Reside, April Elizabeth (2011) ***Assessing climate change vulnerability: novel methods for understanding potential impacts on Australian tropical savanna birds*****. PhD thesis, James Cook University.**

Assessing Climate Change Vulnerability:

Novel methods for understanding potential impacts on Australian Tropical Savanna Birds

Thesis submitted by

April Elizabeth Reside

(BSc Hons)

2011

For the degree of Doctor of Philosophy

School of Marine and Tropical Biology

James Cook University

Townsville, Queensland 4811

Australia

Squatter pigeons (*Geophaps scripta*), a bird of the eastern tropical savannas in Australia.

Statement of contribution of others

Research funding and stipend:

- Climate Adaptation Flagship, CSIRO

Research in-kind support

- CSIRO Ecosystem Sciences

Supervision

- Dr Jeremy VanDerWal, Centre for Tropical Biodiversity and Climate Change, JCU
- Professor Stephen Williams, Centre for Tropical Biodiversity and Climate Change, JCU
- Dr Ian Watson, Ecosystem Sciences, CSIRO

Statistical, analytical and modelling support

- Jeremy VanDerWal
- Justin Perry (GIS)
- Genevieve Perkins (database)

Editorial assistance

- Alex Kutt
- Tony Grice
- Eric Vanderduys
- Colette Thomas
- Nick Webb
- Kristen Williams
- Brooke Bateman
- Rob Puschendorf
- Amanda Elledge

Co-authorship of published manuscripts

Co-authors of published manuscripts within this thesis participated in one or more of the following ways: discussions of concept and study design, advice on methods and editing of manuscripts.

Acknowledgements

This project was initially set up by Alex Kutt and I am indebted to him for his dedication to getting me started on the project and for his initial supervisory role. His knowledge of birds and tropical savannas has been invaluable, as was his help with editing and reviewing chapters. Thanks to Alex securing funding through CSIRO‟s Climate Adaptation Flagship, I was one of the few PhD students without financial worries.

Thanks to my supervisors Jeremy VanDerWal, Ian Watson and Stephen Williams for maintaining good humour despite any hassling they may have received. Thanks Jeremy for introducing me to modelling and answering 5 billion questions about *R* and for your ever-present famous “who cares” statement. Thanks also goes to Iain Gordon for his sage advice and care.

My PhD was my first foray into spatial modelling and lots of people answered dumb questions about GIS, *R*, databases, modelling and other IT-related matters. These people include Justin Perry, Gen Perkins, Brett Abbott, Colin Mayocchi, Scott Hardy, Eric Vanderduys, Amanda Elledge, Johnathan Kool, Kristen Williams and James Moloney. I even fired a few questions towards the ever-patient Chris Stokes. Great proof-reading, comments, general discussion and support was provided by Tony Grice. Gen Perkins was instrumental in setting up the database to house all the bird data.

I was particularly inspired, encouraged and emotionally supported by my genius housemate and friend Piero Visconti. Thanks so much Piero for talking about conservation, analyses and modelling over breakfast, after dinner and while cycling. Other fabulous housemates who provided food, cups of tea and hugs were Kate Nairn and Tom Brewer. Thanks also to Leonie Mynott for feeding me, listening to my woes and keeping me fit. Mel Thomas was also a great cycling buddy.

I really enjoyed the chats, advice, support and friendship from fellow students; in particular Jen Parsons, Tammy Inkster, Leila Brook, Brooke Bateman, Mariana Fuentes, Morena Mills, Marios Aristophanous, Alex Anderson, Kyran Staunton, Amanda Elledge, Heidi Schuttenberg, Deb Bower, Vanessa Valdez, Ally Lankester and Collin Storlie. Advice was also generously granted by Yvette Williams, Rob Puschendorf, Jenny Martin and Euan Ritchie.

I am indebted to all those that read my chapter and provided comments, but of all Nick Webb tirelessly taught me how to write in a structured and logical manner, to which I‟m so very grateful.

Thanks to Mum, Dad and Shane for their encouragement. And finally, a truck load of gratitude goes towards Eric Vanderduys, for, well, everything. Thanks for listening to endless hours of fascinating

(!) thesis discussion, for cooking for me, bandaging my soles (and soul), for fixing my bike, proof-reading my chapters, being my bird expert, introducing me to Mollies steaks, keeping me fascinated by savanna biota, the hugs and the love.

Thanks to Stephen Garnett and Judit Szabo for the use of their bird life history data in my vulnerability analysis, they provided data on species maximum longevity and minimum age of first breeding.

Publications associated with this thesis

Peer-reviewed publications

Reside, A.E., VanDerWal, J.J., Kutt, A.S., and Perkins, G.C. (2010) Weather, not climate, defines distributions of vagile bird species. *PLoS ONE* **5**(10), e13569.

Reside, A. E., VanDerWal, J.J., Watson, I.W., Kutt, A. S. and S. E. Williams (2011) Fire regime shifts affect bird species distributions. *Diversity and Distributions.* early view pp 1-13. DOI: 10.1111/j.1472-4642.2011.00818.x.

Reside, A. E., Watson, I.W., VanDerWal, J.J., and Kutt, A. S. (2011) Incorporating low-resolution historic species location data decreases performance of distribution models. *Ecological Modelling* 222(18): 3444-3448, DOI:10.1016/j.ecolmodel.2011.06.015.

Manuscripts in review

Reside, A.E., VanDerWal, J.J., and Kutt, A.S. (Accepted) Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios. *Ecology and Evolution*.

Manuscripts in preparation

Reside, A. E., VanDerWal, J.J., Kutt, A. S., S. E. Williams and S. Garnett (In Prep) Predicting the vulnerability of Australian tropical savanna birds to climate change.

Popular literature

Reside, A. (2008) Times they are a changing. *Contact Call*, Newsletter for Birds North Queensland.

Conference presentations

Reside, A.E., VanDerWal, J., (2011) Predicting the vulnerability of Australian tropical savanna birds to climate change. Ecological Society of Australia conference, Hobart.

Reside, A., VanDerWal, J., Watson, I. and Kutt, A. (2010) How will climate change impact bird species across Australian tropical savannas? Ecological Society of Australia conference, Canberra.

Reside, A. E., VanDerWal, J. J., Watson, I. and Kutt, A.S. (2010) Incorporating altered fire frequency scenarios in species distribution models improves climate change predictions for tropical savanna birds. Association for Tropical Biology and Conservation, Conference in Bali

Reside, A. E., VanDerWal, J. J., Watson, I. and Kutt, A.S. (2010) Predicting the effects of changing fire regimes on tropical savanna birds using species distribution modelling, Birds Australia Congress, Townsville.

Reside, A. E. (2010) Understanding distributions of vagile species in a dynamic landscape. Seminar to the Spatial Ecology Lab at University of Queensland.

Reside, A.E., VanDerWal, J., Kutt, A. and Williams, S. (2010) Improving species distribution modelling using weather, not climate: Temporal data provides better understanding of bird distributions. CSIRO Climate Adaptation Flagship symposium, Melbourne.

Reside, A.E., VanDerWal, J., Kutt, A. and Williams, S. (2009) Improving species distribution modelling using weather, not climate: Temporal data provides better understanding of bird distributions. The 10th International Congress of Ecology: Ecology in a Changing Climate, Brisbane.

Other peer-reviewed publications generated during my candidature

Godfree, R., Lepschi, B., **Reside, A.**, Bolger, T., Robertson, B., Marshall, D. and Carnegie, M. (2010) Habitat heterogeneity increases resilience and resistance of a keystone grassland species to extreme drought and climate change. *Global Change Biology*. 17: 943-958 DOI: 10.1111/j.1365-2486.2010.02292.x.

Monadjem, A., Schoeman, C., **Reside, A.,** Pio, D., Stoffberg, S., Bayliss, J., Cotterill, FPD., Curran, M., Kopp, M., Taylor, P. (2010) A recent inventory of the bats of Mozambique with documentation of seven new species for the country. *Acta Chiropterologica*. 12: 371-391

Mokany, K., Richardson, A. J., Poloczanska, E. S., Ferrier, S., and the CSIRO CAF Biodiversity Working Group (Elith, J., Robinson, L., **Reside, A.**, Harwood, T.D., Dunstan, P. K., Williams, K. J., Hilbert, D. W., Austin, M. P., Smith, F., Booth, T. H., Ellis, N., Barry, S.) (2010) Uniting marine and terrestrial modelling of biodiversity under climate change. *Trends in Ecology and Evolution*. 25: 550-551

Monadjem, A., **Reside, A.,** Cornut, J. and Perrin, M. R. (2009) Roost selection and home range of an African insectivorous bat *Nycteris thebaica* (Chiroptera, Nycteridae). *Mammalia*. 73:353-359

Monadjem, A., **Reside, A.** (2008) The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. *Acta Chiropterologica*. 10:339-348

Reside, A. E., Lumsden, L. F. (2011) Resource partitioning of two closely-related sympatric freetail bat species, Mormopterus spp. In: *The Biology and Conservation of Australasian Bats*. Eby, P., Law, B., Lumsden, L. and Lunney, D. (Eds). Pp 155-166. Royal Zoological Society NSW

Reside, A.E., Lumsden, L.F. and VanDerWal, J. (In prep) Identifying cryptic taxa: a tool for distinguishing female Freetail bats *Mormopterus* sp. 2 and *Mormopterus* sp. 4 in the wild.

Anderson, A. S., **Reside, A. E.**, VanDerWal, J., Shoo, L. P., Pearson, R. G. And Williams, S. E. (In review) Species distribution modelling predicts dispersal mediation of lowland biotic attrition due to climate change in Australia"s north-eastern rainforest birds. *Global Change Biology.*

Thesis Abstract

The current global biodiversity decline is predicted to be amplified by escalating anthropogenic change. Climate change stands as one of the major threats to biodiversity, and evidence for changing climate such as rising temperatures and altered precipitation have been well-documented. These changes have led to changes in species distributions, assemblages and interactions. The abilities of species to withstand or adapt to climate change are compromised by the synergies between climate change and the other drivers of decline, particularly habitat loss through land modification. The level of threat to biodiversity, coupled with large gaps in the scientific knowledge of many aspects of global biota particularly in the southern hemisphere, necessitates large-scale vulnerability assessments. These vulnerability assessments can be used to focus finite conservation resources to maximise conservation gain.

Tropical northern Australia houses a large proportion of Australia‟s biodiversity, however many species in northern Australia are under threat from climate change, land modification and introduced species. Most of northern Australia is tropical savanna, a biome that covers nearly one-quarter of mainland Australia. Australian Tropical Savannas (ATS) have been substantially less modified than the landscapes of southern Australia, and are consequently considered to be largely intact. However, alarming population declines have been recorded for mammals and granivorous birds that occur within the ATS. Despite the extent and species richness of the ATS, and the need for further conservation attention, no assessments of the vulnerability of ATS fauna to climate change have been conducted to date.

This thesis addresses the need for further understanding of the vulnerability to climate change of birds of the ATS, in two stages. I begin by improving methods for understanding the distributions of ATS birds, firstly by testing whether training distribution models of ATS birds on short-term weather variables better explains distributions when compared with standard long-term climate models (Chapter 2; Reside *et al.*, 2010). Next, I test whether the inclusion of coarse-resolution historic species data decreases the performance of models that are otherwise composed of recent, high-resolution species data (Chapter 3; Reside *et al.*, 2011ba). The second stage of this thesis predicts the impact of major threats to ATS birds: increasing fire frequency (Chapter 4; Reside *et al.*, 2011ab) and climate change (Chapter 5; Reside *et al.*, In Review), by modelling the response of species distributions to predicted change. Finally, I use the predictions of species sensitivity to changes in fire regimes, the predictions of distribution change due to climate change, and information on their

life history and ecology to generate an overall vulnerability assessment (Chapter 6; Reside *et al.*, In prep).

Species distribution modelling (SDM) is a frequently-used tool for estimating species‟ ranges, and predicting how species will respond to future change. However, the SDM process needs to be scrutinised for relevance to the species and system being modelled and the question being addressed. This thesis examines two issues concerning SDM of ATS birds. Firstly, whether the standard method of using long-term (c. 30 year) climate data averages adequately explains the dynamic ranges of ATS birds. ATS birds are highly mobile, with many species tracking resource availability throughout the landscape. Many species have large distributions, and use either nomadic or migratory movements to respond to changes across their range. I found that SDM was improved for ATS birds by training the models on the climatic variables averaged over a short time frame (three, six and 12 months), when compared with models trained on climatic variables averaged over 30 years. The improvement was particularly apparent for modelling distributions of wide-ranging, nomadic and desert species.

The second issue concerning SDM examined in this thesis is whether to include all available species records in the distribution model, or to include species records only with fine spatial resolution. The impact of including historic, coarse-resolution data on model performance was tested using bird location data in a model experiment. I found that models run using both fine- and coarse-resolution data (spatial accuracy ranging from 100 m to 222 km), when compared with models run using only fine-resolution data (mostly with 100 – 500 m accuracy, but with some with 5 km) had significantly lower model performance.

Next, this thesis focuses on two of the major threats to birds of the ATS: increasing fire and climate change. Fire is an integral part of the ATS; however, fire regimes have changed due to shifts in land management practices. Further changes are expected globally, with fire frequency predicted to increase. The impact of increasing fire frequency, and in particular fire frequency confined to the late-dry season, on the distributions of ATS birds was investigated by projecting modelled species distributions onto scenarios of increased fire frequency. Increased annual fire frequency was predicted to result in a distribution decrease for two-thirds of species, but a slight increase in distribution for one-third of species. In contrast, increasing frequency of fire in the late-dry season was predicted to result in 98% of species decreasing in distribution area. These results support the hypothesis that frequent late-dry season fires have a detrimental impact on many species of ATS birds.

The impact of climate change on the distributions of ATS birds was investigated by projecting species distributions to 2080 using a mid-range emissions scenario (A1B) and eight global circulation models.

The impact of dispersal scenario on predictions of species ranges was investigated by comparing future distributions under full dispersal, no dispersal, and a partial dispersal scenario of 30 km per decade. To achieve realistic predictions of species future distributions we assigned each species to the most appropriate of the three dispersal scenarios depending on the mobility and habitat specificity of each species. Under the realistic dispersal scenario, 67% of species were predicted to face distribution decreases by 2080; however many migratory and tropical-endemic species were predicted to increase in distribution.

Finally, I integrated the predictions for changes in species distributions due to changes in fire and climate, and biological and ecological species traits influencing species sensitivity, into a vulnerability assessment of the ATS bird assemblage. The analysis found that overall ATS have low biological sensitivity, but a range of ecological sensitivities. Threatened species have higher ecological sensitivity than non-threatened species, and species restricted to Cape York Peninsula have the highest vulnerability.

Overall, this thesis demonstrates the importance of applying modelling techniques that are relevant to the species and the system being modelled. In particular, the data used in the models and the methods for model training need to be examined to assess their appropriateness in the given ecological context. Additionally, this thesis has made predictions on the vulnerable elements of the ATS bird fauna, specifically in relation to distribution shifts resulting from increased fire frequency and climate change. This information coupled with other extrinsic factors such as land use change through invasive species and land clearing is vital for conservation of the birds of the ATS.

Contents

List of Figures

List of Tables

List of Appendices

Chapter 1: Introduction

Climate change as a threat to biodiversity

Climate change is a major threat to biodiversity globally, and evidence of ecological impacts of recent climate change is steadily accumulating (Walther *et al.*, 2002; IPCC 2007a; Maclean & Wilson, 2011). Global temperatures have already risen by approximately 0.74°C over the past 100 years and the rate of warming since the mid-1970s is greater than at any other time during the last 1 000 years (IPCC 2007b). Furthermore, minimum temperatures are increasing faster than maxima in some regions (Hughes, 2003; Nicholls & Collins, 2006). Atmospheric concentrations of CO_2 have increased by almost 100 ppm from preindustrial levels, and concentrations continue to increase (IPCC 2007a). However, the effects of climate change on biodiversity are not operating in isolation. Ecosystems are also increasingly under threat from the combined effect of disturbances influenced by climate change, such as drought and wildfire, and other drivers of global change, such as land modification, fragmentation and over-exploitation of natural resources (IPCC 2007a). Rapid climate change is likely to overwhelm the capacity for adaptation of many species, and reduce their resilience to further environmental perturbations (Jump & Peñuelas, 2005). Climate change is projected to result in up to 30 percent of species at high risk of extinction, resulting in changes in ecosystem structure and function, biotic interactions and species geographic ranges (Maclean & Wilson, 2011). Currently, the majority of higher-taxa species are in decline, and the drivers of biodiversity loss are either steady or increasing in intensity (Millennium Ecosystem Assessment, 2005). Existing conservation management practices are generally not designed to cope with the predicted degree of change (Coetzee *et al.,* 2009; D'Amen *et al.,* 2011), and responses to facilitate adaptation (e.g. assisted migration) are likely to be costly (Fischer & Lindenmayer, 2000). Given the rapid state of change, conservation action to mitigate threats to biodiversity needs to be efficient and effective; this in turn requires the identification of the most vulnerable elements of the biota. The impact of climate change has been observed and predicted for different regions throughout the world (Root *et al.*, 2003; Parmesan, 2006); however, for many regions the vulnerability of individual taxa is unknown. Therefore, broad-scale vulnerability assessments across assemblages are urgently required.

Vulnerability to climate change differs across ecosystems and species (IPCC 2007a). Tropical biota are expected to be more susceptible to climate change, due to the high species diversity and species with smaller ranges and narrower thermal tolerances (Colwell *et al.,* 2008; Deutsch *et al.,* 2008). In addition, many tropical species are currently living close to their optimal temperature, rendering them more sensitive to changes in temperature (Deutsch et al., 2008). Despite this, there have been few studies either predicting or measuring climate change impacts in tropical areas, where global species richness is at its peak (Maclean & Wilson, 2011). As a consequence of high diversity and species richness, high predicted extinction risk due to climate change, and the paucity of studies, tropical species are a high priority for climate change vulnerability assessments.

Birds and climate change – what is known for Australia?

Studies of the impact of climate change on species generally fall into two broad categories: (1) evidence-based and (2) predictive. Evidence-based studies of climate change impacts on birds have shown changes in timing of migration (Cotton, 2003; Jenni & Kery, 2003; Sparks *et al.*, 2005; Lehikoinen, 2011), migration distances (Visser et al., 2009), timing of breeding (Crick *et al.*, 1997; Visser *et al.*, 1998; Dunn & Winkler, 1999; Both & Visser, 2001) and distributions (Thomas & Lennon, 1999; Parmesan & Yohe, 2003; La Sorte & Thompson, 2007). Studies examining shifts in species migratory timing have found species arriving earlier in the spring (Cotton, 2003; Sparks *et al.*, 2005; Miller-Rushing *et al.*, 2008). Some species have reduced migratory distances (Visser et al., 2009) and changed overwintering distributions (Austin & Rehfisch, 2005). The shifts in timing of breeding events have, in some cases, resulted in the uncoupling of the synchrony of breeding and food supply (Visser *et al.,* 2004; Van Der Jeugd *et al.,* 2009).

Northerly margins of bird distributions have shifted poleward for birds in Finland (Brommer, 2004), the United Kingdom (Thomas & Lennon, 1999), France (Devictor et al., 2008) and across Europe (Maclean et al., 2008). In North America, the northern boundary, centre of occurrence and centre of abundance of winter bird distributions have all moved north (La Sorte & Thompson, 2007). Species have also been recorded at higher altitudes; for example, pre-montane bird species in Costa Rica have moved upslope (Pounds et al., 1999). However, species shifts have lagged behind the rate of shifting climate, suggesting that climate is changing faster than the rate at which species can shift their distributions (Devictor et al., 2008).

Despite the evidence for species responding to climate change, the evidence-based studies have been largely confined to the northern hemisphere where the necessary baseline data exists. In the southern hemisphere, few studies on the effects of climate change on birds have been conducted (Chambers *et al.,* 2005; Beaumont *et al.,* 2006). For the small number of species studied, changes in the arrival and departure dates of some migratory birds have been identified (Chambers, 2005; Beaumont *et al.*, 2006; Chambers, 2008; Chambers, 2010; Chambers & Keatley, 2010). These are in a similar proportion of species and magnitude of change found in the northern hemisphere, with 12 out of 24 species showing advanced spring arrival dates (Beaumont et al., 2006). Other studies of bird movement and breeding phenology in Australia reported no clear pattern for most of the species studied, despite recorded increases in temperatures (Chambers, 2005; Chambers, 2010; Chambers & Keatley, 2010). However, species may be responding idiosyncratically to local climate conditions, as shown for the seven species studied in south-eastern Australia (Chambers & Keatley, 2010).

Species-specific studies have found that populations of Australasian Gannets (*Morus serrator*) have increased (Bunce et al., 2002), Helmeted Honeyeaters (*Lichenostomus melanops cassidix*) have advanced the timing of egg-laying (Chambers et al., 2008) and Little Penguins (*Eudyptula minor*) have delayed breeding (Chambers, 2004). These shifts are all correlated with the observed changes in climate. In addition, there is evidence for climate change contributing to species declines in southern Australia (Mac Nally *et al.*, 2009), Western Australia (Rowley & Russell, 2002), and for seabird populations in north-eastern Australia (Smithers *et al.*, 2003).

The lack of clear trends in phenological and species distribution shifts from the southern hemisphere is in part due to the lack of historical baseline data with which to compare the current patterns (Chambers et al., 2008). This is compounded by high inter-annual variability of climate, rainfall and species phenology, which compromises the ability to detect clear trends over the background variation (Chan, 2001). Australian land birds show high intraspecific and temporal variability in migration patterns, an adaptation favoured by high variability of climatic patterns and resource availability (Chan, 2001). In particular, many Australian bird species track resources rather than follow traditional migration routes as found for bird species in many other parts of the world (Dingle, 2008). Australia has a high proportion of birds species undertaking partial migration, a phenomenon in which some individuals of a species migrate while others are residents (Dingle, 2008). Partial migration occurs where climatic patterns or resource availability are highly variable between years, but never sufficiently variable to eradicate either the migratory or the sedentary behaviour (Chan, 2001). Australian nectarivorous birds in particular respond to the high climatic variability by dispersal, diet switching, and behavioural and life-history traits (Woinarski *et al.*, 2000a). Nectarivorous birds are highly mobile and regularly cover large distances to increase their inter-seasonal access to nectar resources, which show dramatic seasonal and spatial dynamics (Woinarski *et al.*, 2000a). The challenge remains in detecting long-term trends of changing migration or distribution for species displaying high inter-annual variability in activity.

Predictive studies on the impact of climate change on birds have been conducted both globally and regionally, mostly focussing on distribution shifts, and all with varyingly severe predicted outcomes. A global study predicted the combined impact of climate and land-use change would cause up to 10%

of land birds to lose over 50% of their geographic range by 2100 (Jetz et al., 2007). Regional studies have predicted the impact of climate change on the distributions of birds in Europe, North America, South Africa, the South American Cerrado, Central America, the Australian Wet Tropics and south-eastern Australia (Brereton *et al.*, 1995; Erasmus *et al.*, 2002; La Sorte & Thompson, 2007; Huntley *et al.*, 2008; Coetzee *et al.*, 2009; Doswald *et al.*, 2009; Marini *et al.*, 2009b; Gasner *et al.*, 2010). Large range shifts have been predicted, generally in a poleward or upslope direction. However, these trends can be altered by local geography, for example, in South Africa species ranges are predicted to move east as a result of the east-west aridity gradient across the country (Erasmus et al., 2002). Studies have predicted range size decreases for most species, with some local extinctions (Erasmus *et al.,* 2002; Gasner *et al.,* 2010).

Predictions for south-eastern Australia showed that 13 out of the 17 bird species studied are likely to face a bioclimatic range reduction with a temperature rise of 1^{o}C (Brereton et al., 1995). For birds of the Australian tropics, 20% are predicted to be under threat of climate change (Garnett & Brook, 2007). Severe range contractions are predicted for bird species adapted to the high altitude wet tropics even with an increase of only 1^{o}C (Williams *et al.,* 2003; Hilbert *et al.,* 2004). However, birds from most regions in Australia are yet to be the focus of either evidence-based or predictive climate change impact studies. It is likely that the responses of Australian bird species to climate change will be complex and idiosyncratic for species, populations, and individuals. This prediction is supported by the complex and variable movement and breeding strategies displayed by many Australian birds (Dingle, 2008), and the complex and variable changes that have occurred in recent years (Chambers, 2005; Chambers, 2010; Chambers & Keatley, 2010). Further study is required to highlight elements of Australia‟s avifauna that are likely to be under threat as a consequence of either the direct (e.g. changes in temperature) or indirect (e.g. changes in fire, food availability) effects of climate change in order to develop effective conservation strategies.

The Australian tropical savannas context

Over 50% of the world‟s grasslands and savannas have been highly modified (TEEB, 2009) and the global threat to savannas is likely to increase; as they are predicted to face accelerated impacts of habitat modification, climate change, invasive species and pollution (e.g. nitrogen and phosphorus) (Millennium Ecosystem Assessment, 2005). In contrast to the global situation, the tropical savannas of northern Australia are relatively unmodified (Ridpath, 1985; Williams *et al.*, 2005). Consequently, they are of international significance, being one of the most extensive areas of essentially intact vegetation in the world (Franklin, 1999).

Australian tropical savannas encompass almost one-quarter of the continental mainland, covering most of northern Australia (Franklin, 1999; Williams *et al.*, 2005) (Figure 1.1). Australian tropical savannas (ATS) are defined as consisting of single-stemmed woody plants greater than 3 m tall with 0.2 to 90% cover, and a graminoid layer covering more than 2% of the ground (Walker & Gillison, 1982). The vegetation largely consists of open eucalypt woodland with annual or perennial grasses dominating the ground layer (Ash *et al.,* 1997; Williams *et al.,* 2005). The ATS display subtle longitudinal variation in vegetation communities and topography (Woinarski *et al*., 2005). The savannas are characterised by sharply contrasting wet summer and dry winter seasons (Woinarski, 2000; Bowman, 2002), which drive biological processes at both annual and evolutionary time-scales (Bowman, 2002). This marked seasonality of rainfall results in conditions of rapid plant growth following summer rain which then declines with the onset of the dry winter (Walker & Gillison, 1982). Rainfall is one of the strongest determinants of vegetation structure and composition (Fensham et al., 2005), along with soil type (Ward & Kutt, 2009). Compounding the largely seasonal rainfall pattern is the high inter-annual variability (McKeon *et al*., 1990).

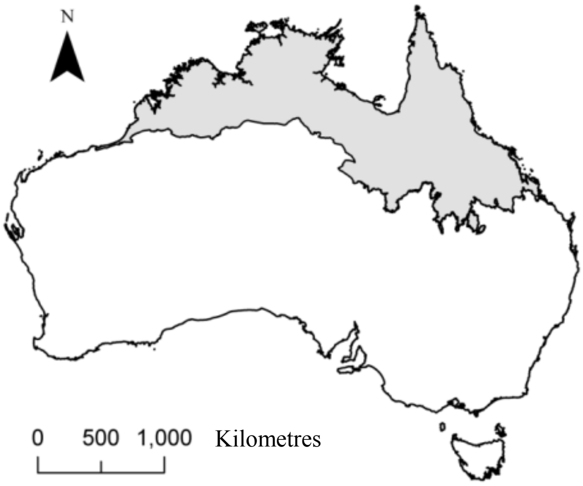


Figure 1.1.

Study area. The location of tropical savannas (in grey) across Australia.

Fire is a regular and important feature of savannas, as the ATS are thought to be „the most extensive and flammable ecosystem in the world‟ (Liedloff & Cook, 2007). As a result, the northern Australian biota are highly fire-adapted (Bowman, 2002). Fire frequency is at its highest in the northern savanna and declines inland with decreasing average annual rainfall and with increasing pastoral intensity (Williams *et al.*, 2002; Felderhof & Gillieson, 2006). Much of the landscape has a long history (c.

40 000 years) of aboriginal stewardship, and the historical fire management resulted in small-scale patches differing in time-since-fire (Woinarski et al., 1999). These small-scale mosaics of fire ages generated by early dry season burns have been shown to increase vegetation diversity and protect mature, long-unburnt habitat from large-scale wildfires (Bird et al., 2008). In contrast, fires occurring in the late dry season are of greater intensity and extent due to the curing of fuel (Williams et al., 2002) and they often have a more detrimental effect on species than other fire regimes (Bradstock et al., 2005).

Australian savannas have received substantially less anthropogenic modification than the grasslands and woodlands of southern Australia (Woinarski & Catterall, 2004) and savannas worldwide (Garnett *et al.*, 2010b). However, around 80% of northern Australia is under pastoral leases (Ash *et al.*, 1997; Franklin, 1999) and the associated effects of long-term pastoral land management such as vegetation clearing, grazing, altered fire regimes, the control of introduced predators and the spread of exotic pasture species, have led to a reduction in the functional integrity of the savannas (Ludwig *et al.*, 2004; Johnson *et al.*, 2007; Garnett *et al.*, 2010b). Substantial changes in both the plant and animal diversity of northern Australia have occurred since European settlement of the area about 150 years ago (Williams *et al.*, 2009a). Altered fire regimes are purported to be one cause, manifesting in two ways: unmanaged wildfire resulting in a simplification of the habitat structure (Woinarski, 2000) or vegetation thickening due to fire exclusion (Fensham & Fairfax, 2005). Grazing has modified savanna and has influenced fire regimes (Roques *et al.*, 2001; Fensham *et al.*, 2002; Sharp & Whittaker, 2003; Kutt & Woinarski, 2007). Savanna biota are also impact by mining, however the factors that relate to the pastoral industry are believed to be of greater threat (Woinarski, 1993a; Woinarski *et al.*, 1999; Smyth & James, 2004; Kutt & Fisher, 2011). As a result of the combined threats, alarming population declines have occurred for groups such as granivorous birds, the small terrestrial mammals, and some obligate-seeding woody plants (Bowman & Panton, 1993; Franklin, 1999; Woinarski & Ash, 2002; Williams *et al.*, 2009a; Woinarski *et al.*, 2010).

The ground and grass-layer foraging granivorous birds of the ATS have shown widespread changes in distribution and abundance, coinciding with the onset of pastoralism and associated management practices (Franklin, 1999). Three of the 49 indigenous and mostly resident granivorous bird species that are widespread generalists have shown distinct increases. Of the 12 species that have declined, one is extinct, two are critically endangered and one endangered (Franklin, 1999). The declines are greatest towards the south-eastern edge of the savannas where the grazing intensity is greatest, and are correlated with greater inter-annual variation in rainfall (Franklin et al., 2005). The declines are believed to be associated with diminishing functional integrity of the ATS, and this is supported by evidence that small mammals of the ATS are also facing alarming declines (Woinarski et al., 2010).

The small mammal declines are attributed to a combination of habitat change, predation by feral cats, poisoning by cane toads *(Rhinella marina)* and novel diseases; but the declines are believed to be ultimately linked to the shift away from indigenous management to pastoralism (Woinarski *et al.*, 2011).

Climate change is expected to impact on ATS biodiversity by amplifying or altering the impact of changed fire regimes, land use intensification, changes in water use, and increasing the spread of exotic plants and feral animals (Williams *et al.*, 2009a). Any change in the wet-dry rainfall cycles has the potential to substantially alter the processes within the savanna, given the role of the rainfall cycle on driving biotic patterns of this biome (Williams *et al.*, 2009a). While tropical species are expected to be the most susceptible to climate change, in part due to a tendency towards restricted distributions (Colwell *et al.,* 2008; Deutsch *et al.,* 2008), most birds that occur in ATS are widespread. However, there are distinct exceptions to this generalisation. Distinct communities of narrow-ranged bird species occur on Cape York, which meet the criteria of tropical species most likely to be threatened by climate change (Colwell et al., 2008). In addition, the widespread species occurring in the ATS are not without vulnerability. Despite their large distributions, habitat suitability can be dynamic and variable across the species‟ ranges, with temporally and spatially patchy resource (e.g. nectar or seed) distributions changing with rainfall patterns (Woinarski *et al.*, 2005). This variability may result in periods where very few areas, or sparsely distributed areas, are suitable for these species (Woinarski *et al.*, 2005). Highly mobile, wide ranging species are also a particular conservation challenge, as designating adequate conservation reserves is problematic (Woinarski *et al.*, 1992).

Modelling: a useful approach to climate change impact studies

With the increasing need for predictive climate change impact studies, the field of species distribution modelling has rapidly expanded resulting in a proliferation of studies refining techniques and improving the standards for best practice (Elith & Leathwick, 2009). Species distribution modelling (SDM), also known as ecological niche modelling, is the process of determining environmental predictors of species distributions and projecting the optimal combination of these predictors through space (Araújo & Guisan, 2006). Distribution modelling is therefore based on concepts of niche theory; the theory that a species‟ fundamental niche is a “hypervolume” in multivariate environmental space, in which a species can exist indefinitely (Hutchinson, 1957). In the broadest sense, species distributions are a spatial manifestation of the niche (Pulliam, 2000; Angert, 2009). This “fundamental niche” concept has a subset “realised niche”, consisting of portions of the fundamental niche where the species actually occupies given the potential for biotic interactions and competitive exclusion. Species distribution modelling can be used to model either the fundamental niche – where a species" physiological requirements are met, or the realised niche – where the species can exist given physiological limitations and biotic interactions (Guisan & Zimmermann, 2000). Note that debate exists on whether it is useful or necessary to distinguish between the fundamental and realised niche (Araújo & Guisan, 2006).

Species distributions are often modelled using climatic factors as the environmental predictors in the model, and are therefore mapping a species "bioclimatic envelope" or "climate space" (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003). Climate is known to be the dominant factor limiting species natural distributions (Kearney & Porter, 2009), as species are connected to climatic conditions through exchanges of energy and mass (Porter *et al.*, 2000; Kearney & Porter, 2009). However, species are also limited by biotic and other abiotic factors (Davis *et al.*, 1998; Pearson & Dawson, 2003), and SDM has been improved by the incorporation of essential biotic interactions (Araújo & Luoto, 2007; Heikkinen *et al.*, 2007) and abiotic factors into models (Austin & Van Niel, 2011). SDMs using only climatic variables can still result in useful models (Pearson & Dawson, 2003). For instance, it has been argued that the inclusion of more appropriate environmental predictors may improve models as much as the inclusion of other species representing the biotic interactions (Guisan & Thuiller, 2005). Further evidence for the argument that bioclimatic models are a sound representation of species distributions is that species distributions have been found to follow the movement of their suitable climate space (Tingley et al., 2009).

There are many different SDM techniques, ranging from the earliest techniques using generalized linear models (GLM), to generalised additive models (GAM), artificial neural nets (ANN), genetic algorithm for rule-set prediction (GARP), bioclimatic models (BIOCLIM), boosted regression trees (BRT), Maxent and some Bayesian approaches (Elith & Leathwick, 2009). Studies have compared techniques across species and biomes to rank their performance (Elith *et al.*, 2006; Guisan *et al.*, 2007b), and although different techniques vary in their performance, there is generally more variation in performance across species within technique than across techniques (Guisan *et al.*, 2007b). However, detailed technique comparisons found that the newer methods, and in particular Maxent, consistently outperformed other techniques (Elith et al., 2006).

SDMs are employed for a range of different purposes, including: predicting a species" current range, determining the environmental determinants of a species" range, and predicting how its range might change given its invasive potential or response to environmental perturbation (Guisan & Thuiller, 2005; Elith *et al.*, 2010). SDMs can also be used for conservation purposes such as mapping locations for conservation reserves and finding potential locations for rare species, including locations for translocation (Elith & Burgman, 2002; Hoegh-Guldberg *et al.*, 2008). SDMs are increasingly being used to predict species responses to anthropogenic climate change. There is evidence to show that this approach is likely to reflect realistic changes, such as the documented shifts in species distributions in recent times (Thomas & Lennon, 1999; Parmesan & Yohe, 2003; La Sorte & Thompson, 2007; Maclean *et al.*, 2008). In addition, the few new phenotypes found in the Pleistocene fossil record corresponding with rapid temperature shifts suggests that species are more prone to shift their ranges to track favourable climatic conditions than to remain in place and evolve new forms (Parmesan, 2006).

The field of distribution modelling is evolving rapidly, with many studies focussing on improving the techniques of SDMs for particular applications (Austin, 2007; Elith & Leathwick, 2009; Elith *et al.*, 2010). Studies have investigated the effect of different scales, sample size of occurrence records, predictors, including biotic interactions, location errors and climatic extremes on model performance (Hernandez *et al.*, 2006; Guisan *et al.*, 2007a; Guisan *et al.*, 2007b; Zimmermann *et al.*, 2009; Austin & Van Niel, 2011). Despite the advances, challenges remain in improving model parameterisation, selection, evaluation and assessing model uncertainty (Elith & Leathwick, 2009). Further advances are also required for modelling difficult-to-model species, and in particular highly mobile bird species that track resource availability. There are also questions about trade-offs between data quantity and data quality. All of these challenges must also be addressed in the context of the model subject and purpose. In particular, it is essential that practitioners understand the idiosyncrasies of the species, system and environment to be modelled in order to make informed judgements during model development (Austin, 2002).

Aims of this study

The overarching goal of this study is to develop a vulnerability assessment for the birds in ATS in the face of climate change. In line with this goal, there are three broad aims of this study: (1) improve methods for species distribution modelling, (2) identify and predict the potential impacts of major threats to ATS birds, and (3) integrate knowledge of threats, potential impacts and life history into a framework to better understand the vulnerability of ATS birds to climate change. In order to achieve these aims, my study has four specific objectives outlined below.

Aim 1. Improve species distribution modelling methods in the context of ATS birds.

Objective 1. Improve SDM methods to account for highly dynamic bird distributions.

The high mobility and variability of movement of ATS birds makes them a challenge for distribution modelling. I improve on SDM methods by incorporating short-term weather variables, instead of using long-term climate averages, as the environmental predictors in the models (Chapter 2). To account for variability in species‟ capacity to track climatically-suitable environments, I assess the effect of different dispersal scenarios on predicted future distributions of species (Chapter 5).

Objective 2. Assess the impact of data selection on model performance.

A largely overlooked component of model assessment and refinement is the impact of including historic species occurrence data in distribution models to increase the data sample size. I test the effect of including historic coarse-resolution occurrence data in addition to recent, fine-resolution data on distribution model outputs for birds in ATS (Chapter 3).

Aim 2. Predict the impact of major threats to ATS birds.

Objective 3. Assess the impact of increases in fire frequency on species distributions.

Shifting fire regimes are a major threat to biodiversity, and climate change is predicted to exacerbate these shifts. I investigate the impact of increasing fire frequency, and in particular the impact of increasing late-dry season fire frequency, on the distributions of ATS birds (Chapter 4).

Objective 4. Predict the impact of climate change on species distributions.

The impact of climate change on ATS bird distributions is predicted by projecting species distributions based on current climate to 2080, based on a future climate scenario. I make predictions on the impact of climate change on species richness and individual species distributions, in particular for threatened species (Chapter 5).

Aim 3. Integrate knowledge of ATS birds into a vulnerability framework.

Objective 5. Develop a vulnerability assessment of ATS birds using knowledge of threats, potential impacts and life history.

I develop an overall assessment of the vulnerability of ATS birds to climate change by incorporating the predictions of future threat impacts (fire: chapter 4, climate change: chapter 5) and life history and ecological characteristics (Chapter 6).

Thesis Structure

This thesis consists of five distinct, stand-alone but hierarchically integrated data chapters, brought together by the overall thesis introduction and discussion. The rationale for this approach is that it facilitates wider dissemination of the research by publication in peer-reviewed journals. The thesis introduction (Chapter 1) gives the necessary background and context of climate change, the particular case of Australian tropical savannas, and the modelling approach. Chapters 2, 3 and 5 improve on SDM techniques, particularly for the problem of highly mobile ATS birds. Chapters 4 and 5 predict the impacts of the major emerging threats to ATS birds: increasing fire frequency and climate change. Chapter 6 brings together the knowledge gained from Chapters 4 and 5, plus additional life history information on species, for an overall vulnerability assessment of the birds of the ATS. The thesis discussion (Chapter 7) provides a synthesis of the preceding chapters, highlighting the main findings and implications of this thesis. The relationships between the chapters are shown in a conceptual framework (Figure 1.2).

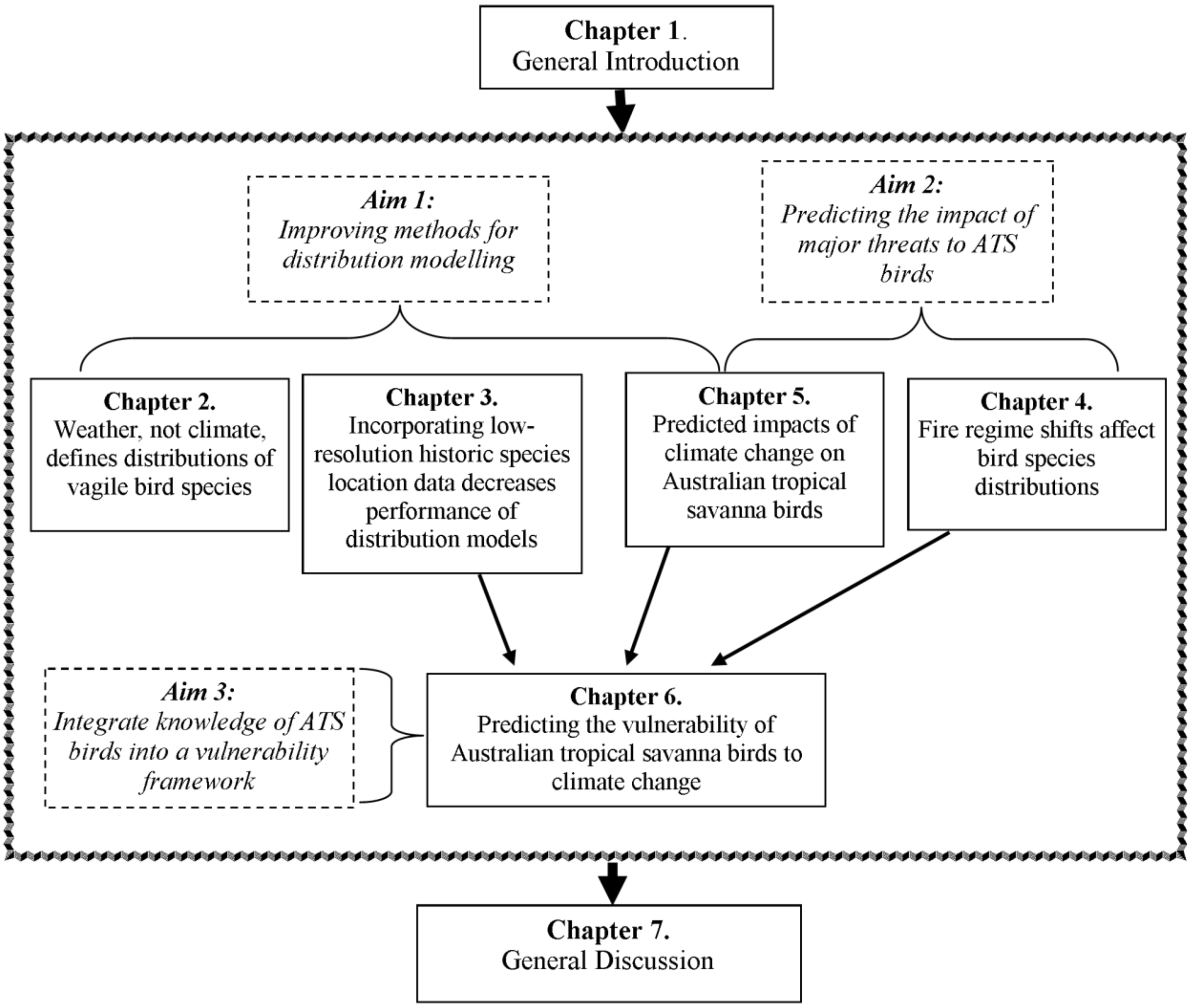


Figure 1.2.

Thesis structure.

