	**Detection Status**	**No.sites 2000**	**No.sites 2008**	**Z-score**	**% change**
Radjah Shelduck	W	H	21	6	2.8*	-56
Australasian Grebe	W	H	8	1	2.3*	-78
Australasian Darter	W	H	13	2	2.8*	-73
Little Egret	W	H	13	2	2.6*	-73
Intermediate Egret	W	H	20	7	2.3*	-48
Black-breasted Buzzard	P	H	8	1	2.0*	-78
Black Kite	P	H	14	1	3.1*	-87
Australian Bustard	N	H	7	0	2.0*	-100
Bush Stone-curlew	S	L	8	0	2.5*	-100
Peaceful Dove	S	H	40	76	3.6**	31
Bar-shouldered Dove	S	H	86	65	2.0*	-14
Galah	N	H	30	12	2.5*	-43
Sulphur-crested Cockatoo	S	H	79	50	2.9*	-22
Rainbow Lorikeet	P	H	184	155	2.5*	-9
Pale-headed Rosella	S	H	47	29	2.0*	-24
Pheasant Coucal	S	H	48	72	2.3*	20
Azure Kingfisher	S	L	10	1	2.4*	-82
Forest Kingfisher	P	H	27	57	3.4**	36
Rainbow Bee-eater	M	H	48	26	2.5*	-30
Brown Treecreeper	S	H	12	4	2.2*	-50
Striated Pardalote	S	M	35	10	4.2***	-56
Weebill	S	L	37	57	2.4*	21
Banded Honeyeater	N	H	24	6	2.8*	-60
White-throated Honeyeater	P	H	118	168	4.5***	17
Blue-faced Honeyeater	P	H	89	59	2.6*	-20
Lemon-bellied Flycatcher	S	H	46	80	3.4**	27
Spangled Drongo	P	H	56	77	2.1*	16
Magpie-lark	P	H	43	27	2.2*	-23
White-bellied Cuckoo-shrike	P	M	106	134	2.2*	12
Yellow Oriole	S	H	48	69	2.6*	18

In the 418 sites sampled in the 2008 survey and used in the analysis, 267 species were recorded in the original survey, and 167 species recorded in the repeat survey. Of the total number of species, 146 had >5 records in the first survey. Of these, 137 were recorded in surveys that were conducted in less than one hour in the first survey, and 30 of the 137 showed significant changes between surveys, with nine showing increases. Of the 30 species that showed significant change, 16 were considered to be sedentary or partially nomadic and highly detectable, and six of the 16 showed a positive change between surveys (Table 7.2). Significant decreases from the previous survey were recorded in reporting of bar-shouldered dove (*Geopelia humeralis*), and Sulphur-crested Cockatoo (*Cacatua galerita*), Rainbow Lorikeet (*Trichoglossus haematodus*), Pale-headed Rosella (*Platycercus adscitus*), Brown Treecreeper, Striated Pardalote (*Pardalotus striatus*), Blue-faced Honeyeater (*Entomyzon cyanotis*) and Magpie-lark (*Grallina cyanoleuca*) (Table 7.2). However, Rainbow Lorikeets, Blue-faced Honeyeaters and Magpie-larks are all partially nomadic and Striated Pardalotes were only moderately detectable and were recorded in fairly low numbers. Therefore, a significant decrease in the number of observations of truly sedentary, highly detectable species was limited to Bar-shouldered Doves, Sulphur-crested Cockatoos, Pale-headed Rosellas and Brown Treecreepers.

There was a strong relationship between the movement patterns of birds and their change in occurrence. Species classed as waterbirds or nomadic showed the greatest propensity for change between surveys (Figure 7.2).

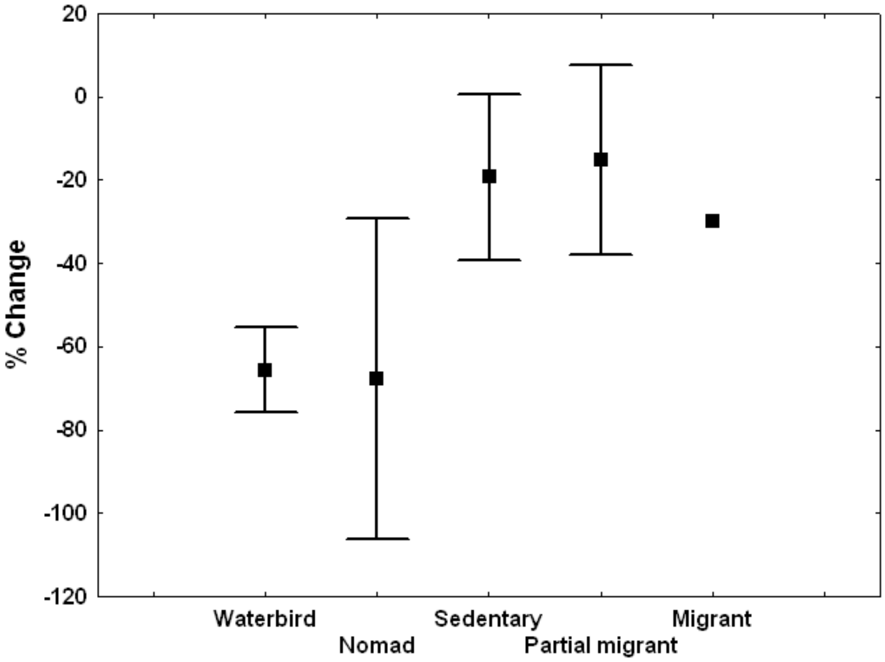
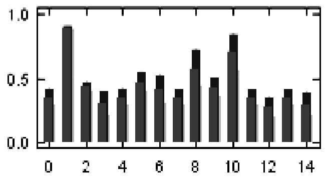
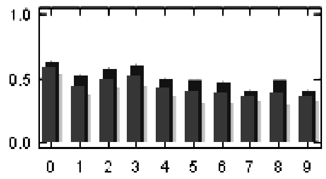
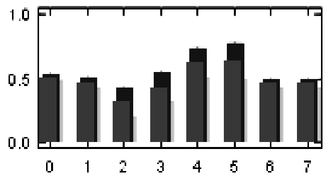
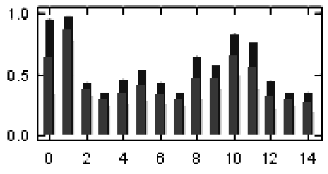
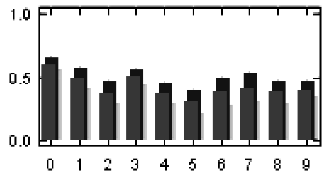
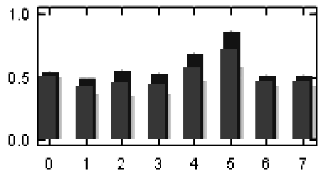
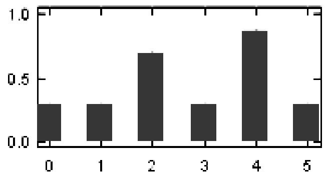
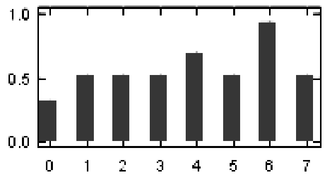
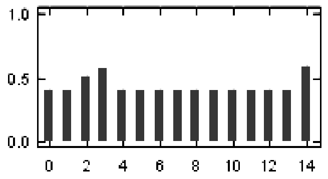
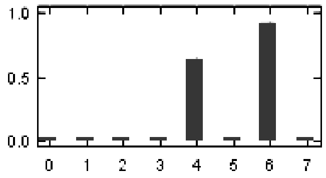
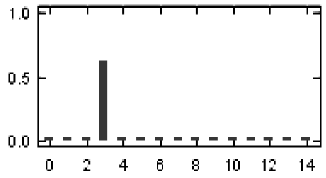
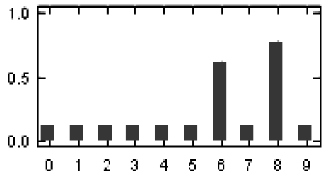


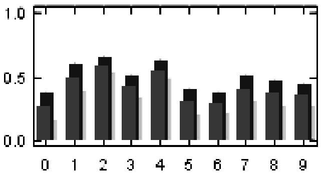
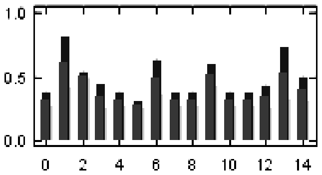
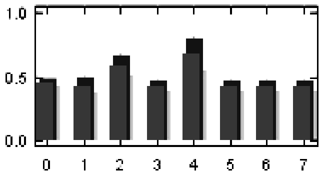
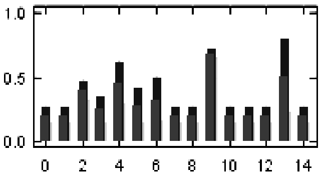
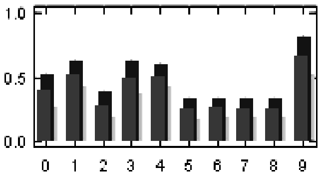
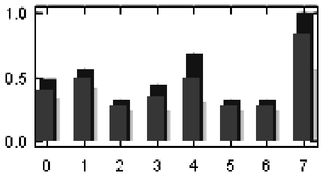
Figure 7.2 Mean (and standard error) in the percentage change for all bird species recorded during the current survey, grouped into four movement categories.

MAXENT models for the four sedentary, detectable species that declined significantly were all primarily influenced by fire frequency and vegetation category rather than climatic variables (Figure 7.3). Similar trends were exhibited by all of the other species that showed significant change between surveys (see Appendix Figure 7.1).