Data used in this study

Australian tropical savannas are home to a diverse assemblage of birds. Australian bird species are generally highly vagile and plastic in their movement and habitat associations (Woinarski, 2006), and therefore the tropical savannas often house birds often associated with other biomes such as rainforest (particularly along riparian areas) and arid zone (Woinarski, 1993b; Woinarski *et al.*, 2000b). In addition, the wetland areas within the tropical savannas are home to a diverse array of waterbirds (Traill *et al.*, 2009). This study focuses on the tropical savanna bird assemblage found within the grassy and woodland savanna, therefore excludes waterbirds and rainforest species that may occur intermittently in the study area. Bird species records were sourced mostly from the Birds Australia Atlas (details given in Chapter 3), with some additional data in recent years from the Queensland Government atlas Wildnet (Environmental Protection Agency, 2004) and on-going CSIRO field data (survey protocol as in Price et al., 2009) collected for the ATS. The data were spread across the time period (Figure S2: Chapter 2). A different number of species was used throughout the chapters, as a consequence of a few factors. Data was collated from Birds Australia over multiple iterations, and the different questions each chapter asked determined which data was suitable for each chapter. For example, Chapter 2 required adequate time-series data, the fire modelling in Chapter 4 was focussed on species limited to the tropics, and chapters 5 and 6 aimed to be as inclusive as possible and consequently had the largest number of species (n=243). Despite the different numbers of species used, the core species are the same throughout the thesis.

Chapter 2: Weather, not climate, defines distributions of vagile bird species[1]

Abstract

Background

Accurate predictions of species distributions are essential for climate change impact assessments. However the standard practice of using long-term climate averages to train species distribution models might mute important temporal patterns of species distribution. The benefit of using temporally explicit weather and distribution data has not been assessed. We hypothesized that short-term weather associated with the time a species was recorded should be superior to long-term climate measures for predicting distributions of mobile species.

Methodology

We tested our hypothesis by generating distribution models for 157 bird species found in Australian tropical savannas (ATS) using modelling algorithm Maxent. The variable weather of the ATS supports a bird assemblage with variable movement patterns and a high incidence of nomadism. We developed "weather" models by relating climatic variables (mean temperature, rainfall, rainfall seasonality and temperature seasonality) from the three month, six month and one year period preceding each bird record over a 58 year period (1950-2008). These weather models were compared against models built using long-term (30 year) averages of the same climatic variables.

Conclusions

Weather models consistently achieved higher model scores than climate models, particularly for wide-ranging, nomadic and desert species. Climate models predicted larger range areas for species, whereas weather models quantified fluctuations in habitat suitability across months, seasons and

---

[1] Reside A. E., Vanderwal J. J., Kutt A. S., Perkins G. C. (2010) Weather, not climate, defines distributions of vagile bird species. PLoS ONE, 5, e13569.

years. Models based on long-term climate averages over-estimate availability of suitable habitat and species‟ climatic tolerances, masking species potential vulnerability to climate change. Our results demonstrate that dynamic approaches to distribution modelling, such as incorporating organism-appropriate temporal scales, improves understanding of species distributions.

Introduction

Impacts of climate change on species are frequently predicted by projecting species distribution models (SDM) onto future climate change scenarios. Meaningful predictions of species‟ distributions require SDM to closely reflect a species‟ environmental limits and requirements; that they reflect the species‟ ecological niche (Hutchinson, 1957). Traditionally, SDM predict the geographic distribution of suitable climatic space for a species by relating species occurrence records to long-term average climate variables. Such models are generally a good representation of a species‟ broad range (Pearson & Dawson, 2003), as species are closely connected to climatic conditions through exchanges of energy and mass (Porter *et al.*, 2000; Kearney & Porter, 2009). The standard approach to SDM incorporates climate variables such as mean annual temperature and annual precipitation averaged over periods of c. 30 years (Elith *et al.*, 2006). SDM generated for climate change predictions commonly use a baseline period of 1961-1991 (Beaumont & Hughes, 2002; Araújo & Luoto, 2007; Marini *et al.*, 2009b). The use of long-term climate averages in SDM has an ecological basis when modelling sessile or sedentary organisms such as plants (Elith & Leathwick, 2009; Zimmermann *et al.*, 2009). However, the application of SDM to more mobile species requires investigation of the appropriateness of long-term climate averages as a one-size-fits-all approach. A small number of studies have accounted for the dynamic nature of species distributions by including climatic variables corresponding to migratory species‟ arrival and breeding times (Heikkinen *et al.*, 2006), and other relevant breeding times (Heikkinen *et al.*, 2007), based on a priori knowledge of species movements. However, for mobile species with less predictable movement patterns, a new approach is needed. The temporal scales important to a mobile individual‟s location are likely to be much shorter than a 30 year average (Mac Nally, 1996; Woinarski *et al.*, 2000a); therefore short-term weather may be more appropriate.

Models tailored to incorporate organism-specific temporal scales are important when modelling species which respond to fluctuations in resource availability following short-term weather events. Weather (defined as the conditions over a short period, for this study it represents a period of 12 months or less) and climate (long-term average, >20 years) both play a large role in the movement of mobile species in search of food and breeding opportunities (Nix, 1976; Wiens, 1976; Maron *et al.*, 2005). However, weather might play a proportionally greater role in movement patterns in regions characterized by high variability in conditions, particularly where rainfall is both variable and limiting (Mac Nally, 1996). Variable rainfall prevents species from relying on regular seasonal migrations to find suitable conditions, instead favouring flexible resource-tracking behaviours (Chan, 2001). Resource tracking is a common trait among birds found within the tropical savannas of northern Australia (Chan, 1999; Dingle, 2008), a region characterised by highly seasonal rainfall, and variable inter-annual weather patterns (Hobbs, 1988; Garnett & Williamson, 2010). The life history of many species is linked with the pulses of nectar, fruit and insect abundance following rainfall events (Nix, 1976; Chan, 1999; Woinarski *et al.*, 2000a; Dingle, 2008).

In addition to climatic variability, Australian land birds are not subject to severe winter conditions like those experienced by their northern hemisphere counterparts (Chan, 2001). The relatively benign winters and stochastic weather patterns within Australia shift the balance in a hypothetical cost-benefit trade off between staying versus relocating from year to year (Mac Nally, 1996), resulting in complex local and continental scale migratory patterns (Griffioen & Clarke, 2002). The flexible nature of movement patterns of Australian birds is reflected in the array of different movement classifications found in the literature (Keast, 1961; Rowley, 1975; Fullagar *et al.*, 1986; Allen & Saunders, 2002; Griffioen & Clarke, 2002). Up to 19 distinct movement patterns have been identified, and many species show variation within populations and across years (Griffioen & Clarke, 2002). Four main categories are consistently used, despite the blurred boundaries between the groupings (Chan, 2001): *migration* is the predictable seasonal movement from a breeding ground to a wintering ground and return within the year; *nomadism* is wandering to wherever conditions are suitable, with yearly variations in routes and distances taken; *sedentary* species remain in the same locality throughout the year; and *partial migration* occurs when some individuals within a species migrate and others are sedentary.

We hypothesise that SDM built using short-term weather variables (weather models) will outperform models built using long-term climate averages (climate models), and this improvement will be strongest for species responding to stochastic weather events. Species more responsive to stochastic weather events are generally nomadic, and in particular those with large distributions covering many biogeographic regions, moving in search of suitable conditions. In particular, the arid zone faces substantial boom-bust cycles (Schwinning *et al.*, 2004), so species associated with arid zones are likely to be particularly responsive to weather patterns. Distributions of 157 bird species were modelled using means and seasonality of temperature and precipitation representing either weather (three, six and twelve month values immediately preceding date of a bird sighting) or climate (30 year average representing 1961-1990). We tested whether a species‟ range size, biogeographic affiliation or movement strategy influenced the relative importance of weather vs. climate variables in defining a species distribution. Range sizes were defined as small (see methods for details), medium or large, and biogeographic affiliations were temperate, tropical and arid (Appendix Figure 2.1, adapted from Schodde, 1982). A further affiliation, "ubiquitous", was included to account for species encompassing two or more zones. Species were classified into a movement category: sedentary, nomadic and partially migratory; and a category combining species which are both sedentary and nomadic. Very few species could be classified as true migrants within our study area (see methods) so were not included in this study. Model performance (defined as the models" discriminancy and consistency (Ling *et al.*, 2003)) was evaluated by the area under the receiver operator curve (AUC): an AUC score of 1 is a perfect fit of the data, 0.5 is no better than random (Elith *et al.,* 2006; Phillips *et al.,* 2006).

Results

Our results show that short-term weather provides a significant improvement in modelling bird distributions. Overall, weather models outperformed climate models, with a mean improvement in the model test statistic AUC of 0.026 (Wilcoxon signed rank test $p < 0.00001$). Model fit differed between climate and weather models depending on range size, biogeographic region and movement (Figure 2.1). AUC increased more for wide ranging species than for either small or medium-ranging species (Kruskal-Wallis ANOVA $p < 0.0001$). When comparing AUC values for species across their biogeographic zones, weather models outperformed climate models to a greater extent for arid species, followed by ubiquitous and tropical species (Kruskal-Wallis ANOVA, $p < 0.0001$). Weather models outperformed climate for species in three of the four biogeographic zones (Figure 2.1). Temperate species showed a mean negative AUC difference; therefore climate models on average slightly outperformed the weather models for these species. The change in AUC across movement categories identified that nomadic species improved the most, followed by sedentary and then partially migratory species (Kruskal-Wallis ANOVA, $p = 0.0001$). Predictably, the group of species which are both sedentary and nomadic sat in between the purely nomadic and purely sedentary species.

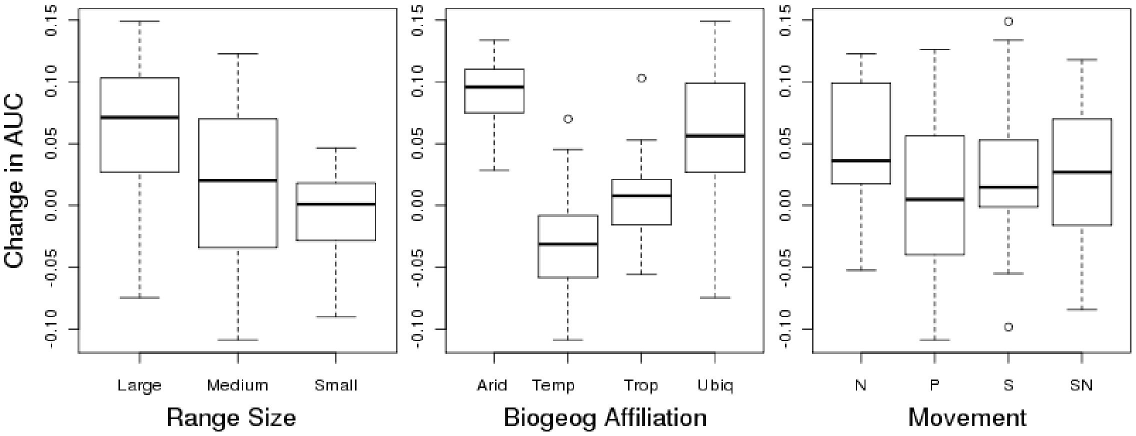


Figure 2.1.

The pairwise differences in AUC values for all species between weather and climate models. Boxplots (mean ± 25th and 75^{th} percentiles) show species are grouped by range size biogeographic region and movement patterns (see methods for description of classes). In most cases the change is positive – showing an improvement of AUC for weather models when compared with the climate models.

Weather models give a more refined understanding of the extent and location of suitable conditions both seasonally and inter-annually, when compared with the distributions generated using long-term climate averages. An example of monthly fluctuations is shown in Figure 2.2 for two birds, the brown songlark (*Cincloramphus cruralis*) and the red-chested button-quail (*Turnix pyrrhothorax*). The weather models demonstrate substantial fluctuations in the distribution of suitable habitat available across months, compared to predictions based on long-term climate averages. The difference in area of suitable habitat for each species as predicted by weather and climate models changes significantly when comparing range sizes (Kruskal-Wallis ANOVA, $p = 0.0001$), biogeographic affiliations ($p = 0.0001$) and movement categories ($p = 0.0002$) (Figure 2.3*A*).

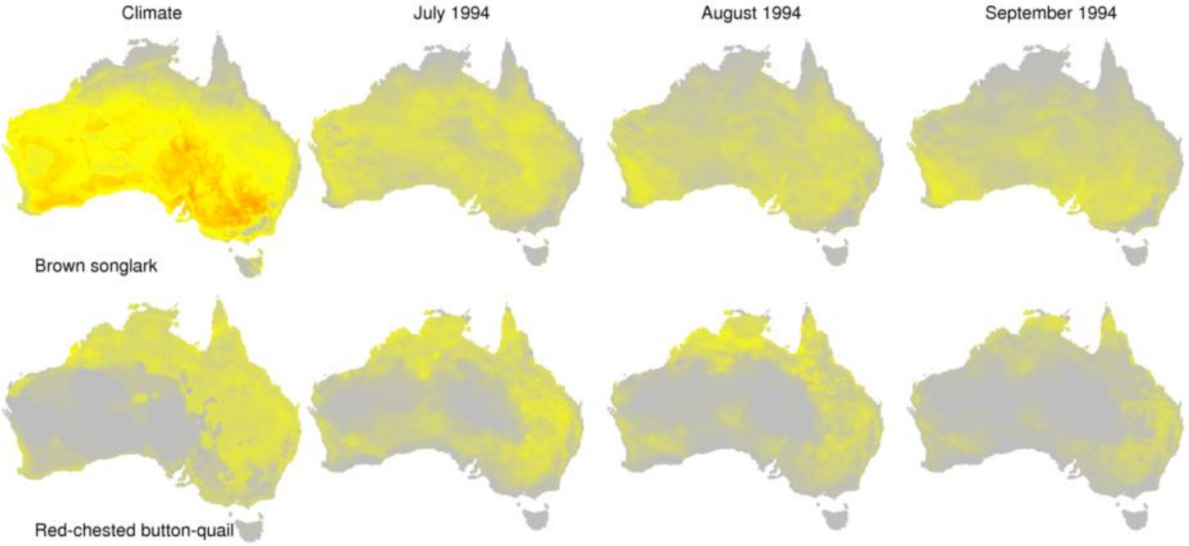


Figure 2.2.

The predicted range for two species determined by the climate model and the weather model. The ranges are shown for brown songlark (*Cincloramphus cruralis*) and the red-chested button-quail (*Turnix pyrrhothorax*). For illustration purposes, the weather model was projected onto 3 consecutive months to illustrate the changes in the distribution of suitable area depending on the weather conditions for a particular month. The probability distribution is shown for each particular month, with grey unsuitable, and increasing suitability shown from yellow to orange (most suitable).

The extent of fluctuation (standard deviation) of suitable conditions when projected onto each month from 1950 – 2008 also varies significantly across these groups (Figure 2.3B). Species with small ranges show little difference between climate and weather area predictions and little fluctuation in area across months. Species with medium ranges show the largest fluctuations, and geographically widespread species show the biggest difference in predicted area yet the least fluctuations across months (Kruskal-Wallis ANOVA, $p < 0.0001$). When species were grouped by biogeographic zones, climate and weather models differed the most for arid and ubiquitous species, but the least fluctuations month to month for weather model predictions ($p = 0.0076$). There was no difference in range fluctuations for species in different movement categories ($p = 0.4612$) It is therefore the wide-ranging, ubiquitous and arid species that have the most marked difference between climate and weather area predictions, the weather models predicting less area, and the least fluctuation across months. By contrast, suitable habitat area predicted for narrow-ranging, temperate and tropical species is quite similar for both weather and climate models.

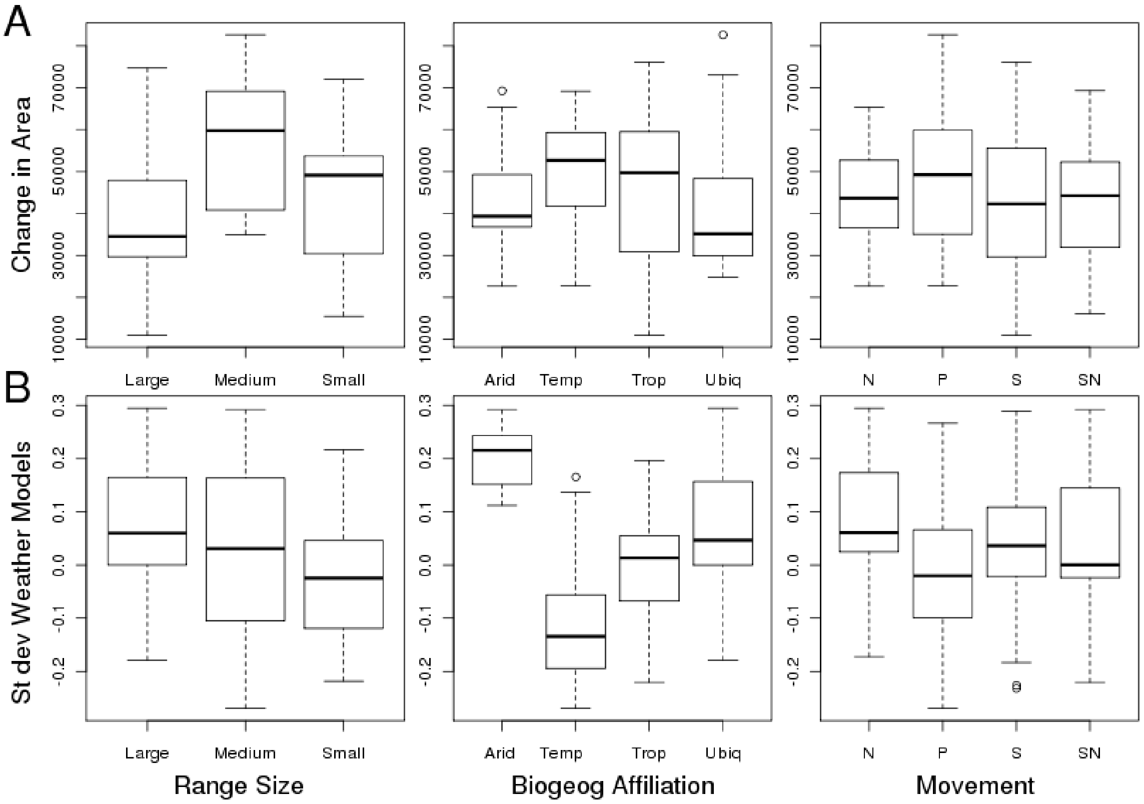


Figure 2.3.

Area predictions for climate and weather models across range sizes biogeographic zones, and movement categories. (*A*) The difference in predicted area (mean ± 25th and 75th percentiles). (*B*) The standard deviation of area for weather models projected onto each month for the period 1950 – 2008, compared across range size biogeographic zone, and movement categories.

Altering the temporal scale of the model variables from 30 year to six month and one year periods changes the relative contributions of the variables. Precipitation contributed significantly more to climate models (Wilcoxon matched pairs test, $p = 0.003$), and precipitation seasonality contributed significantly more to weather models ($p < 0.001$) (Figure 2.4). Temperature was on average the most influential variable across for both climate and weather models, followed by temperature seasonality, precipitation and then precipitation seasonality. We examined the differences in variable contribution to models depending on a species‟ life history, and how this changed with temporal scale. All variables contributed differently for species across biogeographic affiliations to the $p \leq 0.01$ level (Kruskal-Wallis ANOVA; Appendix Figure 2.2). For the other life history characteristics, results were varied. The contribution of temperature differed significantly according to range size (climate models: $p = 0.061$; weather models: $p = 0.019$), and the contribution of precipitation differed according to movement (climate models: $p = 0.01$; weather models: $p = 0.024$).

Table 2.1.

The differences in the variable contributions (mean temperature, temperature seasonality, mean precipitation, precipitation seasonality) to climate and weather models for species across biogeographic zones. The bold values in the climate and weather mean columns are the higher value; bold values in the *p* column indicate a significant difference at the 0.05 level.

Zone	Variable	Climate Mean	Weather Mean	t-value	df	*p*
Tropical	Mean Temp	28.12	**52.25**	-6.73	106	**0.000**
	Temp Season	**48.01**	24.14	6.14	106	**0.000**
	Precipitation	**20.46**	14.58	1.83	106	0.070
	Precip Season	3.42	**9.03**	-4.80	106	**0.000**
Temperate	Mean Temp	**52.23**	35.00	3.81	66	**0.000**
	Temp Season	11.42	**30.35**	-6.30	66	**0.000**
	Precipitation	**29.24**	20.81	2.22	66	**0.030**
	Precip Season	7.11	**13.84**	-4.06	66	**0.000**
Arid	Mean Temp	**40.02**	23.47	2.86	30	**0.008**
	Temp Season	39.08	**43.76**	-0.70	30	0.487
	Precipitation	15.57	**25.81**	-2.15	30	**0.040**
	Precip Season	5.33	**6.97**	-1.18	30	0.248
Ubiquitous	Mean Temp	**47.81**	36.58	2.38	104	**0.019**
	Temp Season	23.00	**37.85**	-4.17	104	**0.000**
	Precipitation	**21.36**	15.53	2.09	104	**0.039**
	Precip Season	7.84	**10.05**	-1.38	104	0.169

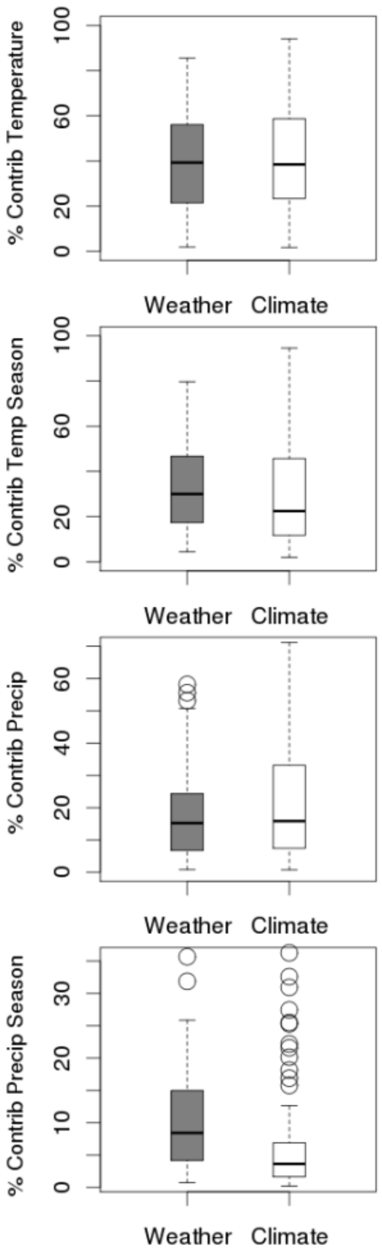


Figure 2.4.

The contribution of different variables to the weather and climate models: mean temperature, temperature seasonality, precipitation and precipitation seasonality (mean ± 25th and 75th percentiles). Bars representing weather are shown in grey, while bars representing climate are white.

Examination of variable contribution to models reveals substantial differences for species within each biogeographic zone (Table 2.1). Mean temperature contributed most to climate models for temperate, arid, and ubiquitous species, whereas temperature seasonality was the most influential for the weather models for species within these zones. The reverse was true for tropical species, as climate models were most influenced by temperature seasonality, and mean temperature was the highest contributor for weather models. The difference in variable contribution for models of species across biogeographic zone was significant for 12 out of 16 cases. As "seasonality" refers to the coefficient of variation for the time period, it is evident that variability in temperature and rainfall are more influential upon bird distributions over short time periods.

Discussion

Successful species distribution models (SDM) require appropriate temporal correspondence between species records and environmental variables (Huston, 1999; Phillips *et al.*, 2006). This correspondence is muted by using long-term climate averages for vagile species, reducing the ability to produce accurate models (Brotons *et al.*, 2007; Ziembicki & Woinarski, 2007; Elith & Leathwick, 2009). Here we demonstrate a technique that uses an organism-relevant temporal scale to model species. The approach more precisely reflects the scope and variability of species" environmental requirements and habitat suitability. We find that weather models largely outperform climate models, and this improvement is most apparent for wide-ranging, nomadic and desert species, and species that traverse multiple biogeographic zones. These species are likely to be the most responsive to weather events and corresponding resource fluctuations (Wiens, 1974). Interestingly, weather models also outperformed climate models for sedentary species. Sedentary species may undertake local movements in response to weather events (Woinarski *et al.*, 2000a), and their distribution might be limited by climatic extremes (Zimmermann *et al.*, 2009), two factors that are better accounted for with weather models than climate. Extreme conditions, for example a period of extreme high temperatures coupled with rainfall deficits, may limit species directly due to their own biological threshold (Jiguet *et al.,* 2006; Zimmermann *et al.,* 2009) or indirectly by limiting food or other habitat resources (Fensham *et al.*, 2009).

Weather models did not outperform climate models or result in larger predicted areas for species with smaller ranges or for temperate species. This suggests that these species" ranges fluctuate less in the short-term; in other words, these species are not tracking resources on this temporal scale and are therefore better explained by long-term averages. Temperate and more restricted species are likely to be adapted to local conditions (Wiens, 1976), possibly by diet switching rather than relocating when resource availability changes (Davies, 1984; Woinarski *et al.*, 2000a). Evidence for diet flexibility has been shown for small-range species in both tropical (Weaver, 1982) and temperate Australia (Lowry & Lill, 2007).

Climate models predicted a greater amount of suitable space than weather models for most species. The larger distributions predicted by climate models result in an over-estimate of the availability of suitable habitat. In contrast, the weather models refine the suitability criteria of an area by incorporating the temporal component to produce smaller predicted areas. Weather models identify the shifting environmental suitability within the species" broader climatic range, and that suitability shifts across time. Climate models have the assumption that a location is always suitable for a species if the species was recorded there. However this assumption is invalid for species that undertake large movements to find suitable conditions because of vast temporal fluctuation in conditions (Franklin *et al.*, 1989). Climate models mask the highly fragmented distributions of key refugial habitats during a resource nadir, leading to an inflated understanding of a species" resistance to extinction. This over-estimation of species" ranges leads to inaccurate assessments of species conservation status, vulnerability to climate change and the degree of protection existing conservation reserves provide.

Robust predictions of the impacts of climate change on species require SDM that account for temporal fluctuations in habitat suitability. Climate change predictions for northern Australia include increasing climatic variability with greater frequency and severity of extreme events (Collins *et al.,* 2000; Cai *et al.,* 2004-2005), and increase in drought conditions due to increase in temperature, decrease in rainfall and increased evapotranspiration (Watterson *et al.*, 2007). Tropical savanna bird species have adapted to highly variable conditions through plastic migratory and nomadic movement behaviour (Chan, 2001). However, flexible movement behaviour relies on patches of suitable conditions being within reasonable proximity, because movement has inherent risks and food supplies must be found before energy stores drop critically low (Petrie & Rogers, 2004; Roshier *et al.*, 2008). Increased climatic variability in combination with increased drought conditions could result in areas of suitable conditions becoming further apart in space, or staying unsuitable for longer periods of time. Vagile species may therefore need to move more frequently to find new suitable conditions. While predictions have been dire for species with narrow niche requirements, such as those relying on montane microclimates (Williams *et al.,* 2003; Hilbert *et al.,* 2004), wide-ranging species have attracted much less concern. However, species undertaking large-scale movements for specific niche requirements may be vulnerable to increased weather variability. This may result in suitable conditions becoming more energetically expensive to find (Petrie & Rogers, 2004). Highly dispersive land birds, such as specialist nectarivores the regent honeyeater (*Xanthomyza phrygia*) and the swift parrot (*Lathamus discolour*) have shown declines due to anthropogenic changes in the landscape (Franklin *et al.*, 1989; Mac Nally & Horrocks, 2000; Woinarski *et al.*, 2000a). Increased variability may lead to other vagile species, such as those in tropical savannas, showing similar declines. Changing patterns of climatic variation are likely to be the crucial element of species persistence, especially in highly variable areas. Therefore, modelling techniques that do not incorporate the short-term weather fluctuations are likely to underestimate climate change implications.

Examining the relative contributions of the different variables to the model can help tease out what is most influential to species distributions. Temperature is known to have a great influence on where a species can occur due to thermal constraints on energetics (Porter *et al.*, 2000). It is interesting to note that temperature seasonality, the coefficient of variation of temperature across a given time period, was also highly influential to species" ranges. This highlights that it is both the mean temperature and the variations in temperature that are highly influential to species" ranges. As expected, the contribution of each variable differs across biogeographic affiliations, as the regions themselves differ climatically.

Including temporal variations in habitat suitability of mobile species is essential for understanding a species" actual conservation status, and the extent that the species is protected by conservation reserves. Mobile species present both monitoring and conservation challenges (Woinarski *et al.*, 1992), as suitable habitat may need to be retained in geographically disjointed locations (Woinarski *et al.*, 1992; Price *et al.*, 1999; Ziembicki & Woinarski, 2007; Nebel *et al.*, 2008). Maintenance of suitable habitat for mobile species will require an extensive reserve network in conjunction with conservation-compatible non-reserve land management to accommodate species that track suitable conditions (Woinarski *et al.,* 1992; Margules *et al.,* 1994). Conservation planning needs to incorporate dynamic processes, particularly shifting species distributions (Nicholls, 1998; Pressey *et al.*, 2007). This is evident for northern Australia (Woinarski *et al.*, 1992), however it is also true for the conservation of vagile species in other parts of the world including the northern hemisphere (Austin & Rehfisch, 2005). Our weather modelling technique is a tool for greater understanding of species range dynamics and therefore vital to conservation planning for mobile species.

The need to incorporate specific climatic conditions relevant to species in order to accurately model distributions is increasingly being recognised (Heikkinen *et al.*, 2006). Both spatial (Osborne *et al.*, 2007; Foody, 2008) and temporal heterogeneity (Heikkinen *et al.,* 2006; Heikkinen *et al.,* 2007) are being incorporated into models, but accounting for interannual climatic variability is still largely lacking. Accounting for this variability is likely to be important to a range of taxa. Studies have shown that species across taxonomic groups: from plants, insects, fish, amphibians, reptiles, mammals and birds; have all shown shifts in distributions in the direction expected as a response to climate change, albeit at different temporal scales (Parmesan & Yohe, 2003). This suggests that species" ranges are responding to fluctuations in climate; therefore accounting for this in SDM is important. Birds are an extreme example of mobility compared to other terrestrial species due to their lower costs of transport (Porter *et al.*, 2000), however many marine species (particularly pelagic species, and including marine mammals) are highly dispersive (Carr *et al.*, 2003) and correlating their occurrences to their physical environment at short-term intervals is likely to greatly increase model performance and understanding of their distributions. Mobile mammals such as ungulates undertake movements in response to rainfall fluctuations (Ogutu *et al.*, 2008), and other volant and dispersive species, such as bats and some invertebrates, are likely to be responsive to weather variation (Woinarski *et al.*, 1992; Green, 2008). While the benefits of incorporating short-term weather in SDM may be intuitive for highly dispersive species, we have shown that the weather models also outperformed the climate models for sedentary bird species, suggesting that our weather modelling technique could be beneficial for species more affected by short-term weather fluctuations and variability than long-term averages. This may be particularly true of species with short generation times.

Our results show that understanding how species respond to weather conditions over short- and medium-term temporal scales is essential for quantifying species climatic limits. It is also important for understanding species‟ responses to rapid climate change and understanding their conservation status. Modellers should consider temporal scales appropriate to their organism when generating SDM and making climate change predictions.

Methods

Over four million occurrence records of 157 Australian tropical savanna bird species were collated across the period 1950 to 2008 from the Birds Australia Atlas (Blakers *et al.,* 1984; Barrett *et al.,* 2003), the Queensland Governmental atlas WildNet (Environmental Protection Agency, 2004) and CSIRO (protocol as in Price *et al.,* 2009). The data were spread across the time period (Appendix Figure 2.3). Species‟ range sizes were defined as either small (less than two million square kilometres; $n = 62$), medium (between two and four million square kilometres; $n = 53$), and large (greater than four million square kilometres; $n = 42$). Species range sizes were those reported in the New Atlas of Australian birds (Barrett *et al.*, 2003) and these categories appeared to adequately represent the spread of species‟ ranges. Species were categorised by movement life history (nomadic ($n = 25$), sedentary ($n = 54$), partially migratory ($n = 59$), and species that were both nomadic and sedentary ($n = 19$)) according to the literature (Marchant & Higgins, 1990; Marchant & Higgins, 1993; Higgins, 1999; Higgins *et al.*, 2001; Higgins & Peter, 2002; Maron *et al.*, 2005; Higgins *et al.*, 2006). The study focused on bird species using the savannas, therefore excluded waterbirds and rainforest species. Species with inadequate data coverage were excluded from the analyses. Due to the blurred boundaries between movement categories (Davies, 1984; Fullagar *et al.*, 1986; Woinarski, 2006), we only used species that could be reliably characterized as nomadic, sedentary, both nomadic and sedentary, or partially migratory in the movement comparisons; very few species within this assemblage could be classified as true migrants and therefore were not the focus of this study. All species in the study occur within Australian tropical savannas, however most species also occur over large areas outside this region. Species were therefore also categorized by which biogeographic affiliation best described their overall range, based on those defined by (Schodde, 1982) (original names in parentheses): tropical (Torresian), for distributions across northern Australia ($n = 54$); temperate (Bassian), for those down the eastern and southern coastal woodlands and forested areas ($n = 34$); arid (Eyrean), for those predominantly in arid inland Australia ($n = 16$); and ubiquitous for species that encompassed two or more of the above categories ($n = 53$).

Daily precipitation and temperature minima and maxima from 1950 until 2008 at a 0.05° grid scale were accessed from the Australian Water Availability Project (AWAP) (Jones *et al.,* 2007; Grant *et al.,* 2008). From this, we calculated annual mean temperature, temperature seasonality, annual precipitation and precipitation seasonality over the baseline period of 1961 – 1990 as our climate data. Temperature and precipitation seasonalities were the coefficient of variation over the given time period. Our weather data were created by calculating the above variables for three, six, nine, twelve months; and three, six, nine years previous to each month that a bird was recorded within the period 1950 to 2008. We reduced the number of variables to minimize the chance of over-fitting the model. We removed variables three, six and nine years as they were all highly correlated with one year (see Appendix Table 2.1.A). We also removed nine months for all variables and three months for mean temperature and precipitation due to the correlations between the months (see Appendix Table 2.1.B). Although the remaining variables (six months and one year for all variables, and three months for temperature and rainfall seasonalities) still had some high correlations, the SDM algorithm can handle such correlation (Phillips *et al.*, 2004).

Species distribution models were run using the presence-only modelling program Maxent (Phillips *et al.*, 2006). Maxent uses species presence records to statistically relate species occurrence to environmental variables on the principle of maximum entropy. The climate data contained unique combinations of latitude and longitude for each species and the corresponding values for the four climate variables. The weather data files consisted of each unique combination of month, year, latitude and longitude of each bird sighting, and the corresponding weather or climate variables for each relevant time period (three, six and twelve months, depending on the variable). All default settings were used except for background point allocation. Background points (pseudo-absences) can be selected in a number of ways; here we used a target group background (Phillips & Dudik, 2008). By using the locations and dates of all bird records („target group") as our background points, it is assumed that any sampling bias (spatially or temporally) in our occurrence records for a single species can also be observed in our background points; in effect cancelling out the effect of any spatial or temporal sampling bias in the modelling exercise. The models were projected onto spatial surfaces consisting of the model variables across Australia for each calendar month between 1950 and 2008.

AUC is potentially influenced by the number of model variables, as increasing the number of variables can lead to an over-fitted model. We investigated whether the higher AUC of our weather models was due to the greater number of variables than in our climate models by running our weather models for each species with only four weather variables. The proportional increase in AUC of the four-variable weather model to the climate model, compared with the AUC increase of the weather model to the climate model, was 0.83 (± 0.11 SE). Therefore on average, 83% of the AUC improvement was due to the weather models having a better fit of the data, and 17% of the increase in AUC was due to the increased number of variables.

Threshold values based on balancing training omission rate, predicted area and logistic threshold value were incorporated to convert the Maxent default probability distribution to a binary presence/absence (Liu *et al.*, 2005). This provided realistic predictions of species distributions (Prates-Clark *et al.*, 2008; VanDerWal *et al.*, 2009b). The threshold was read in from the Maxent Results output file, so that every pixel in the ascii output above the threshold was counted as "presence", and every pixel below the threshold was scored as "absence". The mean and standard deviation of suitable area (measured as the number of 5^{o} cells, which is roughly equivalent to 58,000 km^2) were then calculated for each species. We used Wilcoxon signed rank tests to compare model performance of weather vs. climate models, as this method is widely used for comparing AUCs in similar studies (Araújo & Luoto, 2007; Heikkinen *et al.*, 2007; Zimmermann *et al.*, 2009). Wilcoxon signed rank tests were also used for comparing the difference in variable contribution between weather and climate models. When comparing AUCs, area, or variable contributions of weather and climate models against a grouping variable, we used the Kruskal-Wallis ANOVA. We used 0.05 as our alpha-level significance value. Analyses were conducted using R version 2.9.0 (www.r-project.org) and Statistica version 8.

Author contributions

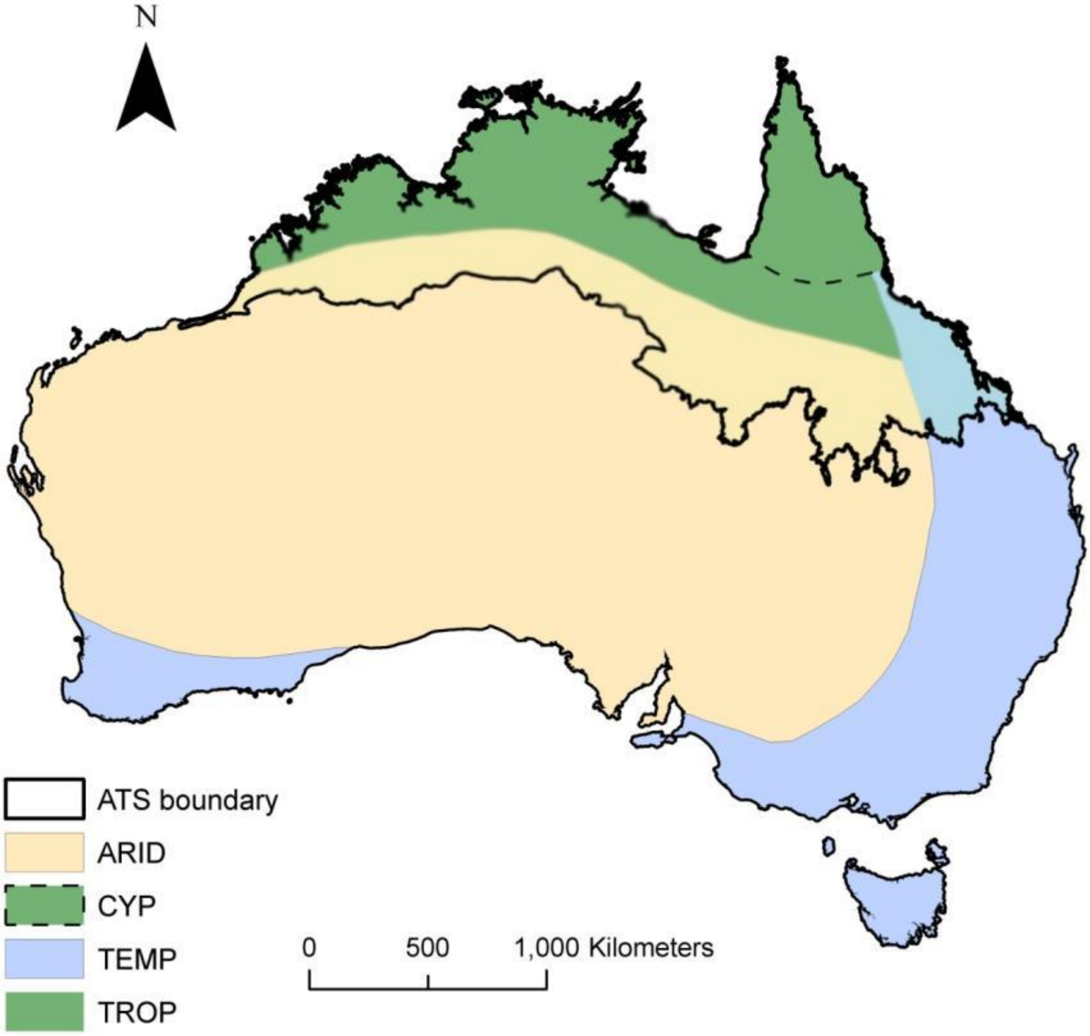
AR and JV conceived and designed the study; AR, JV and GP managed the data; AR performed the modelling; AR and AK analysed the data; AR wrote the paper; JV, AK and GP edited the paper.

Appendix Table 2.1.

The correlation matrices for four climate variables over different time periods. A) shows the correlations between each of the four variables between the four time periods in years (one, three, six and nine years). B) shows the correlations between the four different time periods in months (one, three, six and nine months).

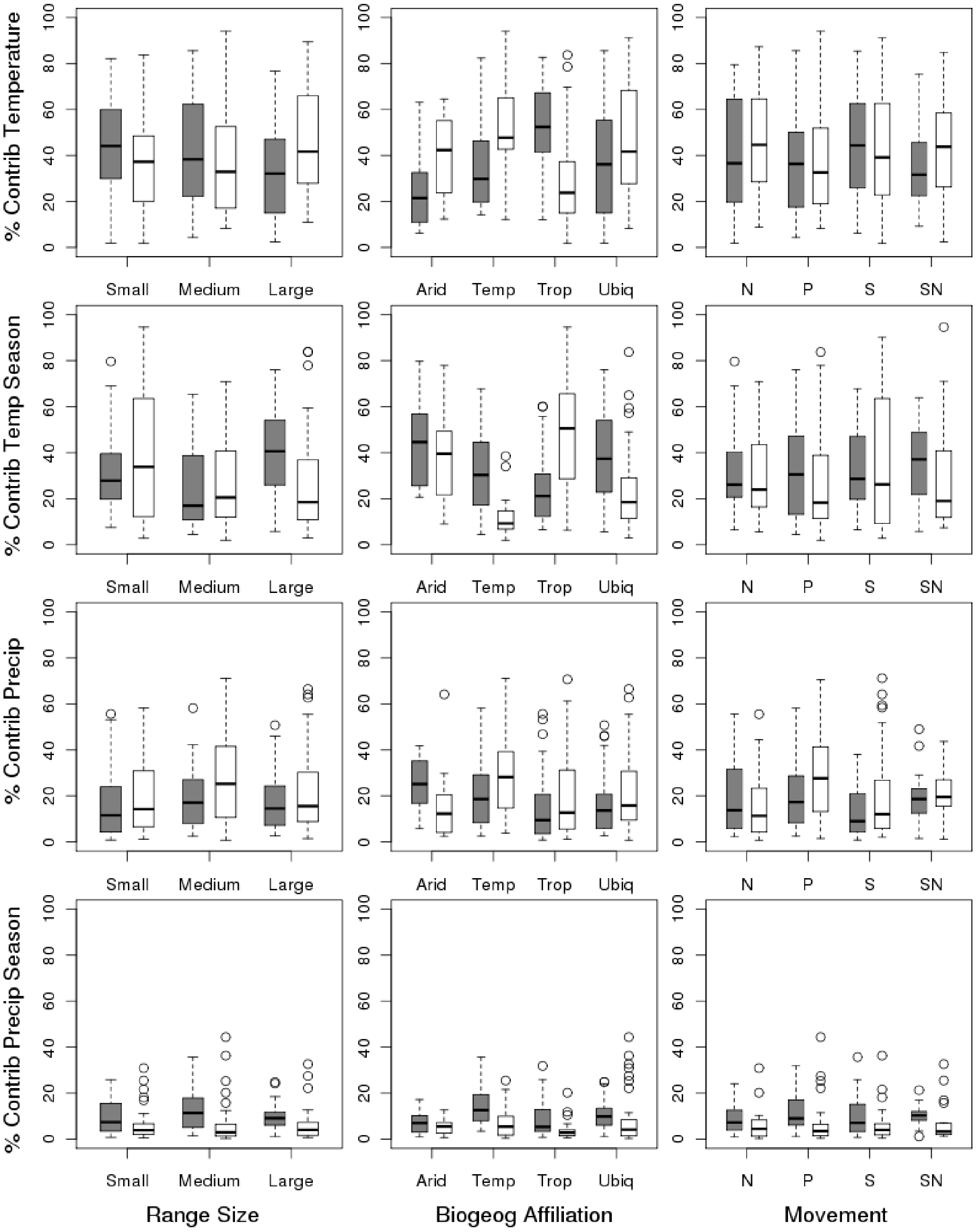
A)	Mean temp 1 yr	Temp seasonality 1 yr	Precipitation 1 yr	Precip seasonality 1 yr
3 yr	0.997	0.967	0.995	0.873
6 yr	0.997	0.963	0.992	0.819
9 yr	0.996	0.951	0.981	0.724

B)	Mean temp 1 m	Temp seasonality 1 m	Precipitation 1 m	Precip seasonality 1 m
3 m	0.986		0.93	
6 m	0.937	0.828	0.866	0.675
9 m	0.901	0.643	0.839	0.506



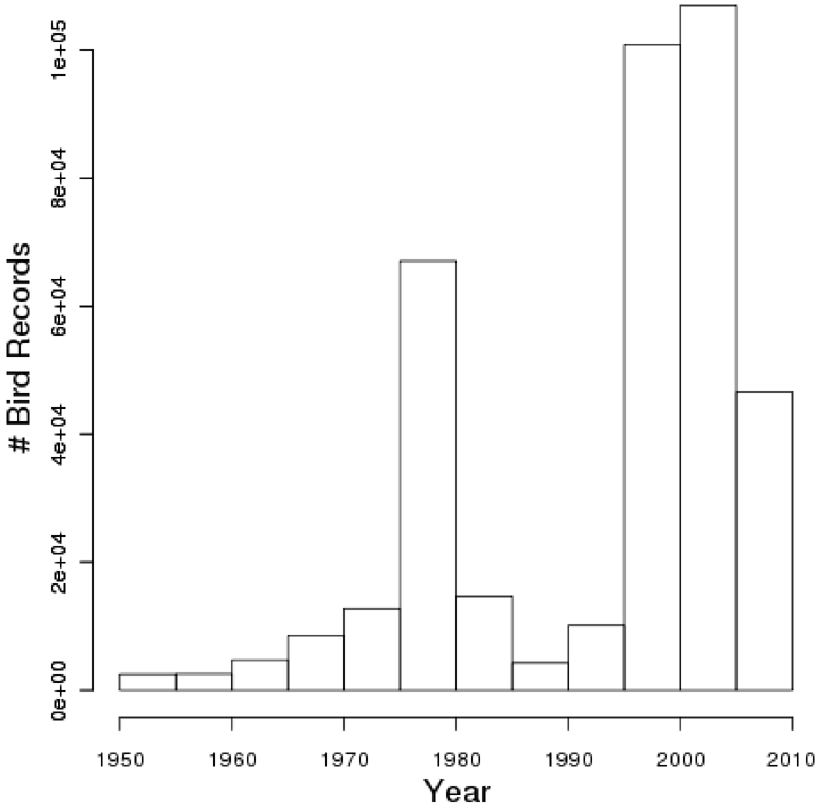
Appendix Figure 2.1.

The broad biogeographic zones that ATS species fall within, adapted from Schodde (1982). All of the biogeographic zones occur within the ATS, and there are large overlaps in the ranges of species across biogeographic zones. The Cape York Peninsula group is a subset of the tropical group, and as such they are treated as part of the tropical group in chapter 2. However they are highlighted in chapter 5 due to the distinctly different patterns they exhibit in the results from chapter 5. The categories are "ARID" = arid, "CYP" = Cape York Peninsula, "TEMP" = temperate, "TROP" = tropical, and ubiquitous, that occur in two or more of the above categories.



Appendix Figure 2.2.

The contribution of the different variables to the weather and climate models, depending on range size, biogeographic affiliation and movement classification (mean ± 25th and 75th percentiles). Bars representing weather are shown in grey, while bars representing climate are white.



Appendix Figure 2.3.

Histogram of bird records across the time period of 1950 to recent.

Chapter 3: Incorporating low-resolution historic species location data decreases performance of distribution models[2]

Abstract

Developing robust species distribution models is important as model outputs are increasingly being incorporated into conservation policy and management decisions. A largely overlooked component of model assessment and refinement is whether to include historic species occurrence data in distribution models to increase the data sample size. Data of different temporal provenance often differ in spatial accuracy and precision. We test the effect of inclusion of historic coarse-resolution occurrence data on distribution model outputs for 187 species of birds in Australian tropical savannas. Models using only recent (after 1990), fine-resolution data had significantly higher model performance scores measured with area under the receiver operating characteristic curve (AUC) than models incorporating both fine- and coarse-resolution data. The drop in AUC score is positively correlated with the total area predicted to be suitable for the species (R^2 = 0.163 - 0.187, depending on the environmental predictors in the model), as coarser data generally leads to greater predicted areas. The remaining unexplained variation is likely to be due to the covariate errors resulting from resolution mismatch between species records and environmental predictors. We conclude that decisions regarding data use in species distribution models must be conscious of the variation in predictions that mixed-scale datasets might cause.

Introduction

Conservation management and planning often rely on results of species distribution modelling (SDM) to help identify and prioritise important biodiversity areas (Sarkar *et al.,* 2006; Pressey *et al.,* 2007). Significant advances in SDM design and applications continue to be made to the three major model components (Austin, 2002): the ecological framework, the data preparation and the statistical model

---

[2] Reside, A. E., Watson, I.W., VanDerWal, J.J., and Kutt, A. S. (2011) Incorporating low-resolution historic species location data decreases performance of distribution models. *Ecological Modelling DOI:10.1016/j.ecolmodel.2011.1006.1015*.

(Stockwell & Peterson, 2002; Araújo *et al.*, 2005b; Austin, 2007; Guisan *et al.*, 2007a; VanDerWal *et al.*, 2009a). However, few studies have tested the effect of including historic species data with low spatial resolution on the model output, an important component of the data preparation (Austin, 2002). The inclusion of more data points in a model to improve sample size, and environmental and geographic coverage must be counter-balanced against the increased chance of error caused by coarse or inaccurate data. Coarse-resolution of species location data results in mismatches between the species occurrence and the corresponding environmental covariates, and therefore poor predictions of species" environmental limits and geographic range (Rabe-Hesketh et al., 2003). Empirical evidence on the effect of including coarse-resolution occurrence data in SDM is required to help inform decisions about the inclusion or exclusion of historic data in these models.

Species data used for SDM commonly come from a variety of sources, including museum databases and wildlife institutions (Araújo & Guisan, 2006; Austin, 2007). Species locality data collected in the last 20 years are generally georeferenced with global positioning system (GPS) technology, and recent species records can have a location precision down to 1 m. On the other hand, historic data are often assigned georeferences post-hoc based on location descriptions that are restricted to coarse estimates of the actual location in relation to land marks (Guisan *et al.*, 2007a; Graham *et al.*, 2008). Datasets available for modelling a species distribution regularly include historic records with coarse-resolutions (sometimes greater than 100 km) in addition to more recent records with much finer resolution and higher accuracy (Graham et al., 2004). The decision facing modellers is whether to include historic data or use only recent, high resolution data (Guisan *et al.*, 2007a).

We compared the performance of distribution models using recent (1990-2009), high resolution data against models run incorporating historic (1950-2009) data in the models for bird species within northern Australia. Our research aimed to determine whether including coarse-resolution historic data resulted in a measureable decrease in model performance.

Methods

Observation data

Bird species records were sourced mostly from the Birds Australia Atlas (described below), with some additional data in recent years from the Queensland Government atlas Wildnet (Environmental Protection Agency, 2004), and on-going CSIRO field data (survey protocol as in Price et al., 2009) collected for the Australian tropical savannas. A subset of 187 tropical savanna bird species was used for this study as defined in Reside et al. (2010). The Birds Australia database contains two Atlas components: the Atlas of Australian Birds (Blakers et al., 1984) consisting of intensive bird survey effort between 1977 and 1981 with some historical records dating back to the 1600s; and the New Atlas of Australian Birds consisting mainly of intensive survey efforts between 1998 - 2002 (Barrett et al., 2003). Both Atlases combined make up one of the largest continent-wide wildlife databases in the world, containing over six million records (Barrett *et al.*, 2003; Dunn & Weston, 2008). There is a strong demarcation in data resolution between data collected prior to 1990, compared to data collected from 1990 to present (Figure 3.1). Few records exist between 1990 and start of the new atlas in 1998. The occurrence records shown in Figure 3.1 are grouped as 1900-1950, then in 10 year blocks between 1950 and 2009. The data post-1990 have consistently finer spatial resolution (mostly within 100 or 500m and some within 5 km), whereas data prior to 1990 had a greater range of resolutions, from one minute grids (c. 1.9 x 1.9 km) to two degree grids (c. 222 x 222 km). The bird location is taken as the midpoint of the grid; therefore the maximum error of the bird location is from the midpoint of the grid to the outer corner. For a one minute grid this maximum error is c. 1.34 km, for a two degree grid, c. 156.98 km.

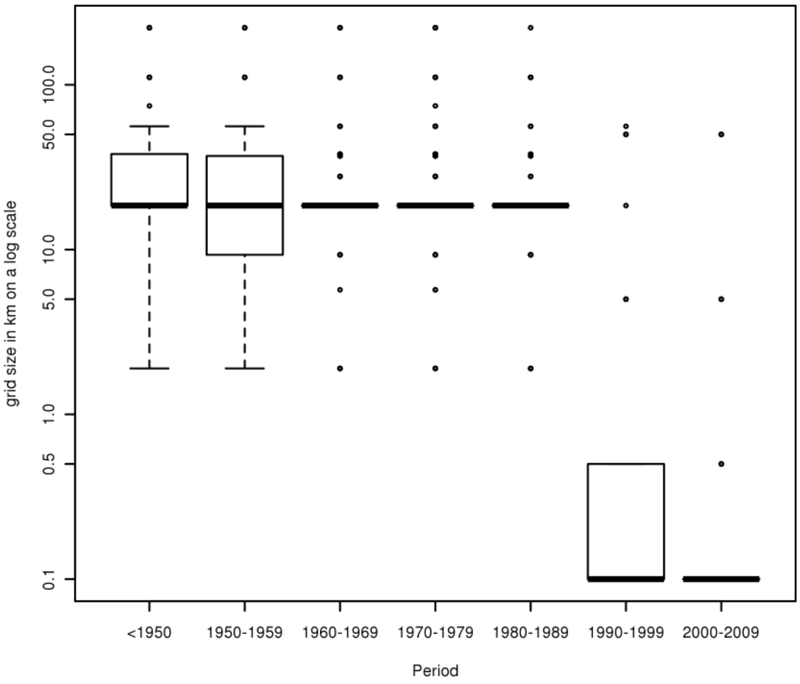


Figure 3.1.

The resolution of bird occurrence data. Bird occurrence data across time (1900-2009) and how it differs in spatial resolution, shown on $\log_{10}$ scale.

Environmental data

Climate and environmental spatial layers were used as environmental predictors of bird species distributions modelled within the tropical savannas across northern Australia, a region covering approximately 2 million km^2. Climate data used in the models were annual mean temperature, temperature seasonality, annual precipitation, precipitation seasonality and precipitation of the driest quarter, estimated using Anuclim 5.1 software (Hutchinson et al., 2000). The climate data were a long term average for the period 1960-1990. Other environmental layers included in the models were major vegetation subgroups (Department the Environment and Water Resources, 2007), land use (Stewart et al., 2001), and fire. The fire data included spatial layers of fire frequency, number of years land was burnt in the period from 1997 to 2008; and late-fire frequency (a subset of fire frequency), the number of years an area was burnt late in the dry season between 1997 and 2008 (Northern Australia Fire Information, NAFI http://138.80.128.152/nafi2/). The late dry-season is defined as the period between August and November (Felderhof & Gillieson, 2006). All spatial layers were reclassified to a resolution of 0.01 degree (c. 1.1 x 1.1 km).

Model experiments

Models were run using the presence-only SDM algorithm Maxent (Phillips et al., 2006). Maxent uses species presence records to statistically relate species occurrence to environmental variables on the principle of maximum entropy. Two sets of Maxent models were run for each of the 187 bird species for comparison: the first using only the data between 1990 and 2009, and the second with data from 1950-2009. These time periods were selected to represent only fine-resolution data, and both fine- and coarse-resolution data respectively. The first model set, referred to as the fine-resolution data model set, was run once using all data within the 1990-2009 period. The second model set (data from 1950-2009; the “inclusive” model set) used a random selection of 50% of the data points for each species in order to achieve greater parity of number of data points for the two time periods, since there were approximately double the number of records for most species in the 1950-2009 period. This controls for the effect of a greater number of occurrence records on model performance. One hundred iterations of the inclusive model set were run. This entire model experiment was run for five sets of environmental predictor variables: 1) climate only, 2) fire and climate, 3) land use and climate, 4) vegetation and climate and 5) all environmental variables. This was to control for any particular effects of individual environmental predictors.

Model evaluation and comparison

We evaluated whether the fine- resolution data models outperformed the inclusive data models using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot. An AUC score of 1 indicates a perfect fit of the data, 0.5 is no better than random (Elith *et al.,* 2006; Phillips *et al.,* 2006). AUC values ≥ 0.7 indicate "useful" models, whilst values ≥ 0.9 indicate models with "high" performance (Swets, 1988). The difference between the AUC values for the two sets of models across all species were compared using the Wilcoxon signed rank test.

The model output was further examined by comparing the single AUC for models of the recent data period (1990-2009) for each species to the distribution of AUC scores for 100 outputs from the all-data model runs. Where the AUC score of the single model run fell outside the 95% range of the all-data model AUC distribution (either below 0.025 or above 0.975), they are significantly different.

We tested whether the improvement in AUC score from coarse-resolution data models to fine-resolution data models was related to the change (i.e. decrease) in the proportion of suitable area predicted for the two sets of models as this is a limitation of using AUC to assess such models (see Luoto et al., 2005). Area was calculated as the proportion of the study area that was suitable for the species. The relationship between model scores and the amount of predicted suitable area for each species was examined with linear regression.

Results

On average, the AUC values for the fine-resolution species distribution models were significantly higher than those of the coarse-resolution models (Figure 3.2; Wilcoxon signed rank test, $p < 0.001$). The distance between the fine- resolution data model AUC score and the distribution of AUC scores for the inclusive models is examined in Figure 3.3. This distance calculation is shown in detail for one exemplar species, black-faced woodswallow *Artamus cinereus* (Figure 3.3a). For the black-faced woodswallow the fine- resolution data model output fell beyond the distribution of the model scores for the inclusive models, illustrating that using fine-resolution data provides a significantly better model than including older, coarse-resolution data. Figure 3.3b shows the distribution of these model AUC distance scores across 187 species, showing there is a skew towards significantly greater AUC scores for fine-resolution data models. This result is consistent across models using each set of environmental variables.

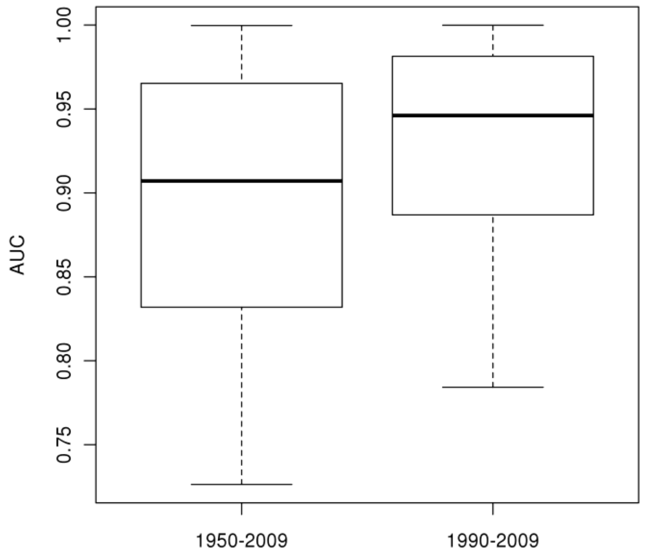


Figure 3.2.

Performance of models. Comparison of model performance for models using data across the period 1950-2009, and only fine resolution data in the period 1990-2009. Model performance is measured by area under the receiver operating characteristic curve (AUC). AUC values ≥ 0.7 indicate "useful" models, whilst values ≥ 0.9 indicate models with "high" performance (Swets, 1988).

The improvement in AUC from the coarse-resolution data models to the fine-resolution data models was significantly related to the decrease in area between the two models (for both climate-only model and all-environmental-variables model $p < 0.001$). However, despite the significant relationship, only 16% and 19% of the variation was explained for the climate-only and all-environment-variables models respectively (climate-only model, $R^2 = 0.163$, all-environment-variables model, $R^2 = 0.187$; Figure 3.4).

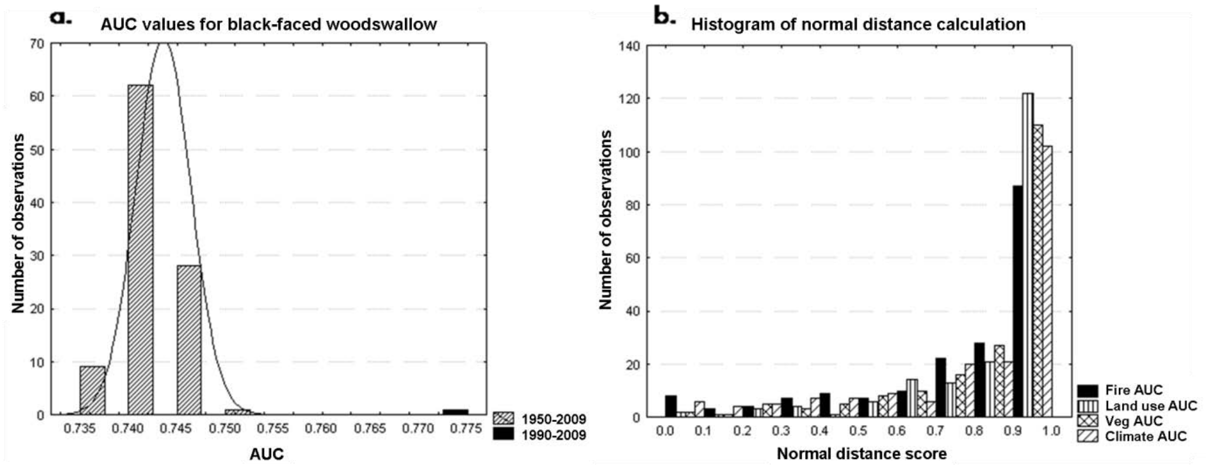


Figure 3.3.

Model performance comparing a single iteration of the models using fine-resolution species data (1990-2009) to the 100 iterations of the models including both fine- and coarse-resolution data (1950-2009). a. Frequency (or the number of times each was observed) of AUC scores for distribution model of the black-faced woodswallow for the model run with bird records from 1950-2009, compared to the model run with bird records from 1990-2009. The difference between the single AUC value from the 1990-2009 models and the frequency of AUC values from the 1950-2009 models is calculated to give a “normal distance” score for each species. b. Histogram showing the normal distance scores for models with each of the variables, for each species. The “inclusive” model (1950-2009) used a random selection of 50% of the data points for each species, and was rerun for 100 iterations. This was done to achieve greater parity of number of data points for the two time periods, since there were approximately twice the number of records for most species in the 1950-2009 period.

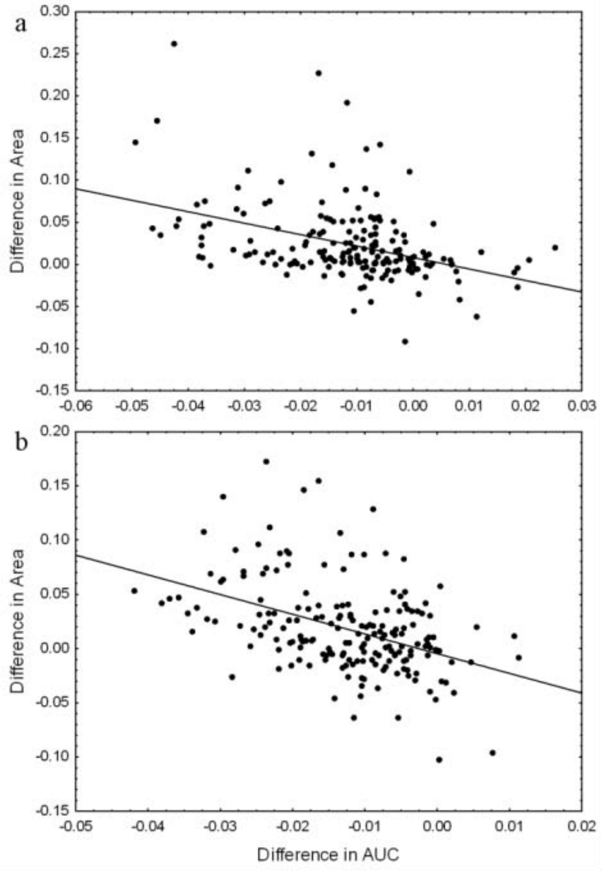


Figure 3.4.

The relationship between the change in area and the change in models performance (AUC) for each species for models using only fine resolution data (1990-2009) and models also incorporating coarse-resolution data (1950-2009). This relationship is shown for the a) climate model ($R^2 = 0.163$, $p < 0.001$), and b) the model incorporating all environmental factors ($R^2 = 0.187$, $p < 0.001$). The change is calculated by subtracting the AUC score of the fine-resolution data model from the mean AUC score of the coarse-resolution data model for each species, and the same for the area calculation of both models.

Discussion

This study has shown that including historic, coarse-resolution data in SDMs decreases model performance when comparing models trained with only recent, fine-resolution data. This change could be explained in part by the greater distributional area predicted by models using coarse-resolution data. Low AUC scores result when the algorithm is unable to discriminate between suitable and unsuitable area. This discrimination can be muted when species are broad in their environmental requirements, when the species data contain location errors, and when covariate errors result from species records at a coarser resolution than the environmental predictors (Rabe-Hesketh et al., 2003). As only less than 20% of the decrease in AUC score was explained by an increase in predicted distributional area, the reduced model performance in our study is likely to be also partly explained by covariate errors resulting from coarse-resolution data.

The effect of coarse-resolution species occurrence data on SDM is not equal across species. This finding is congruent with studies showing that spatial errors effect SDM differently across species and modelling technique (Graham et al., 2008), and that changing the resolution of environmental predictor data has a varying effect on model performance depending on region, technique and species

(Guisan *et al.*, 2007a). In our study, a small number of species‟ inclusive models had significantly higher performance than their respective fine-resolution data models. This was likely to be due to data points in the inclusive models giving a greater environmental coverage. Including some coarse-resolution data in SDM may therefore be beneficial in eliminating spatial bias that might be found in fine-resolution data sets.

Inaccuracies in species models due to over-predicting species ranges and covariate errors have implications when models are used for management decisions. Over-estimating a species range can mask the specificity of species requirements such as association to fine-scale habitat heterogeneity (Price et al., 2010). This can result in poor assessments of a species true vulnerability to perturbations in the environment, in particular climate change (Isaac et al., 2009). However, it is also important that models used in decision making take into account not just the model statistics, but also the biological relevancy: a model may have excellent statistical fit but inaccurate geographic pattern (Austin, 2002). A decrease in model statistics may be inconsequential if the spatial prediction closely matches the species‟ geographic range.

The option of excluding coarse-resolution data may not be available for all studies. Historic data may cover a different geographic distribution, so may represent the full niche requirements of the species, or be needed to show range shifts. The inclusion of coarse-resolution data in a distribution model might be a trade off between representing the full environmental range of a species, against the need for accurate covariates. Excluding coarse-resolution data may be unwise when the initial dataset has a small sample size, as model performance decreases linearly with decreasing sample size for many modelling methods (Guisan *et al.*, 2007a). Where required, coarse-resolution data may be accounted for by down-weighting of coarse or less reliable observations (Araújo & Guisan, 2006) or downscaling the occurrence data (Araújo *et al.*, 2005a). Alternatively, environmental predictor data could be rescaled to match the resolution of the species occurrences (Guisan *et al.*, 2007a). However analysis of temporal trends in species distributions require longitudinal data, and often historical data must be included to represent the time series (Reside et al., 2010).

Conclusion

This study quantitatively demonstrates that inclusion of coarse-resolution data in SDM result in significant over-prediction of species ranges. This variation may be important depending on the scale of the conservation planning decisions, data availability, the species and its life history, and the economic or planning imperatives that are influencing the need for the modelling. We conclude that decisions regarding the inclusion of coarse-resolution data in spatial analysis of species distributions must consider the uncertainty that may result from variable-resolution datasets, and the implications that these data may have on conservation and management uses of the predictions.

Author contributions

AR designed the study, performed the modelling and analysis, and wrote the paper; IW, JV and AK provided advice on the methods and assisted with editing.

Chapter 4: Fire regime shifts affect bird species distributions[3]

Abstract

Aim: Fire is a major driver of ecosystem structure and process, and shifts in fire regimes are implicated in the decline of many species. Shifting fire regimes have been documented around the world, and fire frequency and extent is predicted to increase in many areas due to changes in both climate and land management. Here we evaluate how predicted increases in fire frequency are likely to impact on species distributions.

Location: The tropical savannas of northern Australia.

Methods: We developed distribution models for 44 bird species using the modelling algorithm Maxent. Our models incorporated bird locality records and environmental variables including climate, total fire frequency and the subset of fire frequency occurring late in the dry season. We investigated the effect of increasing total fire frequency, and increasing fire late in the dry season, on species distributions by projecting species model algorithms onto scenarios of incrementally increased total fire frequency.

Results: The probability of presence for most species was higher when fire frequency late in the dry season was low. Species showed a mixed response to an overall increase in total fire frequency, with one-third predicted to increase in distribution. However almost all species (98%) showed a decrease in predicted range with increased late-dry season fire, and species distribution area was generally negatively correlated with an increase in late-dry season fire.

Main conclusion: Our study highlighted the array of responses of species to increasing fire frequency, and suggested that increased fire frequency late in the dry season is detrimental to most savanna-restricted bird species. The understanding of individual species‟ preferences for particular fire frequencies is important for informed conservation planning.

---

[3] Reside A. E., Vanderwal J., Watson I. W., Kutt A. S., Williams S. E. (2011) Fire regime shifts affect bird species distributions. *Diversity and Distributions* 1-13.

Introduction

Shifting fire regimes are a critical conservation issue in many regions of the world, adding to the pressures of climate change, intensifying land use and invasive species on biodiversity (Keith *et al.*, 2002; Stephens & Ruth, 2005; Brook, 2008). The increased frequency and extent of fire in many regions such as western United States (Westerling *et al.,* 2006), Canada (Gillett *et al.,* 2004) and the Neotropics (Barlow & Peres, 2004) has been attributed to recent climate change. Further increases are predicted in areas such as the USA, Brazil, central Asia, south-eastern Europe, southern Africa and Australia (Westerling *et al.,* 2006; Liu *et al.,* 2010). Future fire activity is predicted to vary considerably across regions in response to climate change, and land management will continue to influence the extent of these changes (Liu *et al.,* 2010). Australia, already the world‟s most fire-prone continent, is predicted to face an overall increase in fire (Beer & Williams, 1995; Cary & Banks, 2000; Williams *et al.*, 2001; Cary, 2002; Pitman *et al.*, 2007; Krawchuk *et al.*, 2009), though the spatial and temporal realisation of fire increase across the landscape is uncertain. Managing fire for optimal biodiversity outcomes is an essential conservation issue; yet our knowledge of species requirements of timing, frequency and scale of fire regimes is limited (Clarke, 2008). Information on species‟ sensitivity to fire, and the impact of increased fire frequency on species, is therefore crucial to their conservation.

Fire occurs in almost every biome, but since 1990 86% of fires globally occurred in tropical savannas and grasslands (Mouillot & Field, 2005). For tropical savannas worldwide, fire is a significant determinant of landscape and biodiversity pattern (Davis *et al.*, 2000; Garnett & Brook, 2007), and fire is essential for maintenance of these landscapes (Bond & Parr, 2010). Fires shape savanna vegetation (Woinarski *et al.,* 2004), and fauna that inhabit these tropical savannas are largely resilient to fire (Bond & Parr, 2010).

The frequency of fire in savannas has important implications for biodiversity (Garnett & Brook, 2007; Woinarski *et al.*, 2010). Frequent fires lead to reduced tree density (Davis *et al.,* 2000) and decreased vegetation structural complexity (Bowman, 1998). Too-frequent fires are particularly detrimental to species favouring long-unburnt patches, such as some mammals (Friend & Taylor, 1985; Andersen *et al.*, 2005), fire sensitive plants (Bowman & Panton, 1993), granivorous birds (Fitzherbert & Baker-Gabb, 1988; Franklin *et al.*, 2005) and birds requiring grassy refugia (Garnett & Bredl, 1985; Rowley & Russell, 1993; Jansen *et al.*, 1999). However where fires are sufficiently infrequent, the tree-grass ratio within the savanna could increase (Roques *et al.,* 2001) which can lead to lower bird diversity (O'Reilly *et al.,* 2006) and if excluded for long enough, a shifting of biomes from savanna to rainforest (Woinarski *et al.,* 2004; Accatino *et al.,* 2010).

Fire seasonality can be a major factor determining the impact of fire on biodiversity due to the influence of season on the amount of fuel available to burn and the presence of weather conducive to burning (Bradstock, 2010). In tropical savannas, early dry-season fires tend to be of low intensity, and their occurrence reduces the amount of herbaceous biomass available to burn later in the dry season. In the absence of early-dry season fire, fuel build-up can lead to late-dry season fires that have greater intensity and the capacity to burn larger areas (Williams *et al.,* 2002). The late-dry season fires remove unburnt patches from the landscape (Bird *et al.,* 2008), homogenising the age-class structure of large tracts of savanna (Bradstock *et al.,* 2005).

Understanding the influence of fire frequency and seasonality on savanna biodiversity is a primary conservation objective in tropical savannas (Williams *et al.,* 2002; Uys *et al.,* 2004). In Australia, shifts away from traditional indigenous land management have seen an end to small scale early-dry season fires towards extensive, high intensity late-dry season fires. The increase in late-dry season burning is thought to be a main cause of declines in many vertebrate species populations in the tropical savannas of northern Australia (Franklin, 1999; Woinarski *et al.*, 1999; Woinarski *et al.*, 2001). Experimental and localised studies on fire frequency and fire seasonality and biodiversity in this system have investigated the impact of fire events and regimes on species occurrence (Andersen *et al.*, 2005; Kutt & Woinarski, 2007; Murphy *et al.*, 2010). However, species-level studies and natural experiments should also be complemented by simulation models to investigate landscape-scale fire patterns and its effect on biodiversity (Driscoll *et al.,* 2010). In this study we focus on Australian tropical savanna birds to investigate 1) species sensitivity to fire frequency across their range, and 2) the effect of increased total fire frequency, and in particular increased late-dry season fire frequency (herein “late-fire frequency”), on bird species distributions. To address the first objective we examine species occurrences in relation to total fire frequency and late-fire frequency, and then estimate the probability of presence for each species according to total fire frequency and late-fire frequency. For the second objective, distribution models for Australian tropical savanna birds built using current conditions of fire and climate were projected onto spatial surfaces of simulated total fire frequency increases. Understanding species sensitivities to fire frequency, and how their distributions will be affected with fire frequency increases (a likely scenario under climate change predictions; Krawchuk *et al.,* 2009) is an important step in developing mitigation strategies for bird species conservation (Driscoll *et al.,* 2010).

Methods

Study area

Tropical savannas stretch almost continuously across Australia north of c. 23°S (Franklin *et al.,* 2005), occupying nearly one quarter of the Australian continent (Williams *et al.,* 2005). Savannas are characterised by a discontinuous stratum of trees above a mostly continuous layer of grasses (Williams *et al.,* 2002). Rainfall in the Australian tropical savannas is highly seasonal, with most rain falling in the wet season between December and March (Felderhof & Gillieson, 2006). There is a climatic gradient across the Australian savannas, with a trend of decreasing rainfall and increasing inter-annual rainfall variability with distance from coast (Mott *et al.,* 1985).

Bird data

We focussed our study on 44 bird species that are largely restricted to the northern tropical savanna woodlands (see Appendix Table 4.1 for full list of species), excluding waterbirds and rainforest species that may occur intermittently in savanna regions, and species with ranges that extend substantially into other biogeographic regions. We only included species with distributions almost entirely in the study area as less confidence can be placed in models that are restricted to a small subset of species‟ ranges (Elith & Leathwick, 2009). However, we were interested in investigating the response to the savanna fire patterns on the whole bird assemblage, and whether the pattern of responses found for the core 44 species is reflected across the whole assemblage. So despite the issues associated with modelling only a subset of species‟ ranges, we undertook preliminary investigations for a further 163 species that occur within the savanna but also in other parts of the Australian continent. Because these 163 species occur widely outside the modelled region, the analyses focus on the 44 species, and no detailed analysis was done on the extra 163 species. Occurrence records of all 207 bird species were collated from the Birds Australia Atlas (Blakers *et al.,* 1984; Barrett *et al.,* 2003), the Queensland Governmental atlas WildNet (Environmental Protection Agency, 2004) and CSIRO (protocol as in Reside *et al.,* 2010) for the period from 1997 to 2008. The mean number of locality records per species was 2617, with records well distributed across northern Australia.

Environmental data

The climate data used for modelling were gridded spatial layers of annual mean temperature, temperature seasonality (the mean coefficient of variation of temperature over an annual period), annual precipitation, maximum temperature of the warmest period (measured as the maximum temperature of the warmest month), precipitation seasonality and precipitation of the driest quarter. These variables have been shown to produce robust species distribution models for vertebrates in northern Australia (VanDerWal *et al.*, 2009a; VanDerWal *et al.*, 2009b; Williams *et al.*, 2009b; Reside *et al.*, 2010). The climate layers were derived from monthly climate surfaces obtained from the Australian Water Availability Project (Jones *et al.,* 2007; Grant *et al.,* 2008) averaged over the period 1961 – 1990 at a 0.05° resolution (~5km grid). The climate layers were created using the "climates" package in *R* (VanDerWal *et al.,* 2011), and are equivalent to the bioclim variables derived using Anuclim 5.1 software (McMahon *et al.,* 1995). The fire data were spatial layers of total fire frequency, defined here as the number of years land was burnt in the period from 1997 to 2008; and late-fire frequency (a subset of total fire frequency) which was the number of years an area was burnt late in the dry season, August – November, between 1997 and 2008 (Northern Australia Fire Information, NAFI http://138.80.128.152/nafi2/). The fire layers were derived from the National Oceanic and Atmospheric Administration‟s Advanced Very High Resolution Radiometer (NOAA-AVHRR) from the Bushfire Council of the Northern Territory at a 0.01° resolution. The fire layers were rescaled to a 0.05° resolution by aggregating cells by the mean fire frequency value in ArcGIS v. 9.3.

Environmental space plots

Environmental space plots were produced to visually inspect the species‟ occurrence against fire frequency, regardless of geographic space using the statistical package "R" version 2.9.0 (www.r-project.org). Annual rainfall, total fire frequency and late-fire frequency variables for every pixel of the study area were extracted, and then plotted with rainfall on the x-axis and either total fire frequency or late-fire frequency on the y-axis. This provided the "background" available environmental space. The values of annual rainfall and total fire frequency or late-fire frequency corresponding to each species‟ location were plotted on top of the background. This gave an indication of the selectivity of the species, whether a species was selecting areas with particular fire frequencies, particular annual mean rainfall values, or both. Both the background environmental space and the species‟ occurrence were weighted by frequency of occurrence, so that more frequently recorded combinations of fire and rainfall are represented by different colours than those less frequently recorded.

Distribution models

Species distribution models were run using the presence-only modelling program Maxent (Phillips *et al.,* 2006). Maxent uses species presence records to statistically relate species occurrence to environmental variables on the principle of maximum entropy. All default settings were used, and models were run at a spatial resolution of 0.05 degrees (c. 5 x 5 km). Maxent has the advantage of being insensitive to spatially correlated variables, which can occur when using multiple climate variables (Phillips *et al.,* 2004). Model performance (defined as the models" consistency and ability to identify species actual presence and actual absence; Ling *et al.,* 2003) was evaluated by the area under the receiver operating characteristic curve (AUC): an AUC score of 1 is a perfect fit of the data, 0.5 is no better than random (Elith *et al.,* 2006; Phillips *et al.,* 2006). Models for each species were screened for low AUC (< 0.75) so that underperforming models were not included in further analyses.

The percentage contribution of each environmental variable to the model was used to indicate their proportional influence. The Maxent output response curves were then used to further examine the influence of the fire variables on the model. The response curves show the logistic probability of presence using only one variable at a time so that the contribution of individual variables can be examined when there is autocorrelation in the environmental layers. This was important in this case, as the late-fire frequency variable is a subset of total fire frequency and therefore is highly correlated.

Increased fire and late-fire frequency projections

The impact of increasing total fire frequency and late-fire frequency was predicted by projecting the model algorithm for each species onto a series of spatial surfaces, each consisting of a fire layer with artificially increased fire or late-fire frequency, and all climate variables remaining unchanged. These spatial surfaces were created by increasing each cell of the total fire frequency raster layer by an increment of one (therefore a cell that was burnt five times between 1997 and 2008 then had a total fire frequency of six). This process was repeated six times for both total fire frequency and late-fire frequency. A total of thirteen spatial surfaces were generated: the first with current levels of total fire frequency, late-fire frequency and climate, then six surfaces with increasing total fire frequency, and six with increasing late-fire frequency.

The Maxent default cumulative output value was converted to a binary presence/absence for each species using the threshold that balances training omission rate, predicted area and logistic threshold value (Liu *et al.,* 2005). This threshold value provides realistic predictions of species distributions (Prates-Clark *et al.*, 2008; VanDerWal *et al.*, 2009b). With the binary output, area could be denoted as "suitable predicted area" or "unsuitable predicted area" for each species. This enabled the calculation of the proportion of the whole study area that was suitable. We could then predict the percentage of the study area (Australian tropical savannas) that was suitable under the current conditions, and how this proportional suitability shifted when total fire frequency or late-fire frequency increased incrementally six times. The change in suitable area under the extreme case of a six-increment increase in total fire frequency or late-fire frequency was calculated by subtracting the percentage suitable under the current conditions from that calculated for a six-increment increase.

In addition to the change between current and the extreme case, we examined the change in the percent of suitable area for each species with each increment of increasing total fire frequency and late-fire frequency. We calculated the Pearson correlation between increasing fire and increasing late-fire frequency from current to a maximum increase of six years burnt, with the percentage of suitable area predicted by the model for each species. The Pearson correlations (ρ) for all species are displayed in a histogram. All analyses were conducted using the statistical package "R" version 2.9.0 (www.r-project.org). Images of the suitable area, unsuitable area, and area that changed in suitability depending on fire frequency as predicted by the Maxent model were produced for each species. Four exemplar species with a range of fire sensitivities are presented as case studies to demonstrate the results.

Results

Environmental space plots

Birds in Australian tropical savannas show a broad range of responses to existing fire frequencies (Figure 4.1). The environmental space plots show that species were recorded in a smaller total fire frequency envelope than the entire range of fire frequencies. The highest concentration of species" occurrence points generally clustered around the lower fire frequencies. Some species, for example Gouldian finch *Erythrura gouldiae*, were found fairly broadly across fire frequencies (zero to ten years out of twelve burnt) but were not found in areas with late-fire frequency greater than six years out of twelve. In contrast, red-backed fairy-wren *Malurus melanocephalus* showed broad tolerance for fire, being recorded at every total fire frequency and most frequencies of late-dry season fire. A few species were less tolerant, such as the white-streaked honeyeater *Trichodere cockerelli* which was recorded almost exclusively in locations with fire frequencies less than five years out of 12.

Probability of presence curves

The logistic probability of species presence depending on the total fire frequency calculated by Maxent is shown in Figure 4.1. Gouldian finch and red-backed fairy-wren showed slight increases in the probability of presence as total fire frequency increases, but decreasing in probability of presence as late-fire frequency increases. In contrast, star finch *Neochmia ruficauda*, and white-streaked honeyeater both show decreases in probability of presence with increases in both total fire frequency and late-fire frequency. White-streaked honeyeater is predicted to not occur where total fire frequency or late-fire frequency exceed eight or seven years respectively. The response curves are generally consistent the environmental space plots. For example, Gouldian finch is frequently recorded at fire frequencies between two and nine. The Maxent probability of presence peaks between fire frequencies of seven and ten. Gouldian finch is recorded only where late-fire frequency is between zero and six, and the probability of presence decreases after late-fire frequency exceeds three. On the other hand, red-back fairy-wren is recorded at every total fire frequency, and correspondingly, total fire frequency has little effect on their probability of presence.

Distribution models

Model performance across the core 44 savanna bird species was high, with all species‟ model AUC scores above 0.75 (range 0.76 – 0.99). The environmental factors of total fire frequency and late-fire frequency had a small but meaningful mean contribution in the models: 3.9% (range 0.6 – 23.1%) and 3.1% (range 0.04 – 11.9%) respectively (Table 4.1). Climate provided most of the explanatory power to the distribution models, which is to be expected for models at this scale (Pearson & Dawson, 2003). Annual precipitation showed the highest average contribution (37.8%), followed by temperature seasonality (24.3%).

Table 4.1.

The mean, standard deviation and range of percentage contributions that each variable made to the Maxent models for the 44 species.

Variable	Mean ± Standard Deviation (%)	Range (%)
Fire frequency	3.9 ± 4.5	0.6 – 23.1
Late-fire frequency	3.1 ± 2.7	0.04 – 11.9
Mean annual temperature	7.9 ± 10.1	0.3 – 61.5
Temperature seasonality	24.3 ± 17.2	0.9 – 67.5
Max temp warmest period	8.9 ± 8.3	0.8 – 38.2
Annual precipitation	37.8 ± 22.1	2.6 – 78.3
Precipitation seasonality	10.6 ± 11.5	0.3 – 50.7
Precipitation driest quarter	3.3 ± 3.4	0.1 – 15.0

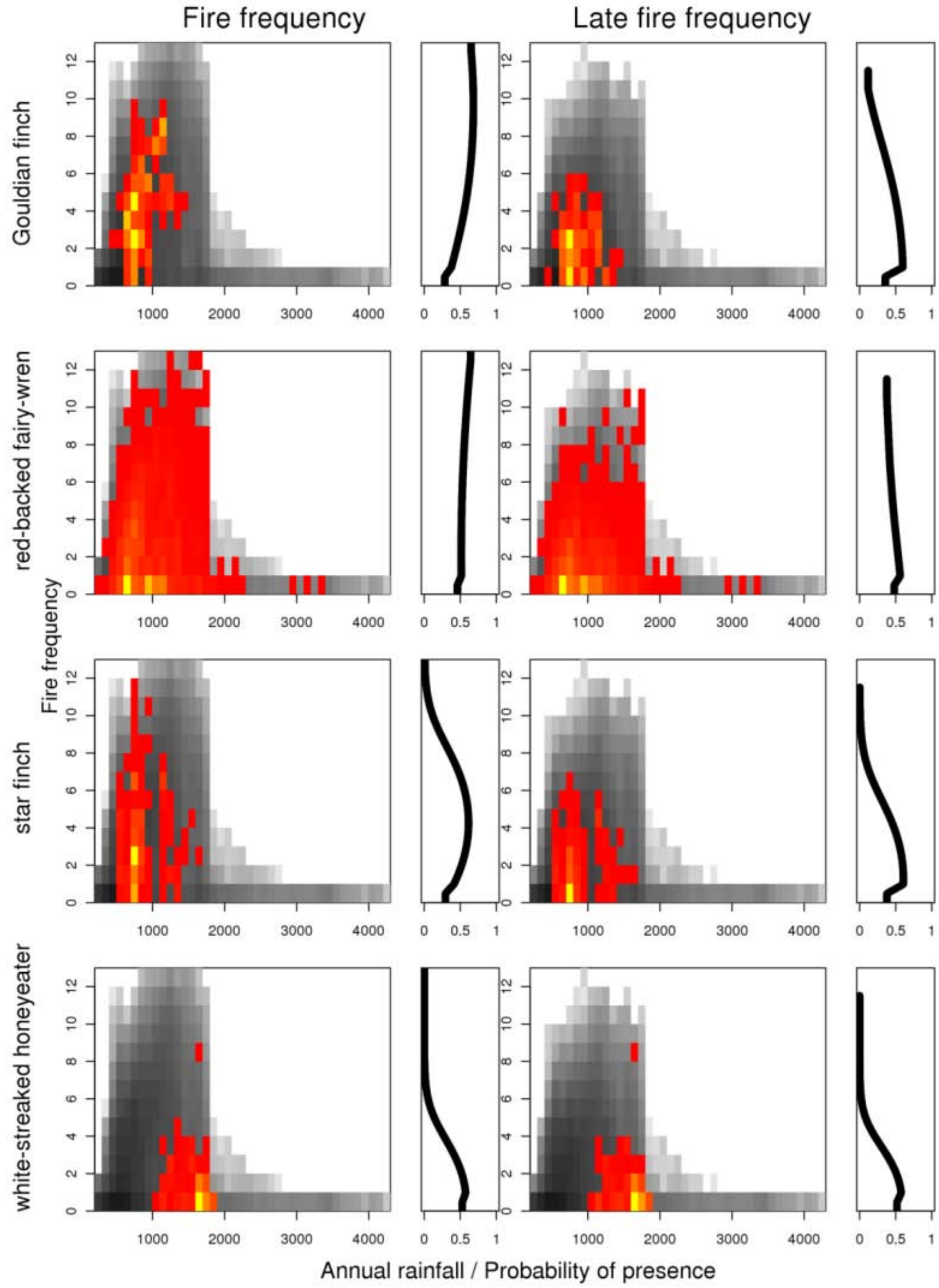


Figure 4.1.