Bar-Shouldered Dove - 2000		
 Vegetation Category	 Fire Frequency 00 - 08	 Early Fire Frequency 00 - 08
50.2%	17.5%	9.6%
Bar-Shouldered Dove - 2008		
 Vegetation Category	 Fire Frequency 00 - 08	 Early Fire Frequency 00 - 08
55.6%	19.4%	10.0%

Brown Treecreeper - 2000		
 **Storm Fire Frequency 00 - 08**	 **Early Fire Frequency 00 - 08**	 **Vegetation Category**
47.2%	27.8%	2.7%
Brown Treecreeper - 2008		
 **Early Fire Frequency 00 - 08**	 **Vegetation Category**	 **Fire Frequency 00 - 08**
41.4%	37.0%	8.7%

Pale-headed Rosella - 2000

 **Fire Frequency 00 - 08**	 **Vegetation Category**	 **Early Fire Frequency 00 - 08**
42.0 %	20.9%	19.6%
Pale-headed Rosella - 2008		
 **Vegetation Category**	 **Fire Frequency 00 - 08**	 **Early Fire Frequency 00 - 08**
35.3%	29.2%	25.5%

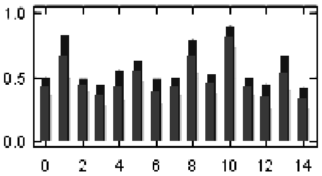
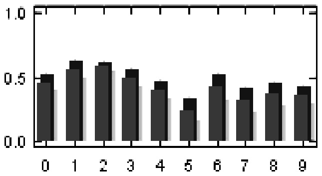
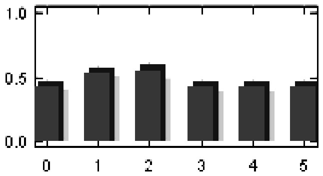
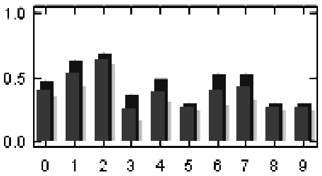
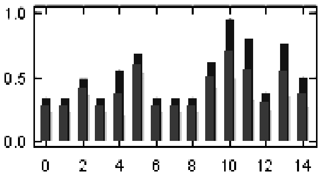
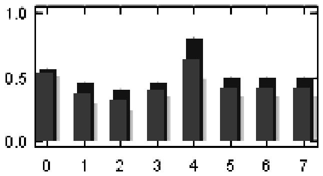
Sulphur-crested Cockatoo - 2000		
 **Vegetation Category**	 **Fire Frequency 00 - 08**	 **Storm Fire Frequency 00 - 08**
38.0%	28.5%	12.1%
Sulphur-crested Cockatoo - 2008		
 **Fire Frequency 00 - 08**	 **Vegetation Category**	 **Early Fire Frequency 00 - 08**
34.5%	33.3%	13.1%

Figure 7.3 Response histograms (mean, central bars, +/- one standard deviation, offset bars) from maximum entropy (MAXENT) species habitat modelling for species recorded as having significant increase or decline in reporting rate across the two surveys. Model percentage represents the percent variance explained by each variable. x- axis values represent fire frequency (early – January to August, storm – November to January and all) between 2000 and 2008, mean annual rainfall, mean annual temperature, vegetation category (Miscellaneous = 0, Beach Scrub= 1, *Eucalyptus* Woodland - Flats = 2, *Eucalyptus* Woodland - Hills = 3, *Eucalyptus* Woodland – Wet = 4, Closed Forest = 5, Grassland = 6, *Acacia* = 7, Mangrove = 8, Ti Tree = 9, Bare and Rock = 10, Dry Scrub = 11, Heath = 12, Wetland = 13, *Eucalyptus*

Forest = 14), and foliage projective cover (ranging from 0 – 100%). Y- axis values represent likelihood value between 0 – 1.

For Brown Treecreepers, the presence of Eucalyptus woodlands and forests had a greater influence on the model in the original survey and Eucalyptus woodlands on hills were more important in the repeat survey. Pale-headed Rosellas showed a slight increase in likelihood of association with annually burnt sites, and had a more pronounced association with frequent early dry season fires. In addition, the likelihood of Pale-headed Rosellas being associated with low lying Eucalyptus woodlands was lower in 2008 than in the 2000 survey. Model contribution and likelihood estimates for Bar-shouldered Doves remained stable, with only a slight increase evident in association with a broader range of vegetation categories. Sulphur-crested Cockatoos also maintained a fairly similar set of habitat characteristics, although there was a shift in likelihood for low fire frequency areas and a considerable decrease in the likelihood of Cockatoos using lowland eucalypt woodland.

Red-backed Fairy-wrens, Pied Butcherbirds and Black-backed Butcherbirds are species that have been singled out as fire reactive on Cape York Peninsula. These species did not exhibit significant declines or increases between surveys. Pied Butcherbirds have been responsible for the deaths of Golden-shouldered Parrots (*Psephotus chrysopterygius*) at the nest, and are more successful in thickened habitats associated with a cessation in burning on pastoral lands (Crowley et al. 2009). My data do not indicate a greater prevalence of these birds at a landscape scale. Pied Butcherbirds exhibited a relatively equal likelihood of being associated with high low fire frequency.

Observations of Black-backed Butcherbird also remained stable between surveys and this species does not exhibit strong associations with any particular fire frequency. The model for this species was more influenced by vegetation type, with a higher likelihood of association with lowland eucalypt woodlands in the first survey period and wet Eucalyptus woodlands in the recent survey.

Discussion

This study has shown that there has been relatively little change in the bird assemblage on Cape York Peninsula over two sampling periods separated by 8 years, though several species declined or increased in reporting frequency. One possible cause for the lack of a clear pattern is subtle differences in survey methods and observer bias. A recent review of bias in bird surveys indicated that there are four issues of concern: lack of replication; different skill levels; single observer site-sampling; and weather patterns (Lindenmayer et al. 2009). Despite these factors, Lindenmayer et al. (2009) concluded that inferences made about environmental relationships were not substantially affected. I do not believe that the lack of substantial change in the avifauna between the two surveys was a result of observer bias or issues of detectability but rather it was a function of the general stability of the current avifauna assemblage on Cape York Peninsula.

Temporal variation, either at daily or seasonal temporal scales can influence the patterns of avian assemblages and the interpretation of permanent versus cyclical changes (Chambers 2008; Chan 2001; Maron et al. 2005). This is particularly apparent for waterbirds or nomadic arid-zone species that follow rainfall events (Kingsford 1995). Given that the initial survey period was generally wetter than the second survey period it is likely that significant changes in waterbird populations in this study are likely to be linked to the increased availability of surface water during the first survey period. Similarly, local and regional patterns of migration in birds can be affected by inter-annual and seasonal weather patterns (Chan 1999), which in turn are driven by annual to decadal La Niña and El Niño climatic patterns (Chambers et al. 2005). I recorded a suite of species whose reporting rate changed between the two surveys periods (e.g. Australian Bustard (*Ardeotis australis*), Black Kite (*Milvus migrans*), Rainbow Lorikeet, White-throated Honeyeater (*Melithreptus albogularis*), Banded Honeyeater (*Cissomela pectoralis*), and the patterns of movement of these species are reported as being associated with longer term, landscape scale changes in weather and resources (Chan 2001; Woinarski et al. 2000; Ziembicki and Woinarski 2007). The broad scale changes in species richness across the entire study area (i.e. general decrease in species richness in the Lakefield region and increase in Coen–Lockhart region) suggest landscape scale temporal variation has had an influence on the broad survey results.

Despite the limitations identified here, I am confident that my data do provide scope to make comparisons about change over the two periods sampled. In particular, there was a suite of species that changed in frequency of recording and that are easily detected and largely sedentary, and typical of the tropical savanna woodlands of northern Australia (Kutt et al. 2005; Woinarski and Tidemann 1991). Several these species have been associated with changes in the structural pattern of vegetation caused by encroachment of woody weeds and mechanical clearing (e.g. bar-shouldered dove, brown treecreeper, bush-stone curlew, weebill, Tassicker et al. 2006), and fire and grazing (e.g. striated pardalote, pale-headed rosella, Kutt and Woinarski 2007). This provides confidence that impacts such as fire and grazing, and stochastic forces such as extreme climatic events, might be responsible for some of the changes reported here. Existing information for Cape York Peninsula indicates that population patterns in species such as the Brown Treecreeper and Bush Stone-curlew are a result of changing fire regimes and associated changes in vegetation structure (Garnett and Crowley 1995a; Kutt et al. 2005). In the current survey, the Brown Treecreeper was restricted to a single vegetation type: Stringy Bark (*Eucalyptus tetradonta*) woodland on rocky hills.

Most of species recorded in my current survey did not demonstrate any significant variation in reporting rate, which tends to suggest that the avifauna of Cape York Peninsula remained fairly stable in the 8 years between the two surveys. There are two possible explanations for this. Firstly, fauna populations of Australian tropical savannas are widespread and interconnected across northern Australia and are considered to show very little spatial variation over vast distances (Woinarski et al. 2005). Most of the species reported more frequently were common, widespread and partially migratory species (e.g. Pale-headed Rosella, Forest Kingfisher, Weebill, White-throated Honeyeater, White-bellied Cuckoo-shrike (*Coracina papuensis*) and Lemon-bellied Flycatcher (*Microeca flavigaster*)). The general stability of vegetation structure in Cape York Peninsula woodlands between 1966 and 1995 (Crowley and Garnett 1998) suggests that the bird assemblage associated with the extant woodlands on Cape York Peninsula may not have changed dramatically over time. Large changes in savanna bird composition are linked to more significant woodland disturbance, such as mechanical clearing and thinning (Tassicker et al. 2006).

The second explanation for a lack of clear variation in the two periods is that substantial change might have already occurred in many species: I am simply recording the new status quo. There have been significant break-points in land management in northern Australia, such as the shift to *Bos indicus* cattle, improved cattle husbandry (Ash and McIvor 1998) and shifts in the frequency and scale of fires owing to cattle grazing and disruption to traditional management by Aboriginal people (Garnett et al. 2010). Changes in populations of Brown Treecreeper between the 1920s and early 1990s have been recorded (Garnett and Crowley 1995a; Thomson 1935). Further, the decrease in populations of granivorous birds from about the 1970s to the 1990s is well established (Franklin 1999). Many avian species considered of concern were not recorded in high numbers in the first survey (Brown Treecreeper, n = 12 sites; Crimson Finch, 5 sites; Star Finch, 6 sites; Black-faced Woodswallow, 3 sites). These species were recorded in equally low numbers in the current survey, with two showing further worrying declines (Brown Treecreeper, Black-faced Woodswallow). It is difficult to then interpret what this stability between surveys indicates: a healthy landscape typical of the dispersed, fluid tropical savannas, an environment in an ecological coma, or a system that is in gentle decline.

In the models examining what factors contributed most to species presence, fire frequency and vegetation categories generally contributed more explanatory power than climatic variables (see Appendix Figure 7.1). Though modelling change over a fairly short period might lead us to be more circumspect over the certainty of the result, it does hint that landscape configuration and changes to vegetation caused by management of fire and grazing might have a larger influence on bird assemblages in the short-term than climate, an outcome recently reported for arid Australian birds

(Pavey and Nano 2009). It is more likely that long-term extreme weather events (i.e. long-term rainfall deficit) and short-term (monthly or yearly) weather will have a greater influence on the distribution of birds across the landscape (Chan 1999). This could mean that land management decisions regarding grazing, use of fire and periodic natural catastrophes, such as flood or cyclone (Cook and Goyens 2008), will affect avian community composition more than short-term natural variation in weather.

Conclusion

Increasing attention has been given to tracking temporal changes in Australian biota in relation to land management (Bastin 2008; Beeton et al. 2006). This study has shown that there was little change in the avifauna at sites sampled in the 2000 survey and 2008 on Cape York Peninsula. This includes many species that were originally recorded in very low numbers (Brown Treecreeper, Black-faced Woodswallow, Star Finch, and Crimson Finch) and thought to be in decline. Fire and vegetation types were consistent predictive model variables for species either declining or increasing in reporting rate, and this suggests that changes in land management, especially in the use of fire, are likely to affect the distribution and abundance of avian populations on Cape York Peninsula. However, the lack of change in the overall bird community could be a function of either the general biotic constancy of the tropical savanna landscapes or a new equilibrium of depletion. The lack of robust longitudinal surveys of fauna, and poor understanding of how patterns relate to land management in northern Australia, undermine our ability to take remedial action if required. I believe that this study represents an opportunity to develop a temporally significant monitoring program for birds on Cape York Peninsula. In combination with the original survey I have developed a methodology and a representative set of sites for collecting and analysing data on Cape York Peninsula birds. However the trajectory, cause and patterns of change will not be evident unless repeated monitoring occurs in the future.

Author contributions

Justin Perry, Alex Kutt, Stephen Garnett, and Gay Crowley devised the study. Eric Vanderduys, Genevieve Perkins, Alex Kutt and Justin Perry conducted the surveys. Justin Perry managed the data, conducted the analysis and wrote the paper. All authors edited the paper.

Appendix Table 7.1. Complete list of birds recorded in the original survey and 2008 survey. Under Change, + indicates significant change between the 2000 and 2008 surveys, 0 indicates no significant change: ‡ indicates a species recorded in 2000 but not in the 2008 surveys (no species was recorded in the 2008 survey only).

Family	**Scientific name**	**common name**	**Change**
Casuariidae	*Dromaius novaehollandiae*	Emu	0
Megapodiidae	*Alectura lathami*	Australian Brush-turkey	0
Megapodiidae	*Megapodius reinwardt*	Orange-footed Scrubfowl	0
Phasianidae	*Coturnix ypsilophora*	Brown Quail	0
Anseranatidae	*Anseranas semipalmata*	Magpie Goose	0
Anatidae	*Dendrocygna eytoni*	Plumed Whistling-Duck	+
Anatidae	*Dendrocygna arcuata*	Wandering Whistling-Duck	0
Anatidae	*Tadorna radjah*	Radjah Shelduck	+
Anatidae	*Nettapus pulchellus*	Green Pygmy-goose	0
Anatidae	*Anas superciliosa*	Pacific Black Duck	0
Podicipedidae	*Tachybaptus novaehollandiae*	Australasian Grebe	+
Columbidae	*Chalcophaps indica*	Emerald Dove	+
Columbidae	*Phaps chalcoptera*	Common Bronzewing	+
Columbidae	*Geopelia cuneata*	Diamond Dove	+
Columbidae	*Geopelia striata*	Peaceful Dove	+
Columbidae	*Geopelia humeralis*	Bar-shouldered Dove	+
Columbidae	*Ptilinopus magnificus*	Wompoo Fruit-Dove	0
Columbidae	*Ptilinopus superbus*	Superb Fruit-Dove	+
Columbidae	*Ptilinopus regina*	Rose-crowned Fruit-Dove	0
Columbidae	*Ducula bicolor*	Pied Imperial-Pigeon	0
Podargidae	*Podargus strigoides*	Tawny Frogmouth	0
Podargidae	*Podargus papuensis*	Papuan Frogmouth	0
Caprimulgidae	*Caprimulgus macrurus*	Large-tailed Nightjar	+
Aegothelidae	*Aegotheles cristatus*	Australian Owlet-nightjar	+
Apodidae	*Apus pacificus*	Fork-tailed Swift	0
Anhingidae	*Anhinga novaehollandiae*	Australasian Darter	+
Phalacrocoracidae	*Microcarbo melanoleucos*	Little Pied Cormorant	0
Phalacrocoracidae	*Phalacrocorax sulcirostris*	Little Black Cormorant	+
Phalacrocoracidae	*Phalacrocorax varius*	Pied Cormorant	+
Pelecanidae	*Pelecanus conspicillatus*	Australian Pelican	+
Ciconiidae	*Ephippiorhynchus asiaticus*	Black-necked Stork	0
Ardeidae	*Ardea pacifica*	White-necked Heron	+
Ardeidae	*Ardea modesta*	Eastern Great Egret	0
Ardeidae	*Ardea intermedia*	Intermediate Egret	+
Ardeidae	*Ardea ibis*	Cattle Egret	+
Ardeidae	*Butorides striata*	Striated Heron	+
Ardeidae	*Egretta picata*	Pied Heron	0

Family	**Scientific name**	**common name**	**Change**
Ardeidae	*Egretta novaehollandiae*	White-faced Heron	0
Ardeidae	*Egretta garzetta*	Little Egret	+
Ardeidae	*Nycticorax caledonicus*	Nankeen Night-Heron	0
Threskiornithidae	*Plegadis falcinellus*	Glossy Ibis	+
Threskiornithidae	*Threskiornis molucca*	Australian White Ibis	0
Threskiornithidae	*Threskiornis spinicollis*	Straw-necked Ibis	0
Threskiornithidae	*Platalea regia*	Royal Spoonbill	0
Accipitridae	*Pandion cristatus*	Eastern Osprey	+
Accipitridae	*Hamirostra melanosternon*	Black-breasted Buzzard	+
Accipitridae	*Haliaeetus leucogaster*	White-bellied Sea-Eagle	0
Family	Scientific name	common name	Change
Accipitridae	*Haliastur sphenurus*	Whistling Kite	0
Accipitridae	*Haliastur indus*	Brahminy Kite	0
Accipitridae	*Milvus migrans*	Black Kite	+
Accipitridae	*Accipiter fasciatus*	Brown Goshawk	+
Accipitridae	*Accipiter novaehollandiae*	Grey Goshawk	+
Accipitridae	*Circus approximans*	Swamp Harrier	+
Accipitridae	*Erythrotriorchis radiatus*	Red Goshawk	0
Accipitridae	*Aquila audax*	Wedge-tailed Eagle	+
Falconidae	*Falco cenchroides*	Nankeen Kestrel	0
Falconidae	*Falco berigora*	Brown Falcon	0
Falconidae	*Falco longipennis*	Australian Hobby	0
Falconidae	*Falco peregrinus*	Peregrine Falcon	+
Gruidae	*Grus rubicunda*	Brolga	0
Rallidae	*Porphyrio porphyrio*	Purple Swamphen	+
Otididae	Ardeotis australis	Australian Bustard	‡
Burhinidae	*Burhinus grallarius*	Bush Stone-curlew	‡
Haematopodidae	*Haematopus longirostris*	Australian Pied Oystercatcher	+
Haematopodidae	*Haematopus fuliginosus*	Sooty Oystercatcher	+
Recurvirostridae	*Himantopus himantopus*	Black-winged Stilt	+
Charadriidae	*Charadrius leschenaultii*	Greater Sand Plover	+
Charadriidae	*Elseyornis melanops*	Black-fronted Dotterel	+
Charadriidae	*Vanellus miles*	Masked Lapwing	0
Jacanidae	*Irediparra gallinacea*	Comb-crested Jacana	0
Scolopacidae	*Numenius phaeopus*	Whimbrel	+
Scolopacidae	*Tringa nebularia*	Common Greenshank	0
Scolopacidae	*Tringa stagnatilis*	Marsh Sandpiper	+
Scolopacidae	*Calidris ruficollis*	Red-necked Stint	+
Scolopacidae	*Calidris acuminata*	Sharp-tailed Sandpiper	+
Turnicidae	*Turnix pyrrhothorax*	Red-chested Button-quail	+
Glareolidae	*Stiltia isabella*	Australian Pratincole	+
Laridae	*Gelochelidon nilotica*	Gull-billed Tern	+
Laridae	*Hydroprogne caspia*	Caspian Tern	+
Laridae	*Chlidonias leucopterus*	White-winged Black Tern	+
Laridae	*Thalasseus bergii*	Crested Tern	+