Environmental space plots and Maxent variable response curves for four exemplar species within the Australian tropical savannas. The species shown are Gouldian finch *Erythrura gouldiae*, red-backed fairy-wren *Malurus melanocephalus*, star finch *Neochmia ruficauda* and white-streaked honeyeater *Trichodere cockerelli*. The environmental space plots show the available fire frequency and late-fire frequency versus annual rainfall. Results for the whole ATS region in greyscale. Darker grey represents greater prevalence. The values of fire frequency and late-fire frequency versus annual rainfall for which the species have been recorded is shown in yellow-to-red scale. For the species, the lighter colour (yellow) represents the most records, where the red represents fewer. The response curves show the probability of presence of each species depending on the fire frequency or late-fire frequency, assuming that each of these variables in turn are the only variable in the model, and are displayed to the right of each corresponding environmental space plot.

Increased fire and late-fire frequency projections

Predicted changes in the percentage area suitable for the core 44 species under a six-increment increase in total fire frequency and late-fire frequency are shown in Table 4.2. Two-thirds of these species faced a decrease in suitable area with increased total fire frequency, and the mean change in area was slightly greater for the species with decreased ranges (9.4% of suitable area lost, versus 4.4% gained) than the species that increased in predicted range. Where late-fire frequency increased, the decreases in suitable area were more pronounced, with 98% of species showing decreases. The mean change in suitable area was also more dramatic for the species facing a decrease in suitable area, at 7.2% of area lost versus 0.8% of area gained for the one species (long-tailed finch *Poephila acuticauda*) that showed increases in suitable area.

Table 4.2.

The number (and percentage) of the 44 modelled species predicted to face an increase or decrease in suitable area as a result of a factor of six increase in both fire frequency and late-fire frequency. The mean change in suitable area (either increase or decrease) and standard error are shown.

	Fire frequency increase	**Mean change in suitable area**	**Late-fire frequency increase**	**Mean change in suitable area**
# increasing species	15 (34%)	4.4% ± 3.2	1 (2%)	0.8% ± 0
# decreasing species	29 (66%)	9.4% ± 7.4	43 (98%)	7.2% ± 6.2

The effect of increasing total fire frequency and late-fire frequency at each of the increments is shown in detail for the four exemplar species (Figure 4.2). Species showed a variety of responses to increased total fire frequency. Gouldian finch showed a slight increase in suitable area with increasing total fire frequency (Figure 4.2a). Red-backed fairy-wren showed little change (Figure 4.2c), whereas the suitable area for star finch (Figure 4.2e) and white-streaked honeyeater (Figure 4.2g) decreased. All four species showed a trend of decreasing suitable area associated with an increase in late-fire frequency. Star finch showed a particularly strong decline with late-fire frequency (Figure 4.2f). White-streaked honeyeater showed strong declines with both increasing fire and late-fire frequencies (Figure 4.2g and 4.2h).

The strength of the relationship between increasing total fire frequency or late-fire frequency and the percentage suitable area across the 44 species is shown with Pearson correlations (ρ) in Figure 4.3. Two-thirds of species were negatively correlated between increased total fire frequency and the percentage suitable area, and one-third positively correlated. In contrast, the majority of species show a negative correlation between increasing late-fire frequency and the percentage suitable habitat. The ρ are also shown for all 207 of species that also occur in Australian tropical savannas in Figure 4.3. The same pattern is observed across the 207 species as that seen for the core 44 savanna specialist species – a mixed response to increasing total fire frequency. However, under increasing late-fire frequency most species show a strong decline in suitable area.

Some species may face substantial distribution loss with increases in total fire frequency (Figure 4.3). In the extreme event of a six-increment increase in total fire frequency, 11out of the core 44 species are predicted to lose more than 10% of their range within the tropical savannas (Appendix Table 4.1). These same 11 species are also predicted to lose more than 10% of their range within the study area in the case of a six-increment increase in late-fire frequency. Under both scenarios, three species are predicted to lose more than 20% of their distribution: yellow honeyeater *Lichenostomus flavus*, black-throated finch *Poephila cincta* and oriental cuckoo *Cuculus saturatus*. A six-increment increase in total fire frequency may prove beneficial for some species, although predicted increases in suitable area are comparably small. Thirteen species showed very slight increases, with the most substantial increase shown by long-tailed finch *Poephila acuticauda*, with an increase of 10%. Long-tailed finch was the only species to show an increase in area due to a six-increment increase in late-fire frequency; however this increase was minimal (Table 4.1).

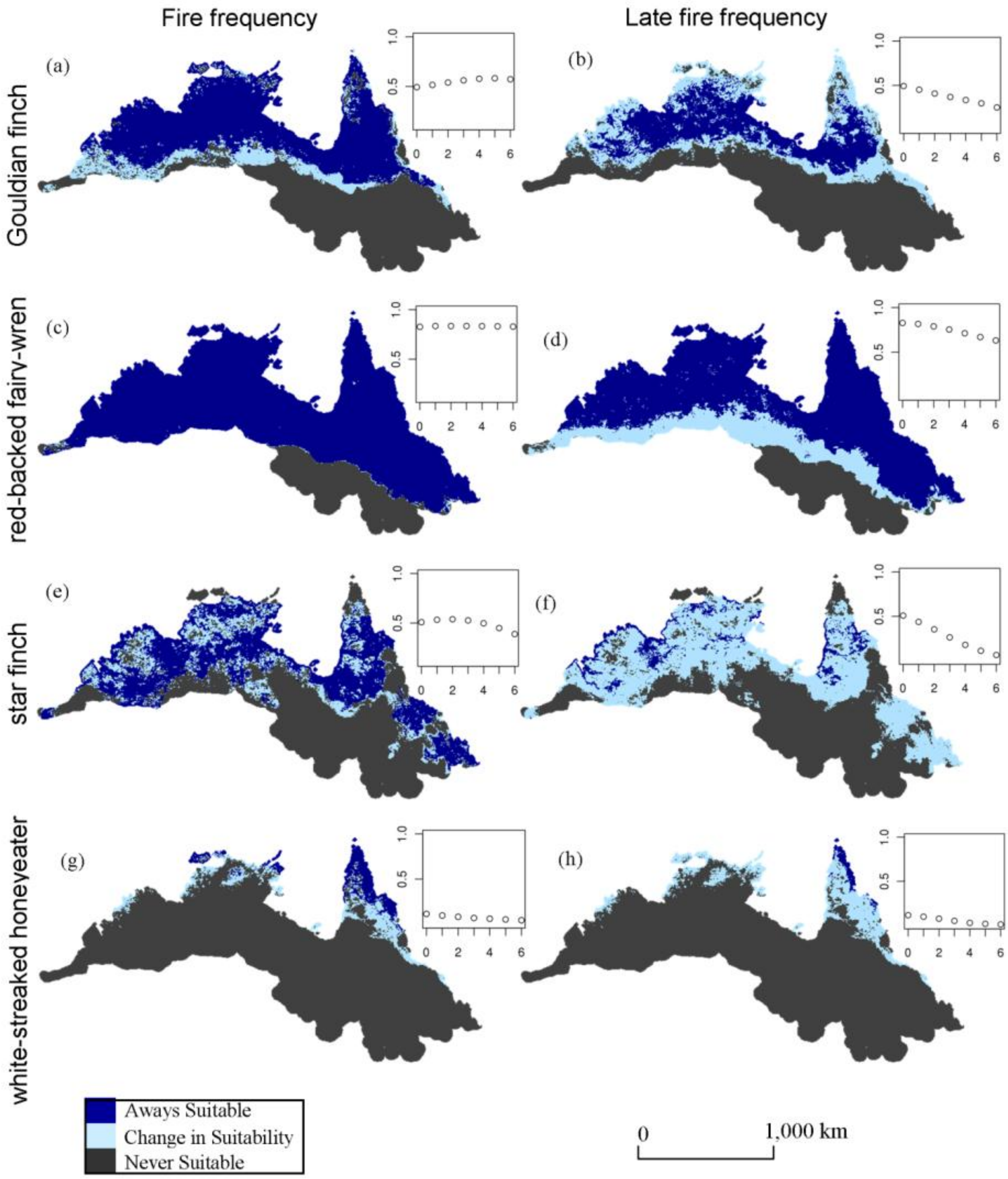


Figure 4.2.

The proportional change in suitable area for species from the current levels of fire frequency (a, c, e, g) and late-fire frequency (b, d, f, h), to a six-increment increases in fire frequency variables, for the same four species within Australian tropical savannas as in Fig 4.1. In the maps, the dark blue represents area that is always suitable, the dark grey is always unsuitable, and the light blue is the area that has changed in suitability. For the plots, the Y-axis represents the proportion of the entire Australian tropical savanna region that is suitable, depending whether the fire frequency is at current levels (0) or increasing by each factor 1 – 6.

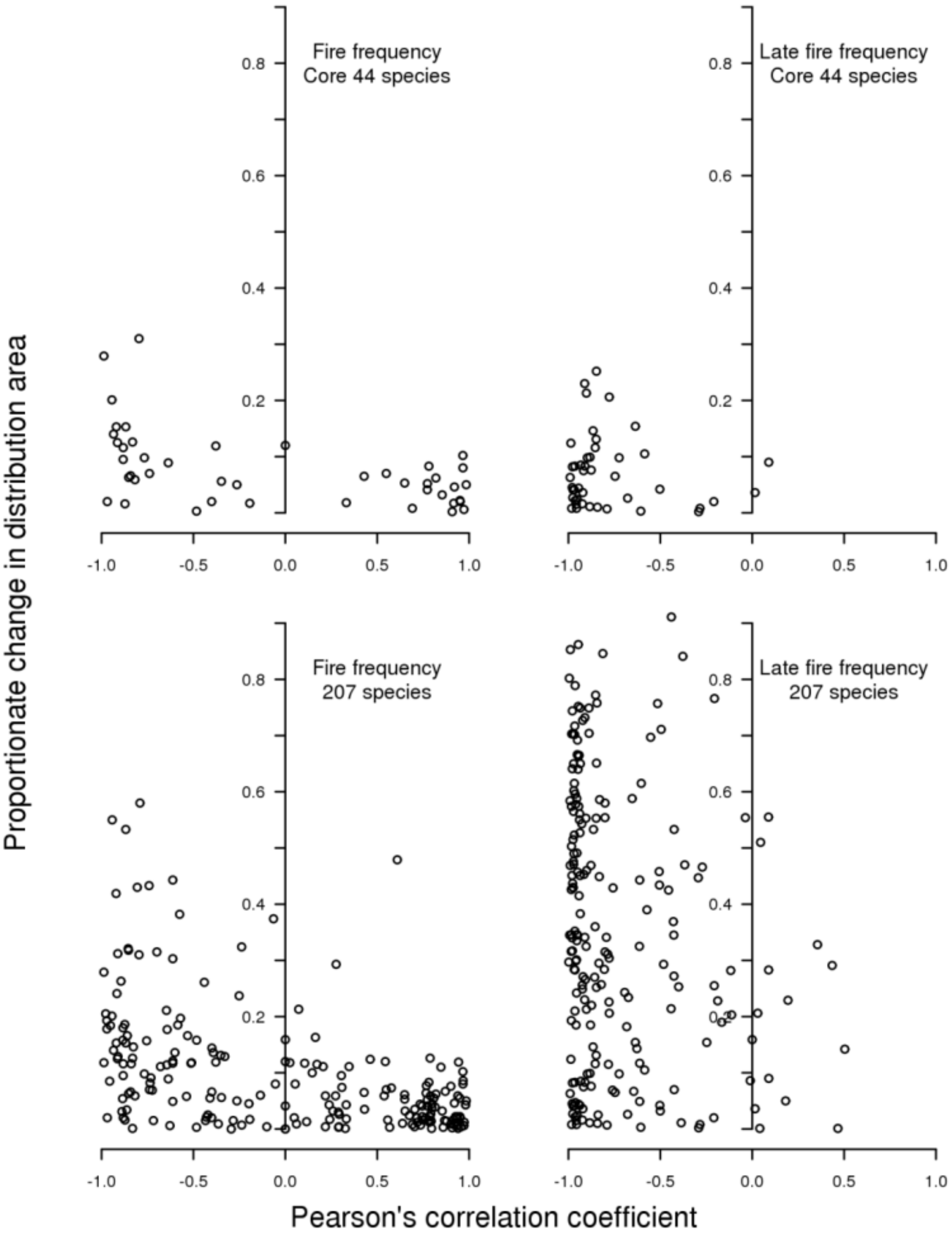


Figure 4.3.

Plots representing the Pearson correlation (ρ) for the relationship between increasing fire frequency or late-fire frequency and the proportion of suitable area for each species, against the change in suitable area. The top row shows the plots for 44 species largely confined to the northern Australian savannas, whereas bottom row shows the plots for 207 species (inclusive of the original 44), which incorporates species that also occur outside the savanna. Models of the 163 species that occur outside the savanna are less reliable as only a subset of their geographic extent has been modelled.

Discussion

This study indicates that on broad bioclimatic scale many Australian tropical savanna birds have low sensitivity to fire frequency and fire frequency increase, with increasing fire predicted to result in one-third of species increasing in range, and many only decreasing by a small percentage. Many species within Australian tropical savannas are known for their resilience to fire, and this is likely due to the long history of coexisting with fire (Andersen & Hoffmann, 2011). Birds within this biome possess attributes associated with high resilience to fire, such as high mobility (Moretti & Legg, 2009). Many species are attracted to recently burnt areas as fire can make food resources, such as seeds and small animals, more accessible due to removal of the grass layer (Braithwaite & Estbergs, 1985; Braithwaite & Estbergs, 1987; Dean, 1987; Woinarski, 1990). Some of the species predicted to experience range increases due to increases in total fire frequency are associated with vegetation close to water, such as long-tailed finch, purple-crowned fairy-wren *Malurus coronatus*, Gouldian finch, northern rosella *Platycercus venustus*, silver-crowned friarbird *Philemon corniculatus* and crimson finch *Neochmia phaeton*. These species may be more resilient to frequent fires due to their proximity to water courses. Previous studies have found that black-tailed treecreeper *Climacteris melanura* in particular has been associated with frequent burning (Woinarski *et al.,* 1999). Species responses to fire predicted by our study appeared to be independent of functional groups, as granivorous, insectivorous and foliage insectivore/nectarivore species showed both positive and negative relationships with increasing total fire frequency in our study.

Seasonality of fire can have a marked effect on how it impacts on species. Our study demonstrated that increasing late-dry season fire has a detrimental effect on the majority of species. These findings are consistent with other studies which highlight the impact of late-dry season fire on bird species in Australian tropical savannas (Bradstock *et al.,* 2005). High late-fire frequency can influence bird composition and assemblage pattern by changing habitat structure through the decline in fire sensitive vegetation (Bowman *et al.*, 1988; Russell-Smith & Bowman, 1992; Price & Bowman, 1994), increasing tree mortality (Williams *et al.,* 2002), and a reduction in structural diversity (Woinarski, 1990; Valentine *et al.*, 2007). Other studies have shown late-dry season fires to be detrimental to tropical savanna bird species such as black-tailed treecreeper (Garnett & Crowley, 1995), red-backed fairy-wren (Murphy *et al.,* 2010), lemon-bellied flycatcher *Microeca griseoceps* and Australian owlet-nightjar *Aegotheles cristatus* (Andersen *et al.,* 2005).

In contrast, early-dry season burns may have a beneficial effect on particular species. The main benefit of early-dry season burns may be that they reduce the extent and impact of late-dry season fires (Williams *et al.,* 2002; Bird *et al.,* 2008). A mosaic of burnt and unburnt habitat created by early-dry season burns is required for species to survive the actual fire event (Murphy *et al.,* 2010). In addition, fire may facilitate access to foraging resources, but be detrimental to nesting sites (Woinarski, 1990), and species benefit most with access to both burnt and unburnt areas within their home range (Murphy *et al.,* 2010). Wet season burns are also likely to be beneficial. Areas that have undergone wet season burns have higher bird abundance than unburnt sites immediately post-fire, and maintain similar vegetation structure and bird assemblages as unburnt sites several years following the burning event (Valentine *et al.,* 2007).

One quarter of species were predicted to lose more than 10% of their range with fire frequency increases, regardless of the seasonality of fire. These species may be of particular conservation concern because in addition to their sensitivity to increased fire frequency, nine out of the eleven have small geographic distributions (Barrett *et al.,* 2003), and two of these species have endangered subspecies (crimson finch and black-throated finch). In particular, star finch may be dependent on areas left unburnt for at least a year which provide a food source in the wet season (Garnett *et al.,* 2005). Although not found in our study, foliage-gleaners, branch gleaners and foliage-gleaner/nectarivores have been found in association with unburnt plots (Woinarski, 1990). Four out of the 11 predicted to lose the most range could be described as foliage-gleaner/nectarivores (yellow honeyeater, brown-backed honeyeater *Ramsayornis modestus*, helmeted friarbird *Philemon buceroides* and red-headed honeyeater *Myzomela erythrocephala*).

Fire frequency and late-fire frequency had a relatively small proportional contribution to the distribution model of most species, as was expected as species distributions are predominantly governed by climate at large spatial scales (Pearson & Dawson, 2003). For some species, total fire frequency contributed substantially to the model (e.g. >20% for the northern rosella). However, percentage contributions for individual variables can be misleading when variables are highly correlated, as with total fire frequency and late-fire frequency, or mean annual temperature and maximum temperature of the warmest period. Despite the relatively small contribution of the fire variables, simulating changes in total fire frequency resulted in substantial changes in the distribution models for many species. Our study is correlative by nature, and while correlative distribution models explain species distributions on par with mechanistic distribution models (Hijmans & Graham, 2006; Kearney *et al.*, 2010); correlative models do not facilitate separating correlation from causality. Detailed mechanistic studies are needed for thorough understanding of the effects of fire frequency and seasonality on individual species (Driscoll *et al.,* 2010); these would determine the importance of interactions of local factors e.g. burnt patch size, proximity to unburnt refugia or habitat heterogeneity to species resilience to fire (Murphy *et al.,* 2010).

For many species likely to lose suitable habitat as total fire frequency and late-fire frequency increases, decreases mostly occurred in the southern parts of their distribution. The southern section of the tropical savannas is largely semi-arid, with generally a much lower fire frequency than in the north (Felderhof & Gillieson, 2006). Fire can have a severe impact on these habitats, as lower and less consistent rainfall can slow the post-fire regeneration process (Noble, 1989). Many semi-arid plant species are fire-killed, such as acacia (e.g. *Acacia aneura*), and spinifex (e.g. *Triodia* spp), and high fire frequency coupled with the lack of post-fire rain can prevent resprouting (Allan & Southgate, 2002). The bird species‟ intolerance of high fire frequencies on the southern edge of the savannas is likely to be linked to the more dramatic impact of fire on semi-arid savanna vegetation. Marked changes in vegetation are expected to impact on birds, as birds are highly responsive to vegetation structure (Martin & Possingham, 2005; Sirami *et al.*, 2009). The greater impact of fire on semi-arid savanna could also explain why our study (which encompassed both semi-arid and mesic savanna) found detrimental effects of late fire on some species, for example blue-winged kookaburra (*Dacelo leachii*) and forest kingfisher (*Todiramphus macleayii*), while in the northern mesic savannas of the Northern Territory experimental studies (Corbett *et al.,* 2003) found no effect of fire on these species.

While our study is likely to reflect real-world sensitivities of species to fire, it is not without limitation. One issue is that the spatial scale – 5 km pixels – may miss the detail of fine burnt and unburnt mosaics that are likely to be influential to bird species. However given the mobility of birds, individuals of many species are operating on a spatial scale of hundreds of kilometres (Griffioen & Clarke, 2002), therefore although a 5 km x 5 km scale may be missing some detail, it should be fine enough to be relevant to the species studied. Another limitation is the bird data and the fire data are from the same period, therefore this study might not be capturing the lag-effect of past fire influences on habitat structure and therefore the birds. However the broad patterns of fire frequencies across the savanna have been consistent over the last 20 years (Russell-Smith, 2002; Felderhof & Gillieson, 2006), therefore the fire history prior to our study is likely to be broadly reflected in the vegetation patterns.

Conclusion

Australian tropical savannas have “fire weather” conducive to burning for most of the dry season, but burning is limited by the number of ignitions and fuel reduction by previous fires or intensive grazing (Ash *et al.*, 1997; Bradstock, 2010). Therefore a regime of moderate fire frequency early in the dry season may be the best way to prevent the large destructive late-dry season fires (Williams *et al.,* 2002; Bird *et al.,* 2008). Our study has shown that frequent fires late in the dry season are likely to be detrimental to many bird species within savannas. In addition, we have identified species that are particularly sensitive to high fire frequency, and those that benefit from frequent fire when it occurs outside the late-dry season. Our study could therefore aid design of fire regimes tailored to the management of species, particularly threatened or endemic species that are fire sensitive (Garnett & Crowley, 2002; Perry *et al.*, 2011a), although further work on the impact of the less likely scenario of decreased fire frequency on birds may be necessary. The relative congruence in species‟ sensitivities to the range of fire frequencies as demonstrated by our three modelling approaches (environmental occurrence, their probability of presence, and change in suitable area under hypothetical fire frequency increases) gives us confidence that our methods show meaningful patterns. We suggest that this approach may be useful for identifying at risk species in other biomes facing changes in fire regimes.

Author contributions

AR conceived the study, performed the modelling and analyses, and wrote the paper; JV assisted with the analyses; JV, AK, IW and SW provided advice and editorial assistance.

Appendix Table 4.1.

The responses of each species to increases in fire frequency and late fire frequency. "% area fire frequency 0-6" refers to the percentage of area lost between the original fire frequency scenario, and the scenario where fire was increased by a factor of six.

Common Name	**Scientific name**	**% area fire frequency 0-6**	**ρ for fire frequency**	**% area late fire frequency 0-6**	**ρ for late fire frequency**
brahminy kite	*Haliastur indus*	-15.3	-1.00	-14.6	-0.98
red goshawk	*Erythrotriorchis radiatus*	-1.7	-0.17	-3.6	-0.93
red-backed button-quail	*Turnix maculosa*	-12.6	-0.87	-13.1	-0.76
bar-shouldered dove	*Geopelia humeralis*	5.2	0.92	-0.8	-0.76
varied lorikeet	*Psitteuteles versicolor*	-5.3	-0.95	-6.5	-0.92
double-eyed fig-parrot	*Cyclopsitta diophthalma*	-8.9	-0.86	-9.8	-0.51
northern rosella	*Platycercus venustus*	7	0.94	-0.6	-0.50
golden-shouldered parrot	*Psephotus chrysopterygius*	-9.5	-1.00	-9.8	-0.98
oriental cuckoo	*Cuculus saturatus*	-31	-1.00	-25.2	-0.97
little bronze-cuckoo	*Chrysococcyx minutillus*	-12	-1.00	-12.2	-0.97
rufous owl	*Ninox rufa*	-5.9	-1.00	-7.6	-0.96
grass owl	*Tyto capensis*	-5.6	-0.41	-7.5	-0.84
blue-winged kookaburra	*Dacelo leachii*	-2	-0.79	-4.4	-0.95
forest kingfisher	*Todiramphus macleayii*	-12.5	-0.99	-12.4	-0.97
black-tailed treecreeper	*Climacteris melanura*	5	0.96	-0.8	-0.48
purple-crowned fairy-wren	*Malurus coronatus*	8.3	0.99	-0.2	-0.64
red-backed fairy-wren	*Malurus melanocephalus*	0.2	-0.02	-2.7	-0.94
fairy gerygone	*Gerygone palpebrosa*	-6.6	-0.93	-8.3	-0.98
silver-crowned friarbird	*Philemon argenticeps*	6.2	0.84	-0.7	0.19
helmeted friarbird	*Philemon buceroides*	-14	-1.00	-14.2	-0.98
yellow-spotted honeyeater	*Meliphaga notata*	-9.8	-1.00	-9.9	-0.98
graceful honeyeater	*Meliphaga gracilis*	-6.3	-1.00	-8	-0.43
white-gaped honeyeater	*Lichenostomus unicolor*	2.2	0.67	-1.6	-0.94
yellow honeyeater	*Lichenostomus flavus*	-20.1	-1.00	-20.6	-0.94
white-throated honeyeater	*Melithreptus albogularis*	0.6	0.64	-2.4	-0.04
white-streaked honeyeater	*Trichodere cockerelli*	-7	-0.99	-8.5	-0.95
brown-backed honeyeater	*Ramsayornis modestus*	-15.3	-1.00	-15.4	-0.94
bar-breasted honeyeater	*Ramsayornis fasciatus*	4.1	0.81	-1.1	0.02
tawny-breasted honeyeater	*Xanthotis flaviventer*	-1.6	-1.00	-3.6	-0.78
rufous-throated honeyeater	*Conopophila rufogularis*	-1.8	-0.96	-4.1	-0.65
rufous-banded honeyeater	*Conopophila albogularis*	-2	-0.93	-4.2	-0.40
banded honeyeater	*Certhionyx pectoralis*	3.2	0.93	-1.5	-0.25
red-headed honeyeater	*Myzomela erythrocephala*	-11.6	-0.93	-10.5	-0.98
lemon-bellied flycatcher	*Microeca flavigaster*	-6.5	-0.99	-8.2	-0.99
northern fantail	*Rhipidura rufiventris*	0.8	0.27	-2.2	-0.01
yellow oriole	*Oriolus flavocinctus*	-2	-0.97	-4.5	-0.76
black-backed butcherbird	*Cracticus mentalis*	-5	-0.98	-6.3	-0.95

Common Name	**Scientific name**	**% area fire frequency 0-6**	**ρ for fire frequency**	**% area late fire frequency 0-6**	**ρ for late fire frequency**
great bowerbird	*Ptilonorhynchus nuchalis*	-1.7	-0.72	-4.1	0.18
long-tailed finch	*Poephila acuticauda*	10.2	0.99	0.8	0.09
black-throated finch	*Poephila cincta*	-27.9	-0.99	-23	-0.90
star finch	*Neochmia ruficauda*	-11.9	-0.80	-11.6	-1.00
crimson finch	*Neochmia phaeton*	4.6	0.69	-1	0.09
pictorella mannikin	*Heteromunia pectoralis*	0.3	0.95	-2.6	-0.96
Gouldian finch	*Erythrura gouldiae*	8	0.93	-0.3	-0.44

Chapter 5: Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios[4]

Abstract

Identifying the species most vulnerable to extinction as a result of climate change is a necessary first step in mitigating biodiversity decline. Species distribution modelling (SDM) is a commonly used tool to assess potential climate change impacts on distributions of species. We use SDMs to predict geographic ranges for 243 birds of Australian tropical savannas, and to project changes in species richness and ranges under a future climate scenario between 1990 and 2080. However, realistic predictions require recognition of the variability in species capacity to track climatically-suitable environments. Here we assess the effect of dispersal on model results by using three approaches: full dispersal, no dispersal and a partial-dispersal scenario permitting species to track climate change at a rate of 30 km per decade. As expected, the projected distributions and richness patterns are highly sensitive to the dispersal scenario. Projected future range sizes decreased for 66% of species if full dispersal was assumed, but for 89% of species when no dispersal was assumed. However, the realistic future predictions should not assume a single dispersal scenario for all species and as such, we assigned each species to the most appropriate dispersal category based on individual mobility and habitat specificity; this permitted the best estimates of where species will be in the future. Under this „realistic‟ dispersal scenario, projected ranges sizes decreased for 67% of species but showed that migratory and tropical-endemic birds are predicted to benefit from climate change with increasing distributional area. Richness hotspots of tropical savanna birds are expected to move, increasing in southern savannas and southward along the east coast of Australia, but decreasing in the arid zone. Understanding the complexity of effects of climate change on species‟ range sizes by incorporating

---

[4] Reside, A.E., VanDerWal, J.J., and Kutt, A.S. (Accepted) Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenario. *Ecology and Evolution*.

dispersal capacities is a crucial step toward developing adaptation policies for the conservation of vulnerable species.

Introduction

Global climate change is already having an effect on species and communities, with increasingly severe impacts expected across taxonomic groups with increasingly rapid climate change (Walther *et al.,* 2002; Thomas *et al.,* 2004). Climate change has resulted in species‟ Grinnellian niche - defined as the environmental conditions characterising its occurrence (Grinnell, 1917) - shifting to new geographic locations (Tingley *et al.*, 2009). The Grinnellian niche is well represented by climate for many species, and is commonly referred to as its suitable climate space (Root, 1988; Kearney & Porter, 2009). Many species have been documented as tracking the shifts in their suitable climate space to new geographic locations (Tingley *et al.*, 2009) and generally this shift is towards the poles or to higher altitudes as temperatures increase (Parmesan & Yohe, 2003). However, rising temperatures combined with changing precipitation patterns can have more complex effects on species distributional shifts, and some species‟ suitable climate spaces are projected to disappear altogether (Williams *et al.*, 2003; Malcolm *et al.*, 2006; Williams & Middleton, 2008; Coetzee *et al.*, 2009). The increased extinction risk predicted for many species due to climate change has resulted in conservation initiatives to incorporate vulnerability to climate change as a factor for listing a species as threatened and requiring management intervention (Brook *et al.*, 2009; Hawke, 2009). With up to 50% of the world‟s biodiversity already threatened with extinction (Millennium Ecosystem Assessment, 2005) and biodiversity continuing to decline (Secretariat of the Convention on Biological Diversity, 2010), broad-scale predictions of species‟ responses to climate change are needed to prioritise those in need of urgent conservation action.

Tropical biota are expected to have higher than average sensitivity to climate change, due to the high species diversity, smaller ranges and narrower thermal tolerances (Colwell *et al.,* 2008; Deutsch *et al.,* 2008). Species restricted to high altitude tropical regions face “mountain top extinctions” as their suitable climate space shifts upslope with rising temperatures (Williams *et al.*, 2003). Tropical lowlands are predicted to decrease in species richness, as there are no species currently in hotter places available to replace those that move to higher latitudes or altitudes (Colwell *et al.*, 2008). In Australia, modelling studies on climate change impacts on tropical rainforest fauna forecast severe declines in the area of suitable climate space and possible species extinctions (Williams *et al.,* 2003; Hilbert *et al.,* 2004). For species confined to tropical uplands, some are likely to lose substantial proportions of suitable habitat (Shoo *et al.*, 2005). However, most of tropical Australia is savanna and few assessments of the consequences of climate change for species occupying this biome have been conducted. One example examining kangaroo (Macropodidae) distribution in northern Australia predicted average range reductions per species of 48% with 2°C of warming (Ritchie & Bolitho, 2008). A more in-depth understanding of the climate change threat to species persistence in Australian tropical savannas is imperative, as many vertebrate populations are declining at sufficient rates to be cause for concern. In particular, small mammals (Woinarski *et al.,* 2010; Woinarski *et al.,* 2011) and granivorous birds (Franklin *et al.*, 2005) are declining as a result of altered habitat conditions due to changed fire regimes and widespread cattle grazing, despite most of the region being relatively unmodified by intensive agriculture or urbanisation (Fensham *et al.*, 1999; Russell-Smith, 2002).

Many studies have documented mobile species such as birds shifting their ranges and migration strategies in response to change in climate and weather patterns (Dunlop & Wooller, 1986; Pounds *et al.*, 1999; Thomas & Lennon, 1999; Cotton, 2003; Reid, 2003; Brommer, 2004; Austin & Rehfisch, 2005; Visser *et al.*, 2009). These responses are likely to amplify as global climates continue to change in line with projections (IPCC 2007a). Birds are an exemplar study group for understanding and anticipating the potential effect of climate change because more is known about their distributions and life histories than many other taxa (Webb & Gaston, 2000). In Australia, range shifts of birds have been documented in recent years; but attributing this observation to climate change is confounded by the relative effects of land use change on bird movements and distributions (Chambers *et al.*, 2005). Despite this complexity, there is evidence for climate change contributing to species declines in southern Australia (Mac Nally *et al.*, 2009), Western Australia (Rowley & Russell, 2002), and for seabird populations in the north-east (Smithers *et al.*, 2003).

Birds of the Australian tropical savanna biome have complex and flexible movement patterns and are therefore highly adapted to variable resource distributions (Woinarski *et al.*, 2000a; Chan, 2001). Despite the general mobility of savanna bird species, some are habitat or food specialists with restricted distributions (Weaver, 1982; Rowley & Russell, 1993; Perry *et al.*, 2011a). While some species have the adaptive capacity to track suitable climate space as it shifts geographically, some species may be constrained by the time required for habitats (e.g. vegetation) to change in response to changing climate (Warren *et al.*, 2001). Therefore forecasting actual climate change responses by individual species requires realistic dispersal scenarios. These realistic dispersal scenarios improve projections by predicting not only the direction in which species‟ suitable climate spaces are shifting, but also the ability of species to track the shift, including accounting for species‟ habitat limitations (Midgley *et al.*, 2006). Generally species are expected to move to higher latitudes (Parmesan & Yohe, 2003). For birds of the Australian tropical savanna, direct poleward movement of many species may be impeded by the arid zone on the southern boundary of the biome, and the severe disjunction between wooded savanna and largely treeless grassland and desert (Mott *et al.*, 1985). While global studies on future climate suggest that while the broad climatic biome classification of northern Australia are unlikely to shift substantially (Rubel & Kottek, 2010), this region is expected to experience climates that are relatively novel (Williams *et al.*, 2007). However, it is unknown how the suitable climate space of savanna birds will change on a regional scale, how well different species will be able to track that movement, and as a consequence, what will happen to the species richness of the tropical savannas. In this study we investigate the impact of future climate change on the bird fauna of Australian tropical savannas. We use distribution models for 243 species to: 1) estimate the change in species richness between 1990 and 2080; 2) investigate the effects of different dispersal scenarios on species potential response to climate change; and 3) using a realistic dispersal scenario for each species, estimate the potential impact of climate change on individual species, and across groupings of: a) autecology and b) current conservation concern under Australian and international listings.

Methods

Study area

The Australian tropical savannas occur north of c. 23°S (Franklin *et al.*, 2005), occupying nearly one quarter of the continent (Williams *et al.*, 2005). Savannas are characterised by a discontinuous stratum of trees above a mostly continuous layer of grasses (Williams *et al.*, 2002). Rainfall is highly seasonal and largely occurs in the wet season between December and March (Felderhof & Gillieson, 2006). A climatic gradient extends from the higher rainfall savannas near the coast, to the semi-arid savannas inland with increased inter-annual rainfall variability (Mott *et al.*, 1985).

Bird data

We focussed our study on 243 bird species occurring within the northern tropical savanna woodlands excluding waterbirds and rainforest species that may occur intermittently in savanna regions. Bird occurrence records were collated from the Birds Australia Atlas (Blakers *et al.,* 1984; Barrett *et al.,* 2003), the Queensland Governmental atlas WildNet (Environmental Protection Agency, 2004) and CSIRO (protocol as in Reside *et al.*, 2010). Species were grouped according to their movement life history (migratory, nomadic, sedentary, partially migratory, and species that were both nomadic and sedentary). Most species that occur within Australian tropical savannas also occur beyond the savanna region, many occurring widely across Australia. The species were grouped into five broad biogeographic groups describing their broader range: arid, temperate, tropical, Cape York Peninsula (a subset of the tropical biogeographic region which has a distinct species assemblage) and ubiquitous for species that encompassed two or more of the above categories (Appendix Figure 2.1); according to the literature (Schodde, 1981; Marchant & Higgins, 1990; Marchant & Higgins, 1993; Higgins & Davies, 1996; Higgins, 1999; Higgins *et al.*, 2001; Higgins & Peter, 2002; Higgins *et al.*, 2006). The details for each species are provided in Appendix Table 5.1. While we focused our study on the suite of species that occur in the tropical savannas, we investigated the effect of climate change on species‟ broader ranges, even when they extend beyond the savanna and across the rest of Australia. Detailed explanations of the biogeographic groupings can be found in Reside *et al.* (2010). Species conservation status was also compiled. Nineteen of 243 species in our study are listed as having a significant conservation status under the Australian Commonwealth Government (EPBC: Environment Protection and Biodiversity Conservation Act, 1999), Queensland Sate (NCA: Nature Conservation Act, 1992) or international (IUCN, 2001) categories of endangered, vulnerable or near-threatened (Table 5.2).

Climate data

The climate data used for modelling were gridded spatial layers of annual mean temperature, temperature seasonality (the standard deviation of the weekly mean temperatures expressed as a percentage of the annual mean), maximum temperature of the warmest period, annual precipitation, precipitation seasonality and precipitation of the driest period. The maximum temperature of the warmest period is the highest temperature of any monthly maximum temperature; precipitation of the driest period is the precipitation of the driest month. These variables have been shown to produce robust species distribution models for vertebrates in northern Australia (VanDerWal *et al.*, 2009a; VanDerWal *et al.*, 2009b; Williams *et al.*, 2009b; Reside *et al.*, 2010). The climate layers were derived from monthly climate surfaces obtained from the Australian Water Availability Project (Jones *et al.,* 2007; Grant *et al.,* 2008) averaged over the period 1961 – 1990 at a 0.05° resolution (~5km grid). The climate layers were created using the "climates" package in *R* (VanDerWal *et al.,* 2011), and are equivalent to the bioclim variables derived using Anuclim 5.1 software (Hutchinson *et al.*, 2000).

Future climate

Future climate layers consisted of climate surfaces for ten year intervals between 1990 and 2080. The future climate surfaces were based on the IPCC Special Report on Emission Scenarios (SRES) scenario A1B, which represents a medium-severity projection of both fossil fuel and non-fossil fuel energy sources (Nakicenovic *et al.*, 2000). Future climate surfaces were based on eight global circulation models (GCM) (Cubash *et al.*, 2001), some with multiple realisations (Table 5.1), resulting in 30 projections per ten year interval. Figure 5.1 presents the weighted mean change in each climate variable between 1990 and 2080. The weighting was based on the number of realisations per GCM to remove any possible GCM-specific bias. By 2080, both mean annual temperature and temperature of the warmest period are projected to increase the most in the Pilbara and Great Sandy Desert bioregions of north-western Australia, by up to 3.4°C (Figure 5.1). The increase in temperature declines with decreasing distance to the coast. This is in broad agreement with other work projecting future climate in Australia (Whetton *et al.*, 2005). Temperature seasonality is projected to decrease in northern Australia (less variation throughout the year in temperature) and increase across the south.

The climate projections for rainfall are variable, from widespread severe decreases to widespread increases in annual rainfall (Appendix Figure 5.1). The weighted means indicate that precipitation may increase across the central tropical savanna by up to 5%; but decrease across north-western Australia and southern Australia (Figure 5.1). Precipitation seasonality is projected to decrease slightly in northern savannas, and precipitation of the driest period is predicted to decrease across most of the continent. The extreme changes in temperature (maximum and minimum, Appendix Figure 5.1) show similar spatial patterns in increases in annual mean temperature between 1990 and 2080, with varying degrees of warming. Changes in annual precipitation are more varied: the minimum shows the whole continent getting drier, with large tracts of inland Australia receiving half the current annual rainfall; whereas the maximum shows most of the continent receiving more rainfall by up to 184%.

Table 5.1.

The eight global circulation models used for the projections of future climate. The number of runs for the 20th (C20) and 21st (C21) century, and the total number of realisations, used for the future projections are shown for each GCM (Cubash *et al.* 2001).

Global circulation model	# runs for C20	# runs for C21	# realisations
BCCR-BCM 2.0	1	1	1
CSIRO-Mk 3.0	3	1	3
CSIRO-Mk 3.5	3	1	3
GISS AOM	2	2	4
INM CM 3.0	1	1	1
MIROC 3.2 (hires)	1	1	1
MIROC 3.2 (medres)	3	3	9
NCAR CCSM 3.0	2	4	8

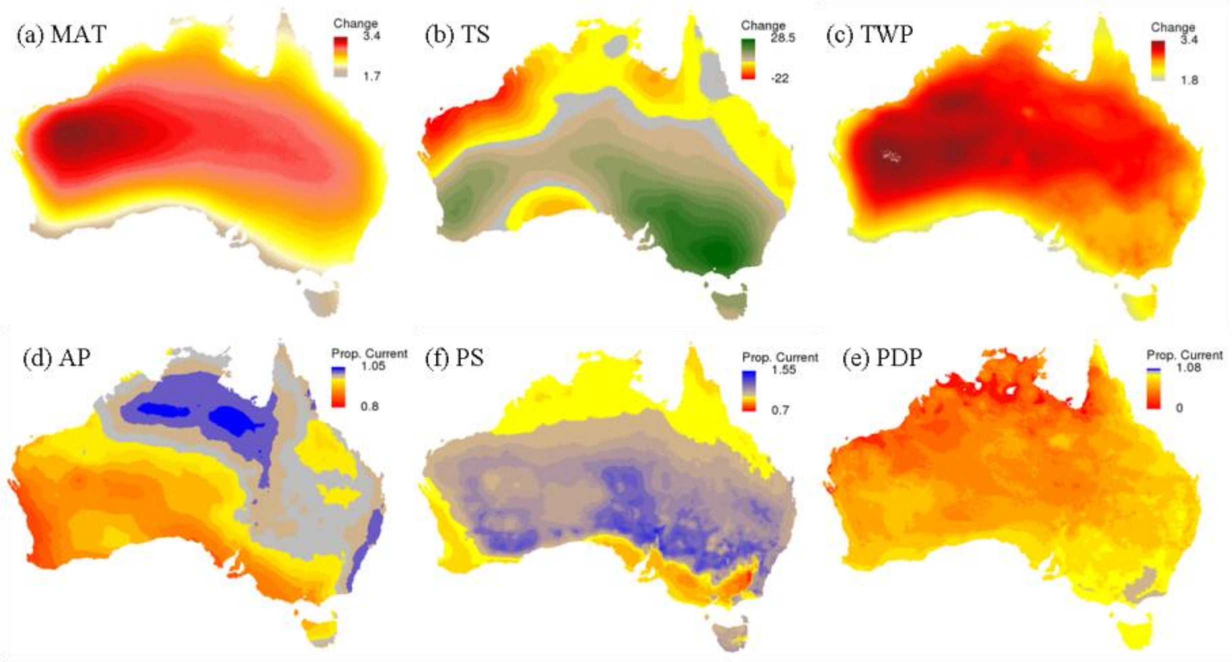


Figure 5.1.

The change in climate between mean projections for 1990 and 2080, modelled at a 0.05° resolution. Thirty climate projections representing eight different global circulation models (GCMs) and multiple realisations for each GCM were summarised first within GCM and then across GCMs to give the mean projection for each year. The climate variables used are mean annual temperature (MAT), temperature seasonality (TS), temperature of the warmest period (TWP), annual precipitation (AP), precipitation seasonality (PS) and precipitation of the driest period (PDP). The scale bars show the absolute change in temperate variables between the 1990 baseline and the 2080 projection for 1. (a) – (c); and for 1. (d) – (e) the proportional change between 1990 and 2080 for rainfall variables. The units for the temperature variables are degrees Celsius. Higher values for seasonality correspond with increasing seasonality.