Family	Scientific name	common name	Change
Cacatuidae	*Probosciger aterrimus*	Palm Cockatoo	0
Cacatuidae	*Eolophus roseicapillus*	Galah	+
Cacatuidae	*Cacatua galerita*	Sulphur-crested Cockatoo	+
Psittacidae	*Trichoglossus haematodus*	Rainbow Lorikeet	+
Psittacidae	*Aprosmictus erythropterus*	Red-winged Parrot	0
Psittacidae	*Platycercus adscitus*	Pale-headed Rosella	+
Cuculidae	*Centropus phasianinus*	Pheasant Coucal	+
Cuculidae	*Eudynamys orientalis*	Eastern Koel	0
Cuculidae	*Scythrops novaehollandiae*	Channel-billed Cuckoo	0
Cuculidae	*Chalcites basalis*	Horsfield's Bronze-Cuckoo	+
Cuculidae	*Chalcites minutillus*	Little Bronze-Cuckoo	+
Cuculidae	*Cacomantis castaneiventris*	Chestnut-breasted Cuckoo	+
Cuculidae	*Cacomantis flabelliformis*	Fan-tailed Cuckoo	+
Cuculidae	*Cacomantis variolosus*	Brush Cuckoo	0
Strigidae	*Ninox rufa*	Rufous Owl	+
Strigidae	*Ninox connivens*	Barking Owl	+
Strigidae	*Ninox novaeseelandiae*	Southern Boobook	+
Alcedinidae	*Ceyx azureus*	Azure Kingfisher	+
Halcyonidae	*Dacelo novaeguineae*	Laughing Kookaburra	0
Halcyonidae	*Dacelo leachii*	Blue-winged Kookaburra	0
Halcyonidae	*Syma torotoro*	Yellow-billed Kingfisher	+
Halcyonidae	*Todiramphus macleayii*	Forest Kingfisher	+
Climacteridae	*Climacteris picumnus*	Brown Treecreeper	+
Meropidae	*Merops ornatus*	Rainbow Bee-eater	+
Coraciidae	*Eurystomus orientalis*	Dollarbird	0
Pittidae	*Pitta versicolor*	Noisy Pitta	+
Ptilonorhynchidae	*Ailuroedus melanotis*	Spotted Catbird	+
Ptilonorhynchidae	*Ptilonorhynchus nuchalis*	Great Bowerbird	0
Maluridae	*Malurus melanocephalus*	Red-backed Fairy-wren	0
Maluridae	*Malurus amabilis*	Lovely Fairy-wren	0
Acanthizidae	*Sericornis beccarii*	Tropical Scrubwren	+
Acanthizidae	*Smicrornis brevirostris*	Weebill	+
Acanthizidae	*Gerygone magnirostris*	Large-billed Gerygone	0
Acanthizidae	*Gerygone albogularis*	White-throated Gerygone	0
Pardalotidae	*Pardalotus rubricatus*	Red-browed Pardalote	0
Pardalotidae	*Pardalotus striatus*	Striated Pardalote	+
Meliphagidae	*Meliphaga lewinii*	Lewin's Honeyeater	+
Meliphagidae	*Meliphaga notata*	Yellow-spotted Honeyeater	0
Meliphagidae	*Meliphaga gracilis*	Graceful Honeyeater	0
Meliphagidae	*Lichenostomus unicolor*	White-gaped Honeyeater	0
Meliphagidae	*Lichenostomus flavus*	Yellow Honeyeater	0
Meliphagidae	*Lichenostomus flavescens*	Yellow-tinted Honeyeater	‡
Meliphagidae	*Ramsayornis modestus*	Brown-backed Honeyeater	0
Meliphagidae	*Ramsayornis fasciatus*	Bar-breasted Honeyeater	0
Meliphagidae	*Conopophila albogularis*	Rufous-banded Honeyeater	0

Family	Scientific name	common name	Change
Meliphagidae	*Myzomela obscura*	Dusky Honeyeater	0
Meliphagidae	*Myzomela erythrocephala*	Red-headed Honeyeater	+
Meliphagidae	*Cissomela pectoralis*	Banded Honeyeater	+
Meliphagidae	*Lichmera indistincta*	Brown Honeyeater	+
Meliphagidae	*Trichodere cockerelli*	White-streaked Honeyeater	+
Meliphagidae	*Melithreptus albogularis*	White-throated Honeyeater	+
Meliphagidae	*Entomyzon cyanotis*	Blue-faced Honeyeater	0
Meliphagidae	*Philemon buceroides*	Helmeted Friarbird	0
Meliphagidae	*Philemon argenticeps*	Silver-crowned Friarbird	0
Meliphagidae	*Philemon corniculatus*	Noisy Friarbird	+
Meliphagidae	*Philemon citreogularis*	Little Friarbird	0
Meliphagidae	*Xanthotis flaviventer*	Tawny-breasted Honeyeater	0
Pomatostomidae	*Pomatostomus temporalis*	Grey-crowned Babbler	0
Neosittidae	*Daphoenositta chrysoptera*	Varied Sitella	0
Campephagidae	*Coracina novaehollandiae*	Black-faced Cuckoo-shrike	0
Campephagidae	*Coracina papuensis*	White-bellied Cuckoo-shrike	+
Campephagidae	*Lalage sueurii*	White-winged Triller	+
Campephagidae	*Lalage leucomela*	Varied Triller	0
Pachycephalidae	*Pachycephala rufiventris*	Rufous Whistler	0
Pachycephalidae	*Colluricincla megarhyncha*	Little Shrike-thrush	0
Pachycephalidae	*Colluricincla harmonica*	Grey Shrike-thrush	0
Oriolidae	*Oriolus flavocinctus*	Yellow Oriole	+
Oriolidae	*Oriolus sagittatus*	Olive-backed Oriole	0
Artamidae	*Artamus cinereus*	Black-faced Woodswallow	+
Artamidae	*Artamus minor*	Little Woodswallow	‡
Artamidae	*Cracticus mentalis*	Black-backed Butcherbird	0
Artamidae	*Cracticus nigrogularis*	Pied Butcherbird	0
Artamidae	*Cracticus tibicen*	Australian Magpie	0
Artamidae	*Strepera graculina*	Pied Currawong	0
Rhipiduridae	*Rhipidura rufifrons*	Rufous Fantail	‡
Rhipiduridae	*Rhipidura leucophrys*	Willie Wagtail	0
Corvidae	*Corvus orru*	Torresian Crow	0
Monarchidae	*Myiagra ruficollis*	Broad-billed Flycatcher	+
Monarchidae	*Myiagra rubecula*	Leaden Flycatcher	0
Monarchidae	*Myiagra cyanoleuca*	Satin Flycatcher	+
Monarchidae	*Myiagra alecto*	Shining Flycatcher	+
Monarchidae	*Myiagra inquieta*	Restless Flycatcher	+
Monarchidae	*Symposiarchus trivirgatus*	Spectacled Monarch	0
Monarchidae	*Grallina cyanoleuca*	Magpie-lark	+
Monarchidae	*Machaerirhynchus flaviventer*	Yellow-breasted Boatbill	+
Paradisaeidae	*Ptiloris magnificus*	Magnificent Riflebird	0
Petroicidae	*Microeca fascinans*	Jacky Winter	0
Petroicidae	*Microeca flavigaster*	Lemon-bellied Flycatcher	+
Petroicidae	*Poecilodryas superciliosa*	White-browed Robin	+
Cisticolidae	*Cisticola exilis*	Golden-headed Cisticola	0

Family	Scientific name	common name	Change
Timaliidae	*Zosterops luteus*	Yellow White-eye	+
Nectariniidae	*Dicaeum hirundinaceum*	Mistletoebird	0
Nectariniidae	*Nectarinia jugularis*	Olive-backed Sunbird	0
Estrildidae	*Taeniopygia bichenovii*	Double-barred Finch	0
Estrildidae	*Neochmia phaeton*	Crimson Finch	0
Estrildidae	*Neochmia ruficauda*	Star Finch	+
Estrildidae	*Neochmia temporalis*	Red-browed Finch	0
Estrildidae	*Lonchura castaneothorax*	Chestnut-breasted Mannikin	+
Motacillidae	*Anthus novaeseelandiae*	Australasian Pipit	+

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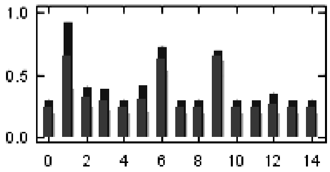
<td>

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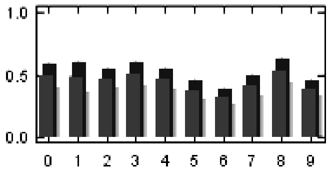
<td>

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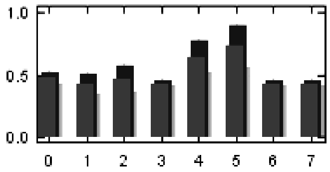
<td>

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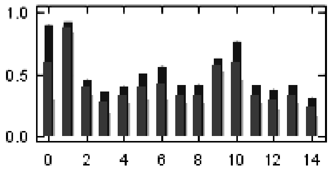
<td>

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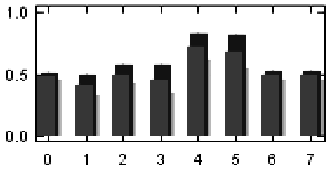
<td>

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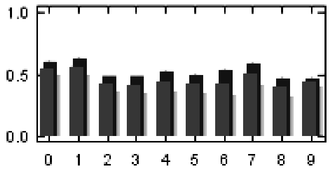
<td>

Fire Frequency 00 - 08</td>
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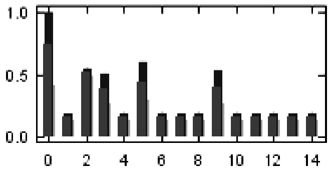
<td>

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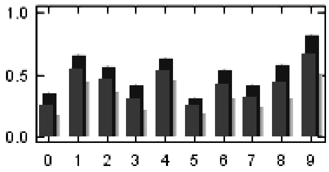
<td>

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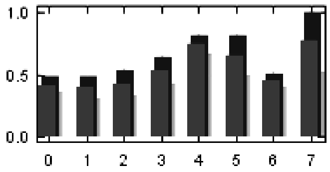
<td>

Early Fire Frequency 00 - 08</td>
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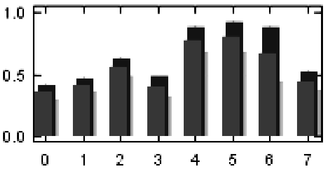
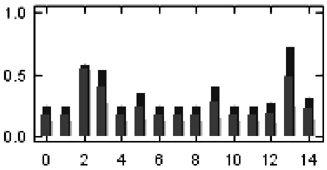
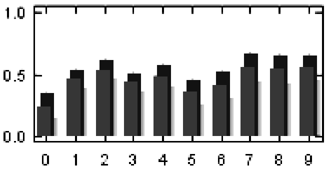
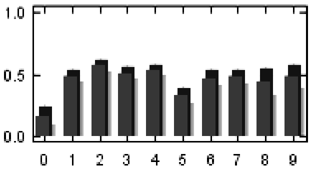
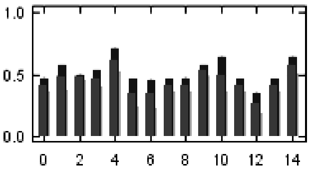
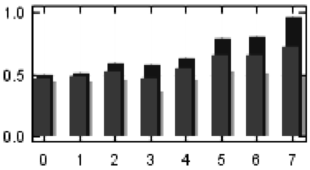
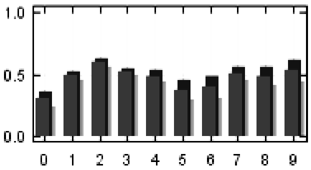
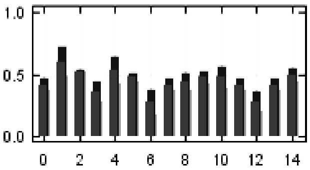
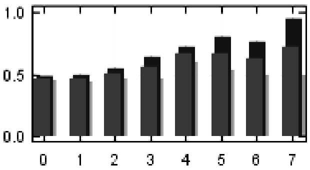
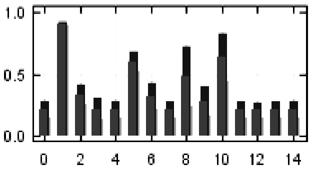
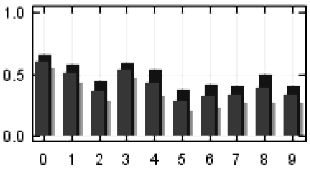
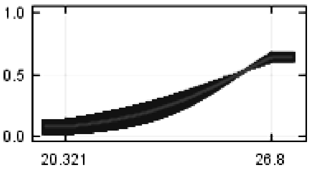
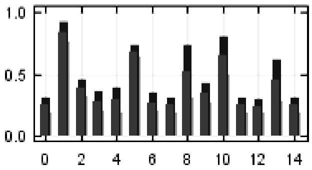
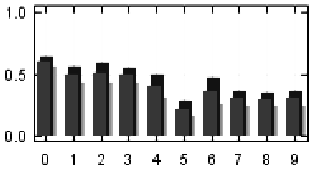
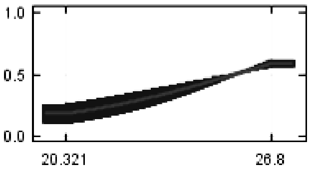
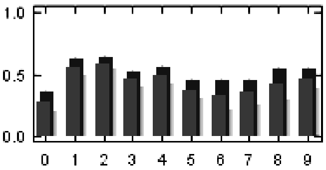
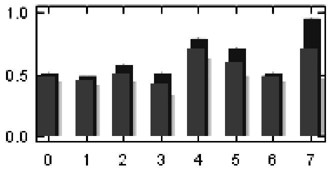
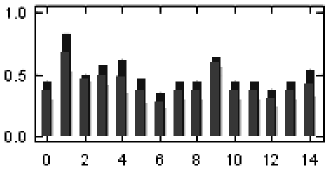
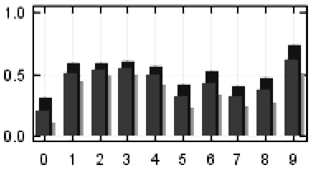
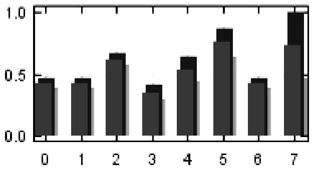
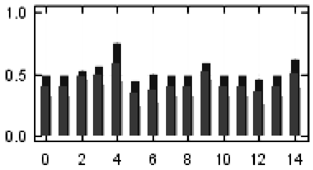
30.9%	26.8%	23.1%
Weebill 2008		
 **Early Fire Frequency 00 - 08**	 **Vegetation Category**	 **Fire Frequency 00 - 08**
32.6%	30.8%	20.6%
White-throated Honeyeater 2000		
 **Fire Frequency 00 - 08**	 **Vegetation Category**	 **Early Fire Frequency 00 - 08**
39.1%	19.2%	13.5%
White-throated Honeyeater 2008		
 **Fire Frequency 00 - 08**	 **Vegetation Category**	 **Early Fire Frequency 00 - 08**
33.7%	22.2%	18.1%
Yellow Oriole 2000		
 **Vegetation Category**	 **Fire Frequency 00 - 08**	 **Mean Temperature**

63.5%	13.1%	7.2%
Yellow Oriole 2008		
 **Vegetation Category**	 **Fire Frequency 00 - 08**	 **Mean Temperature**
50.0%	20.5%	11.0%
Black-backed Butcherbird 2000		
 **Fire Frequency 00 - 08**	 **Early Fire Frequency 00 - 08**	 **Vegetation Category**
35.9%	26.4%	21.8%
Black-backed Butcherbird 2008		
 **Fire Frequency 00 - 08**	 **Early Fire Frequency 00 - 08**	 **Vegetation Category**
41.2%	31.1%	15.0%