Distribution models

Species distribution models incorporating baseline climate data and species occurrences were created using Maxent (Phillips *et al.*, 2006). Maxent uses presence-only data to statistically relate distribution records to environmental variables on the principle of maximum entropy. Models were run at a spatial resolution of 0.05 degrees (c. 5 x 5 km). Model performance was evaluated by the area under the receiver operating characteristic curve (AUC). AUC measures each models‟ consistency and predictive accuracy (Ling *et al.*, 2003). An AUC score of 1 is a perfect model fit of the data; 0.5 is no better than random (Elith *et al.,* 2006; Phillips *et al.,* 2006). AUC values ≥ 0.7 indicate "useful" models, whilst values ≥ 0.9 indicate models with "high" performance (Swets, 1988). Models for each species were screened for low AUC (< 0.7) so that underperforming models were not included in further analyses. Model performance was generally high: AUC scores ranged from 0.66 to 0.99, with 82 species having AUC scores greater than 0.95. Eleven species had AUC scores less than 0.7 and so were excluded from species-specific analyses.

Species' range projections

Species models were projected onto each of the 300 future climate surfaces (30 realisations across 8 GCMs per decade). These were averaged to examine the weighted mean and extremes as an ensemble model. The mean was weighted by the number of realisations per GCM to avoid undue influence by GCMs with more realisations; and the extremes were calculated as the minimum and maximum projections. The projections represent "potential" future distribution ranges, which is the suitable climate space based on the historical Grinnellian niche for the species. Potential distributions are often an over-estimate of species actual, "realised" distribution (Anderson *et al.*, 2003); therefore realised distributions were created by clipping the historical potential distribution to the sub-bioregions (Environment Australia, 2000) in which the presence of the species was recorded. The future species" range projections were clipped to three dispersal scenarios: full dispersal (no clipping), a realistic dispersal scenario of 3 km per year (applied as 30 km per decade), and no dispersal (i.e., species were constrained to the sub-bioregions that they currently occur in). Different studies documenting range shifts of birds have found that, averaged across the assemblage for each study, birds can shift their ranges from between 100 m to 5 km per year (Thomas & Lennon, 1999; Brommer, 2004; Devictor *et al.*, 2008; Tingley *et al.*, 2009; Zuckerberg *et al.*, 2009; Martinez-Morales *et al.*, 2010). We chose 3 km per year as an intermediate of these observed dispersal distances. The 3 km per year dispersal scenario was generated by buffering the cells on the outer edge of the modelled realised species distribution. For each 10 year period from 1990 to 2080, the buffer matrix was extended by 30 km, resulting in 10 dispersal masks for each species. The full dispersal models were clipped by the dispersal masks to create decadal dispersal scenarios for each species. Each species was assigned to one of the three dispersal categories (full, 3km per year, or no dispersal) as a best-estimate of likelihood of dispersal ability, herein referred to as "realistic" dispersal. This estimate was based on the long-distance movements recorded in the literature, and by the current habitat specificity of the species (Marchant & Higgins, 1990; Marchant & Higgins, 1993; Higgins & Davies, 1996; Higgins, 1999; Higgins *et al.*, 2001; Higgins & Peter, 2002; Higgins *et al.*, 2006). Species with greater habitat specificity were assumed to be less able to establish a new range without corresponding shifts in their preferred habitat, while species with generalist habitat associations are more likely to be able to track their climatic niche as it shifts (Warren *et al.*, 2001). Estimates of realistic dispersal from the literature were corroborated with expert opinion (Eric Vanderduys pers. comm.).

The default Maxent distribution output is a continuous prediction of environmental suitability for the species. A binary distribution output was created by applying an appropriate threshold obtained from the Maxent results output file. The threshold showing the most realistic distributions for the species was the "equate entropy of threshold and original distributions logistic threshold". All areas for the distribution of each species that the probability of presence fell below this species-specific threshold were accorded a "0", and all areas equal to and greater than this threshold were accorded "1" or presence. The details of the threshold value for each species are given in the Appendix Table 5.1.

Summary characteristics of each species projected distribution range, such as the total area, number of patches, proportion of the landscape and statistics related to fragmentation were calculated using the "ClassStat" function of the SDMTools package from the CRAN website http://cran.r-project.org/web/packages/SDMTools/. Species richness maps were created by stacking all the binary distribution outputs for each species for each 10 year interval. The species richness maps included all 243 species to achieve more realistic species richness estimates, including species with low AUC scores as accuracy of individual species models was not vital given the of the large scale of the output. All analyses were conducted using the statistical package "R" version 2.12.1 (www.r-project.org).

Results

Species richness

Species richness of the savanna bird assemblage is projected to change across the region with some notable shifts projected between 1990 and 2080 for the realistic dispersal scenario (Figure 5.2, 5.3d). Savanna bird species richness is projected to decrease in the arid zone, particularly in western regions. This contrasts with the increase in species richness projected for the southern savannas, and eastward and southward along the east coast of the continent by 2080 (Figure 5.2b). Projected increases in species richness correspond with projected increases in annual precipitation within the savannas (Figure 5.1d). Savanna regions in which a decrease in species richness is projected are those likely to experience the greatest increase in temperatures, both annually (MAT) and during the humid summer (TWP) (Figure 5.1a, c).

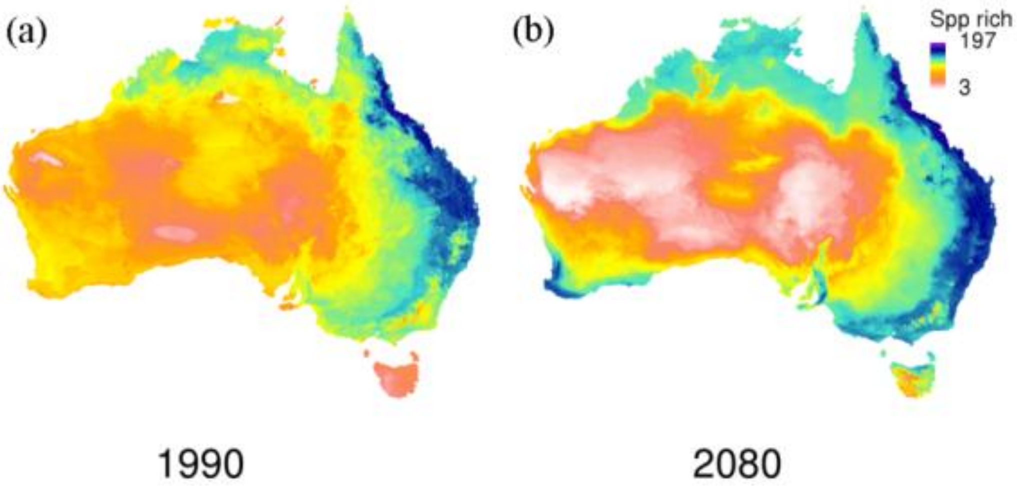


Figure 5.2.

Species richness of savanna bird species, calculated by stacking each species‟ Maxent model for 1990 (a), compared to the species richness projected for 2080 (b).

The extent of potential decreases and increases in species richness of savanna birds varies greatly depending on the dispersal scenario (Figure 5.3). Assuming full dispersal is possible for all species; most of the tropical savannas are projected to increase in species richness (Figure 5.3a). Under the full dispersal scenario, most of the decreases in species richness are confined to the arid zone. Increases in species richness of savanna species are projected for most of eastern Australia, Tasmania and south-west Western Australia. Few areas are projected to increase in species richness if all species are restricted to a dispersal rate of 3 km per year (Figure 5.3b). The arid interior of the Australian continent remains the region of greatest potential loss of savanna species, with some small increases in species richness throughout the savanna and southward along the east coast. If no dispersal occurs, most of Australia will decrease in savanna species, with some areas predicting no change (Figure 5.3c). The near-coastal northern savanna and south-eastern Australia will face the least decrease in savanna species richness. Under restricted or no-dispersal scenarios, species will be unable to move to similar climate-niche areas of south-western Australia, and south-eastern Australia including Tasmania (Figure 5.3b, c). Our realistic dispersal scenario shows species richness changes somewhat intermediate between the full dispersal and the 3km per year dispersal scenarios (Figure 5.3d). The reduction in species richness of savanna birds in the arid zone is greater for the realistic dispersal scenario compared with full dispersal, but many regions are projected to show increases in species richness.

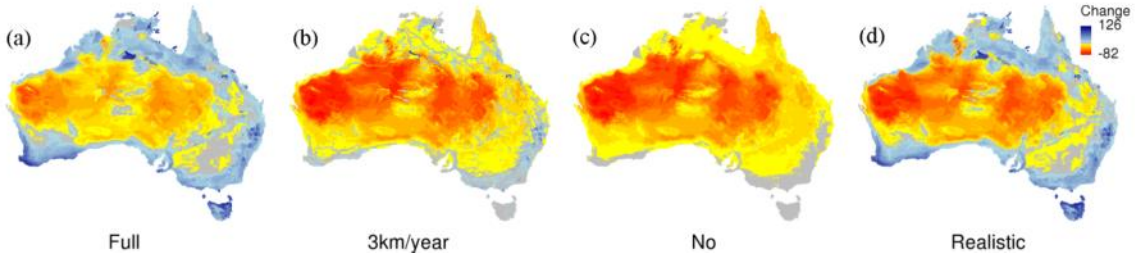


Figure 5.3.

The change in species richness of savanna bird species between 1990 and 2080 depending on dispersal scenario. “Full” is unlimited dispersal (a), “3km/year” is dispersal at a rate of 3km per year (b), “No” is no dispersal (c) and “Realistic” (d) is the best-estimate of dispersal ability for each species. Warm colours indicate a reduction in species richness (yellow is the least lost and red the most); cool colours indicate an increase in species richness.

Projected changes for species

The proportional change in individual species distributions between 1990 and 2080 varied greatly depending on which dispersal scenario was used (Figure 5.4). Under a full dispersal scenario, 154 species are expected to experience a decrease in their suitable climate space (Figure 5.4a). Of the 78 distributions projected to increase, the average increase of suitable climate space is 35% and the greatest increase is 164%. The number of species projected to increase in suitable climatic space is reduced to 66 species with an average of 16 % with dispersal limited to 3km per year (Figure 5.4b). By definition, no increase in distribution is possible under a no-dispersal scenario (Figure 5.4c). With a 3km dispersal scenario, the suitable climate spaces for 166 species are projected to decrease, and with no dispersal this increases to 207 species.

Under the realistic dispersal scenario, the overall mean area percentage shift in suitable climate space for species is -13%. Decreases are projected for 155 (c. 67%) bird species by 2080, by an average of 34%. One third of species are projected to increase their area of suitable climate space by 2080. The average projected increase is 30%, and 16 species are likely to increase by 50%. Despite the large proportion of declines and the number of severe declines, 47 (20%) species are projected to change very little by 2080, only increasing or decreasing the size of their suitable climate space by less than 10%. From here on, all results will be discussed in terms of the realistic dispersal scenario for each species.

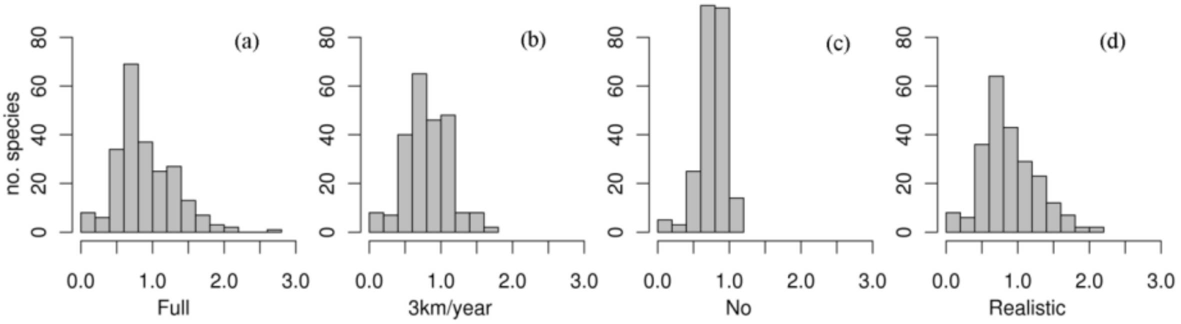


Figure 5.4.

Histograms representing the proportional change in species‟ suitable climate area between 1990 and 2080 according to the full (a), 3km per year (b), no (c) and realistic (d) dispersal scenarios. The scale on the x-axis represents the proportional change, with 1 representing no change, 0 representing a complete loss of suitable climate space, and 3 representing a tripling of suitable climate space.

Autecology and biogeography for shifting species

Migratory species are projected to have the greatest distribution increases, with no difference between other movement categories (Figure 5.5a, $F = 2.73$, $p = 0.03$). Species with a “tropical” biogeographic affiliation showed on average the greatest increases in distribution, while “Cape York Peninsula” (CYP) species decreased the most (Figure 5.5b, $F = 29.45$, $p < 0.001$). Of the eight species projected to lose more than 80% of their suitable climate space, six are largely restricted to northern CYP (black-backed butcherbird *Cracticus mentalis*, Figure 5.6a; palm cockatoo *Probosciger aterrimus*; golden-shouldered parrot *Psephotus chrysopterygius*, Figure 5.6b; tawny-breasted honeyeater *Xanthotis flaviventer;* white-streaked honeyeater *Trichodere cockerelli* and buff-breasted button-quail *Turnix olivii*), and the remaining two (black honeyeater *Sugomel niger*, Figure 5.6c, and crimson chat *Epthianura tricolor*) are distributed throughout arid Australia. The CYP species that are expected to experience decreases in their suitable climate space are projected to lose the western edge of their range; becoming restricted to the cooler upland “refugial” areas of the Eastern Cape (Figure 5.6a,b). The CYP decreasers are unlikely to be able to extend their distributions directly south to adjacent regions, as these will face greater increases in temperature than the rate of change in their current distribution (Figure 5.1). Many species distributed along the east coast and partly occurring on CYP are projected to lose the CYP part of their range in the same manner as the CYP restricted species;

that is, the western edge of their range is eroded while the cooler upland suitable climate space is retained.

Many species occurring across the arid zone are projected to lose the part of their range that encompasses western Australia, around the Pilbara and Great Sandy Desert bioregions (approximately 21°00′S, 124°00′E). This region is expected to experience the greatest increase in mean temperatures (Figure 5.1a,c), and declines in species richness projections (Figure 5.2b). Many species with distributions currently extending down the east coast of Australia are projected to lose the inland edge of their range, presumably related to the higher temperature gradient.

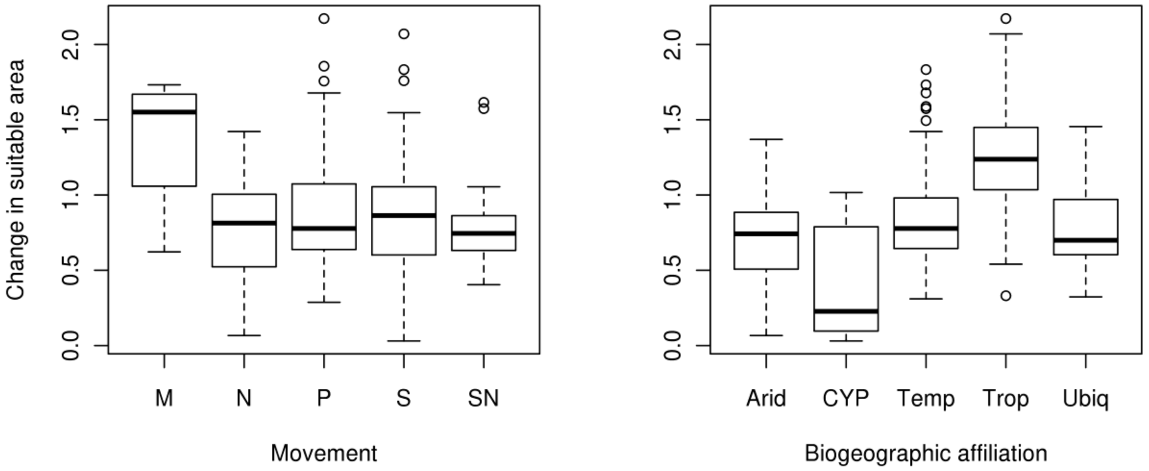


Figure 5.5.

Boxplots showing the proportional change in species climatic niche area in relation to species movement life history and biogeographic affiliation, using a realistic dispersal scenario. Movement categories are migratory (M), nomadic (N), partially migratory (P), sedentary (S), and both sedentary and nomadic (SN). Biogeographic affiliation categories are arid, Cape York Peninsula (CYP), temperate (Temp), tropical (Trop) and ubiquitous (Ubiq).

Currently threatened species

Of the nineteen species currently listed as threatened, eight are projected to decrease in distribution by 2080, ten are projected to increase and one is likely not to change in distribution (Table 5.2). Three threatened species are within the group projected to decline on CYP (golden-shouldered parrot, Figure 6b; buff-breasted button quail and palm cockatoo). Two species listed as endangered, Gouldian finch

Erythrura gouldiae and red goshawk *Erythrotriorchis radiatus*, are projected to increase in suitable climate space (Figure 5.6j,l).

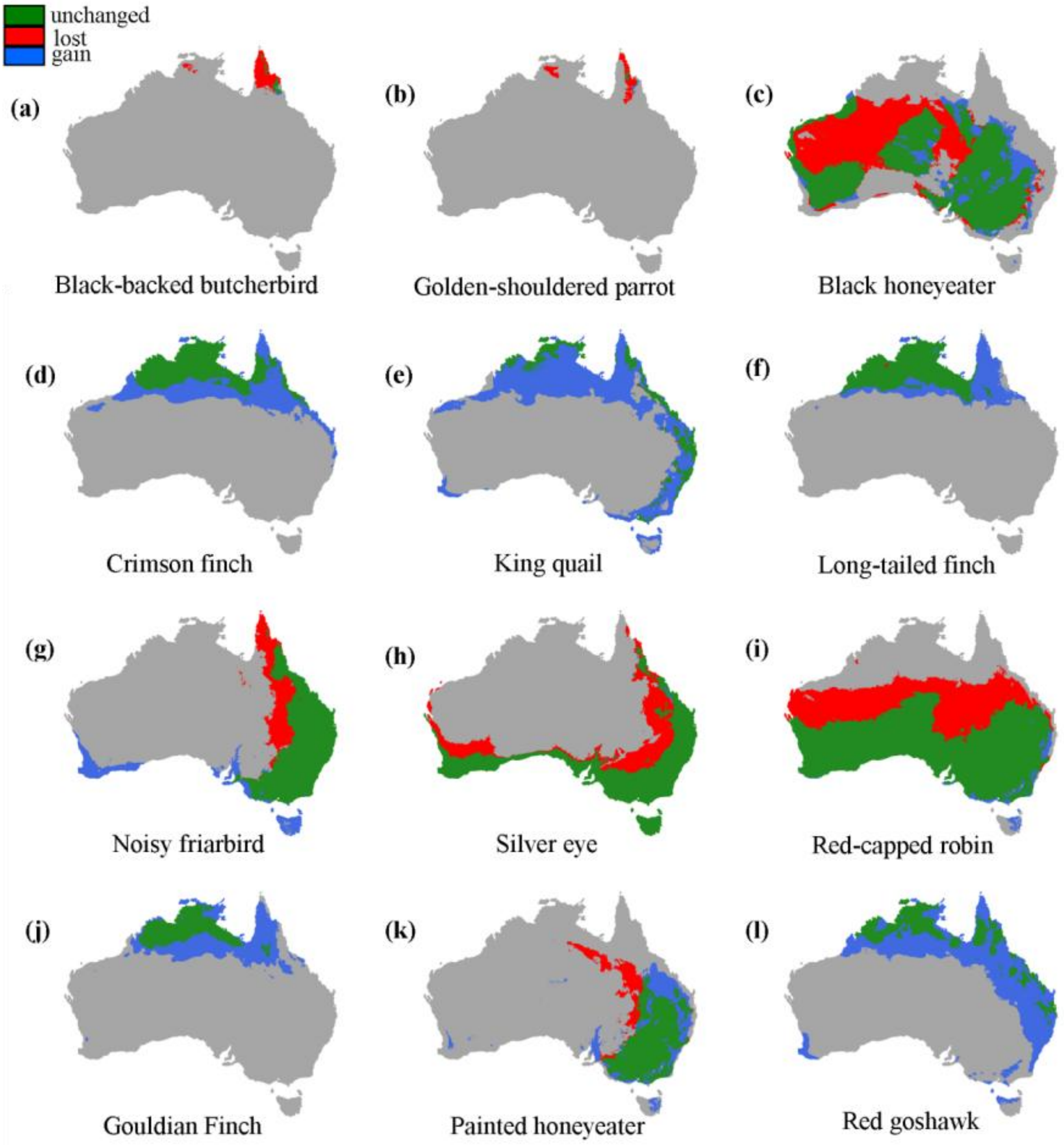


Figure 5.6.

Examples of current and future predicted distributions showing some of the patterns found among tropical savanna birds using a realistic dispersal scenario. The green colour indicates area that is suitable both in 1990 and 2080, red indicates area that was suitable in 1990 but not in 2080, and blue areas are gained by 2080. Examples shown are: Cape York species predicted to have the greatest proportional decrease in climatic niche (a) and (b); (c) shows an arid species predicted to face a severe decline in range; (d) through to (f) show examples of tropical species predicted to increase in range. (g) through to (i) show species predicted to lose the Cape York section of their range or the inland margin. Some of the changes to threatened species climatic niche changes are shown in (j) through to (l).

Discussion

This study has demonstrated that decreases in distribution are expected for over two-thirds of Australian tropical savanna birds by 2080 based on their suitable climate space. However it should be noted that all the projections for species shown here are based on the weighted mean of 30 climate realisations derived from 8 different GCMs each with several realisations (Table 5.1), and therefore the actual manifestation of future climate could diverge from these mean projections. The projections used here are based on the SRES A1B emissions scenario, which is a conservative mid-range scenario. This contrasts with the current rate of increase in global CO_2 emissions since 2000 which is greater than the most severe projection developed by the IPCC in the late 1990s (Raupach *et al.*, 2007). As a consequence, our projections for birds of the Australian tropical savanna are conservative. There is a significant potential for faster and more extreme change in suitable climate space further reducing the ability of many species to track this change.

The choice of dispersal scenario affects the predicted change in species richness, which varies from continent-wide decreases to large areas of increasing species richness. Many studies include a no-dispersal scenario in their projections which is likely to be unrealistic given the natural plasticity in the distribution of most birds (Webb & Gaston, 2000; Jetz & Rahbek, 2002; Coetzee *et al.*, 2009; Marini *et al.*, 2009a). Bird species have been recorded shifting their ranges in the Northern Hemisphere (Thomas & Lennon, 1999; Brommer, 2004; Tingley *et al.*, 2009; Zuckerberg *et al.*, 2009; Martinez-Morales *et al.*, 2010), though these range shifts have lagged behind the spatial shifts of climate (Devictor *et al.*, 2008). For this reason we chose an intermediate dispersal scenario to simulate a realistic projection into future locations of species ranges. Ideally, the dispersal scenario should be tailored to be as accurate for individual species as current knowledge will allow, in order to account for variation in individual species dispersal ability (le Roux & McGeoch, 2008). In this study, the species richness projection for 2080 based on realistic dispersal scenarios for each species is most similar to the full dispersal projection, although declines in the arid zone are similar to those projected for the 3 km per year dispersal scenario (Figure 5.3).

The projected increases in species richness of savanna birds extend across most of the tropical savanna region under a realistic dispersal scenario. This is true for the coastal lowlands and the mid-elevational regions, coinciding with the projected increases in rainfall in the region. In contrast to the prediction that tropical lowlands are likely to lose the most species (Colwell *et al.*, 2008), our study projects that it is the higher elevation areas within the region that are predicted to face a reduction in species richness. However, our study only looks at projections of tropical savanna bird species, therefore the actual bird species richness of the region may differ due to different responses by birds that are currently restricted to rainforest or arid areas.

Tropical savanna bird species which migrate annually north beyond the Australian continent (e.g. eastern koel *Eudynamys orientalis*, oriental cuckoo *Cuculus saturatus* and dollarbird *Eurystomus orientalis*) are projected to benefit the most from climate change. These species are expected to extend their range down the east coast and into areas in which rainfall is projected to increase; a response to climate change that may already be occurring (Reid, 2003). Aside from assigning each species to a dispersal scenario, our modelled projections of future range are based on the bioclimatic correlates of current distribution for each species and do not take behaviour into account. However, migratory behaviour is likely to enhance species‟ adaptive capacity in response to climate change; as migratory species already disperse to suitable habitat with changing weather patterns (Şekercioğlu, 2007).

In general, species distributed predominantly across northern Australia, the "tropical" distribution (e.g. Figure 5.6d,f,j), are projected to fare the best with future range expansion south and east in tandem with increasing rainfall. In contrast, large range decreases are projected for the narrow-ranged species currently found on Cape York Peninsula. These species are likely to be the most vulnerable to extinction. This fits with the theory that diverse tropical assemblages consisting of small-ranged species have the highest vulnerability to climate change (Colwell *et al.*, 2008). These species may be on the edge of their thermal tolerances, as they occupy one of the hottest regions in the continent (Deutsch *et al.*, 2008). The western side of the Cape currently has higher annual mean temperature and lower dry-season precipitation than the eastern side, and these western regions are projected to become unsuitable (Appendix Figure 5.1). For the three species on Cape York Peninsula projected to face severe declines that are currently listed as threatened (golden-shouldered parrot, buff-breasted button quail and palm cockatoo), the combination of climate change and their current threatening processes (e.g. inappropriate fire regimes and grazing; Garnett & Crowley, 2002; Mathieson & Smith, 2009) is likely to lead to a high risk of extinction. For those that rely on specific nesting requirements, e.g. termite mounds for golden-shouldered parrot and hollow-bearing trees for palm cockatoo, their vulnerability is exacerbated by the risk that climate change will interrupt the crucial biotic interactions they depend upon through changes in fire or cyclonic activity (Weaver, 1982; Murphy & Legge, 2007).

Table 5.2.

The species in our study listed as critically endangered (CE), endangered (E), vulnerable (V) or near-threatened (NT) under the federal (EPBC: Environment Protection and Biodiversity Conservation Act, 1999), state (NCA: Nature Conservation Act, 1992) or international (IUCN, 2001) classifications, including those with threatened subspecies (subsp). The "Proportion of current" column gives the proportional change that the future range is projected to be in 2080 in relation to the current range size.

Species	EPBC	NCA	IUCN	Proportion of current	Direction of change in area
Buff-breasted button quail *Turnix olivii*	E	V	E	0.17	Decrease
Golden-shouldered parrot *Psephotus chrysopterygius*	E	E	E	0.06	Decrease
Gouldian finch *Erythrura gouldiae*	E	E	E	1.76	Increase
Red goshawk *Erythrotriorchis radiatus*	V	E	V	1.32	Increase
Painted honeyeater *Grantiella picta*		V		0.62	Decrease
Purple-crowned fairy-wren *Malurus coronatus*	V subsp	V		1	No change
Yellow chat *Epthianura crocea*	CE subsp	V		1.62	Increase
Crimson finch *Epthianura tricolor*	V subsp	V		1.55	Increase
Grey goshawk *Accipiter novaehollandiae*		NT		1.33	Increase
Grey falcon *Falco hypoleucos*		NT	NT	0.89	Decrease
Square-tailed kite *Lophoictinia isura*		NT		1.07	Increase
Palm cockatoo *Probosciger aterrimus*		NT		0.05	Decrease
Pictorella mannikin *Heteromunia pectoralis*		NT		1.45	Increase
Australian Bustard *Ardeotis australis*			NT	1.24	Increase
Bush stone curlew *Burhinus grallarius*			NT	1.14	Increase
Squatter pigeon *Geophaps scripta*	V subsp	V subsp	V subsp	0.71	Decrease
Double-eyed fig-parrot *Cyclopsitta diophthalma*	E subsp	E, V, NT subsp		0.80	Decrease
Black-throated finch *Poephila cincta*		E subsp	E subsp	0.40	Decrease
Star finch *Neochmia ruficauda*	E subsp	E subsp		1.24	Increase

These projected species-specific responses are likely to result in substantial changes in species composition across the Australian tropical savannas and the rest of Australia. Migratory and tropical species are likely to become more widespread while species inhabiting the savannas at the southern edge (e.g. arid-affiliated species) are likely to be lost from the savanna region. Northern Australia may receive more migrants from Papua New Guinea and south-east Asia, which may expand their ranges south. Potential changes could result in "no-analogue" species assemblages due to community reorganisation (le Roux & McGeoch, 2008). Compositional changes in bird species assemblages have already occurred in response to climatic change in other regions (Albright *et al.*, 2010). In particular, generalist species have increased while specialists decreased (Christian *et al.*, 2009). This has been shown for butterfly populations, where increases in species richness lag behind the predicted increases, with the resultant species assemblages showing a greater dominance of generalist species (Warren *et al.,* 2001; Menéndez *et al.,* 2006). In Australia, widespread generalist bird species, such as crested pigeon (*Ocyphaps lophotes*) and galah (*Eolophus roseicapillus*), have increased their ranges across Australia largely as a result of land use change (Franklin, 1999); generalists in Australia might benefit from the synergy between climate and land-use change.

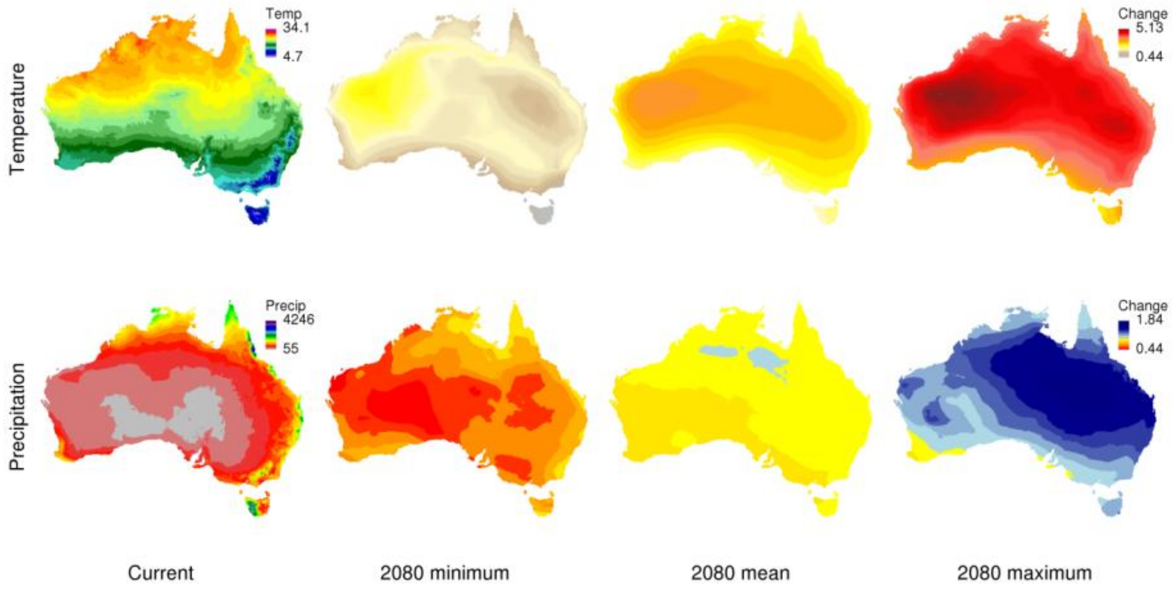
Despite the potential for many birds of tropical savannas to track the geographic shift in their suitable climate space, the realisation of this range shift may depend on whether land is available or has been anthropogenically modified to the extent of being unsuitable habitat (Pearson, 2006). Many Australian tropical savanna bird species are predicted to show similar patterns to those documented elsewhere (Parmesan & Yohe, 2003); tracing the movement of their suitable climate space across increasing latitudes. However, the projected future locations of greatest species richness - down the east coast and in far south-western Australia - are heavily modified in comparison to the current savanna biome, with extensive urbanisation and more intensive agriculture (Berry & Roderick, 2006), a pattern predicted for tropical savanna birds in other parts of the world (Marini *et al.*, 2009a). The location of conservation reserves in Australia and globally will need to be re-evaluated to assess their efficacy in light of the increasing evidence for species movements with shifting climate (Coetzee *et al.*, 2009). Such re-evaluation may highlight the need for restoration of urban and agricultural areas to create suitable habitat to facilitate movements by range-shifting species (Shoo *et al.*, 2011).

Conclusions

Projected increases in extinction risk due to climate change have necessitated comprehensive climate change impact assessments across species assemblages (IPCC 2007a). The birds of Australian tropical savannas are projected to shift out of the arid zone as mean temperature increases, some into the southern savanna where rainfall is projected to increase, and others southward toward and along the east coast of Australia. Using realistic dispersal scenarios makes a substantial difference to the range projections when compared with no dispersal scenarios, and therefore appropriate dispersal scenarios are important for meaningful projections of species" range-shifts. Overall, birds occurring in Australian tropical savannas are projected to decline in distribution size, and this response is reflected in assemblage measures such as species richness. While many species are predicted to change marginally, others species found in particular biogeographic zones (e.g. Cape York Peninsula and the arid zone), are predicted to show severe contraction and become increasingly vulnerable. Therefore an integrated understanding of species dispersal capacities and the patchiness of available habitat in future destinations for these species is important in planning for the long-term persistence of species. Studies such as these support conservation adaptation programs by anticipating the effectiveness of current conservation for range-shifting species.

Author contributions

AR conceived the study, performed the modelling and analyses, and wrote the paper; JV assisted with the modelling and analyses, AK and JV assisted with editing the paper.



Appendix Figure 5.1.
Mean annual temperature and annual precipitation for current (1990), and the minimum, mean and maximum projections for 2080. The colour scale bars show absolute values of current annual mean temperature (degrees Celsius) and current annual rainfall (mm). The colour scale bars show the minimum, mean and maximum predicted absolute change in annual mean temperate between the 1990 baseline and the 2080 projection; and proportional change between 1990 and 2080 for predicted minimum, mean and maximum rainfall.

Appendix Table 5. 1

Details for each species in the study. “Move” refers to a species movement behaviour; either sedentary (S), nomadic (N), migratory (M), partially migratory (P) or both sedentary and nomadic (SN). “Biogeog” refers to a species broad biogeographic affiliation; temperate (Temp), arid (Arid), tropical (Trop), predominantly found on Cape York Peninsula (CY), or ubiquitous (Ubiq) which includes species found in two or more categories. “Dispers” refers to our expert-opinion estimates of a species ability to track their climate niche into the future depending on their habitat specificity and movement behaviour; species were assigned to either full-, 3km per year- or no-dispersal. “N” refers to the number of records used in the Maxent model for each species. “AUC” is the area under the receiver operating characteristic curve. “Threshold” is the value calculated by Maxent‟s „Equate entropy of threshold and original distributions logistic threshold‟ for each species; when creating a binary presence/absence distribution for each species, the probability of presence scores above the threshold are predicted „presence‟, and those below the threshold are „absence‟. “Change” is the proportional change in suitable climate space for each species between 1990 and 2080; a value of 1 is no change, 0 is a complete loss in climate space and 2 is a doubling of climate space.

Scientific name	Common name	Move	Biogeog	Dispers	N	AUC	Threshold	Change
Struthidea cinerea	apostlebird	SN	Temp	full	6408	0.88	0.20	0.70
Alectura lathami	Australian brush-turkey	S	Temp	3km	1506	0.98	0.16	0.69
Ardeotis australis	Australian bustard	N	Arid	full	3537	0.71	0.27	1.24
Falco longipennis	Australian hobby	P	Ubiq	full	5845	0.77	0.30	0.97
Alisterus scapularis	Australian king parrot	P	Temp	full	3989	0.97	0.14	0.69
Cracticus tibicen	Australian magpie	SN	Ubiq	full	32039	0.80	0.29	0.53
Aegotheles cristatus	Australian owlet-nightjar	S	Ubiq	full	4464	0.73	0.29	0.60
Anthus novaeseelandiae	Australian pipit	P	Ubiq	full	6299	0.77	0.23	0.52
Corvus coronoides	Australian raven	S	Arid	full	21518	0.84	0.22	0.44
Acrocephalus stentoreus	Australian reed-warbler	P	Temp	full	4484	0.87	0.19	1.29
Barnardius zonarius	Australian ringneck	S	Ubiq	full	3335	0.84	0.21	0.32
Ceyx azureus	azure kingfisher	P	Temp	full	2998	0.93	0.17	1.05
Certhionyx pectoralis	banded honeyeater	N	Trop	full	1049	0.95	0.15	1.26
Ramsayornis fasciatus	bar-breasted honeyeater	P	Trop	full	764	0.96	0.15	1.62
Ninox connivens	barking owl	S	Temp	full	1110	0.86	0.17	1.83
Tyto alba	barn owl	N	Ubiq	full	2528	0.80	0.22	1.00
Geopelia humeralis	bar-shouldered dove	S	Temp	full	5968	0.92	0.14	1.16
Falco subniger	black falcon	P	Ubiq	full	1905	0.78	0.26	1.45
Certhionyx niger	black honeyeater	N	Arid	full	1336	0.79	0.20	0.07
Milvus migrans	black kite	P	Ubiq	full	8627	0.69	0.32	
Cracticus mentalis	black-backed butcherbird	S	CY	3km	305	0.99	0.13	0.03
Hamirostra melanosternon	black-breasted buzzard	P	Arid	full	1482	0.77	0.22	0.63
Melithreptus gularis	black-chinned honeyeater	N	Temp	full	2131	0.86	0.20	0.81
Chrysococcyx osculans	black-eared cuckoo	P	Ubiq	full	1750	0.76	0.22	1.26
Coracina novaehollandiae	black-faced cuckoo-shrike	P	Temp	full	25175	0.75	0.36	0.93
Monarcha melanopsis	black-faced monarch	P	Temp	full	1679	0.99	0.14	0.79
Artamus cinereus	black-faced woodswallow	P	Ubiq	full	4413	0.69	0.34	
Elanus axillaris	black-shouldered kite	P	Ubiq	full	8261	0.84	0.22	0.66
Climacteris melanura	black-tailed treecreeper	S	Trop	full	889	0.94	0.20	2.07

Scientific name	**Common name**	**Move**	**Biogeog**	**Dispers**	**N**	**AUC**	**Threshold**	**Change**
Poephila cincta	black-throated finch	SN	Temp	full	293	0.97	0.17	0.40
Entomyzon cyanotis	blue-faced honeyeater	P	Temp	full	6625	0.89	0.17	0.77
Dacelo leachii	blue-winged kookaburra	S	Trop	full	3897	0.90	0.19	1.42
Neopsephotus bourkii	Bourke's parrot	N	Arid	full	846	0.88	0.16	0.28
Haliastur indus	brahminy kite	P	Trop	full	1718	0.97	0.16	1.86
Lichenostomus frenatus	bridled honeyeater	P	Temp	3km	172	1.00	0.09	0.83
Myiagra ruficollis	broad-billed flycatcher	S	Trop	3km	248	0.98	0.17	1.03
Falco berigora	brown falcon	P	Ubiq	full	16123	0.70	0.42	
Accipiter fasciatus	brown goshawk	P	Ubiq	full	8306	0.80	0.25	0.93
Lichmera indistincta	brown honeyeater	SN	Ubiq	full	11383	0.81	0.20	0.72
Coturnix ypsilophora	brown quail	P	Ubiq	full	3335	0.86	0.20	1.10
Cincloramphus cruralis	brown songlark	N	Ubiq	full	6102	0.77	0.25	0.45
Climacteris picumnus	brown treecreeper	S	Ubiq	full	6967	0.91	0.15	0.56
Ramsayornis modestus	brown-backed honeyeater	P	Temp	full	415	0.99	0.13	0.43
Melithreptus brevirostris	brown-headed honeyeater	P	Temp	full	6941	0.92	0.16	0.42
Cacomantis variolosus	brush cuckoo	P	Temp	full	2750	0.94	0.19	1.68
Melopsittacus undulatus	budgerigar	N	Arid	full	7331	0.70	0.25	
Turnix olivii	buff-breasted button-quail	N	CY	3km	3	0.98	0.15	0.17
Acanthiza reguloides	buff-rumped thornbill	S	Temp	full	4377	0.95	0.17	0.59
Burhinus grallarius	bush stone-curlew	S	Ubiq	full	2091	0.84	0.21	1.14
Scythrops novaehollandiae	channel-billed cuckoo	P	Temp	full	2584	0.94	0.15	0.98
Cacomantis castaneiventris	chestnut-breasted cuckoo	P	CY	3km	41	0.99	0.10	0.50
Lonchura castaneothorax	chestnut-breasted mannikin	SN	Temp	full	1417	0.96	0.17	1.57
Acanthiza uropygialis	chestnut-rumped thornbill	S	Arid	full	7675	0.85	0.20	0.39
Coracina tenuirostris	cicadabird	P	Temp	full	2084	0.97	0.18	0.82
Nymphicus hollandicus	cockatiel	P	Arid	full	8345	0.74	0.30	1.37
Accipiter cirrhocephalus	collared sparrowhawk	P	Ubiq	full	4990	0.78	0.27	1.01
Phaps chalcoptera	common bronzewing	P	Ubiq	full	11740	0.83	0.23	0.53
Eudynamys scolopacea	common koel	M	Temp	full	2971	0.95	0.16	1.49
Oreoica gutturalis	crested bellbird	SN	Arid	full	8610	0.78	0.23	0.41
Ocyphaps lophotes	crested pigeon	S	Ubiq	full	22994	0.74	0.33	1.00
Falcunculus frontatus	crested shrike-tit	S	Temp	full	3678	0.95	0.14	0.57
Epthianura tricolor	crimson chat	N	Arid	full	4281	0.74	0.17	0.11
Neochmia phaeton	crimson finch	S	Trop	full	925	0.96	0.17	1.55
Geopelia cuneata	diamond dove	P	Ubiq	full	5280	0.71	0.22	0.55
Stagonopleura guttata	diamond firetail	P	Temp	full	2553	0.96	0.18	0.44
Eurystomus orientalis	dollarbird	M	Temp	full	5184	0.92	0.18	1.73
Taeniopygia bichenovii	double-barred finch	N	Temp	full	6612	0.88	0.17	1.42
Cyclopsitta diophthalma	double-eyed fig-parrot	SN	Temp	3km	214	1.00	0.09	0.80
Myzomela obscura	dusky honeyeater	SN	Trop	full	1554	0.98	0.16	0.90
Artamus cyanopterus	dusky woodswallow	P	Arid	full	8641	0.92	0.15	0.43

Scientific name	Common name	Move	Biogeog	Dispers	N	AUC	Threshold	Change
Eopsaltria australis	eastern yellow robin	P	Temp	full	7560	0.96	0.17	0.63
Dromaius novaehollandiae	emu	S	Ubiq	full	9317	0.74	0.22	0.47
Gerygone palpebrosa	fairy gerygone	S	Temp	3km	672	0.99	0.13	0.51
Hirundo ariel	fairy martin	P	Ubiq	full	8439	0.77	0.32	1.09
Cacomantis flabelliformis	fan-tailed cuckoo	P	Temp	full	7771	0.93	0.17	0.58
Ptilonorhynchus cerviniventris	fawn-breasted bowerbird	S	CY	no	32	1.00	0.10	0.98
Sphecotheres viridis	figbird	P	Trop	full	3069	0.97	0.17	0.99
Phaps histrionica	flock bronzewing	P	Ubiq	full	261	0.89	0.19	1.40
Todiramphus macleayii	forest kingfisher	P	Trop	full	2465	0.96	0.14	0.54
Lichenostomus fuscus	fuscous honeyeater	P	Temp	full	2270	0.97	0.16	0.64
Eolophus roseicapillus	galah	SN	Ubiq	full	27732	0.75	0.38	0.75
Cisticola exilis	golden-headed cisticola	P	Temp	full	3907	0.91	0.17	1.33
Psephotus chrysopterygius	golden-shouldered parrot	S	CY	3km	16	0.96	0.09	0.06
Erythrura gouldiae	Gouldian finch	S	Trop	full	201	0.97	0.16	1.76
Tyto capensis	grass owl	P	Trop	full	86	0.92	0.12	1.76
Ptilonorhynchus nuchalis	great bowerbird	S	Trop	full	2591	0.94	0.13	1.23
Cracticus torquatus	grey butcherbird	SN	Temp	full	17661	0.81	0.20	0.78
Falco hypoleucos	grey falcon	P	Arid	full	439	0.74	0.26	0.89
Rhipidura fuliginosa	grey fantail	P	Temp	full	19316	0.88	0.19	0.71
Accipiter novaehollandiae	grey goshawk	S	Temp	full	1575	0.95	0.16	1.33
Colluricincla harmonica	grey shrike-thrush	S	Ubiq	full	23727	0.81	0.32	0.57
Pomatostomus temporalis	grey-crowned babbler	S	Temp	3km	8356	0.79	0.24	0.93
Lichenostomus plumulus	grey-fronted honeyeater	SN	Arid	full	1894	0.81	0.21	0.77
Lichenostomus keartlandi	grey-headed honeyeater	SN	Arid	3km	1596	0.90	0.16	0.53
Coracina maxima	ground cuckoo-shrike	N	Arid	full	1911	0.73	0.27	0.56
Philemon buceroides	helmeted friarbird	N	Trop	full	805	0.98	0.12	0.94
Chrysococcyx basalis	Horsfield's bronze-cuckoo	P	Ubiq	full	8949	0.75	0.33	0.62
Mirafra javanica	Horsfield's bushlark	P	Temp	full	1188	0.81	0.23	1.06
Microeca fascinans	jacky winter	P	Ubiq	full	10255	0.82	0.23	0.61
Amytornis ballarae	Kalkadoon grasswren	S	Trop	no	62	1.00	0.13	0.33
Coturnix chinensis	king quail	P	Trop	full	120	0.95	0.14	2.17
Caprimulgus macrurus	large-tailed nightjar	S	Trop	full	354	0.98	0.13	0.93
Dacelo novaeguineae	laughing kookaburra	S	Temp	full	17173	0.90	0.14	0.65
Myiagra rubecula	leaden flycatcher	P	Temp	full	4990	0.93	0.15	1.32
Microeca flavigaster	lemon-bellied flycatcher	S	Trop	3km	1139	0.97	0.16	1.05
Elanus scriptus	letter-winged kite	N	Arid	full	240	0.79	0.25	0.88
Meliphaga lewinii	Lewin's honeyeater	P	Temp	full	3821	0.98	0.17	0.79
Chrysococcyx minutillus	little bronze-cuckoo	P	Trop	full	737	0.97	0.15	1.33
Turnix velox	little button-quail	P	Ubiq	full	1938	0.70	0.26	
Cacatua sanguinea	little corella	P	Ubiq	full	7720	0.71	0.35	0.91