Blue-faced Honeyeater 2000

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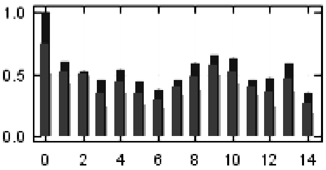
<td>
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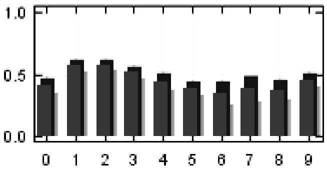
<td>
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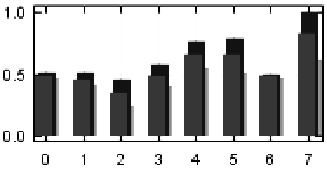
<td>
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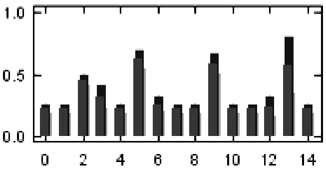
<td>
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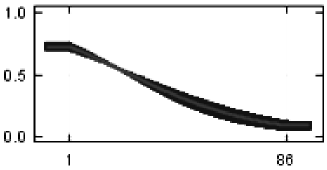
<td>
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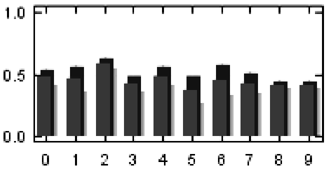
<td>
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<tr><td>32%</td><td>19.9%</td><td>15.1%</td></tr>
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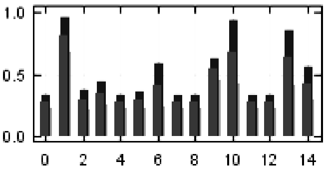
<td>
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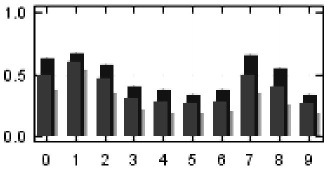
<td>
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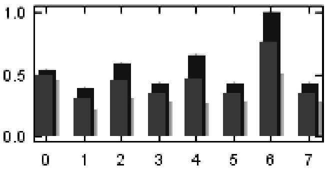
<td>
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<tr><td>44.7%</td><td>23.7%</td><td>18.9%</td></tr>
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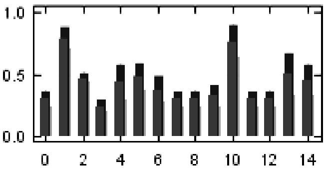
<td>
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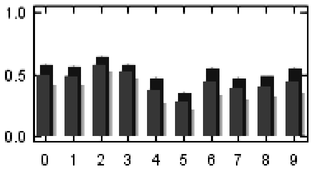
<td>
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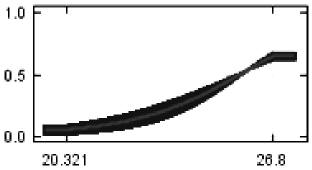
<td>
Mean Temperature</td>
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<tr><td>36.6%</td><td>21.5%</td><td>20.4%</td></tr>
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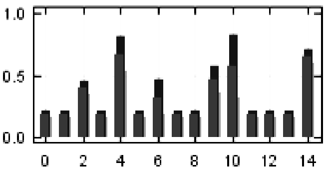
<td>
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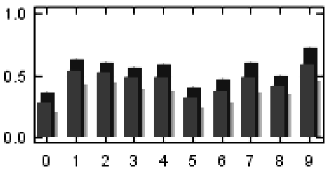
<td>
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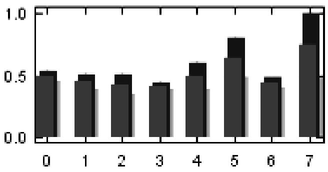
<td>
Early Fire Frequency 00 - 08</td>
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<tr><td>43.2%</td><td>20.6%</td><td>11.9%</td></tr>
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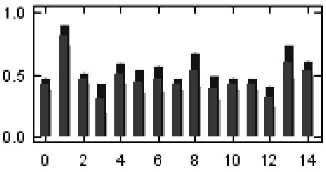
<td>
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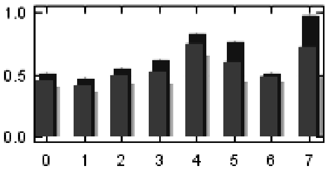
<td>
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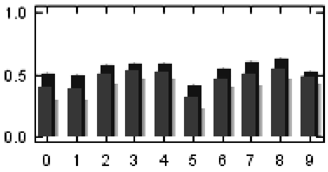
<td>
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<tr><td>26.3%</td><td>23.2%</td><td>17.5%</td></tr>
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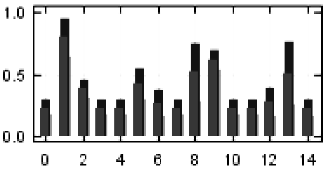
<td>
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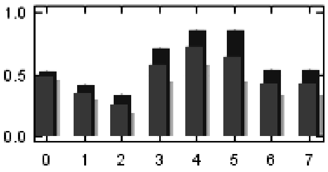
<td>
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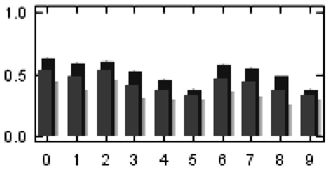
<td>
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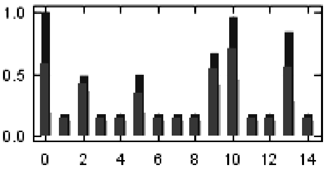
<td>
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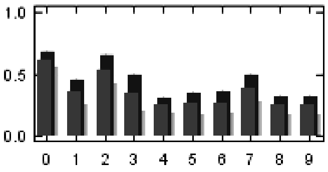
<td>
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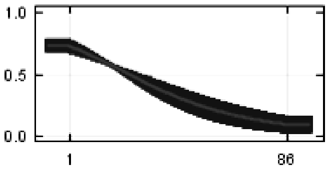
<td>
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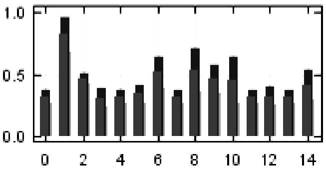
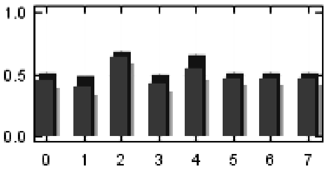
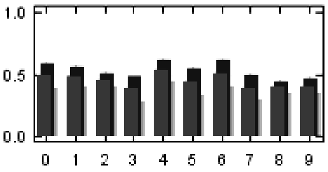
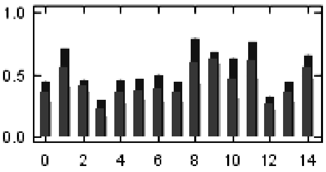
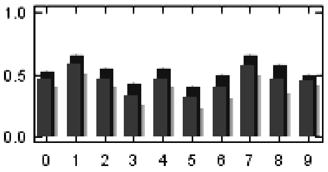
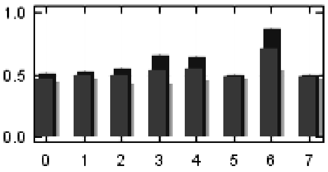
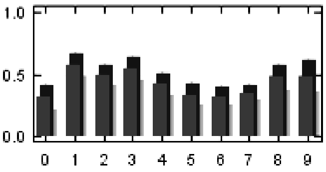
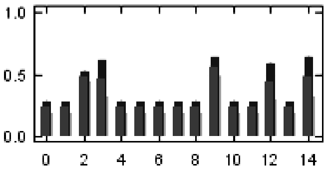
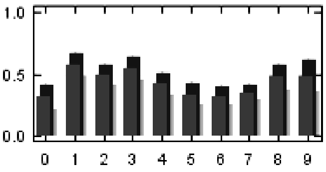
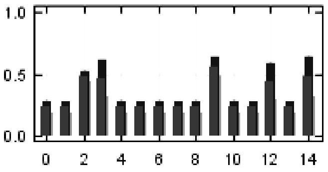
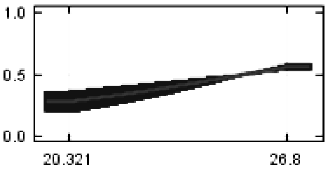
39.9%	29.4%	13.7%
Pheasant Coucal 2000		
 **Vegetation Category**	 **Early Fire Frequency 00 - 08**	 **Fire Frequency 00 - 08**
36.7%	22.5%	18.7%
Pheasant Coucal 2008		
 **Vegetation Category**	 **Fire Frequency 00 - 08**	 **Early Fire Frequency 00 - 08**
43.7%	30.7%	8.6%
Pied Butcherbird 2000		
 **Fire Frequency 00 - 08**	 **Vegetation Category**	 **Mean Temperature**
38.4%	32.1%	18.5%
Pied Butcherbird 2008		
 **Fire Frequency 00 - 08**	 **Vegetation Category**	 **Mean Temperature**

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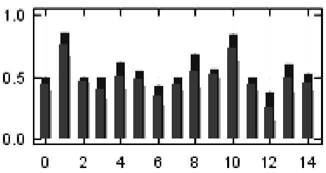
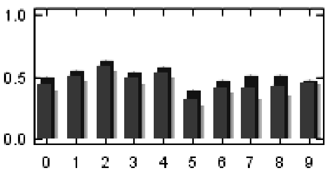
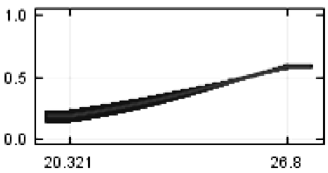
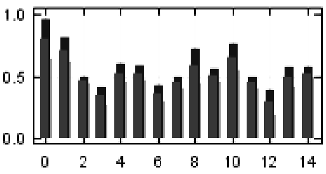
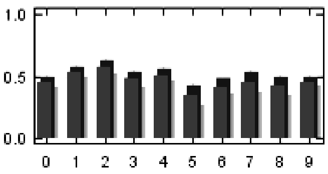
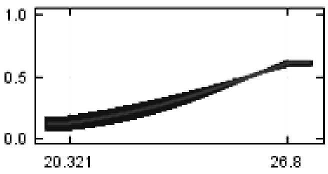
<tr><td>

Vegetation Category</td><td>

Fire Frequency 00 - 08</td><td>

Mean Temperature</td></tr>
<tr><td>38.4%</td><td>30.6%</td><td>12.7%</td></tr>
<tr><td colspan="3">Rainbow Lorikeet 2008</td></tr>
<tr><td>

Vegetation Category</td><td>

Fire Frequency 00 - 08</td><td>

Mean Temperature</td></tr>
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Appendix Figure 7.1. Response curves and histograms (mean, central bars, +/- one standard deviation, offset bars) from maximum entropy (MAXENT) species habitat modelling for species recorded as having significant increase or decline in reporting rate across the two surveys. Model percentage represents the percent variance explained by each variable. x- axis values represent fire frequency (early – January to August, storm – November to January and all) between 2000 and 2008, mean annual rainfall, mean annual temperature, vegetation category (Miscellaneous = 0, Beach Scrub= 1, *Eucalyptus* Woodland - Flats = 2, *Eucalyptus* Woodland - Hills = 3, *Eucalyptus* Woodland – Wet = 4, Closed Forest = 5, Grassland = 6, *Acacia* = 7, Mangrove = 8, Ti Tree = 9, Bare and Rock = 10, Dry Scrub = 11, Heath = 12, Wetland = 13, *Eucalyptus* Forest = 14), and foliage projective cover (ranging from 0 – 100%). Y- axis values represent likelihood value between 0 – 1.

Chapter 8. General discussion

A substantial body of research has shaped my understanding of fire in savanna ecosystems across the globe. This research has spanned decades and has included an examination of the social, cultural and environmental impacts of fire (Andersen et al. 2005; Bond et al. 2005; Bowman et al. 2011; Bowman et al. 2009; Driscoll et al. 2010; Hill and Baird 2003; Lehmann et al. 2014; Lehmann et al. 2011; Murphy et al. 2013; Parr et al. 2002; Price et al. 2007; Russell-Smith et al. 2013; Russell-

Smith et al. 1997; Russell-Smith et al. 2009; Yibarbuk et al. 2001). There is also a reasonably well-developed understanding of the evolutionary processes that shaped these ecosystems, including the role of fire in determining vegetation structure and composition, and the associated vertebrate responses to these changes (Krawchuk et al. 2009; Moritz et al. 2012; Pepper et al. 2008). It is clear from previous research that there are interacting links between fire, climate, vegetation and vertebrate species distributions.

Despite the broad and well-developed research base that encompasses the multi-faceted outcomes from altered fire regimes, there is still debate about the best way to manage fire, particularly in reference to biodiversity and cultural outcomes. One of the most interesting manifestations of the collective research is the overwhelming acceptance by land managers that the best way to manage fire for biodiversity is to create a random mosaic of burning at a landscape scale (Levin et al. 2012; Parr and Andersen 2006). In essence, the idea is theoretically sound, i.e., fire patchiness should create a more heterogeneous matrix of fire scar ages, which should support a wider range of habitat niches. In reality, however, the nature of the weather and vegetation in northern Australia supports an annual replenishment of biomass (Felderhof and Gillieson 2006), potentially quickly homogenising habitats altered by fire. The assumption that fire mosaics promote biodiversity also assumes that savanna ecosystems lack heterogeneity, despite the vast climatic gradient that supports a wide range of ecosystems, ranging from arid deserts to tropical rainforest patches (Woinarski et al. 1999b). Additionally, in savannas, human intervention is rarely the primary driver of fire heterogeneity, rather, fire patterns follow the natural boundaries that break up landscapes (Price et al. 2005; Price et al. 2003; Price et al. 2007). Human intervention and the ability to manipulate fire to alter habitat structure generally operates within the boundaries of natural climatic, geological and topographical features (Murphy et al. 2013), such that complete change in habitat is difficult to implement (i.e., it is difficult to change a grassland into a rainforest by preventing fire, but altering the number of trees growing in a woodland may be possible by manipulating fire) and even more difficult to maintain (Russell-Smith and Whitehead 2015).

Even with the well-documented changes to fire management strategies across Australia since European colonisation that has led to the dominance of large and intense wildfire (Russell-Smith et al. 2013; Russell-Smith and Whitehead 2015), there are still examples of areas where unusual circumstances have led to fire exclusion in very fire prone landscapes. These areas can provide insights into the potential implications of changed fire regimes for vertebrate fauna (Woinarski et al. 2004b). Many of the species found in these areas exist because of natural or induced barriers to fire within naturally fire prone landscapes. The areas that inherently exclude fire are generally relict landscapes that offer a window into a different climatic period (Trainor et al. 2000). Recent changes to land management and climate promote larger, more intense fires that have reduced the protection that these landscapes once afforded (Robinson et al. 2013; Whitehead et al. 2005). The focus of landscape-scale fire management rarely focuses on these unique areas, which represent only a small fraction of the total savanna ecosystem. In fact, recently, the dominant fire management paradigm has largely shifted to meet the requirements of the federally regulated Emissions Reduction Fund for managing fire for greenhouse gas abatement (Australian.Government 2015). The assumption that there are biodiversity and cultural co-benefits associated with this methodology opens up a new, and yet to be adequately explored, research area that I have begun to explore in this thesis.

To understand the best way to manage fire both now and into the future we need to clearly state the objectives of fire management and then assess the relationships between the stated objectives and the actual outcomes. This is particularly important where there are assumed co-benefits for biodiversity and culture from enacting a single fire management strategy, such as the greenhouse gas abatement method (Australian.Government 2015).

Summary of research findings

This thesis extends the established fire ecology and biodiversity conservation research in northern Australia from the Northern Territory and Western Australia to Cape York Peninsula, an important and iconic bioregion in Australia. The data used in this thesis represent the most comprehensive, systematically collected, multi-taxa vertebrate fauna survey ever completed for Cape York Peninsula, which will form the basis for future ecological research in the region. In addition, I have used analysis of these data to extend the broader understanding of the impact of commonly applied fire management methods to terrestrial fauna beyond the relatively well-studied mesic savanna of the Northern Territory.

Hypothesis one:

i. The probability of fire weather that can alter fire frequency in northern Australia has changed (led to conditions that support more frequent fire or less frequent fire) in recent history (the past 60 years).

ii. The probability of fire weather that supports increased fire frequency has increased unequally across the rainfall gradient which supports a range of fire frequencies.

Widespread changes in pyrogeography are expected under future climate scenarios. Most researchers predict a net increase in fire frequencies worldwide driven by increasing temperatures and rates of drying of biomass. Savannas are usually cited as the exception: they are expected to become less fire prone, or show little change in fire frequency under future climate scenarios, in part due to a perception that large parts of savanna systems are already at, or close to, fire maximum and therefore fire activity can only remain static or decrease (Cary et al. 2012). In **Chapter 2** I found that the average area of land presently experiencing weather conditions suitable for fire every year has increased by 972,774 km^2 since 1950, and 27% of the savanna biome is now at fire maximum, compared to 15% in the 1950's. Another 118,215 km^2 will probably achieve fire maximum within the next 20 years; even beyond 2030, the fire maximum front may expand. Between 1950 and 1990 the area classified as increasing to a fire maximum (over a 5 year moving window) grew, but showed considerable variation, that is, large parts of the landscape experienced fire maximum conditions for short intervals but intermittently experienced years that were less conducive to burning (i.e., they did not stay in the fire maximum category). Post 1990, variation decreased markedly, indicating that large parts of the landscape achieved fire maximum conditions and stayed there for the remainder of the 60 year period.

Seasonally, patterns of weather conducive to fire appeared to be relatively stable in the fire maximum region (areas that have always been suitable for fire since 1950). I did not detect any lengthening of the number of months over the dry season when weather conducive to burning was experienced in this region. In the western savannas, the fire maximum front has shifted south nearly 2° latitude over the past 60 years. The most dramatic expansions occurred in the 1970s and in the 2000s, which were wetter than average. Fire is limited at the climate extremes, i.e., where conditions are consistently too wet or too dry to support frequent fire. In these areas it is only during abnormal conditions (those that reflect the nearly annual cycle in the mesic savanna) that such areas are suitable for fire.

These results have significant implications for carbon accounting that relies on static values defined by rainfall gradients and the month of the late dry season. The logical next step for this research is to use the model results (monthly fire probability) to assess the spatial and temporal variance in fire weather in the context of regionally specific dry season dates that can be used to better account for greenhouse gas emissions.

Hypothesis two: Contemporary fire management strategies applied by Aboriginal land managers, such as early dry season burning done from a helicopter using incendiary, do not closely replicate traditional Aboriginal burning across northern Australia.

No assessment of burning in northern Australia would be complete without acknowledging the fundamental role played by Aboriginal people in informing contemporary and historical fire management strategies. There is an assumption that the random patch mosaic burning strategy commonly applied by land managers is representative of indigenous burning, and that this management strategy is inherently good for biodiversity conservation. In **Chapter 3** I collaborate with traditional owners from the Wik people of Cape York Peninsula, a human geographer and an anthropologist that has worked with Wik and Wik Waya people for over 30 years. Together we identified contemporary fire management strategies and put these into context with traditional Wik fire management. We found that the current land management methods, including the management of fire, were largely governed by federal and state policy via government funded ranger programs and had very little relationship to traditional burning. Traditionally, Wik people managed fire for very specific purposes and an example of fire management for the protection of an important Yam species was discussed. This chapter outlines some of the key philosophical and practical challenges of fire management using traditional Aboriginal methods within the context of contemporary land management. Because many fire management programs list the re-instatement of traditional Aboriginal burning as a key objective, it is very important to illustrate the fundamental differences in these methods, which is what I have done here.

In this chapter I used interviews with traditional owners, and a critical examination of contemporary fire management strategies, to show that contemporary fire management is applied across traditional cultural boundaries using methods that limit participation by traditional owners, such as the use of aerial incendiary techniques. Financial incentives and contractual obligations associated with fire management are externally driven or include modern considerations such as the protection of infrastructure as reasons for burning. In contrast, traditional fire management was the prerogative of traditional owners and was applied at fine scales for specific outcomes. Fire management was governed by rules that determined how people moved across the landscape and how resources were partitioned and shared. Although there is a clear separation between the two fire management paradigms (modern and traditional) this isn't necessarily seen as a conflict by Wik people. However, it is clear that there is an imbalance in the application fire management based on externally driven outcomes that have associated financial resources. Supporting the implementation of Aboriginal burning alongside current fire management practices could lead to significant community engagement in such activities and is likely to have much better biodiversity and social outcomes.

Proposition 3. The vertebrate taxa of northern Australia vary in response to fire management and there are no simple linear relationships between fire metrics that relate to optimum outcomes for all taxa.

In **Chapter 4** I set out to understand the overall responses of three vertebrate taxa (birds, reptiles and mammals) in relation to fire management on Cape York Peninsula. Specifically, I tested the assumption that there is a positive relationship between the fire management methods used to abate greenhouse gases in northern Australia and vertebrate fauna. I systematically sampled 202 sites on Cape York Peninsula, and examined the relationship between vertebrate fauna abundance and diversity, fire, and environmental metrics. I found that within the approved greenhouse gas abatement methodology vegetation type, open woodlands in tropical savanna woodland, early and late dry season fire frequency was not a strong predictor of bird, mammal and reptile richness and abundance. Additionally, the response of each taxa to fire frequency was different across broad structural vegetation categories (closed forest, tropical woodland and grassland) suggesting that a more nuanced species-specific monitoring approach is required to expose links between savanna burning for carbon abatement and burning for biodiversity benefit.

Fire is an important management tool for biodiversity conservation in the savanna biome and is an unavoidable reality for anyone managing broad natural systems in this region. To effectively use fire as a tool, land managers need to clearly define the desired response and understand the likelihood of success in various persistent vegetation types. The success of a fire management program with biodiversity conservation goals can only be measured in this context.

Chapter 4 demonstrated that there were was a complex relationship between fire and vertebrate fauna and this was taxon specific, so in the next three chapters (Chapters 5 – 7) I sought to contextualise the patterns of each taxa within the framework of individual species response to fire and other environmental factors.