Scientific name	**Common name**	**Move**	**Biogeog**	**Dispers**	**N**	**AUC**	**Threshold**	**Change**
Corvus bennetti	little crow	N	Arid	full	5248	0.76	0.21	0.80
Hieraaetus morphnoides	little eagle	P	Ubiq	full	5790	0.77	0.30	0.70
Philemon citreogularis	little friarbird	P	Temp	full	8083	0.85	0.20	0.78
Megalurus gramineus	little grassbird	P	Temp	full	2489	0.88	0.17	0.55
Glossopsitta pusilla	little lorikeet	N	Temp	full	2559	0.97	0.16	0.70
Artamus minor	little woodswallow	P	Arid	full	2600	0.80	0.19	0.87
Cacatua tenuirostris	long-billed corella	S	Temp	full	2416	0.97	0.15	0.65
Poephila acuticauda	long-tailed finch	S	Trop	full	1274	0.96	0.21	1.23
Xanthotis macleayana	Macleay's honeyeater	S	Temp	3km	244	1.00	0.09	0.89
Grallina cyanoleuca	magpie-lark	P	Ubiq	full	27896	0.75	0.34	0.73
Poephila personata	masked finch	S	Trop	full	789	0.97	0.18	1.24
Artamus personatus	masked woodswallow	N	Ubiq	full	4892	0.68	0.30	
Dicaeum hirundinaceum	mistletoebird	N	Ubiq	full	14263	0.76	0.30	0.62
Falco cenchroides	nankeen kestrel	P	Ubiq	full	20114	0.71	0.37	0.65
Philemon corniculatus	noisy friarbird	P	Temp	full	7848	0.94	0.14	0.72
Manorina melanocephala	noisy miner	S	Temp	full	11968	0.92	0.15	0.72
Rhipidura rufiventris	northern fantail	P	Trop	full	1231	0.97	0.15	1.37
Platycercus venustus	northern rosella	S	Trop	3km	656	0.97	0.20	1.04
Drymodes superciliaris	northern scrub-robin	S	CY	3km	22	1.00	0.10	0.85
Oriolus sagittatus	olive-backed oriole	P	Temp	full	6650	0.91	0.15	1.07
Nectarinia jugularis	olive-backed sunbird	P	Temp	full	815	0.99	0.15	0.52
Cuculus saturatus	oriental cuckoo	M	Trop	full	222	0.96	0.16	1.61
Aviceda subcristata	Pacific baza	P	Trop	full	1333	0.97	0.18	1.54
Turnix varia	painted button-quail	P	Temp	full	1391	0.94	0.15	0.57
Emblema pictum	painted finch	N	Arid	full	747	0.91	0.15	0.98
Grantiella picta	painted honeyeater	M	Ubiq	full	435	0.90	0.15	0.62
Platycercus adscitus	pale-headed rosella	S	Temp	full	4106	0.95	0.13	0.80
Cuculus pallidus	pallid cuckoo	P	Ubiq	full	8866	0.74	0.34	0.64
Probosciger aterrimus	palm cockatoo	S	CY	3km	133	1.00	0.14	0.05
Podargus papuensis	Papuan frogmouth	P	CY	3km	175	0.99	0.13	0.29
Geopelia striata	peaceful dove	S	Ubiq	full	12385	0.79	0.25	1.02
Falco peregrinus	peregrine falcon	P	Ubiq	full	4002	0.85	0.18	0.99
Centropus phasianinus	pheasant coucal	S	Temp	3km	4154	0.93	0.15	1.01
Heteromunia pectoralis	pictorella mannikin	P	Trop	full	333	0.94	0.15	1.45
Cracticus nigrogularis	pied butcherbird	S	Ubiq	full	17479	0.75	0.25	0.75
Strepera graculina	pied currawong	P	Temp	full	9363	0.94	0.16	0.72
Certhionyx variegatus	pied honeyeater	N	Arid	full	1714	0.79	0.20	0.60
Neochmia modesta	plum-headed finch	N	Temp	full	889	0.94	0.12	1.00
Malurus coronatus	purple-crowned fairy-wren	S	Trop	no	132	0.98	0.17	1.00
Merops ornatus	rainbow bee-eater	P	Ubiq	full	13878	0.76	0.28	0.71
Trichoglossus haematodus	rainbow lorikeet	SN	Temp	full	8680	0.91	0.14	1.00

Scientific name	**Common name**	**Move**	**Biogeog**	**Dispers**	**N**	**AUC**	**Threshold**	**Change**
Erythrotriorchis radiatus	red goshawk	S	Trop	full	72	0.93	0.13	1.32
Turnix maculosa	red-backed button-quail	P	Trop	full	132	0.96	0.17	1.42
Malurus melanocephalus	red-backed fairy-wren	S	Trop	no	4878	0.92	0.14	1.00
Todiramphus pyrrhopygia	red-backed kingfisher	P	Ubiq	full	4754	0.66	0.28	
Neochmia temporalis	red-browed finch	SN	Temp	full	6536	0.96	0.15	0.62
Pardalotus rubricatus	red-browed pardalote	N	Arid	full	2737	0.77	0.18	1.11
Petroica goodenovii	red-capped robin	P	Arid	full	10446	0.80	0.19	0.65
Geoffroyus geoffroyi	red-cheeked parrot	S	CY	full	21	1.00	0.11	0.73
Turnix pyrrhothorax	red-chested button-quail	P	Temp	full	254	0.79	0.22	1.05
Myzomela erythrocephala	red-headed honeyeater	SN	Trop	full	304	0.98	0.17	1.05
Calyptorhynchus banksii	red-tailed black-cockatoo	P	Temp	full	4517	0.86	0.21	0.69
Aprosmictus erythropterus	red-winged parrot	N	Temp	full	5303	0.85	0.14	0.98
Myiagra inquieta	restless flycatcher	P	Temp	full	9979	0.84	0.18	0.76
Rhipidura rufifrons	rufous fantail	P	Temp	full	3023	0.97	0.15	0.93
Ninox rufa	rufous owl	S	Trop	3km	96	0.98	0.12	1.07
Cincloramphus mathewsi	rufous songlark	P	Ubiq	full	7856	0.75	0.31	0.64
Pachycephala rufiventris	rufous whistler	P	Ubiq	full	21943	0.75	0.32	0.63
Conopophila albogularis	rufous-banded honeyeater	S	Trop	full	360	0.99	0.15	1.08
Stipiturus ruficeps	rufous-crowned emu-wren	S	Arid	no	216	0.88	0.19	0.49
Conopophila rufogularis	rufous-throated honeyeater	P	Trop	full	1741	0.93	0.16	1.21
Todiramphus sanctus	sacred kingfisher	P	Temp	full	10706	0.84	0.24	0.98
Colluricincla woodwardi	sandstone shrike-thrush	S	Trop	no	274	0.97	0.19	1.00
Myiagra cyanoleuca	satin flycatcher	P	Temp	full	1885	0.96	0.14	0.71
Trichoglossus chlorolepidotus	scaly-breasted lorikeet	SN	Temp	full	2881	0.98	0.16	0.83
Myzomela sanguinolenta	scarlet honeyeater	P	Temp	full	2703	0.98	0.17	0.78
Chrysococcyx lucidus	shining bronze-cuckoo	P	Temp	full	4750	0.94	0.15	0.59
Philemon argenticeps	silver-crowned friarbird	N	Trop	full	1495	0.96	0.18	1.35
Zosterops lateralis	silvereye	S	Temp	full	13044	0.92	0.14	0.62
Lichenostomus virescens	singing honeyeater	S	Arid	full	17111	0.72	0.23	0.80
Ninox novaeseelandiae	southern boobook	P	Ubiq	full	7506	0.80	0.26	0.82
Dicrurus bracteatus	spangled drongo	P	Trop	full	3374	0.97	0.16	0.78
Chthonicola sagittata	speckled warbler	S	Temp	full	2106	0.97	0.16	0.93
Geophaps plumifera	spinifex pigeon	S	Arid	full	1320	0.89	0.17	1.27
Eremiornis carteri	spinifexbird	S	Arid	full	474	0.92	0.15	0.86
Acanthagenys rufogularis	spiny-cheeked honeyeater	P	Arid	full	14144	0.78	0.18	0.71
Ptilonorhynchus maculatus	spotted bowerbird	SN	Temp	full	1657	0.92	0.14	0.76
Circus assimilis	spotted harrier	P	Ubiq	full	4003	0.70	0.33	0.70
Eurostopodus argus	spotted nightjar	P	Ubiq	full	1667	0.69	0.32	
Pardalotus punctatus	spotted pardalote	P	Temp	full	11151	0.93	0.18	0.57
Lophoictinia isura	square-tailed kite	P	Ubiq	full	1119	0.82	0.21	1.07

Scientific name	Common name	Move	Biogeog	Dispers	N	AUC	Threshold	Change
Geophaps scripta	squatter pigeon	SN	Temp	3km	754	0.96	0.16	0.71
Neochmia ruficauda	star finch	S	Trop	full	299	0.95	0.19	1.24
Pardalotus striatus	striated pardalote	P	Ubiq	full	23388	0.81	0.24	0.67
Plectorhyncha lanceolata	striped honeyeater	SN	Arid	full	4456	0.93	0.14	0.90
Coturnix pectoralis	stubble quail	N	Ubiq	full	2871	0.88	0.17	0.52
Cacatua galerita	sulphur-crested cockatoo	S	Temp	full	13161	0.89	0.17	0.91
Circus approximans	swamp harrier	P	Ubiq	full	4156	0.89	0.17	1.15
Podargus strigoides	tawny frogmouth	S	Ubiq	full	5563	0.82	0.23	0.72
Megalurus timoriensis	tawny grassbird	P	Temp	full	1031	0.97	0.19	1.59
Xanthotis flaviventer	tawny-breasted honeyeater	S	CY	3km	131	1.00	0.13	0.13
Corvus orru	Torresian crow	S	Arid	full	10180	0.84	0.26	0.82
Lichenostomus versicolor	varied honeyeater	S	Temp	3km	84	0.99	0.10	0.83
Psitteuteles versicolor	varied lorikeet	N	Trop	full	1235	0.95	0.18	1.14
Daphoenositta chrysoptera	varied sittella	SN	Ubiq	full	7408	0.85	0.22	0.71
Lalage leucomela	varied triller	P	Trop	full	1957	0.97	0.17	1.53
Malurus lamberti	variegated fairy-wren	S	Ubiq	3km	10244	0.71	0.28	0.71
Aquila audax	wedge-tailed eagle	S	Ubiq	full	18059	0.74	0.34	0.67
Smicrornis brevirostris	weebill	SN	Ubiq	full	16533	0.78	0.26	0.64
Hirundo neoxena	welcome swallow	P	Temp	full	19878	0.86	0.20	0.89
Gerygone fusca	western gerygone	P	Ubiq	full	5098	0.89	0.19	0.57
Haliastur sphenurus	whistling kite	P	Ubiq	full	12594	0.73	0.30	0.74
Coracina papuensis	white-bellied cuckoo-shrike	P	Temp	full	4981	0.89	0.13	1.07
Artamus leucorynchus	white-breasted woodswallow	P	Temp	full	4893	0.80	0.25	0.68
Poecilodryas superciliosa	white-browed robin	S	Trop	no	257	0.97	0.20	1.00
Sericornis frontalis	white-browed scrubwren	S	Temp	3km	9002	0.95	0.20	0.60
Artamus superciliosus	white-browed woodswallow	P	Ubiq	full	5002	0.84	0.23	0.59
Phylidonyris nigra	white-cheeked honeyeater	S	Temp	full	1971	0.98	0.17	0.74
Lichenostomus leucotis	white-eared honeyeater	P	Temp	full	7053	0.93	0.14	0.63
Monarcha leucotis	white-eared monarch	P	Trop	full	320	0.99	0.08	1.33
Phylidonyris albifrons	white-fronted honeyeater	P	Arid	full	3961	0.84	0.19	0.56
Lichenostomus unicolor	white-gaped honeyeater	S	Trop	full	1724	0.95	0.16	1.28
Melithreptus lunatus	white-naped honeyeater	P	Temp	full	5615	0.96	0.15	0.64
Lichenostomus penicillatus	white-plumed honeyeater	S	Arid	full	14374	0.81	0.25	1.00
Trichodere cockerelli	white-streaked honeyeater	N	CY	3km	119	1.00	0.12	0.14
Gerygone olivacea	white-throated gerygone	P	Temp	full	5294	0.93	0.15	1.03
Melithreptus albogularis	white-throated honeyeater	P	Trop	full	4197	0.94	0.14	1.23
Eurostopodus mystacalis	white-throated nightjar	P	Temp	full	503	0.97	0.19	0.87
Corcorax melanorhamphos	white-winged chough	SN	Temp	full	8060	0.92	0.16	0.74
Malurus leucopterus	white-winged fairy-wren	N	Arid	3km	6117	0.76	0.21	0.82
Lalage sueurii	white-winged triller	P	Ubiq	full	10157	0.68	0.38	

Scientific name	**Common name**	**Move**	**Biogeog**	**Dispers**	**N**	**AUC**	**Threshold**	**Change**
Rhipidura leucophrys	willie wagtail	P	Ubiq	full	34330	0.72	0.40	0.60
Epthianura crocea	yellow chat	SN	Trop	full	98	0.91	0.20	1.62
Lichenostomus flavus	yellow honeyeater	S	Temp	full	1096	0.98	0.19	0.31
Oriolus flavocinctus	yellow oriole	S	Trop	full	1110	0.98	0.15	1.45
Acanthiza nana	yellow thornbill	S	Temp	full	6893	0.93	0.14	0.86
Lichenostomus chrysops	yellow-faced honeyeater	P	Temp	full	8136	0.96	0.16	0.66
Microeca griseoceps	yellow-legged flycatcher	S	CY	3km	13	1.00	0.15	1.02
Acanthiza chrysorrhoa	yellow-rumped thornbill	S	Arid	full	16379	0.87	0.20	0.60
Meliphaga notata	yellow-spotted honeyeater	SN	Temp	3km	655	0.99	0.16	0.41
Manorina flavigula	yellow-throated miner	S	Ubiq	full	15607	0.69	0.28	
Lichenostomus flavescens	yellow-tinted honeyeater	P	Trop	full	1531	0.95	0.19	1.22
Taeniopygia guttata	zebra finch	SN	Ubiq	full	12557	0.67	0.26	

Chapter 6: Assessing vulnerability to climate change: a comprehensive examination of the Australian tropical savanna birds

Abstract

Comprehensive assessments of species" vulnerability to climate change are required in order to effectively intervene in the current and alarming decline in biodiversity. Species" vulnerability to climate change will be a consequence of their ecological and biological sensitivity, in combination with their exposure to climate change. I apply an established vulnerability assessment framework to 243 bird species inhabiting the tropical savannas of northern Australia. Biological factors relating to species sensitivity to change (clutch size, age of first reproduction and longevity), ecological factors (distribution size, sensitivity to fire, abundance, movement behaviour, relative dispersal ability and dietary breadth), and proportional changes predicted for their geographic range (i.e. exposure to climate change) are integrated to provide a ranking of vulnerability. My analysis found that birds of Australian tropical savannas have low biological sensitivity, but a range of ecological sensitivities, and the impact of climate change on these species is predicted to be substantial. Threatened species had lower biological sensitivity but higher ecological sensitivity than non-threatened species. Overall, species largely restricted to Cape York Peninsula (a geographically distinct region) had the greatest overall vulnerability; these species were, in general, ecologically sensitive due to small distributions, sensitivity to fire frequency and a lower capacity for dispersal. In addition, these species are predicted to experience the greatest exposure to climate change (i.e. the greatest proportional loss in geographic range due to climate change). It will be important for the future of Australian tropical savanna birds that ecological threats are mitigated and extensive areas of suitable habitat are maintained to facilitate species dispersal.

Introduction

There is scientific consensus that species worldwide are facing an unprecedented threat of extinction as consequence of anthropogenic global change (Barnosky *et al.*, 2011; He & Hubbell, 2011). The majority of well-studied species are in decline, and the drivers of biodiversity loss are either steady or increasing in intensity (Millennium Ecosystem Assessment, 2005; Secretariat of the Convention on Biological Diversity, 2010). Extinction risk is projected to increase with intensifying climate change and associated climate change-induced threats such as changes in sea level, water availability, fire patterns and the frequency of extreme weather events (IPCC 2007a). Therefore comprehensive vulnerability assessments that assess the effect of climate change itself, climate change-induced changes to existing threatening processes, and intrinsic sensitivity of species are required for prioritising conservation action (IPCC 2007a; Brook *et al.*, 2009).

A number of studies have outlined frameworks for assessing vulnerability to climate change (Turner *et al.,* 2003; Schröter *et al.,* 2005; Williams *et al.,* 2008; Isaac *et al.,* 2009). However some refer to integrated human-environment systems rather than to biodiversity per se (Turner *et al.,* 2003; Schröter *et al.,* 2005). Common across most vulnerability assessments is the need to include factors that relate to the sensitivity, resilience, adaptive capacity, and exposure of the study unit to the threat. Sensitivity is governed by intrinsic traits, such as species abundance (Williams *et al.,* 2008); resilience is the capacity to withstand and recover from a disturbance, such as the ability to disperse to new areas (DeAngelis, 1980; Pimm, 1984); adaptive capacity is the flexibility, or ability to adjust, in response to disturbances, such as changing to a new food source (Smit *et al.,* 2001); and exposure is determined by extrinsic factors, for example response to fire frequency (Williams *et al.,* 2008). Here I use the term "resilience" loosely as an antonym of both sensitivity and vulnerability. Additional elements recommended for inclusion into vulnerability analysis are: interacting stressors, the nested scales of dynamics of hazards, and anticipating future scenarios (Turner *et al.,* 2003; Schröter *et al.,* 2005). It is also recognised that vulnerability assessments should be "place-based" due to strong spatial variation in vulnerability (Cutter, 1996; Wilbanks & Kates, 1999; Schröter *et al.*, 2005).

Here I apply these advances in vulnerability assessment methodology to the birds of Australian tropical savannas. Climate change impact studies have covered the biota of iconic areas in Australia (Green & Pickering, 2002; Williams *et al.*, 2003; Malcolm *et al.*, 2006; Anthony *et al.*, 2011) showing that species with narrow thermal niches have high sensitivity to climate change (Williams *et al.,* 2003; Isaac *et al.,* 2009). However, there is no previous research on vulnerability of the biota within the extensive tropical savannas across northern Australia; a region that makes up almost one quarter of mainland Australia (Williams *et al.,* 2005). These tropical savannas are an important conservation resource nationally and internationally, being one of the most extensive areas of essentially intact vegetation in the world (Franklin, 1999). Despite the relative intactness of Australian tropical savannas, the well-studied vertebrates such as birds and mammals are exhibiting concerning population declines (Franklin, 1999; Woinarski *et al.*, 2011). These declines have been attributed to habitat change due to the impacts of livestock grazing and changed fire regimes (Franklin *et al.,* 2005). In particular, the increase in extensive and intense late-dry season fires has been shown to be detrimental to many species, as late-dry season fires burn large areas and remove the unburnt patches from the landscape (Legge *et al.,* 2008; Murphy *et al.,* 2010). Mammal populations have also been negatively affected by the introduction of feral cats (*Felis catus*) and cane toads (*Rhinella marina*) (Johnson *et al.,* 2007; O‟Donnell *et al.,* 2010; Woinarski *et al.,* 2011). The declines are of particular concern due to the level of threat (e.g. species that are endangered), the rate of acceleration of the declines, and uncertainty as to the direct causes of declines (Woinarski *et al.,* 2011). These factors suggest that paradoxically this large extensive biome, though superficially of high environmental integrity, contain a fauna with ecological and biological traits that might be particularly vulnerable to landscape scale change. With the impending threat of climate change, the potential threat to species might be exacerbated and must be investigated in addition to the current threats.

I use information derived and compiled from a range of sources (detailed below) to assess the relative vulnerability of Australian tropical savanna birds. I generate a relative vulnerability score, referred to as an index of vulnerability, by combining two components: relative sensitivity and exposure to climate change. The sensitivity of each species is obtained by using both biological and ecological traits that relate to a species‟ resilience. Biological traits relating to species‟ reproductive rate indicate the ability of a species to maintain or regain viable population size (Crawford, 1997). Ecological traits useful for assessing species sensitivity largely indicate the degree of ecological specialisation. Ecological specialisation is a known predictor of extinction (O'Grady *et al.,* 2004); therefore species showing higher specialisation (e.g. smaller distribution, inflexible movement behaviour, narrow dietary breadth) have greater sensitivity. Species resilience is also associated with ecological traits such as high abundance (Rabinowitz, 1981) and greater dispersal capacity (Knapp *et al.,* 2001). The exposure of species to climate change is generated by the future predictions of species range changes in relation to future climate scenarios in 2080 (Reside *et al.,* In Review). This relative sensitivity derived from species biological and ecological traits, coupled with each species‟ exposure to climate, gives an overall indication of their vulnerability. This analysis provides for the first time a taxa-wide assessment of vulnerability for the ATS to climate change. This information is then used to investigate the relative vulnerability of threatened species and non-threatened species, and variation in vulnerability of birds affiliated to different biogeographic regions. This is extremely timely given the documented declines in key vertebrate taxa in the ATS, and the impact of anthropogenic climate change on biodiversity already documented worldwide (Maclean & Wilson, 2011).

Methods

Sensitivity index

I draw upon information on Australian tropical savanna birds generated from previous work (for an index of fire sensitivity; Reside *et al.*, 2011a), abundance data, and species life history information from the literature, to score each species for its relative sensitivity. For simplicity, I categorise all the sensitivity traits as relating to a species‟ biology, or its ecology. I allocate a score to each species according to its relative sensitivity for each of the biological and ecological factors to calculate an index of sensitivity. This index of sensitivity, coupled with each species" exposure to climate change, gives an overall indication of its vulnerability. The sensitivity index uses the number of eggs per clutch, age of first reproduction and longevity as the biological factors; and distribution size, sensitivity to fire, abundance, movement behaviour, relative dispersal ability and dietary breadth as the ecological factors (Appendix 6.1). The scoring of each factor is detailed below in the analysis section.

Biological factors

The biological factors relating to a species" sensitivity included the number of eggs per clutch, age of first reproduction and longevity. Clutch size was gained from the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB) (Marchant & Higgins, 1990; Marchant & Higgins, 1993; Higgins & Davies, 1996; Higgins, 1999; Higgins *et al.*, 2001; Higgins & Peter, 2002; Higgins *et al.*, 2006). Data on the age of first reproduction and longevity were assembled by S. T. Garnett and J. K. Szabo (unpublished compilation of data). The scores for each factor were rescaled from zero to one. For the age of first reproduction, an inverse score was taken, as species with a higher first age of reproduction were believed to have greater sensitivity. Incorporating the inverted first age of reproduction score, for all scores lower values equate to greater sensitivity or the converse, low resilience.

Ecological factors

Ecological factors relating to a species sensitivity included were distribution size, sensitivity to fire, abundance, movement behaviour, relative dispersal ability and dietary breadth. Species distribution sizes were measured as the number of 1^{o} grid cells, each of which equates to roughly 100 x 100 km, as reported in the New Atlas of Australian birds (Barrett *et al.,* 2003).

Species sensitivity to fire was obtained from Reside *et al*. (2011a). The species fire sensitivity score used here is the Pearson correlation between fire frequency increase (or late-dry season fire frequency increase) and the proportional change in species distribution (Reside *et al.*, 2011a). The Pearson correlation was rescaled as a sensitivity score from zero to one, with a sensitivity score of zero equating with a Pearson correlation of -1, and a sensitivity score of 1 equalling the Pearson correlation score of 1.

Abundance data were collected throughout the tropical savanna region of Queensland by the biodiversity team at CSIRO, using a standard bird census technique developed for tropical savannas (Kutt & Fisher, 2011). Abundance is scored as the average number of individuals per hectare where the species was found.

Species were placed in one of five movement behaviour categories (migratory, partially migratory, sedentary, nomadic, or both nomadic and sedentary) as per information outlined in HANZAB (references as above) and Maron et al. (2005). Species were allocated a score between zero and one depending on which category they fell into: sedentary species were scored a zero, the assumption being that sedentary species are less likely to follow their shifting climate space. Nomadic species were believed to be the best adapted for finding new suitable environments so were accorded a score of one. Species that were migratory, partially migratory, or both sedentary and nomadic were believed to have intermediate adaptive capacity and so were given a score of 0.5.

Relative dispersal ability of each species was assigned in Reside *et al.* (In Review). I assigned each species into one of three dispersal-ability categories of good, fair and poor, assigning an arbitrary resilience score of 1, 0.66 and 0.33 respectively. The estimate of relative dispersal ability was based on the long-distance movements and the current habitat specificity of the species, as per HANZAB. Species with greater habitat specificity were assumed to be less able to establish a new range without corresponding shifts in their preferred habitat, while species with generalist habitat associations are more likely to be able to track their climatic niche as it shifts (Warren *et al.,* 2001). Estimates of relative dispersal ability from the literature were corroborated with expert opinion (Eric Vanderduys pers. comm.).

Diet breadth was calculated using Simpson‟s Diversity index, as derived by Costa *et al.* (2008):

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where p is the proportion of prey category i and n is the number of prey categories. Prey categories were seed, mistletoe, nectar, pollen, fruit, flower, arthropod and chordate. I used the proportion of prey categories by frequency of occurrence from collations of diet studies in the literature (Barker & Vestjens, 1989; Barker & Vestjens, 1990). Low scores equate to narrow diet breadth, and high scores to a broad diet.

Climate change sensitivity

Projections of species ranges with respect to future climate change were included as an addition to a species‟ vulnerability to account for a species‟ "exposure" to climate change. These projections were generated in Reside *et al.* (In Review) as the proportion al change of projected range between 1990 and 2080 using a realistic dispersal scenario and the A1B emissions scenario. I use this proportional change in species range as an index of their sensitivity to climate change, rescaled from zero to one to be consistent with the other factors. Low scores (close to zero) relate to decrease in projected range in 2080 and high scores (close to one) indicate projected range increase, on a continuous scale.

Threatened species

The conservation status of each of the ATS bird species was compiled. Threatened species are defined as having a significant conservation status under the Australian Government legislation (Environment Protection and Biodiversity Conservation Act, 1999), Queensland State legislation (Nature Conservation Act, 1992) or international categories of endangered, vulnerable or near-threatened (IUCN, 2001). Further details are presented in Reside *et al.* (In Review).

Analyses

The scores of each of the biological and ecological factors for each of the 243 species were rescaled from zero to one by dividing each score by the highest value in the category. This was to ensure equal relative weighting of each factor for each species. I opted to include as many species as possible despite missing information on particular factors for some species. Where there were missing values for species biological or ecological factors, the species was given the median score (missing values shown in Appendix Table 6.1). All biological scores were summed to give an overall "biological sensitivity rank"; likewise for ecological scores to give an "ecological sensitivity rank". The biological and ecological scores were again scaled from zero to one, and the overall sensitivity index was generated by summing the biological and ecological sensitivity rank scores for each species. The rescaling of the biological and ecological sensitivity scores is necessary as it allows for their direct comparison, as there were more factors used to assess ecological sensitivity. For all factors, low scores relate to a heightened extinction risk (i.e. greater sensitivity, greater vulnerability) whereas high scores equate to greater resilience. A species" overall vulnerability to climate change is then calculated by summing the climate change sensitivity score and overall sensitivity score. Chi-square tests were used to assess whether species sensitivity, overall vulnerability, and vulnerability combined with climate change sensitivity differed from the normal distribution.

I investigated whether species vulnerability was influenced according to which region they were predominantly distributed, as some species occurring in the tropical savannas were also distributed beyond this biome (Reside *et al.,* 2010). Therefore each species was assigned a biogeographic affiliation (arid, Cape York Peninsula, temperate, tropical, and ubiquitous for species that encompassed two or more of the above categories, Appendix Figure 2.1) which best describes its broader distribution. A one-way analysis of variance was conducted to look for difference across biogeographic groups and post-hoc Tukey-Kramer HSD tests were used to assess which of the groups were significantly different. All analyses were conducted using the statistical package "R" version 2.12.1 (www.r-project.org).

Results

Overall scoring

Overall, species biological scores were significantly skewed towards high resilience (Chi-square = 29.53, df = 5, $p < 0.001$; Figure 6.1), with the mean score of 0.68. In contrast, species were normally distributed across ecological scores (Chi-square = 4.95, df = 6, $p = 0.55$, mean = 0.54), as was overall sensitivity (Chi-square = 2.02, df = 5, $p = 0.85$, mean = 0.53). Climate change impacts were skewed towards greater impact than expected (Chi-square = 24.75, df = 4, $p < 0.001$). Therefore by this metric, the tropical savanna bird fauna have high biological resilience but many are likely to experience a high exposure to climate change.

Comparison across biogeographic affiliation

There was no difference in the spread of biological scores across biogeographic groups (F = 0.71, $p = 0.59$; Figure 6.2). However the ecological scores were significantly different (F = 26.18, $p < 0.01$), as were the overall sensitivity scores (F = 12.75, $p < 0.01$) and the climate change impact scores (F = 30.43, $p < 0.01$). The paired comparisons found that all groups differed in their ecological scores except for arid and ubiquitous species, which fared the best (Table 6.1). Cape York Peninsula (CYP) species had the lowest ecological scores, followed by tropical species and then temperate species. For the overall sensitivity, tropical and CYP species had the lowest scores, while arid and ubiquitous species had the highest. For predicted climate change impact, tropical species had the highest score, and again CYP species are predicted to experience the greatest impact.

In comparing CYP species with all the other species to see which factors were driving their greater ecological sensitivity, it was found that CYP species had greater sensitivity to fire frequency ($p = 0.02$), smaller distributions ($p < 0.01$) and are likely to have lower capacity for dispersal ($p < 0.01$) than the other species combined (Figure 6.3).

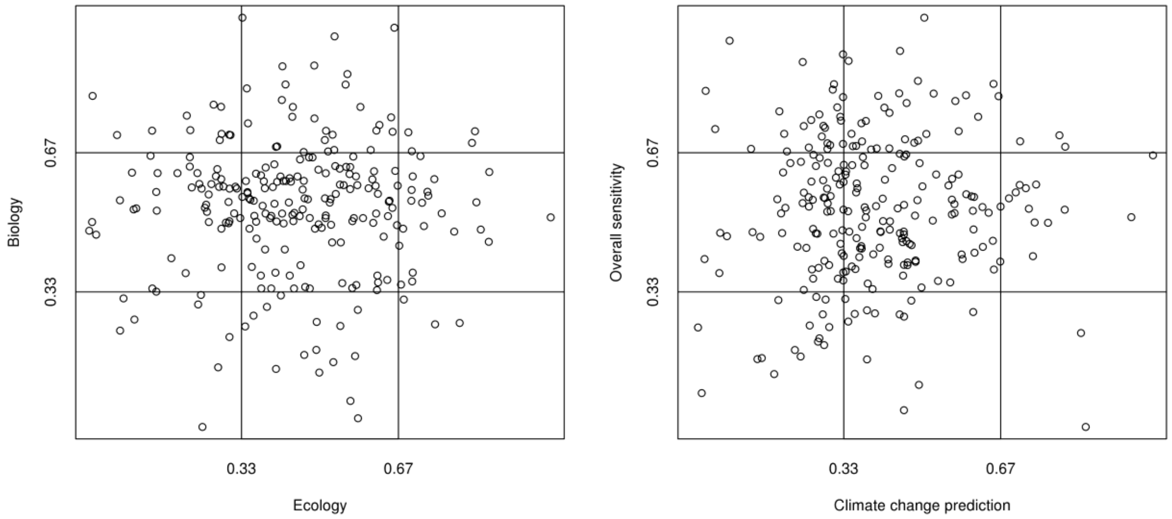


Figure 6.1.

The sensitivity and overall vulnerability of Australian tropical savanna birds. The plot on the left shows the components of species sensitivity – the biological and ecological resilience scores - across all species. The plot on the right shows the spread of species overall sensitivity against their "climate change impact". Climate change impact is measured by the proportional shift in distribution size predicted by 2080 (obtained from Reside *et al.* In Review).

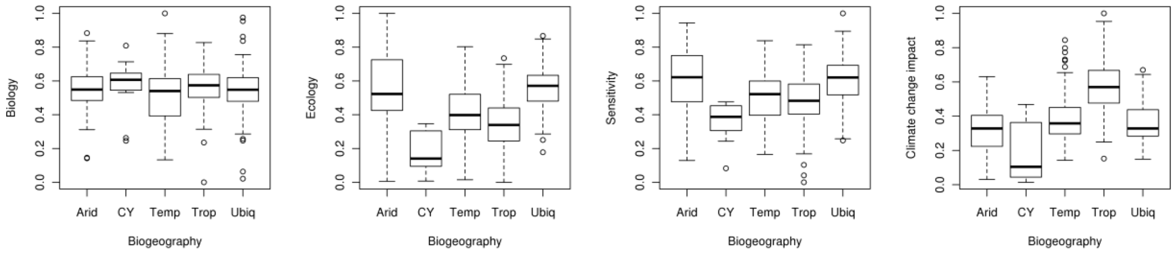


Figure 6.2.

The spread of sensitivity scores across biogeographic zones. The biological and ecological sensitivity, the overall sensitivity, and the climate change impact scores plotted against the different biogeographic affiliations of species.

Table 6.1.

Results from the Post-hoc Tukey-Kramer HSD tests assessing the difference between sensitivity factors among the biogeographic groups. The table shows each of the *p* values from the different tests, with significant differences highlighted in bold.

	Biology *p*	Ecology *p*	Sensitivity *p*	Climate change *p*
CYP – Arid	0.96	**<0.01**	**<0.01**	**0.04**
Temp – Arid	0.99	**<0.01**	**<0.01**	0.12
Trop - Arid	0.88	**<0.01**	**<0.01**	**0.00**
Ubiq – Arid	0.99	0.99	0.99	0.79
Temp – CYP	0.88	**<0.01**	**0.02**	**<0.01**
Trop – CYP	0.99	**0.02**	0.15	**<0.01**
Ubiq – CYP	0.98	**<0.01**	**<0.01**	**<0.01**
Trop – Temp	0.54	**0.04**	0.81	**<0.01**
Ubiq - Temp	0.95	**<0.01**	**<0.01**	0.57
Ubiq - Trop	0.92	**<0.01**	**<0.01**	**<0.01**

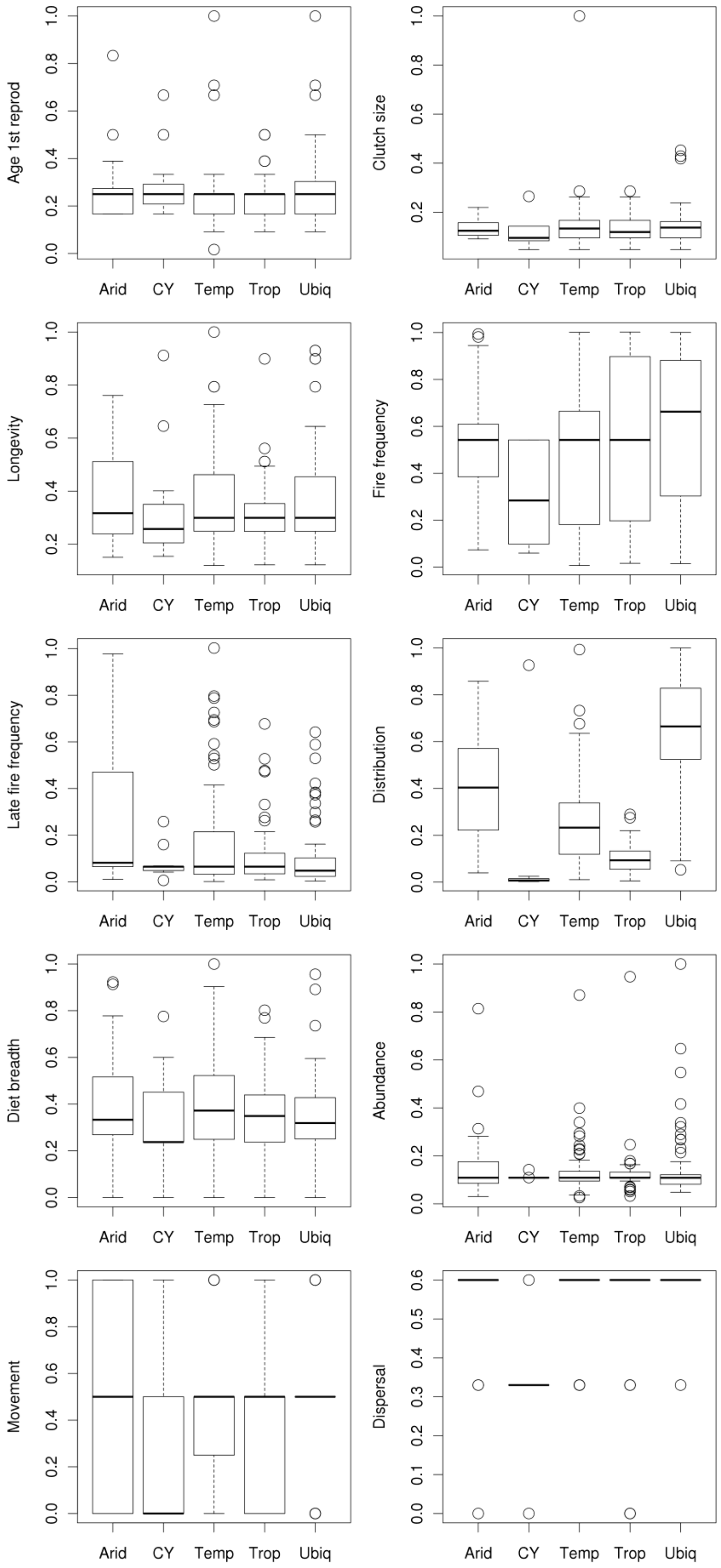


Figure 6.3.

Each of biological and ecological factor scores plotted across biogeographic affiliations.

Threatened species

Threatened species on average had lower biological sensitivity ($p = 0.02$), but greater ecological sensitivity ($p = 0.02$) than non-threatened species (Figure 6.4). Overall, there was no difference in the overall sensitivity or sensitivity to climate change between threatened and non-threatened species ($p = 0.57$ and $p = 0.22$ respectively). Across all threatened species, there were a wide range of biological and ecological sensitivity scores (Figure 6.5). With respect to overall sensitivity, the palm cockatoo (*Probosciger aterrimus*), had both the greatest biological and ecological sensitivity of all threatened species, closely followed by the grey goshawk (*Accipiter novaehollandiae*), which had high ecological sensitivity but moderate biological sensitivity. Red goshawk (*Erythrotriorchis radiatus*), yellow chat (*Epthianura crocea*), buff-breasted button-quail (*Turnix olivii*), double-eyed fig-parrot (*Cyclopsitta diophthalma*), purple-crowned fairy-wren (*Malurus coronatus*) and squatter pigeon (*Geophaps scripta*) all show moderate ecological and biological sensitivity. A number of species were highly resilient in either biological or ecological factors such as the square-tailed kite (*Lophoictinia isura*) and Pictorella mannikin (*Heteromunia pectoralis*) (i.e. low biological and moderate ecological sensitivity) or low ecological and moderate biological sensitivity, such as for Australian bustard (*Ardeotis australis*).

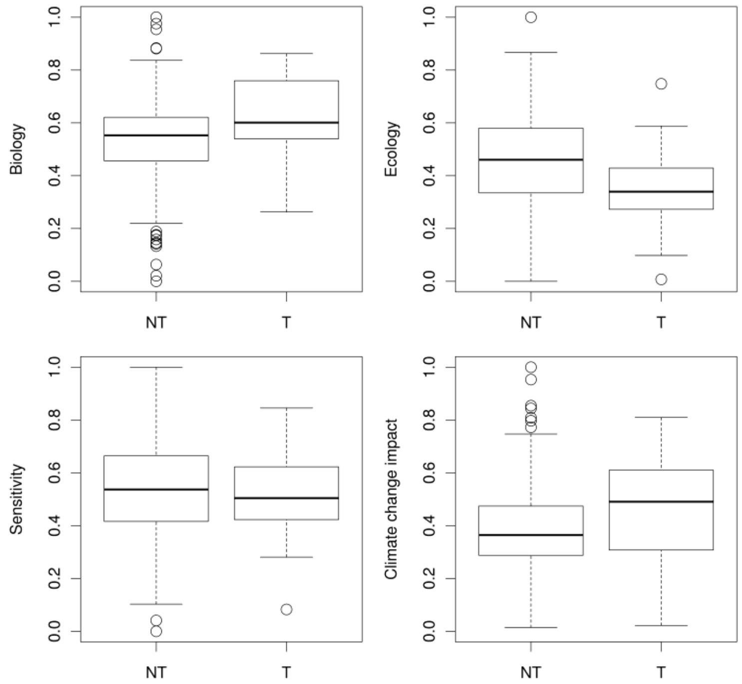


Figure 6.4.

The resilience scores across threatened (T) and non-threatened (NT) species. The biological and ecological sensitivity, overall sensitivity, and the climate change impact scores are shown.