In **Chapter 5** I used the best available data to develop a better understanding of the historical changes in small- to medium-sized mammals on Cape York Peninsula. The Australian Government has placed significant resources and emphasis on halting small mammal declines in northern Australia. In my study, mammals were generally scarce across the sites I surveyed on Cape York Peninsula and were more abundant and species rich in wet coastal grasslands or closed forests than tropical savanna woodlands. The vegetation complexity (number of vegetation types within 1km) surrounding the sampling site was a consistent landscape scale predictor of mammal richness and abundance; increasing ground cover and woody complexity were significant at the site-scale (1ha plots). Notwithstanding interpretational constraints related to the limited evidence base of historic sampling, the mammal fauna recorded in this study for Cape York Peninsula was similar in composition to the mammal fauna described from 1948–1980 and surveys in 1985, with some species seemingly declining (e.g. *Melomys burtoni, Dasyurus hallucatus, Sminthopsis virginiae*) and others stable (e.g. *Rattus sordidus*) or more common (e.g. *Rattus tunneyi*); however, across all sites abundance was low, and many sites had few or no mammals. In the absence of consistent long-term systematic monitoring it is difficult to determine if this survey and historical surveys represent pre-European patterns for mammals. The absence or low abundance of mammals in most sites suggests that contemporary patterns may not represent an intact mammal fauna. Due to the equivocal nature of these findings a critical next step is to establish robust monitoring and experimental work to reveal the response of mammals to management interventions.

The taxon least likely to avoid fire, due to generally small home ranges, is reptiles. In **Chapter 6** I explored relationships between reptile diversity and fire. This taxon should demonstrate a strong relationship with vegetation. I found some effect of remotely sensed fire frequency on vegetation structure in the most and least fire prone habitats, but in the largely undifferentiated and most extensive habitat – open Eucalyptus woodlands – there was an intermediate and less conclusive effect of fire frequency on reptile diversity. Reptile assemblages were partitioned along an environmental gradient within broad vegetation groups from least complex (grassland) to most complex (closed forest). Reptile diversity was highest at intermediate to low tree cover and density and low in sites with very low or very high tree cover (though these areas contained unique or specialised species). The implication of this result is that vegetation types with intermediate to low cover, were most suitable for heliothermic and thigmothermic species (because such habitats were neither too exposed nor too covered) and fire frequency measured by remote sensing is a poor surrogate for predicting reptile patterns except at the extremes of vegetation cover (high or low). This study suggests that fire management that aims to reduce fire frequency at a landscape scale may not lead to changes in reptile diversity unless the intervention is extreme (burning every year or not burning at all).

Chapter 7 illustrated that the most vagile taxa, birds, remained relatively stable in the tropical woodlands of Cape York Peninsula. I recorded little change in the avifauna at sites sampled during a survey conducted by volunteers and ornithologists in the year 2000 and a survey I did in 2008 on Cape York Peninsula. This included many species that were originally recorded in very low numbers (Brown Treecreeper, Black-faced Wood Swallow, Star Finch, and Crimson Finch) and thought to be in decline. Fire and vegetation types were consistent significant predictive model variables for species either declining or increasing in the reporting rate, and this suggests that changes in land management, especially in the use of fire, could affect the distribution and abundance of avian populations on Cape York Peninsula, however most species remained unchanged across time.

In my study, changes in mean species richness varied across the study area (decreased in 59 grid cells and increased in 43) with no apparent pattern. Significant change in reporting rates was recorded in 30 species. Four sedentary and highly detectable species declined (Bar-shouldered Dove, Brown Treecreeper, Pale-headed Rosella and Sulphur-crested Cockatoo) and five increased (Peaceful Dove, Pheasant Coucal, Weebill, White-throated Honeyeater and Yellow Oriole). Habitat preference for the species that changed in abundance remained relatively stable between the two survey periods. Some species that were recorded in very low numbers in the original survey and are threatened (Brown Treecreeper, Black-faced Woodswallow) remained in very low numbers or decreased in my survey, suggesting that there has been no regional recovery of these species. Long-term monitoring can describe important patterns of species change over time, though in the case of large, highly seasonal environments like the tropical savannas, signals of change may manifest over decades rather than annually. This study demonstrated that for most savanna birds, which are resource-tracking generalists, the general distribution and abundance of most species was stable despite broad scale changes to land management in recent history. This suggests that savanna birds may be less sensitive to change than other vertebrate taxa.

Future research directions.

In this study, I identified some fundamental assumptions about fire heterogeneity, the influence of humans on this and the implications for biodiversity of commonly applied fire management strategies. As with all good research studies, my work uncovered more questions than it answered. Critically, I exposed fundamental gaps in the collective knowledge regarding the impacts of suggested fire management strategies and the effects on vertebrate fauna. For example, often there is an assumption that a response in vegetation linked to altered fire management impacts other elements of biodiversity. My research has demonstrated that there isn’t a clear linear relationship between fire and vertebrate fauna at the temporal scales in which fire is generally managed and measured.

During the course of this PhD I have witnessed a dramatic shift in fire management following the development of the Savanna Burning for Greenhouse Gas Abatement methodology. In this thesis I have identified issues with some of the critical assumptions of this methodology particularly with the assumptions that burning for greenhouse gas abatement is similar to traditional Aboriginal burning and that it has overall benefits for terrestrial fauna. This thesis has raised four important research areas that need significant and rapid attention.

1. Unequal and predictable spatial and temporal variance in weather conducive to fire identified in Chapter 2 needs to be included in the approved savanna fire carbon accounting methodology.
2. Biodiversity co-benefits associated with the savanna burning for greenhouse gas emission methodology need to be robustly measured. This will require species- and taxon-specific research that accounts for underlying niche selection, evolutionary processes, and hysteresis.
3. The lack of longitudinal studies of vertebrate fauna patterns in northern Australia means that we have very little data to discuss potential changes in fauna patterns over time. This severely hinders the ability to measure the impact of management interventions and to advise policy and land managers about the best way to manage fire for biodiversity. Long-term funding for robust, and systematic biodiversity surveys is required to support informed decisions making for climate adaptation policy and management.
4. Dedicated research and management funding is required to involve Aboriginal people in developing fire management strategies for the future. We need to support the re-invigoration of traditional burning and develop collaborative research programs to understand the biodiversity and carbon benefits of fire management chosen by traditional owners. Participatory approaches are required to clearly understand and articulate the evolving role of Aboriginal people in contemporary fire and land management and acknowledge that adaptation to modern requirements (enterprise development, carbon abatement and infrastructure protection) is a critical part of this.

Concluding remarks

In this thesis, I have exposed the complex ecology of fire and fauna. I have more clearly defined the role of Aboriginal people in northern fire management, exposing the divergence of fire management strategies despite the explicit aim of including Aboriginal people in land management decision making. I have, yet again, raised the importance of longitudinal studies and systematic monitoring as critical inputs for understanding the complex relationships between environmental and anthropogenic influences. In short, models need data and the data need to adequately sample the environmental space including seasonal and annual variation across climate and vegetation gradients. We currently don't have enough data to make sense of the variance in these dynamic and rapidly changing systems.

With the dramatic changes to weather that I illustrated in chapter 2, the continuation of research and monitoring that quantify the patterns and trends of ecological systems will be essential for developing adaptation strategies for dynamic future challenges. Without these critical feedback mechanisms we will be developing policy and management interventions blindly, and risk the significant loss of species. For example, if the Northern Territory Government hadn't invested in fundamental biodiversity monitoring over many decades, we wouldn't even know that small mammals have dramatically declined in the past 20 years. Now that we are aware of the issues, future research needs to aggressively search for solutions. This will require a concerted effort and collaborations across research and management sectors, especially in a fiscally impoverished research sector characterised by unfortunate re-appropriation of research funding, and concerted effort to tackle these critical issues. Northern Australia has avoided broad-scale development, and as such, represents one of the most intact natural systems in the world. At the same time, Australian Aboriginal people in this region have largely maintained their culture and traditional knowledge of landscapes and management. The future of the natural and cultural assets of this globally significant region will depend on the ability of research and management sectors to identify and respond to the challenges that will come with economic development and rapid climate change.

Appendices

Appendix 1. A bird survey method for Australian tropical savannas

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Perry, J.J., Kutt, A.S., Perkins, G.C., Vanderduys, E.P. & Colman, N.J. (2012). A bird survey method for Australian tropical savannas. *Emu*, 112, 261-266.

Abstract

The tropical savannas of northern Australia are extensive and relatively homogenous open woodlands. The bird fauna of this biome are dispersed and spatially uneven in the landscape. A standard bird count method using eight repeated counts has been used extensively over the past decade or more, but has never been critically examined. I used data collected from across northern Queensland from 2004 and 2010 comprising >500 single survey sites, and 60 sites resampled four times to examine species records and accumulation with respect to time of day, increasing repeat counts, species turnover, vegetation density effects and distance to first observation. This study demonstrated that repeated sampling over multiple days, and at different times of the day, provided the best estimate of species present at a site, and improved detection estimates.

Keywords: species accumulation, repeat counts, spatial and temporal variation, detection

Appendix 2. Status and habitat of the Carpentarian grasswren (*Amytornis dorotheae*) in the Northern Territory

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Abstract.

Birds with restricted geographical distributions are particularly vulnerable to environmental change. In order to evaluate their conservation status it is necessary to have accurate records of their distribution and how that distribution has changed over time. The determinants of the distribution and abundance of the Carpentarian grasswren (*Amytornis dorotheae*) are poorly known. In this study, I revisited eight locations in the Northern Territory where populations of this species had been previously recorded. I examined the habitat and management characteristics of the sites where it was present or absent at both a local and landscape scale. Non detection of Carpentarian grasswren at seven out of the eight sites suggests that this species has undergone an extensive range retraction since they were last surveyed in 1986. An increase in the frequency of large late dry season fires in northern Australia seems to have had a profound effect on the distribution of this species and suggests it is extremely vulnerable to environmental change.

Key Words: Fire, Northern Australia, grasswren, habitat, *Triodia*

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