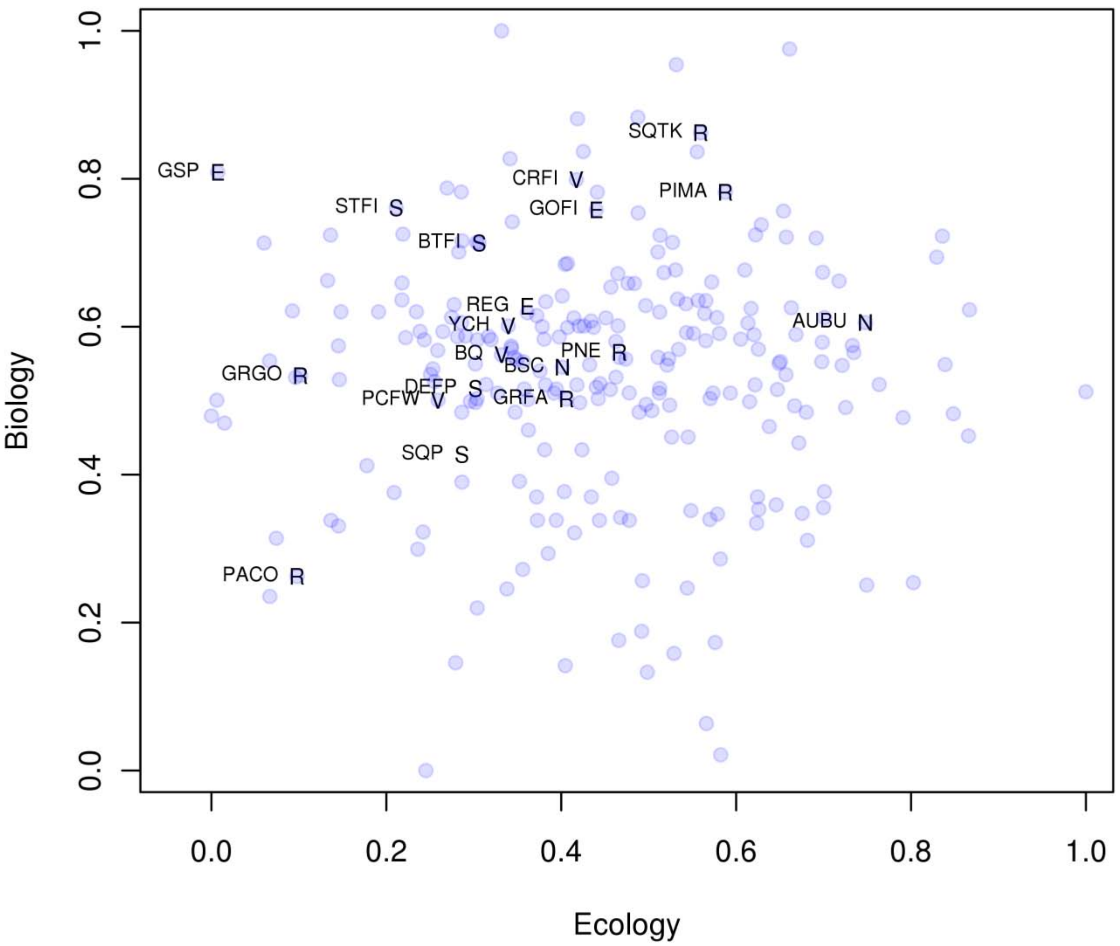


Figure 6.5.

The relative biological and ecological resilience of threatened species (denoted as a letter representing species threatened status), plotted over the spread of scores for all species (pale blue circles). The threatened species are: “AUBU” = Australian Bustard, “BQ”= Buff-breasted button quail, “BSC” = Bush stone curlew, “BTFI” = Black-throated finch, “CRFI” = Crimson finch, “DEFP” = Double-eyed fig-parrot, “GOFI” = Gouldian finch, “GRFA” = Grey falcon, “GRGO” = Grey goshawk, “GSP” = Golden-shouldered parrot, “PACO” = Palm cockatoo, “PCFW” = Purple-crowned fairy-wren, “PIMA” = Pictorella mannikin, “PNE” = Painted honeyeater, “REG” = Red goshawk, “SQP” = Squatter pigeon, “SQTK” = Square-tailed kite, “STFI” = Star finch, “YCH” = Yellow chat. The threatened status of each species is marked: E = endangered, R = rare, N = near-threatened, S = endangered subspecies, V = vulnerable.

Most vulnerable species overall

Sixteen species were found in the lowest one third for both sensitivity and climate change impact (Figure 6.1), and so are categorised as being of highest conservation concern with respect to vulnerability to climate change. Black-backed butcherbird (*Cracticus mentalis*), a narrow-ranged species occurring on CYP, is predicted to have the greatest vulnerability overall. Only one of the sixteen most vulnerable species is listed under existing conservation legislation and assessments; palm cockatoo, another species occurring on CYP, is listed as near-threatened. Half of the most vulnerable species are in the lowest quartile of body size of all ATS birds, including three thornbill species (buff-rumped thornbill (*Acanthiza reguloides*), chesnut-rumped thornbill (*Acanthiza uropygialis*) and yellow-rumped thornbill (*Acanthiza chrysorrhoa*)), fairy gerygone (*Gerygone coronatus*), silvereye (*Zosterops lateralis*), rufous-crowned emu-wren (*Stipiturus ruficeps*), white-browed scrubwren (*Sericornis frontalis*) and red-browed finch (*Neochmia temporalis*). Five species are in the next lowest quartile of body size: two honeyeaters, yellow and yellow-spotted (*Lichenostomus flavus* and *Meliphaga notata* respectively), brown treecreeper (*Climacteris picumnus*), Kalkadoon grasswren (*Amytornis ballarae*) and eastern yellow robin (*Eopsaltria australis*). Two are in the uppermost quartile: laughing kookaburra (*Dacelo novaeguineae*) and palm cockatoo.

Three species are categorised as least vulnerable by the present analysis and these are crimson finch (*Epthianura tricolor*), dollarbird (*Eurystomus orientalis*) and Gouldian finch (*Erythrura gouldiae*). Two of these are listed as threatened by conservation legislation – the Gouldian finch is listed as endangered and the crimson finch having a vulnerable subspecies.

Discussion

Overall, Australian tropical savanna bird species are relatively biologically robust but with varying ecological sensitivity, dominated by intermediate sensitivity scores. In particular, threatened species were found to have both high biological resilience and low ecological resilience when compared with non-threatened species. This suggests that it is threats to ecological factors (i.e. dispersal, diet, sensitivity to landscape change) driving the overall sensitivity of the birds in this assemblage. It is worth noting that the variables used are likely to influence the results; including other variables such as the plasticity in breeding timing or overall habitat specificity may provide different rankings of sensitivity. Species in this study were generally clustered around the mid-range of ecological and biological sensitivity scores, which differs from other studies that have found species to be clustered around very high or very low vulnerability (Kattan, 1992; Yu & Dobson, 2000; Isaac *et al.*, 2009). This method also differed from other vulnerability studies, mainly by using more factors in my model, particularly place-based threats such as fire frequency and late-dry season fire frequency. The greater number of factors in this study may have caused the sensitivity to be more centred, due to the potential for factors to cancel each other out. Despite variation in methodology, the results from this study are likely to be highlighting the distinctive ecological of the Australian tropical savanna birds. Australian tropical birds generally have larger ranges than species in other tropical areas, possibly as a result of the relatively flat landscape and limited range of climatic regimes across northern Australia (Hawkins *et al.,* 2003; Woinarski *et al.,* 2005). Consequently, Australian tropical savanna birds tend to be widespread, highly mobile, with flexible diets (Woinarski *et al.*, 2000a); all characteristics that confer high resilience. The species that deviate from this general pattern (e.g. CYP and threatened species) are those with the greatest vulnerability, largely due to greater ecological sensitivity. However, it should not be assumed that the widespread, highly mobile and dietary generalist species in this assemblage are invulnerable to climate change. These ecological characteristics are likely to be a consequence of temporally and spatially patchy resource distributions (Woinarski *et al.,* 2005), and habitat suitability is dynamic and variable across the species‟ range (Reside *et al.,* 2010). This variability may result in periods when very few areas, or sparsely distributed areas, are suitable (Woinarski *et al.,* 2005). For example, many species of widely distributed granivores that feed on a range of seed species have dramatically declined due to a critical resource bottlenecks or resource losses caused by extreme climate cycles and inappropriate land management (Franklin, 1999; Dostine *et al.*, 2001).

Extinction risk in birds has been shown to have a strong geographic pattern (Şekercioğlu *et al.,* 2004; Foden *et al.,* 2008). In this study, the species found on CYP were found to have the greatest sensitivity, the greatest climate change exposure and therefore are the most vulnerable overall. The low ecological resilience of CYP species is largely explained by small distributions, sensitivity to fire frequency and a lower capacity for dispersal. This is consistent with observations that vulnerability traits are often correlated (Manne & Pimm, 2001). Small distribution size is a key contributor to vulnerability to extinction (Rabinowitz, 1981; McKinney, 2006; Garnett & Brook, 2007), as recognised by the Red List criteria for threatened species devised by the IUCN (2001). Restricted-range species are more vulnerable to extinction due to stochastic events (McKinney, 2006), and are especially vulnerable to climate change (Manne & Pimm, 2001; Williams *et al.*, 2003; Thomas *et al.*, 2004). Species with small ranges tend to be less abundant than species with larger ranges, and have higher habitat specificity (Brown, 1984).

The CYP species‟ overall vulnerability was compounded by their sensitivity to fire frequency. The sensitivity to fire frequency of the granivorous CYP species may be due to the relationship between fire and the availability of grass seeds, a key food resource for granivorous birds such as Gouldian finch and golden-shouldered parrot (*Psephotus chrysopterygius*) (Crowley & Garnett, 1999). There is also evidence that shifting fire frequencies affect non-granivorous species on CYP. The second most vulnerable species in this study, brown treecreeper, has a subspecies confined to CYP which has declined possibly because of too-frequent fires (Garnett & Crowley, 1995; Perry *et al.*, 2011b).

With both ecological and biological sensitivity combined, the overall sensitivity of threatened species was no different from non-threatened species. Of the 16 species in the "most vulnerable" category, only one – palm cockatoo – is already listed as threatened so it should be given conservation action priority due to susceptibility to current threats and predicted susceptibility to future threats. For the remainder, this analysis identifies the importance of undertaking climate change vulnerability analysis for threatened species assessments (Garnett & Brook, 2007). A number of currently widespread and common species such as yellow-rumped thornbill, chesnut-rumped thornbill and laughing kookaburra are classified as highly vulnerable in this study, but are considered common and widespread and of least concern under current conservation listings (Garnett *et al.*, 2010a). The situation is similar to that found in other studies, where climate change is a threat but species are largely unaffected by other, extrinsic threats (Williams *et al.*, 2003; Garnett & Brook, 2007), and high vulnerability scores do not necessarily equate to current conservation listing (Yu & Dobson, 2000; Garnett & Brook, 2007; Isaac *et al.*, 2009). A shift in the rank of importance of the major threatening processes is predicted to occur in the coming decades (Garnett & Brook, 2007), resulting in an increasing need to understand susceptibility to future threats.

Further detailed analyses of extinction threat requires understanding of the full range of extrinsic threatening processes (for example, fire frequency or habitat modification) and how these currently interact to impact species. Information on vulnerability to these extrinsic threats would complement the species" biological and ecological sensitivity assessment and predicted climate change exposure information compiled here. For some species, it is the combination of high vulnerability to climate change and high exposure to extrinsic threats that will determine their long term persistence. One of the most pertinent threatening processes for birds in Australian tropical savannas is habitat modification through grazing (Woinarski, 1993a; Franklin, 1999), land clearing (McAlpine *et al.,* 2002; Hannah *et al.,* 2007) and invasive weeds (Kutt & Fisher, 2011), which are known to threaten these species both within and outside the savanna biome. Many species are affected by the combination of grazing and fire; for example variegated fairy-wren (*Malurus lamberti*), which has high vulnerability in this study (Kutt & Woinarski, 2007). In the south-east of the Australian tropical savannas the predominant threat affecting species is habitat loss through extreme landscape modification and in particular vegetation clearing (Evans *et al.,* 2011), which are also major threats to the species that also occur in south-eastern Australia (Fischer *et al.,* 2010). Two species with moderately high vulnerability in this study – grey shrike thrush (*Colluricincla harmonica*) and grey fantail (*Rhipidura fuliginosa*) – have declined where vegetation clearing has occurred in the south-eastern savanna region (Woinarski *et al.,* 2006). Some Australian tropical savanna birds are threatened by interspecific competition (Brazill-Boast *et al.,* 2011; Maron *et al.,* 2011) and predation (Fraser & Whitehead, 2005). For example, competitive interference at nest sites reduced recruitment of the endangered Gouldian finch (Brazill-Boast *et al.,* 2011). The presence of aggressive native birds from the *Manorina* genus is also a major factor influencing the richness, abundance and assemblage composition of woodland birds, especially where there is a level of habitat disturbance (Maron *et al.,* 2011; Kutt *et al.,* In Review). Understanding the current additive and interactive effect of these extrinsic factors on species, how climate change will influence the effect of these extrinsic factors, and the combination of these existing and future threats is the next step towards comprehensive conservation assessment.

The need to incorporate extrinsic factors into a comprehensive assessment is especially high for the species that were found to have low predicted ecological, biological and climate change vulnerability, but are showing population decline. Most pertinent are the threatened species Gouldian and crimson finch that show low overall vulnerability but are of current conservation concern. The inclusion of species-specific extrinsic factors in the vulnerability assessment (for example, grass seed availability), and how these might change under future climate scenarios, will enhance the focus of such an assessment. In addition, species with low vulnerability such as double-barred finch (*Taeniopygia bichenovii*), crested bellbird (*Oreoica gutturalis*) and spiny-cheeked honeyeater (*Acanthagenys rufogularis*) are sensitive to current land management change like vegetation thinning (Tassicker *et al.,* 2006) and clearing (Woinarski *et al.,* 2006). Of lesser concern are those that have low vulnerability and have been recorded increasing due to habitat modification, such as brown quail (*Coturnix ypsilophora*), dollarbird, galah (*Cacatua roseicapilus*) (Woinarski *et al.,* 2006), Australian magpie (*Cracticus tibicen*) and yellow-throated miner (*Manorina flavigula*) (Kutt & Fisher, 2011). In the latter case, increasing populations of hyper-aggressive native species can have cascading negative effects on the native bird assemblage (Maron *et al.,* 2011; Kutt *et al.,* In Review).

Implications

With high biological resilience and moderate overall sensitivity, there is hope for the future persistence of many bird species within Australian tropical savannas. The notable exceptions are those largely confined to CYP. Therefore conservation efforts should be concentrated on CYP species, particularly those endemic to Australia. Despite the overall low sensitivity of Australian tropical savanna birds, many are likely to face large shifts in their suitable climatic space area. This leads to the conclusion that future conservation efforts should be concentrated on controlling current threats, such as the impacts of unsuitable fire and grazing regimes. This is difficult to do solely with the use of conservation reserves, as designing adequate conservation reserves is problematic for highly mobile ATS bird species (Woinarski *et al.,* 1992). ATS birds often require large areas of intact habitat in order to track resource availability, and therefore generally require conservation outside of specific reserves (Woinarski *et al.,* 1992). Additionally, larger areas of suitable habitat will be required to facilitate species tracking their climate space as anthropogenic climate change progresses (Garnett *et al.*, 2010b). Many species are likely to require landscape-scale connectivity in order to establish populations in future climatically-suitable areas (Garnett *et al.*, 2010b).

Appendix Table 6.1.

The species used in the vulnerability analysis, detailing all the biological and ecological factors used in the analysis. The standardised biological sensitivity (“biology”), ecological sensitivity (“ecology”), overall sensitivity (“Sensitiv”), and vulnerability (“Vulner”) scores are given. Codes are as follows:

NCA = listing under the Nature Conservation Act, state legislation for threatened species. C: common, E: endangered, Es: endangered subspecies, NT : near threatened, V: vulnerable, Vs: vulnerable subspecies, Ces: critically endangered subspecies

EPBC = listing under the Environmental Protection and Biodiversity and Conservation Act, Australian federal legislation

Age = minimum age of first reproduction

Clutch = the mean number of eggs per clutch

Longev = the maximum known longevity

Distrib = the number of 1° grid cells the species occurs in

Diet = the diet breadth of the species

Move = S: sedentary, N: nomadic, M: migratory, P: partially migratory, SN: both sedentary and nomadic

Biogeog = the biogeographic affiliation of the species. Temp: Temperate, Arid: Arid, Trop: Tropical, CY: Cape York, Ubiq: Ubiquitous. Note that species under the “Temperate” categorisation is those that occur down the east coast, even if limited to the tropics; this is to try to represent the longitudinal differences in species communities

CC = the climate change impact score. This is the proportion in which the species range is expected to change by 2080 under a realistic dispersal scenario and the A1B emissions scenario.

FFR = the correlation coefficient between species range area with a 6-fold increase in fire frequency

LFR = the correlation coefficient between species range area with a 6-fold increase in late-dry season fire frequency

Abund = mean relative abundance calculated as the number of individuals per hectare

Biology = the sum of each biological trait score, scaled across species

Ecology = the sum of each ecological trait score, scaled across species

Sensitiv = the sum of the biological and ecological sensitivity scores

Vulner = the sum of the Sensitivity and climate change impact scores

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Struthidea cinerea	apostlebird	C		2	3.9	4.38	225	0.52	SN	Temp	full	0.70	-0.91	-0.97	3.74	0.88	0.42	1.30	2.00
Alectura lathami	Australian brush-turkey	C		2	21	25	76	0.90	S	Temp	3km	0.69				1.00	0.33	1.33	2.02
Ardeotis australis	Australian bustard	C		5	2	26.17	396	0.51	N	Arid	full	1.24	0.80	-0.94	0.59	0.61	0.75	1.35	2.60
Falco longipennis	Australian hobby	C		1.64	2.8	13.61	558	0.47	P	Ubiq	full	0.97	-0.64	-0.95	0.86	0.51	0.48	0.99	1.96
Alisterus scapularis	Australian king parrot	C		1	4.5	15.12	95	0.64	P	Temp	full	0.69	0.16	0.18		0.44	0.67	1.11	1.81
Cracticus tibicen	Australian magpie	C		1.5	3.3	10.3	665	0.34	SN	Ubiq	full	0.53	-0.97	-0.95	0.74	0.61	0.43	1.04	1.57
Aegotheles cristatus	Australian owlet-nightjar	C		1	3	9.8	519	0.24	S	Ubiq	full	0.60	-0.74	-1.00	0.79	0.54	0.25	0.79	1.38
Anthus novaeseelandiae	Australian pipit	C		1	2.8	7.96	657	0.28	P	Ubiq	full	0.52			0.85	0.58	0.57	1.15	1.66
Corvus coronoides	Australian raven	C		2.25	4.4	19.8	440	0.92	S	Arid	full	0.44	-0.86	-0.29	0.56	0.49	0.50	0.99	1.43
Acrocephalus stentoreus	Australian reed-warbler	C		1.5	3.1	10.3	292	0.25	P	Temp	full	1.29				0.60	0.44	1.04	2.33
Barnardius zonarius	Australian ringneck	C		1	5	10.3	424		S	Ubiq	full	0.32				0.61	0.29	0.89	1.21
Ceyx azureus	azure kingfisher	C		1.5	5.5	10.3	204	0.47	P	Temp	full	1.05	0.54	-0.98		0.70	0.51	1.21	2.26
Certhionyx pectoralis	banded honeyeater	C		1.5	2	10.3	100	0.63	N	Trop	full	1.26	0.85	-0.96	1.13	0.55	0.70	1.25	2.51
Ramsayornis fasciatus	bar-breasted honeyeater	C		1.5	2	10.1	83	0.44	P	Trop	full	1.62	0.77	-0.88		0.56	0.51	1.07	2.69
Ninox connivens	barking owl	C		1	2.2	15.9	190	0.40	S	Temp	full	1.83	-0.53	-0.83		0.32	0.24	0.56	2.40
Tyto alba	barn owl	C		1	4	17.92	318	0.44	N	Ubiq	full	1.00	-0.88	-0.50		0.34	0.57	0.91	1.91
Geopelia humeralis	bar-shouldered dove	C		1	2	14	252	0.27	S	Temp	full	1.16	0.77	-0.96	0.70	0.37	0.37	0.74	1.90
Falco subniger	black falcon	C		1.64	3.3	13.61	257	0.40	P	Ubiq	full	1.45	-0.40	-0.55		0.53	0.46	0.99	2.45
Certhionyx niger	black honeyeater	C		1.5	1.91	10.3	204	0.69	N	Arid	full	0.07	0.17	0.09		0.55	0.84	1.39	1.45
Milvus migrans	black kite	C		2	3	30.92	504	0.43		Ubiq	full	0.77	0.24	-0.98	1.01	0.06	0.57	0.63	1.40
Cracticus mentalis	black-backed butcherbird	C		1.5	3	22.2	704	0.33	S	CY	3km	0.03	-0.26	-0.99	1.03	0.25	0.34	0.58	0.61
Hamirostra melanosternon	black-breasted buzzard	C		3	2	8.2	254	0.24	P	Arid	full	0.63	0.29	-0.98	0.67	0.84	0.43	1.26	1.89
Melithreptus gularis	black-chinned honeyeater	C		1.5	2.5	12.3	223	0.59	N	Temp	full	0.81	0.24	-0.94		0.52	0.65	1.16	1.97

Scientific name	**Common name**	**NCA**	**EPBC**	**Age**	**Clutch**	**Longev**	**Distrib**	**Diet**	**Move**	**Biogeog**	**Dispers**	**CC**	**FFR**	**LFR**	**Abund**	**biology**	**ecology**	**Sensitiv**	**Vulner**
Chrysococcyx osculans	black-eared cuckoo	C		1.5	1	10.3	305	0.28	P	Ubiq	full	1.26	0.67	-0.44	0.45	0.51	0.59	1.10	2.36
Coracina novaehollandiae	black-faced cuckoo-shrike	C		1.5	2.49	8.98	755	0.34	P	Temp	full	0.93	0.80	-0.98	1.02	0.61	0.70	1.31	2.24
Monarcha melanopsis	black-faced monarch	C		1	2.33	11.4	76	0.24	P	Temp	full	0.79	-0.42	-0.42	0.50	0.46	0.36	0.82	1.61
Artamus cinereus	black-faced woodswallow	C		1.5	3.4	8.2	659	0.28	P	Ubiq	full	1.29	0.79	-0.95	2.51	0.67	0.70	1.37	2.66
Elanus axillaris	black-shouldered kite	C		2	3.4	5.18	500	0.37	P	Ubiq	full	0.66	0.29	-0.98		0.84	0.56	1.39	2.06
Climacteris melanura	black-tailed treecreeper	C		2	2	14	87	0.24	S	Trop	full	2.07	0.98	-0.28	0.31	0.52	0.44	0.96	3.03
Poephila cincta	black-throated finch	Es		1	5.18	6.9	28	0.41	SN	Temp	full	0.40	-0.99	-0.91	3.19	0.71	0.31	1.02	1.42
Entomyzon cyanotis	blue-faced honeyeater	C		1.5	2.56	8.3	270	0.37	P	Temp	full	0.77	0.90	-0.96	1.29	0.64	0.57	1.20	1.98
Dacelo leachii	blue-winged kookaburra	C		1	3	15.2	220	0.36	S	Trop	full	1.42	0.95	-0.94	0.48	0.38	0.40	0.78	2.20
Neopsephotus bourkii	Bourke's parrot	C		1	4.5	7.28	131	0.27	N	Arid	full	0.28				0.67	0.52	1.19	1.47
Haliastur indus	brahminy kite	C		2	1.5	30.92	108	0.24	P	Trop	full	1.86	-0.92	-0.87		0.00	0.25	0.25	2.10
Lichenostomus frenatus	bridled honeyeater	C		1.5	2	17.6	8	0.61	P	Temp	3km	0.83			2.15	0.34	0.39	0.73	1.56
Myiagra ruficollis	broad-billed flycatcher	C		1	2	8.6	43	0.24	S	Trop	3km	1.03				0.53	0.15	0.67	1.71
Falco berigora	brown falcon	C		1.6	2.7	18.01	755	0.45	P	Ubiq	full	0.72	0.64	-0.97	0.68	0.38	0.70	1.08	1.79
Accipiter fasciatus	brown goshawk	C		2	3	14.86	569	0.46	P	Ubiq	full	0.93	0.56	-0.83	0.75	0.54	0.66	1.19	2.12
Lichmera indistincta	brown honeyeater	C		1.5	1.94	13.2	494	0.46	SN	Ubiq	full	0.72	0.77	-0.97	0.91	0.46	0.64	1.10	1.83
Coturnix ypsilophora	brown quail	C		1	9.5	4.2	375	0.53	P	Ubiq	full	1.10	0.74	-0.98	2.72	0.98	0.66	1.64	2.73
Cincloramphus cruralis	brown songlark	C		1	3.07	7.1	460	0.32	N	Ubiq	full	0.45	-0.57	-0.89	1.13	0.62	0.56	1.18	1.63
Climacteris picumnus	brown treecreeper	C		1	3	14	209	0.26	S	Ubiq	full	0.56	-0.87	-0.76	0.93	0.41	0.18	0.59	1.15
Ramsayornis modestus	brown-backed honeyeater	C		1.5	1.92	10.1	24	0.54	P	Temp	full	0.43	-0.87	-0.64	1.27	0.56	0.35	0.90	1.33
Melithreptus brevirostris	brown-headed honeyeater	C		1.5	2.5	12.3	216	0.42	P	Temp	full	0.42				0.52	0.46	0.97	1.39
Cacomantis variolosus	brush cuckoo	C		1	1	7.4	177		P	Temp	full	1.68	0.94	-0.96	0.35	0.52	0.42	0.94	2.62

Scientific name	**Common name**	**NCA**	**EPBC**	**Age**	**Clutch**	**Longev**	**Distrib**	**Diet**	**Move**	**Biogeog**	**Dispers**	**CC**	**FFR**	**LFR**	**Abund**	**biology**	**ecology**	**Sensitiv**	**Vulner**
Melopsittacus undulatus	budgerigar	C		1	4.5	5.6	505	0.29	N	Arid	full	0.18	-0.43	-0.51	7.63	0.72	0.84	1.56	1.74
Turnix olivii	buff-breasted button-quail	V	E	1	3	8.9	2		N	CY	3km	0.17				0.56	0.33	0.89	1.06
Acanthiza reguloides	buff-rumped thornbill	C		1	3.6	23.51	150	0.25	S	Temp	full	0.59	0.33	0.19	2.75	0.16	0.53	0.69	1.27
Burhinus grallarius	bush stone-curlew	C		3	1.86	17.92	260	0.39	S	Ubiq	full	1.14	0.77	-0.95	0.56	0.55	0.40	0.95	2.08
Scythrops novaehollandiae	channel-billed cuckoo	C		1	2.55	7.4	167	0.57	P	Temp	full	0.98	-0.96	-0.95	0.38	0.59	0.32	0.90	1.88
Cacomantis castaneiventris	chestnut-breasted cuckoo	C		1	2.7	7.4	7	0.24	P	CY	3km	0.50				0.59	0.26	0.86	1.36
Lonchura castaneothorax	chestnut-breasted mannikin	C		1	5	4.11	116	0.27	SN	Temp	full	1.57	-0.73	-0.93		0.79	0.27	1.06	2.63
Acanthiza uropygialis	chestnut-rumped thornbill	C		1	3.3	23.51	356	0.39	S	Arid	full	0.39	-0.70	-0.80		0.15	0.28	0.42	0.81
Coracina tenuirostris	cicadabird	C		1.5	1	9	123	0.38	P	Temp	full	0.82	0.35	-0.92	0.60	0.55	0.43	0.98	1.80
Nymphicus hollandicus	cockatiel	C		1	4.5	19.6	525	0.28	P	Arid	full	1.37	0.97	-0.88	2.21	0.31	0.68	0.99	2.36
Accipiter cirrhocephalus	collared sparrowhawk	C		1.5	2.9	10.3	504	0.24	P	Ubiq	full	1.01	0.72	-0.91	0.67	0.59	0.58	1.17	2.18
Phaps chalcoptera	common bronzewing	C		1	1.83	10.1	539	0.74	P	Ubiq	full	0.53	0.79	-0.61	0.93	0.48	0.79	1.27	1.80
Eudynamys scolopacea	common koel	C		1.5	1	10.3	162	0.38	M	Temp	full	1.49	0.87	-0.90	0.31	0.51	0.51	1.02	2.52
Oreoica gutturalis	crested bellbird	C		1	2.61	12.07	460	0.46	SN	Arid	full	0.41	0.85	0.44	0.37	0.45	0.87	1.32	1.73
Ocyphaps lophotes	crested pigeon	C		1	2	10.1	649	0.89	S	Ubiq	full	1.00	0.75	-0.98	1.31	0.48	0.68	1.16	2.17
Falcunculus frontatus	crested shrike-tit	C		1.5	2.5	11.94	131	0.27	S	Temp	full	0.57				0.53	0.26	0.78	1.35
Epthianura tricolor	crimson chat	C		1.5	2.73	10.1	404	0.28	N	Arid	full	0.11			2.94	0.59	0.67	1.26	1.37
Neochmia phaeton	crimson finch	V	Vs	1	5.4	4.3	75	0.49	S	Trop	full	1.55	0.92	-0.84		0.80	0.42	1.22	2.76
Geopelia cuneata	diamond dove	C		1	2	14	451	0.24	P	Ubiq	full	0.55	0.70	-0.94	3.17	0.37	0.62	0.99	1.55
Stagonopleura guttata	diamond firetail	C		1	5.1	5.4	99	0.47	P	Temp	full	0.44	0.00	-0.50		0.75	0.49	1.24	1.68

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Eurystomus orientalis	dollarbird	C		2	3.5	9.17	230	0.24	M	Temp	full	1.73	0.94	-0.94	0.77	0.72	0.51	1.24	2.97
Taeniopygia bichenovii	double-barred finch	C		1	4.3	5.4	269	0.34	N	Temp	full	1.42	0.78	-0.99	2.11	0.72	0.69	1.41	2.83
Cyclopsitta diophthalma	double-eyed fig-parrot	Es	Es	1	2.5	8.6	9	0.62	SN	Temp	3km	0.80	-0.64	-0.72		0.55	0.30	0.85	1.65
Myzomela obscura	dusky honeyeater	C		1.5	2	12	77	0.47	SN	Trop	full	0.90	0.31	-0.98	1.17	0.50	0.44	0.95	1.85
Artamus cyanopterus	dusky woodswallow	C		1.5	2.92	8.19	264	0.26	P	Arid	full	0.43	-0.24	-0.51	1.00	0.65	0.46	1.11	1.54
Eopsaltria australis	eastern yellow robin	C		1.25	2.3	18.3	138	0.27	P	Temp	full	0.63			0.89	0.29	0.39	0.68	1.31
Dromaius novaehollandiae	emu	C		2	8.78	19	498	0.96	S	Ubiq	full	0.47	-0.92	-0.60	1.07	0.66	0.48	1.14	1.61
Gerygone palpebrosa	fairy gerygone			1	2	10.6	44	0.24	S	Temp	3km	0.51	-0.84	-0.96		0.47	0.01	0.48	1.00
Hirundo ariel	fairy martin	C		1.5	3.4	10.3	525	0.24	P	Ubiq	full	1.09	-0.59	-0.95	2.18	0.61	0.45	1.06	2.15
Cacomantis flabelliformis	fan-tailed cuckoo	C		1	1	7.4	274	0.25	P	Temp	full	0.58	-0.92	-0.43		0.52	0.38	0.90	1.49
Ptilonorhynchus cerviniventris	fawn-breasted bowerbird	C		1.5	1.5	10.3	4	0.43	S	CY	no	0.98				0.53	0.10	0.63	1.61
Sphecotheres viridis	figbird	C		1.5	2.7	10.3	121	0.37	P	Trop	full	0.99	-0.89	-0.79		0.58	0.30	0.89	1.88
Phaps histrionica	flock bronzewing	C		1	2	10.1	40	0.32	P	Ubiq	full	1.40	0.28	-0.37		0.48	0.49	0.97	2.37
Todiramphus macleayii	forest kingfisher	C		1	4.5	8.54	118	0.24	P	Trop	full	0.54	-0.91	-0.99	0.64	0.64	0.22	0.85	1.39
Lichenostomus fuscus	fuscous honeyeater	C		1.5	2.4	17.59	87	0.39	P	Temp	full	0.64	0.46	0.50		0.36	0.70	1.06	1.69
Eolophus roseicapillus	galah	C		1.5	3.7	10.3	690	0.27	SN	Ubiq	full	0.75	0.22	-0.95	2.00	0.62	0.62	1.24	1.99
Cisticola exilis	golden-headed cisticola	C		1	3.64	8.5	244	0.24	P	Temp	full	1.33			1.36	0.60	0.43	1.03	2.36
Psephotus chrysopterygius	golden-shouldered parrot	E	E	1.5	5.55	6.7	3	0.24	S	CY	3km	0.06	-0.88	-0.90		0.81	0.01	0.82	0.88
Erythrura gouldiae	Gouldian finch	E	E	0.86	5	4.41	20	0.47	S	Trop	full	1.76	0.97	-0.61		0.76	0.44	1.20	2.96
Tyto capensis	grass owl	C		1.5	5.5	10.3	24	0.24	P	Trop	full	1.76	-0.35	-0.92		0.70	0.28	0.98	2.74
Ptilonorhynchus nuchalis	great bowerbird	C		1.5	1.3	10.3	149	0.64	S	Trop	full	1.23	0.92	-0.97	0.54	0.52	0.44	0.97	2.19
Cracticus torquatus	grey butcherbird	C		1.5	3.2	22.2	557	0.42	SN	Temp	full	0.78	0.98	-0.21	0.67	0.25	0.80	1.06	1.84

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Falco hypoleucos	grey falcon	NT	NT	1.6	2.6	13.61	118	0.42	P	Arid	full	0.89	-0.36	-0.65		0.50	0.41	0.91	1.80
Rhipidura fuliginosa	grey fantail	C		0.1	2.66	9.69	472	0.25	P	Temp	full	0.71	-0.98	-0.92	0.92	0.39	0.35	0.74	1.46
Accipiter novaehollandiae	grey goshawk	NT		2	3	14.9	127	0.24	S	Temp	full	1.33	-0.89	-0.95	0.74	0.53	0.10	0.64	1.96
Colluricincla harmonica	grey shrike-thrush	C		1	3	19.3	674	0.30	S	Ubiq	full	0.57	0.54	-0.97	0.70	0.26	0.49	0.75	1.32
Pomatostomus temporalis	grey-crowned babbler	C		2	2.8	14.4	403	0.27	S	Temp	3km	0.93	0.79	-0.99	1.64	0.54	0.38	0.92	1.85
Lichenostomus plumulus	grey-fronted honeyeater	C		1.5	2	17.6	204	0.33	SN	Arid	full	0.77	-0.28	-0.63	1.55	0.34	0.44	0.78	1.55
Lichenostomus keartlandi	grey-headed honeyeater	C		1.5	2	17.6	169	0.37	SN	Arid	3km	0.53			1.65	0.34	0.37	0.71	1.24
Coracina maxima	ground cuckoo-shrike	C		1.5	2.82	9	297	0.27	N	Arid	full	0.56	0.02	-0.27	0.47	0.63	0.66	1.29	1.85
Philemon buceroides	helmeted friarbird	C		1.5	4	10.6	47	0.77	N	Trop	full	0.94	-0.93	-0.90	1.41	0.63	0.50	1.13	2.07
Chrysococcyx basalis	Horsfield's bronze-cuckoo	C		1.5	1	10.3	639	0.26	P	Ubiq	full	0.62	0.29	-0.91	0.55	0.51	0.57	1.08	1.70
Mirafra javanica	Horsfield's bushlark	C		1	3.1	6.6	324		P	Temp	full	1.06				0.63	0.38	1.02	2.08
Microeca fascinans	jacky winter	C		1.25	1.96	5.31	464	0.24	P	Ubiq	full	0.61	0.79	-0.96	0.80	0.66	0.57	1.23	1.85
Amytornis ballarae	Kalkadoon grasswren	C		2.3	2	17	4		S	Trop	no	0.33			1.58	0.48	0.00	0.48	0.81
Coturnix chinensis	king quail	C		1	6	4.2	25	0.24	P	Trop	full	2.17				0.83	0.34	1.17	3.34
Caprimulgus macrurus	large-tailed nightjar	C		3	2	12	49	0.24	S	Trop	full	0.93				0.73	0.22	0.94	1.88
Dacelo novaeguineae	laughing kookaburra	C		1	3	15.24	287	0.43	S	Temp	full	0.65	-0.99	-0.86	0.64	0.38	0.21	0.58	1.23
Myiagra rubecula	leaden flycatcher	C		1	1.72	8.6	224	0.25	P	Temp	full	1.32	0.94	-0.95	0.76	0.52	0.51	1.03	2.35
Microeca flavigaster	lemon-bellied flycatcher	C		1.25	1	5.3	82	0.24	S	Trop	3km	1.05	0.43	-0.98	0.94	0.62	0.19	0.81	1.87
Elanus scriptus	letter-winged kite	C		2	4.5	5.18	30	0.29	N	Arid	full	0.88				0.88	0.49	1.37	2.25
Meliphaga lewinii	Lewin's honeyeater	C		1.5	2.15	15.88	88	0.62	P	Temp	full	0.79			0.81	0.40	0.46	0.85	1.65
Chrysococcyx minutillus	little bronze-cuckoo	C		1.5	1	10.3	89	0.24	P	Trop	full	1.33	0.00	-0.98	0.57	0.51	0.33	0.84	2.17

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Turnix velox	little button-quail	C		1	3.5	8.9	377	0.47	P	Ubiq	full	0.85	-0.05	-0.43	1.55	0.58	0.61	1.19	2.03
Cacatua sanguinea	little corella	C		4.25	2.5	27.3	474	0.33	P	Ubiq	full	0.91	0.82	-0.92	9.38	0.48	0.85	1.33	2.24
Corvus bennetti	little crow	C		2.25	4.5	19.8	409	0.78	N	Arid	full	0.80			0.29	0.49	0.73	1.22	2.02
Hieraaetus morphnoides	little eagle	C		4	2	32	478	0.39	P	Ubiq	full	0.70	0.33	-0.85		0.29	0.58	0.87	1.57
Philemon citreogularis	little friarbird	C		1.5	2.86	10.61	325		P	Temp	full	0.78	0.73	-0.97	1.21	0.58	0.46	1.04	1.82
Megalurus gramineus	little grassbird	C		1	2.93	7.1	237	0.24	P	Temp	full	0.55				0.61	0.41	1.03	1.58
Glossopsitta pusilla	little lorikeet	C		1	4	6.44	103	0.61	N	Temp	full	0.70	-0.61	-0.39	1.52	0.68	0.61	1.29	1.99
Artamus minor	little woodswallow	C		1.5	2.5	8.2	299	0.24	P	Arid	full	0.87	0.80	-0.97	2.31	0.64	0.56	1.19	2.06
Cacatua tenuirostris	long-billed corella	C		4.25	2.9	27.3	86	0.64	S	Temp	full	0.65	-0.61	-0.61		0.50	0.30	0.80	1.44
Poephila acuticauda	long-tailed finch	C		1	4.5	6.9	71	0.37	S	Trop	full	1.23	0.97	-0.76		0.68	0.40	1.09	2.32
Xanthotis macleayana	Macleay's honeyeater	C		1.5	2	8	8	0.62	S	Temp	3km	0.89				0.62	0.23	0.85	1.74
Grallina cyanoleuca	magpie-lark	C		1	3.75	12.14	679	0.37	P	Ubiq	full	0.73	0.29	-0.94	0.72	0.50	0.62	1.11	1.84
Poephila personata	masked finch			1	5.25	6.9	68	0.40	S	Trop	full	1.24			1.68	0.72	0.29	1.00	2.24
Artamus personatus	masked woodswallow	C		1.5	2.2	8.2	483	0.32	N	Ubiq	full	0.74	0.70	-0.80	5.13	0.62	0.87	1.49	2.23
Dicaeum hirundinaceum	mistletoebird	C		1	2.8	9.1	640	0.58	N	Ubiq	full	0.62	-0.24	-0.97	1.06	0.55	0.72	1.27	1.89
Falco cenchroides	nankeen kestrel	C		1.64	3.8	13.61	756	0.42	P	Ubiq	full	0.65	0.27	-0.96	0.78	0.55	0.65	1.20	1.86
Philemon corniculatus	noisy friarbird	C		1.5	3	10.6	198	0.39	P	Temp	full	0.72	-0.97	-0.40	1.26	0.59	0.40	0.98	1.70
Manorina melanocephala	noisy miner	C		2	2.9	13.6	200	0.30	S	Temp	full	0.72	-0.41	-0.80	1.71	0.57	0.26	0.83	1.54
Rhipidura rufiventris	northern fantail	C		0.55	2.1	9.7	86	0.24	P	Trop	full	1.37	0.69	-0.96	0.67	0.43	0.42	0.86	2.23
Platycercus venustus	northern rosella	C		1	2.5	10.24	52	0.35	S	Trop	3km	1.04	0.55	-0.21		0.50	0.36	0.86	1.90
Drymodes superciliaris	northern scrub-robin	C		1.25	2	6.7	3	0.24	S	CY	3km	0.85	-0.61	-0.61		0.62	0.09	0.71	1.57
Oriolus sagittatus	olive-backed oriole	C		1	2.8	7.15	291	0.60	P	Temp	full	1.07	0.90	-0.97	0.59	0.60	0.61	1.22	2.28

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Nectarinia jugularis	olive-backed sunbird	C		1	2	6.2	38	0.43	P	Temp	full	0.52			1.44	0.60	0.41	1.01	1.53
Cuculus saturatus	oriental cuckoo	C		1.5	2.7	10.3	46	0.24	M	Trop	full	1.61	-0.80	-0.85		0.58	0.24	0.83	2.43
Aviceda subcristata	Pacific baza	C		3	3	11.5	113	0.35	P	Trop	full	1.54	-0.84	-0.94	1.42	0.78	0.29	1.07	2.61
Turnix varia	painted button-quail	C		1.5	4	10.3	142	0.52	P	Temp	full	0.57	-0.39	-0.11	1.04	0.64	0.53	1.17	1.74
Emblema pictum	painted finch	C		1	3.69	5.4	101	0.24	N	Arid	full	0.98	0.21	0.36	4.40	0.69	0.83	1.52	2.51
Grantiella picta	painted honeyeater	V		1.5	2	10.1	69	0.57	M	Ubiq	full	0.62	-0.89	-0.04		0.56	0.47	1.03	1.65
Platycercus adscitus	pale-headed rosella	C		1.5	6	10.24	123	0.30	S	Temp	full	0.80	-0.95	-0.91	1.44	0.72	0.14	0.86	1.66
Cuculus pallidus	pallid cuckoo	C		1	1	12.92	633	0.25	P	Ubiq	full	0.64	0.96	-0.97	0.57	0.36	0.65	1.01	1.65
Probosciger aterrimus	palm cockatoo	NT		4	1	31.36	11	0.60	S	CY	3km	0.05	-0.88	-0.94		0.26	0.10	0.36	0.41
Podargus papuensis	Papuan frogmouth	C		3	1	13.8	19	0.24	P	CY	3km	0.29			1.33	0.63	0.28	0.91	1.19
Geopelia striata	peaceful dove	C		1	2	14	485	0.24	S	Ubiq	full	1.02	0.65	-0.97	1.08	0.37	0.43	0.80	1.82
Falco peregrinus	peregrine falcon	C		2	2.86	15.32	384	0.24	P	Ubiq	full	0.99	-0.81	-0.85		0.52	0.36	0.87	1.87
Centropus phasianinus	pheasant coucal	C		1	3.4	6.17	238	0.34	S	Temp	3km	1.01			0.25	0.66	0.22	0.88	1.89
Heteromunia pectoralis	pictorella mannikin	NT		1	5	4.3	50	0.44	P	Trop	full	1.45	-0.48	-0.68	8.88	0.78	0.59	1.37	2.81
Cracticus nigrogularis	pied butcherbird	C		1.5	3	22.16	617	0.37	S	Ubiq	full	0.75	0.86	-0.91	0.76	0.25	0.54	0.79	1.55
Strepera graculina	pied currawong	C		1.5	3	24.15	179	0.66	P	Temp	full	0.72	-0.51	-0.48	0.73	0.19	0.49	0.68	1.40
Certhionyx variegatus	pied honeyeater	C		1.5	2.38	10.1	269	0.91	N	Arid	full	0.60				0.57	0.73	1.31	1.91
Neochmia modesta	plum-headed finch	C		1	5	4.3	93	0.24	N	Temp	full	1.00	-0.48	-0.79		0.78	0.44	1.22	2.23
Malurus coronatus	purple-crowned fairy-wren	V	Vs	2.3	2.5	17	23	0.26	S	Trop	no	1.00	0.78	-0.29		0.50	0.26	0.76	1.76
Merops ornatus	rainbow bee-eater	C		1.17	4.5	5.92	615	0.25	P	Ubiq	full	0.71	0.79	-0.98	1.02	0.74	0.63	1.37	2.08
Trichoglossus haematodus	rainbow lorikeet	C		1.5	2	20.58	262	1.00	SN	Temp	full	1.00	0.97	-0.96	1.66	0.25	0.75	1.00	2.00
Erythrotriorchis radiatus	red goshawk	E	V	3	1.5	14.9	15	0.35	S	Trop	full	1.32	-0.19	0.02		0.62	0.36	0.98	2.30

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Turnix maculosa	red-backed button-quail	C		1	3.6	8.9	44	0.44	P	Trop	full	1.42	-0.83	-0.85		0.59	0.29	0.88	2.30
Malurus melanocephalus	red-backed fairy-wren	C		2.3	3.5	17	209	0.25	S	Trop	no	1.00	0.91	-0.98	2.31	0.54	0.25	0.80	1.80
Todiramphus pyrrhopygia	red-backed kingfisher	C		1.5	4.5	10.3	507	0.42	P	Ubiq	full	0.81	-0.43	-0.90	0.61	0.66	0.48	1.13	1.95
Neochmia temporalis	red-browed finch	C		1	5	23.44	130	0.33	SN	Temp	full	0.62	-0.86	-0.96	2.29	0.22	0.30	0.52	1.15
Pardalotus rubricatus	red-browed pardalote	C		1.5	3	6.25	314	0.27	N	Arid	full	1.11	-0.20	-0.96	0.80	0.71	0.53	1.24	2.35
Petroica goodenovii	red-capped robin	C		1.5	2.5	10.9	500	0.24	P	Arid	full	0.65	-0.83	-0.46	1.39	0.56	0.47	1.03	1.68
Geoffroyus geoffroyi	red-cheeked parrot	C		2	3	8.8	2		S	CY	full	0.73	-0.72	-0.76		0.71	0.06	0.77	1.50
Turnix pyrrhothorax	red-chested button-quail	C		1	3.5	8.9	84	0.41	P	Temp	full	1.05	-0.79	-0.38	0.89	0.58	0.38	0.96	2.02
Myzomela erythrocephala	red-headed honeyeater	C		1.5	2	12	41	0.34	SN	Trop	full	1.05	-0.88	-0.59		0.50	0.30	0.81	1.86
Calyptorhynchus banksii	red-tailed black-cockatoo	C		4	1	34.4	270	0.35	P	Temp	full	0.69	0.95	-0.95	1.49	0.17	0.58	0.75	1.44
Aprosmictus erythropterus	red-winged parrot	C		2	5	13.44	286	0.50	N	Temp	full	0.98	0.78	-0.98	1.28	0.66	0.72	1.38	2.36
Myiagra inquieta	restless flycatcher	C		1	3.5	8.6	399	0.24	P	Temp	full	0.76	0.74	-0.96	0.82	0.59	0.54	1.14	1.89
Rhipidura rufifrons	rufous fantail	C		0.55	2.1	9.7	140	0.24	P	Temp	full	0.93				0.43	0.38	0.81	1.74
Ninox rufa	rufous owl			1	2	15.9	18	0.43	S	Trop	3km	1.07	-0.82	-0.88		0.31	0.07	0.39	1.46
Cincloramphus mathewsi	rufous songlark	C		1	2.94	7.1	536	0.25	P	Ubiq	full	0.64	0.43	-0.84	0.98	0.61	0.58	1.19	1.83
Pachycephala rufiventris	rufous whistler	C		1.5	2.5	18	701	0.25	P	Ubiq	full	0.63	0.78	-0.86	0.85	0.35	0.68	1.02	1.65
Conopophila albogularis	rufous-banded honeyeater	C		1.5	2.16	9.8	32	0.24	S	Trop	full	1.08	-0.97	-0.50		0.57	0.15	0.72	1.80
Stipiturus ruficeps	rufous-crowned emu-wren	C		2.3	2.5	17	67		S	Arid	no	0.49				0.50	0.01	0.51	0.99
Conopophila rufogularis	rufous-throated honeyeater	C		1.5	2.8	9.8	132	0.42	P	Trop	full	1.21	0.33	-0.97	1.57	0.60	0.46	1.07	2.28
Todiramphus sanctus	sacred kingfisher	C		1	4.38	8.54	514	0.33	P	Temp	full	0.98	0.31	-0.97	0.70	0.63	0.54	1.17	2.15
Colluricincla woodwardi	sandstone shrike-thrush	C		1	2.5	19.3	39	0.27	S	Trop	no	1.00				0.24	0.07	0.30	1.30
Myiagra cyanoleuca	satin flycatcher	C		1	3	8.6	122	0.27	P	Temp	full	0.71	-0.51	-0.69		0.57	0.34	0.91	1.62

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Trichoglossus chlorolepidotus	scaly-breasted lorikeet	C		1	2	20.6	88	0.59	SN	Temp	full	0.83	-0.65	-0.44	1.95	0.18	0.47	0.64	1.47
Myzomela sanguinolenta	scarlet honeyeater	C		1.5	2	12	81	0.61	P	Temp	full	0.78	0.00	-0.25	1.27	0.50	0.57	1.07	1.85
Chrysococcyx lucidus	shining bronze-cuckoo	C		1.5	1	10.3	215	0.24	P	Temp	full	0.59	-0.44	-0.50	0.43	0.51	0.39	0.90	1.49
Philemon argenticeps	silver-crowned friarbird	C		1.5	2.5	10.6	100	0.69	N	Trop	full	1.35	0.82	-0.79	1.06	0.57	0.73	1.30	2.65
Zosterops lateralis	silvereye	C		1	2.92	18.66	281	0.67	S	Temp	full	0.62	-0.63	-0.78	1.56	0.27	0.36	0.63	1.25
Lichenostomus virescens	singing honeyeater	C		1.5	2.2	17.6	652	0.48	S	Arid	full	0.80	0.87	-0.97	0.89	0.35	0.58	0.93	1.73
Ninox novaeseelandiae	southern boobook	C		1	2.5	15.93	552	0.37	P	Ubiq	full	0.82	0.76	-0.98	0.56	0.33	0.62	0.96	1.78
Dicrurus bracteatus	spangled drongo	C		1	3.5	7.9	136	0.35	P	Trop	full	0.78	-0.83	-0.97	0.89	0.61	0.27	0.89	1.66
Chthonicola sagittata	speckled warbler	C		1	3	11.09	85	0.51	S	Temp	full	0.93				0.50	0.30	0.80	1.73
Geophaps plumifera	spinifex pigeon	C		1	2	10.1	135	0.52	S	Arid	full	1.27			1.94	0.48	0.35	0.83	2.10
Eremiornis carteri	spinifexbird	C		1	2.5	7.1	101	0.24	S	Arid	full	0.86			1.08	0.59	0.24	0.83	1.69
Acanthagenys rufogularis	spiny-cheeked honeyeater	C		1.5	2.22	12	537	0.75	P	Arid	full	0.71	0.94	0.47	0.81	0.51	1.00	1.51	2.23
Ptilonorhynchus maculatus	spotted bowerbird	C		1.5	1.95	10.3	136	0.68	SN	Temp	full	0.76	0.11	0.03	0.58	0.55	0.65	1.20	1.96
Circus assimilis	spotted harrier	C		2.4	3.1	16.67	459	0.46	P	Ubiq	full	0.70	0.05	-0.97	0.57	0.55	0.52	1.07	1.77
Eurostopodus argus	spotted nightjar	C		1	1	9.8	321	0.24	P	Ubiq	full	0.64	0.74	-0.89	0.77	0.45	0.53	0.98	1.62
Pardalotus punctatus	spotted pardalote	C		1.5	3	6.25	243	0.26	P	Temp	full	0.57	-0.86	-0.87	1.04	0.71	0.30	1.02	1.59
Lophoictinia isura	square-tailed kite	NT		3	2.6	8.2	175	0.38	P	Ubiq	full	1.07	0.93	-0.81		0.86	0.56	1.42	2.49
Geophaps scripta	squatter pigeon	Vs	Vs	1	2	10.1	65	0.47	SN	Temp	3km	0.71	-0.88	-0.67	1.96	0.48	0.29	0.77	1.49
Neochmia ruficauda	star finch	Es	Es	1	4.5	4.3	45	0.41	S	Trop	full	1.24	-0.38	-0.85		0.76	0.21	0.97	2.21
Pardalotus striatus	striated pardalote	C		1.5	4	6.25	591	0.31	P	Ubiq	full	0.67	0.93	-0.99	1.11	0.76	0.65	1.41	2.08
Plectorhyncha lanceolata	striped honeyeater	C		1.5	3	10.1	158	0.53	SN	Arid	full	0.90	-0.25	-0.83	0.61	0.60	0.42	1.02	1.92

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Coturnix pectoralis	stubble quail	C		1	9	4.2	288	0.60	N	Ubiq	full	0.52	-0.94	-0.85		0.95	0.53	1.49	2.01
Cacatua galerita	sulphur-crested cockatoo	C		6	2.5	27.3	335		S	Temp	full	0.91	0.88	-0.98	0.84	0.74	0.34	1.09	2.00
Circus approximans	swamp harrier	C		2.4	3.6	16.67	289	0.39	P	Ubiq	full	1.15	0.61	-0.96		0.57	0.53	1.10	2.26
Podargus strigoides	tawny frogmouth	C		3	2	13.82	474	0.28	S	Ubiq	full	0.72	0.81	-0.94	0.95	0.67	0.46	1.14	1.85
Megalurus timoriensis	tawny grassbird	C		1	3	7.1	97	0.26	P	Temp	full	1.59				0.61	0.37	0.99	2.57
Xanthotis flaviventer	tawny-breasted honeyeater	C		1.5	2	8	12	0.78	S	CY	3km	0.13	-0.87	-0.92		0.62	0.15	0.77	0.90
Corvus orru	Torresian crow	C		2.25	4.6	19.8	429	0.59	S	Arid	full	0.82	0.65	-0.98	0.78	0.50	0.50	0.99	1.81
Lichenostomus versicolor	varied honeyeater	C		1.5	2	17.6	15	0.24	S	Temp	3km	0.83				0.34	0.14	0.47	1.30
Psitteuteles versicolor	varied lorikeet	C		2	3	8.53	98	0.42	N	Trop	full	1.14	0.65	-0.75	1.31	0.72	0.66	1.38	2.52
Daphoenositta chrysoptera	varied sittella	C		1.5	2.64	7	414	0.24	SN	Ubiq	full	0.71			3.01	0.68	0.53	1.21	1.92
Lalage leucomela	varied triller	C		1.5	1	5.83	97	0.80	P	Trop	full	1.53	-0.74	-0.92	0.94	0.64	0.40	1.04	2.57
Malurus lamberti	variegated fairy-wren	C		2.3	3	17	575	0.27	S	Ubiq	3km	0.71	-0.40	-0.92	2.52	0.52	0.31	0.84	1.54
Aquila audax	wedge-tailed eagle	C		6	2	32	689	0.24	S	Ubiq	full	0.67	-0.68	-0.95	0.61	0.58	0.32	0.90	1.57
Smicrornis brevirostris	weebill	C		1	2.6	7.4	601	0.26	SN	Ubiq	full	0.64	0.58	-0.95	1.65	0.59	0.62	1.21	1.85
Hirundo neoxena	welcome swallow	C		1	3.71	11.5	483	0.24	P	Temp	full	0.89	-0.85	-0.80		0.52	0.39	0.91	1.80
Gerygone fusca	western gerygone	C		1	2.65	10.6	283	0.24	P	Ubiq	full	0.57	-0.58	-0.42	0.78	0.50	0.42	0.92	1.49
Haliastur sphenurus	whistling kite	C		2	2	30.92	599	0.46	P	Ubiq	full	0.74	0.12	-0.97	0.69	0.02	0.58	0.60	1.34
Coracina papuensis	white-bellied cuckoo-shrike	C		1.5	2	9	284	0.32	P	Temp	full	1.07	0.92	-0.98	1.11	0.59	0.55	1.14	2.22
Artamus leucorynchus	white-breasted woodswallow	C		1.5	3.68	8.2	369		P	Temp	full	0.68	0.06	-0.94	1.62	0.69	0.41	1.09	1.77
Poecilodryas superciliosa	white-browed robin	C		1.25	2	9	50	0.25	S	Trop	no	1.00				0.55	0.07	0.62	1.62
Sericornis frontalis	white-browed scrubwren	C		1	2.83	17.6	201	0.37	S	Temp	3km	0.60				0.30	0.24	0.54	1.13
Artamus superciliosus	white-browed woodswallow	C		1.5	2.13	8.2	318		P	Ubiq	full	0.59	-0.91	-0.21	6.07	0.62	0.51	1.13	1.72

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Phylidonyris nigra	white-cheeked honeyeater	C		1.5	2	10.3	75	0.73	S	Temp	full	0.74				0.55	0.36	0.91	1.65
Lichenostomus leucotis	white-eared honeyeater	C		1.5	2.09	17.6	197	0.39	P	Temp	full	0.63	0.00	-0.68		0.34	0.47	0.81	1.44
Monarcha leucotis	white-eared monarch	C		1.5	2.5	10.3	29	0.24	P	Trop	full	1.33				0.57	0.34	0.92	2.24
Phylidonyris albifrons	white-fronted honeyeater	C		1.5	2.09	10.3	307	0.56	P	Arid	full	0.56				0.56	0.52	1.08	1.64
Lichenostomus unicolor	white-gaped honeyeater	C		1.5	2	17.6	114	0.68	S	Trop	full	1.28	0.95	-0.92	1.36	0.34	0.48	0.82	2.09
Melithreptus lunatus	white-naped honeyeater	C		1.5	2.67	12.33	139	0.40	P	Temp	full	0.64			8.16	0.52	0.62	1.14	1.78
Lichenostomus penicillatus	white-plumed honeyeater	C		1.5	2.31	17.6	449	0.38	S	Arid	full	1.00	-0.06	0.05	1.27	0.35	0.55	0.90	1.90
Trichodere cockerelli	white-streaked honeyeater	C		1.5	2	10.1	11	0.47	N	CY	3km	0.14	-0.74	-0.93		0.56	0.35	0.90	1.04
Gerygone olivacea	white-throated gerygone	C		1.5	2.8	10.3	230	0.24	P	Temp	full	1.03	-0.72	-1.00	0.68	0.59	0.28	0.87	1.89
Melithreptus albogularis	white-throated honeyeater	C		1.5	2	12.3	167	0.29	P	Trop	full	1.23	0.97	-0.95	1.34	0.49	0.52	1.02	2.24
Eurostopodus mystacalis	white-throated nightjar	C		1	1	9.8	67	0.24	P	Temp	full	0.87	0.26	0.04		0.45	0.55	1.00	1.86
Corcorax melanorhamphos	white-winged chough	C		2	4.4	14.67	194	0.47	SN	Temp	full	0.74	-0.65	-0.82		0.60	0.38	0.98	1.72
Malurus leucopterus	white-winged fairy-wren	C		2.3	3	17	428	0.32	N	Arid	3km	0.82			2.64	0.52	0.76	1.29	2.11
Lalage sueurii	white-winged triller	C		1.5	2.4	10.3	635	0.28	P	Ubiq	full	0.55	0.57	-0.94	1.17	0.57	0.63	1.20	1.75
Rhipidura leucophrys	willie wagtail			0.55	3.5	9.7	760	0.25	P	Ubiq	full	0.60	0.72	-0.96	0.86	0.49	0.67	1.16	1.76
Epthianura crocea	yellow chat	V	Ces	1.5	3	10.1	19	0.24	SN	Trop	full	1.62				0.60	0.34	0.94	2.56
Lichenostomus flavus	yellow honeyeater	C		1.5	1.82	17.6	48	0.40	S	Temp	full	0.31	-0.94	-0.78	0.90	0.33	0.15	0.48	0.79
Oriolus flavocinctus	yellow oriole	C		1	2.3	7.1	62	0.47	S	Trop	full	1.45	-0.40	-0.98	1.53	0.59	0.22	0.81	2.26
Acanthiza nana	yellow thornbill	C		1	3	23.51	189	0.25	S	Temp	full	0.86	0.15	0.09	2.65	0.13	0.50	0.63	1.49
Lichenostomus chrysops	yellow-faced honeyeater	C		1.5	2.35	17.6	137	0.61	P	Temp	full	0.66	0.22	-0.19	1.18	0.35	0.63	0.98	1.63
Microeca griseoceps	yellow-legged flycatcher	C		1.25	2	5.3	4	0.24	S	CY	3km	1.02				0.66	0.13	0.80	1.81

Scientific name	Common name	NCA	EPBC	Age	Clutch	Longev	Distrib	Diet	Move	Biogeog	Dispers	CC	FFR	LFR	Abund	biology	ecology	Sensitiv	Vulner
Acanthiza chrysorrhoa	yellow-rumped thornbill	C		1	3.21	23.51	434	0.26	S	Arid	full	0.60	-0.75	-0.17	2.07	0.14	0.40	0.55	1.15
Meliphaga notata	yellow-spotted honeyeater	C		1.5	2.04	15.9	25	0.71	SN	Temp	3km	0.41	-0.77	-0.88	0.98	0.39	0.29	0.68	1.09
Manorina flavigula	yellow-throated miner	C		2	3.16	13.6	626	0.32	S	Ubiq	full	0.80	0.98	-0.12	1.14	0.58	0.70	1.28	2.08
Lichenostomus flavescens	yellow-tinted honeyeater	C		1.5	1.6	17.6	102	0.38	P	Trop	full	1.22			1.38	0.32	0.42	0.74	1.95
Taeniopygia guttata	zebra finch	C		1	4.4	5.4	566	0.36	SN	Ubiq	full	1.01	-0.10	-0.88	3.90	0.72	0.62	1.35	2.36

Chapter 7: General discussion

Overview

Rapid anthropogenic climate change is likely to be the biggest single threat to biodiversity (Intergovernmental Panel on Climate Change, 2007a). Changes in climate influence the location of species‟ climate space and the suitability of that climate space (Pounds *et al.*, 1999; Thomas & Lennon, 1999); and these changes are idiosyncratic, differing dramatically between species (Chambers & Keatley, 2010). The individualised species responses alter biotic interactions and result in different species assemblages, communities and ecosystems. In addition, climate change will influence other ecosystem drivers such as fire, further influencing species distributions (Williams *et al.*, 2009a).

Identifying the impacts of climate change on species requires baseline data for species distributions, migration timing, abundance and ecological requirements. Australia lacks the comprehensive baseline data in which to compare current patterns, as found in many regions of the northern hemisphere (Chambers *et al.*, 2005). Data for Australian biota are accumulating and some studies have been able to show changes in species migration timing (Chambers & Keatley, 2010). However, few studies have been able to link species range shifts with climate change. Further understanding of species‟ current ranges can be generated through the use of SDM. SDM is a powerful tool to make projections of species distributions in light of future threats of changing climate and fire, although it is vital that methodological approach is relevant to the species and biomes in question. To date, highly refined techniques exist for modelling static distributions of sedentary species; however, techniques for modelling mobile species still require further development. My thesis has enabled the study of distributions of “difficult-to-model” mobile species by advancing modelling techniques to account for species responding to temporally and spatially patchy resource fluctuations.

The knowledge gained through studying species distributions can form the basis for investigating species vulnerability to extinction in the light of climate change. In addition to modelling the direct responses of species to climate change, SDM can allow investigations into the impact of changes of important landscape processes such as fire. This is crucial where changes in fire regimes are believed to be one of the main threatening processes for biodiversity; and where previously the state of knowledge was limited to small-scale, site-based and often short-term studies, and only known for a small number of species. Making predictions on species distribution shifts as a result of changes in fire and climate can then form the basis of an assessment of species‟ overall vulnerability to climate change. Relevant life history, ecological and threat information for each species can complement these predicted responses to species distributions for comprehensive vulnerability assessment.

This thesis looked at the overall vulnerability of the birds of Australian tropical savannas by compiling information in two stages: firstly, I developed and tested methods for improving approaches to modelling mobile species with highly dynamic ranges; and secondly, I assessed species‟ sensitivity to major threats (changes in fire and climate) through modelling with future scenarios of these threats. Finally the outcomes from these first two stages were integrated with information on species sensitivity, life history and ecology to create a comprehensive overall vulnerability assessment for ATS birds. This chapter presents the major findings of this thesis in line with the overall aims of the study.

Summary of the major findings

Aim 1. Improve species distribution modelling methods in the context of ATS birds.

Objective 1. Improve species distribution modelling (SDM) methods to account for highly dynamic bird distributions.

SDMs trained with long-term (c. 30 year) climate averages carry the assumption that species are responding to averages rather than short-term (months to years) fluctuations in climate. For species with high mobility and high variation in movement patterns, SDMs trained on long-term climate averages neglect important variations in distribution patterns. I showed that training SDMs with short-term weather variables (three, six and 12 month averages of temperature and precipitation) achieves better model predictions than long-term (30 year) climate averages for distributions of wide-ranging, nomadic and arid-affiliated ATS birds. The weather models more adequately represented the fluctuations in habitat suitability across months, seasons and years (Chapter 2).

Accounting for ATS bird species‟ mobile behaviour is also important when making predictions of the distributions into the future. Predicted changes in species distributions depend on assumptions of the ability of species to disperse in relation to shifting climate, as the choice of dispersal scenario heavily influences the size of the predicted future distribution. Most studies use a full dispersal, a no dispersal, or both full and no dispersal scenarios when predicting species future ranges in relation to climate change. I show that using appropriate dispersal scenarios for each species, informed by species‟ dispersal capacity, leads to meaningful and realistic predictions of species future distributions.

Objective 2. Assess the impact of data selection on model performance.

Judicial choices concerning which data should be included, and which data excluded, in species distribution models are important for optimal model outcomes. I found that including historic, coarse-resolution data can lead to a drop in distribution model performance; however this must be weighed against the increase in geographic or environmental coverage the coarse-resolution data may contribute (Chapter 3).

Aim 2. Predict the impact of major threats to the ATS birds.

Objective 3. Assess the impact of increases in fire frequency on species distributions.

Changing fire regimes are listed as one of the main threatening processes for savanna biota; however understanding of the impact of fire on individual species is urgently needed. I found that ATS birds have a range of tolerances to fire frequency increase, with predictions varying from slight increases to moderate decreases in species distributions. Overall many species are predicted to not be substantially affected by increases in annual fire frequency. In contrast, many species were predicted to face severe declines in distribution area with increases in late-dry season fire frequency (Chapter 4).

Objective 4. Predict the impact of climate change on species distributions.

Prior to my work, no study had investigated the impact of climate change on the biota of one of the largest tracts of intact savanna in the world – Australian tropical savannas. I predicted that climate change would result in distribution declines for 67% of ATS bird species by 2080. Generally, migratory and species endemic to the tropical areas are predicted to benefit from climate change, however species found on Cape York Peninsula are predicted to be severely threatened. Species richness of ATS birds is predicted to increase throughout much of the ATS region, and also across southern Australia. Most of inland Australia and particularly the arid zone are predicted to face a decrease in ATS bird species richness. Species assemblages are likely to be very different due to climate change, given the species-specific responses seen for other regions, and predicted for the ATS (Chapter 5).

Aim 3. Integrate knowledge of ATS birds into a vulnerability framework.

Objective 5. Develop a vulnerability assessment of ATS birds using knowledge of threats, potential impacts and life history.

The birds of Australian tropical savannas show a broad range of overall vulnerability to climate change (Chapter 6). The ATS birds have relatively low general biological sensitivity, measured here with relative scoring of life history traits relating to species reproductive rate. ATS birds range in ecological sensitivity, for example vary in their distribution size and dispersal ability. In particular, the ATS bird species found on Cape York Peninsula are of the greatest conservation concern because of their high overall vulnerability and predicted reduction in distribution due to climate change. These species‟ vulnerability is exacerbated by their small distribution size, which often corresponds to biome-specificity or regional endemism, characteristics that greatly increase the extinction risk of species (Malcolm et al., 2006). Regionally endemic species with small distributions have been found to be of the highest conservation concern under climate change, even when they are protected from other threats (Williams et al., 2003). Local extinctions of these species is likely to result in a reduction in the bird diversity of the region, possibly with broader consequences for the ecosystem (Şekercioğlu et al., 2004). This study also found that threatened species had higher ecological sensitivity than non-threatened species. However, some threatened species in this study are predicted to have low vulnerability to climate change. Overall, my study highlights species that are threatened by climate change and less so by land management (for example, species of Cape York Peninsula); and the species that are predicted to be less impacted by climate change, yet are threatened by land management (many threatened species, particularly the threatened finches). The next step for the vulnerability analysis is to include the exposure and sensitivity of species to other extrinsic threats such as land modification through grazing, clearing and invasive species.

Future research directions

This thesis has refined existing and tested novel techniques for modelling the distributions of mobile bird species and used the predicted responses to threatening processes along with life history information for assessing their overall vulnerability. As my thesis concentrated on ATS birds, a clear extension of this work would be to apply the methods developed in my thesis to all bird species across Australia, and potentially other unstudied areas of the globe, and to other taxa. Specifically, I make the following suggestions for further research:

- Use temporally-specific environmental predictor variables, as successfully achieved in Chapter 2 with the weather models, to improve model predictions on the impact of fire and climate change on species distributions. As species distribution models for mobile species have higher model performance when trained on short-term weather variables, it would be ideal to incorporate these dynamic distribution predictions into the future. Using short-term variables to train SDMs would enable a closer investigation into species" responses to fire, and account for fluctuating conditions of climate and fire into future predictions.

- Incorporate future scenarios of fire and climate change together to model their synergistic impact on species distributions. My study showed how these two factors, working independently, can have marked and varied impacts on species distributions. However, understanding the synergistic effect of these two factors is likely to give better predictions on how species will respond to the changes into the future.
- Validate the distribution models developed in this thesis by comparing species abundance across the gradient of environmental suitability as predicted by Maxent. Environmental suitability as predicted by Maxent has been shown to predict the upper limit of abundance for rainforest fauna. However it is likely that for ATS birds, there will be lower correspondence between environmental suitability (as predicted from long-term climate models) and species abundance. The ability of SDM to predict abundance by calculating environmental suitability should be tested using the short-term weather models.
- Apply the modelling techniques developed in this study for birds in other parts of Australia, and to other taxa. Many bird species across Australia are similar to ATS birds in their movement behaviours and dynamic distributions, therefore the techniques used in this study are likely to be well-suited to many Australian bird species. Extending the vulnerability assessment to all fauna species would enable national strategies for the conservation of Australian biota.
- Incorporate extrinsic threats into the vulnerability assessment to highlight species that require changes in land management for their conservation. The vulnerability assessment produced in this thesis showed that there are species with low vulnerability to climate change, yet are threatened with extinction due to other factors. Including these other factors, in particular land management practices, would strengthen the overall understanding of species relative vulnerability.

Concluding remarks

This is the first study to undertake a comprehensive assessment of the vulnerability of savanna biota to climate change. The major impending threats to ATS birds – changes in fire regimes and climate – were investigated so that individual species" sensitivity and exposure to these threats could be assessed. Bringing in these two crucial factors, along with life history and ecological traits of species, I was able to identify the most (and least) vulnerable elements of the assemblage. This work will help to focus conservation efforts and highlights the species in need of monitoring in order to identify appropriate management action to forestall any potential declines.

References cited

Accatino, F., C. De Michele, R. Vezzoli, D. Donzelli & R. J. Scholes (2010) Tree-grass co-existence in savanna: interactions of rain and fire. *Journal of Theoretical Biology* **267**, 235-242.

Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlow & V. C. Radeloff (2010) Effects of drought on avian community structure. *Global Change Biology* **16**, 2158-2170.

Allan, G. E. & R. I. Southgate (2002) Fire regimes in the spinifex landscapes of Australia. *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*. (ed. by R. A. Bradstock, J. E. Williams and A. M. Gill), pp. 145-176. Cambridge University Press.

Allen, C. R. & D. A. Saunders (2002) Variability between scales: predictors of nomadism in birds of an Australian mediterranean-climate ecosystem. *Ecosystems* **5**, 348-359.

Andersen, A. N., G. D. Cook, L. K. Corbett, M. M. Douglas, R. W. Eager, J. Russell-Smith, S. A. Setterfield, R. J. Williams & J. C. Z. Woinarski (2005) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology* **30**, 155-167.

Andersen, A. N. & B. D. Hoffmann (2011) Conservation value of low fire frequency in tropical savannas: Ants in monsoonal northern Australia. *Austral Ecology* **36**, 497-503.

Anderson, R. P., D. Lew & A. T. Peterson (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling* **162**, 211-232.

Angert, A. L. (2009) The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proceedings of the National Academy of Sciences* **106**, 19693-19698.

Anthony, K. R. N., J. A. Maynard, G. Diaz-Pulido, P. J. Mumby, P. A. Marshall, L. Cao & O. Hoegh-Guldberg (2011) Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* **17**, 1798-1808.

Araújo, M. B. & A. Guisan (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography* **33**, 1677-1688.

Araújo, M. B. & M. Luoto (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology & Biogeography* **16**, 743-753.

Araújo, M. B., W. Thuiller, P. H. Williams & I. Reginster (2005a) Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology & Biogeography* **14**, 17-30.

Araújo, M. B., R. J. Whittaker, R. J. Ladle & M. Erhard (2005b) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology & Biogeography* **14**, 529-538.

Ash, A. J., J. G. McIvor, J. J. Mott & M. H. Andrew (1997) Building grass castles: integrating ecology and management of Australia's tropical tall grass rangelands. *Rangeland Journal* **19**, 123-144.

Austin, G. E. & M. M. Rehfisch (2005) Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Global Change Biology* **11**, 31-38.

Austin, M. P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**, 101-118.

Austin, M. P. (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling* **200**, 1-19.

Austin, M. P. & K. P. Van Niel (2011) Impact of landscape predictors on climate change modelling of species distributions: a case study with *Eucalyptus fastigata* in southern New South Wales, Australia. *Journal of Biogeography* **38**, 9-19.

Barker, N. & W. Vestjens (1989) *The food of Australian Birds. I Non-passerines.,* Melbourne, CSIRO.

Barker, R. D. & W. J. M. Vestjens (1990) *The food of Australian birds. II Passerines,* Melbourne, CSIRO Australia.

Barlow, J. & C. A. Peres (2004) Ecological responses to El Niño–induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**, 367-380.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey & E. A. Ferrer (2011) Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51-57.

Barrett, G., A. Silcocks, B. Simon, R. Cunningham & R. Poulter (2003) *The New Atlas of Australian Birds,* Melbourne, Royal Australasian Ornithologists Union.

Beaumont, L. J. & L. Hughes (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biology* **8**, 954-971.

Beaumont, L. J., I. A. W. McAllan & L. Hughes (2006) A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Global Change Biology* **12**, 1339-1354.

Beer, T. & A. L. Williams (1995) Estimating Australian forest fire danger under conditions of doubled carbon dioxide concentrations. *Climatic Change* **29**, 169-188.

Berry, S. L. & M. L. Roderick (2006) Changing Australian vegetation from 1788 to 1988: effects of CO2 and land-use change. *Australian Journal of Botany* **54**, 325-338.

Bird, R. B., D. W. Bird, B. F. Codding, C. H. Parker & J. H. Jones (2008) The fire stick farming hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proceedings of the National Academy of Sciences* **105**, 14796–14801.

Blakers, M., S. J. J. F. Davies & P. N. Reilly (1984) *The Atlas of Australian Birds*, Melbourne University Press: Melbourne.

Bond, W. J. & C. L. Parr (2010) Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biological Conservation* **143**, 2395-2404.

Both, C. & M. E. Visser (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296-298.

Bowman, D. M. J. S. (1998) The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist* **140**, 385-410.

Bowman, D. M. J. S. (2002) The Australian summer monsoon: a biogeographic perspective. *Australian Geographical Studies* **40**, 261-277.

Bowman, D. M. J. S. & W. J. Panton (1993) Decline of *Callitris intratropica* R. T. Baker & H. G. Smith in the Northern Territory: implications for pre- and post-European colonization fire regimes. *Journal of Biogeography* **20**, 373-381.

Bowman, D. M. J. S., B. A. Wilson & R. J. Hooper (1988) Response of Eucalyptus forest and woodland to four fire regimes at Munmarlary, Northern Territory, Australia. *Journal of Ecology* **76**, 215-232.

Bradstock, R. A. (2010) A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology & Biogeography* **19**, 145-158.

Bradstock, R. A., M. Bedward, A. M. Gill & J. S. Cohn (2005) Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* **32**, 409-423.

Braithwaite, R. W. & J. Estbergs (1987) Fire-birds of the Top End. *Australian Natural History* **22**, 299-302.

Braithwaite, R. W. & J. A. Estbergs (1985) Fire patterns and woody vegetation trends in the Alligator Rivers region of northern Australia. *Ecology and Management of the World's Savannas*. (ed. by J. C. Tothill and J. J. Mott), pp. 359-364. Australian Academy of Science, Canberra.

Brazill-Boast, J., E. van Rooij, S. R. Pryke & S. C. Griffith (2011) Interference from long-tailed finches constrains reproduction in the endangered Gouldian finch. *Journal of Animal Ecology* **80**, 39-48.

Brereton, R., S. Bennett & I. Mansergh (1995) Enhanced greenhouse climate change and its potential effect on selected fauna of south-eastern Australia: a trend analysis. *Biological Conservation* **72**, 339-354.

Brommer, J. E. (2004) The range margins of northern birds shift polewards. *Annales Zoologici Fennici* **41**, 391-397.

Brook, B. W. (2008) Synergies between climate change, extinctions and invasive vertebrates. *Wildlife Research* **35**, 249-252.

Brook, B. W., H. R. Akcakaya, D. A. Keith, G. M. Mace, R. G. Pearson & M. B. Araujo (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters* **5**, 723-725.

Brotons, L., S. Herrando & M. Pla (2007) Updating bird species distribution at large spatial scales: applications of habitat modelling to data from long-term monitoring programs. *Diversity and Distributions* **13**, 276-288.

Brown, J. H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist* **124**, 255-279.

Bunce, A., F. I. Norman, N. Brothers & R. Gales (2002) Long-term trends in the Australasian gannet (Morus serrator) population in Australia: the effect of climate change and commercial fisheries. *Marine Biology* **141**, 263-269.

Cai, W., S. J. Crimp, R. Jones, K. McInnes, P. Durack, B. Cechet, J. Bathols & S. Wilkinson (2004-2005) Climate Change in Queensland under Enhanced Greenhouse Conditions. CSIRO Marine and Atmospheric Research

Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner & J. L. Largier (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* **13**, S90-S107.

Cary, G. J. (2002) Importance of a changing climate for fire regimes in Australia. *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*. (ed. by R. A. Bradstock, J. E. Williams and A. M. Gill), pp. 26-46. Cambridge University Press.

Cary, G. J. & J. C. Banks (2000) Fire regime sensitivity to global climate change: an Australian perspective. *Advances in Global Change Research: Biomass Burning and its Inter-Relationships with the Climate System*. (ed. by J. L. Innes, M. Beniston and M. M. Verstraete), pp. 233-246. Springer Netherlands.

Chambers, L. E. (2004) Delayed breeding in little penguins - evidence of climate change? *Australian Meteorological Magazine* **53**, 13-19.

Chambers, L. E. (2005) Migration dates at Eyre Bird Observatory: links with climate change? *Climate Research* **29**, 157-165.

Chambers, L. E. (2008) Trends in timing of migration of south-western Australian birds and their relationship to climate. *Emu* **108**, 1-14.

Chambers, L. E. (2010) Altered timing of avian movements in a peri-urban environment and its relationship to climate. *Emu* **110**, 48-53.

Chambers, L. E., L. Hughes & M. A. Weston (2005) Climate change and its impact on Australia's avifauna. *Emu* **105**, 1-20.

Chambers, L. E. & M. R. Keatley (2010) Australian bird phenology: a search for climate signals. *Austral Ecology* **35**, 969-979.

Chambers, L. E., B. R. Quin, P. Menkhorst, D. C. Franklin & I. Smales (2008) The effects of climate on breeding in the Helmeted Honeyeater. *Emu* **108**, 15-22.

Chan, K. Y. (1999) Bird numbers in drought and non-drought years in tropical Central Queensland, Australia. *Tropical Ecology* **40**, 63-68.

Chan, K. Y. (2001) Partial migration in Australian landbirds: a review. *Emu* **101**, 281-292.

Christian, K., L. V. Isabelle, J. Frédéric & D. Vincent (2009) More species, fewer specialists: 100 years of changes in community composition in an island biogeographical study. *Diversity and Distributions* **15**, 641-648.

Clarke, M. F. (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* **35**, 385-394.

Coetzee, B. W. T., M. P. Robertson, B. F. N. Erasmus, B. J. van Rensburg & W. Thuiller (2009) Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography* **18**, 701-710.

Collins, D. A., P. M. Della-Marta, N. Plummer & B. Trewin (2000) Trends in annual frequencies of extreme temperature events in Australia. *Australian Meteorological Magazine* **49**, 277-292.

Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman & J. T. Longino (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258-261.

Corbett, L. K., A. Andersen & W. J. Muller (2003) Terrestrial vertebrates. *Fire in Tropical Savannas: The Kapalga Fire Experiment*. (ed. by A. Andersen, G. D. Cook and R. J. Williams), pp. 126-152. Springer-Verlag, New York.

Costa, G. C., L. J. Vitt, E. R. Pianka, D. O. Mesquita & G. R. Colli (2008) Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* **17**, 670-677.

Cotton, P. A. (2003) Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 12219-12222.

Crawford, R. M. M. (1997) Habitat fragility as an aid to long term survival in arctic vegetation. *Ecology of Arctic Environments*. (ed. by S. J. Woodin and M. Marquiss), pp. 113-136. Cambridge University Press, Cambridge, UK.

Crick, H. Q., C. Dudley, D. E. Glue & D. L. Thomson (1997) UK birds are laying eggs earlier. *Nature* **388**, 526.

Crowley, G. M. & S. T. Garnett (1999) Seeds of the annual grasses *Schizachyrium* spp. as a food resource for tropical granivorous birds. *Australian Journal of Ecology* **24**, 208-220.

Cubash, U., G. A. Meehl, G. J. Boer, R. J. Stouffer, M. Dix, A. Noda, C. A. Senior, S. Raper & K. S. Yap (2001) Projections of future climate change. *Climate Change 2001: The Scientific Basis*. ed. by J. T. Houghton, Y. Ding, D. J. Griggset al, pp. 525-582. Cambridge University Press, Cambridge.

Cutter, S. L. (1996) Vulnerability to environmental hazards. *Progress in Human Geography* **20**, 529-539.

D'Amen, M., P. Bombi, P. B. Pearman, D. R. Schmatz, N. E. Zimmermann & M. A. Bologna (2011) Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? *Biological Conservation* **144**, 989-997.

Davies, S. J. J. F. (1984) Nomadism as a response to desert conditions in Australia. *Journal of Arid Environments* **7**, 183-195.

Davis, A. J., J. H. Lawton, B. Shorrocks & L. S. Jenkinson (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* **67**, 600-612.

Davis, M. A., D. W. Peterson, P. B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington & P. Bazakas (2000) Restoring savanna using fire: impact on the breeding bird community. *Restoration Ecology* **8**, 30-40.

Dean, W. R. J. (1987) Birds associating with fire at Nylsvley Nature Reserve, Transvaal. *Ostrich* **58**, 103-106.

DeAngelis, D. L. (1980) Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* **61**, 764-771.

Department the Environment and Water Resources (2007) Metadata: Australia - Present Major Vegetation Subgroups - NVIS Stage 1, Version 3.1 - Albers. ed. by Australian Government Canberra.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak & P. R. Martin (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 6668-6672.

Devictor, V., R. Julliard, D. Couvet & F. Jiguet (2008) Birds are tracking climate warming, but not fast enough. *Proceeedings of the Royal Society B* **275**, 2743-2748.

Dingle, H. (2008) Bird migration in the southern hemisphere: a review comparing continents. *Emu* **108**, 341-359.

Dostine, P. L., G. C. Johnson, D. C. Franklin, Y. Zhang & C. Hempel (2001) Seasonal use of savanna landscapes by the Gouldian finch, *Erythrura gouldiae*, in the Yinberrie Hills area, Northern Territory. *Wildlife Research* **28**, 445-458.

Doswald, N., S. G. Willis, Y. C. Collingham, D. J. Pain, R. E. Green & B. Huntley (2009) Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers. *Journal of Biogeography* **36**, 1194-1208.

Driscoll, D. A., D. B. Lindenmayer, A. F. Bennett, M. Bode, R. A. Bradstock, G. J. Cary, M. F. Clarke, N. Dexter, R. Fensham, G. Friend, M. Gill, S. James, G. Kay, D. A. Keith, C. MacGregor, J. Russell-Smith, D. Salt, J. E. M. Watson, R. J. Williams & A. York (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* **143**, 1928-1939.

Dunlop, J. N. & R. D. Wooller (1986) Range extensions and the breeding seasons of seabirds in south-western Australia. *Records of the Western Australian Museum* **12**, 389-394.

Dunn, A. M. & M. A. Weston (2008) A review of terrestrial bird atlases of the world and their application. *Emu* **108**, 42-67.

Dunn, P. O. & D. W. Winkler (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266**, 2487-2490.

Elith, J. & M. A. Burgman (2002) Predictions and their validation: rare plants in the Central Highlands, Victoria, Australia. *Predicting Species Occurrences, Issues of Accuracy and Scale*. (ed. by J. M. Scott, P. J. Heglund, M. L. Morrisonet al), pp. 303-313. Island Press.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz & N. E. Zimmermann (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129-151.

Elith, J., M. Kearney & S. Phillips (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution* **1**, 330-342.

Elith, J. & J. R. Leathwick (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**, 677-697.

Environment Australia (2000) Revision of the Interim Biogeographic Regionalisation of Australia (IBRA) and the Development of Version 5.1. - Summary Report. Department of Environment and Heritage, Canberra.

Environment Protection and Biodiversity Conservation Act (1999). ed. by Australian Government Department of Sustainability Environment Water Population and Communities.

Environmental Protection Agency (2004) WildNet (Database). *Environmental Protection Agency*. http://www.derm.qld.gov.au/wildlife-ecosystems/wildlife/wildlife_online/index.html, Brisbane.

Erasmus, B. F. N., A. S. Van Jaarsveld, S. L. Chown, M. Kshatriya & K. J. Wessels (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology* **8**, 679-693.

Evans, M. C., J. E. M. Watson, R. A. Fuller, O. Venter, S. C. Bennett, P. R. Marsack & H. P. Possingham (2011) The spatial distribution of threats to species in Australia. *BioScience* **61**, 281-298.

Felderhof, L. & D. Gillieson (2006) Comparison of fire patterns and fire frequency in two tropical savanna bioregions. *Austral Ecology* **31**, 736-746.

Fensham, R. J. & R. J. Fairfax (2005) Preliminary assessment of gidgee (*Acacia cambagei*) woodland thickening in the Longreach district, Queensland. *The Rangeland Journal* **27**, 159-168.

Fensham, R. J., R. J. Fairfax & S. R. Archer (2005) Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* **93**, 596-606.

Fensham, R. J., R. J. Fairfax & J. E. Holman (2002) Response of a rare herb (Trioncinia retroflexa) from semi-arid tropical grassland to occasional fire and grazing. *Austral Ecology* **27**, 284-290.

Fensham, R. J., R. J. Fairfax & D. P. Ward (2009) Drought-induced tree death in savanna. *Global Change Biology* **15**, 380-387.

Fensham, R. J., J. E. Holman & M. J. Cox (1999) Plant species responses along a grazing disturbance gradient in Australian grassland. *Journal of Vegetation Science* **10**, 77-86.

Fischer, J. & D. B. Lindenmayer (2000) An assessment of the published results of animal relocations. *Biological Conservation* **96**, 1-11.

Fischer, J., A. Zerger, P. Gibbons, J. Stott & B. S. Law (2010) Tree decline and the future of Australian farmland biodiversity. *Proceedings of the National Academy of Sciences* **107**, 19597-19602.

Fitzherbert, J. C. & D. J. Baker-Gabb (1988) Australasian grasslands and their avifauna. *Ecology and Conservation of Grassland Birds*. (ed. by P. D. Goriup), pp. 227-250. International Council for Bird Preservation, Cambridge.

Foden, W., G. M. Mace, J.-C. Vie, A. Angulo, S. H. M. Butchart, L. DeVantier, H. T. Dublin, A. Gutsche, S. Stuart & E. Turak (2008) Species susceptibility to climate change impacts. *The 2008 Review of The IUCN Red List of Threatened Species*. ed. by J.-C. Vie, C. Hilton-Taylor and S. Stuart, IUCN Gland, Switzerland.

Foody, G. M. (2008) Refining predictions of climate change impacts on plant species distribution through the use of local statistics. *Ecological Informatics* **3**, 228-236.

Franklin, D., P. Menkhorst & J. L. Robinson (1989) Ecology of the Regent Honeyeater *Xanthomyza phrygia*. *Emu* **89**, 140-154.

Franklin, D., P. Whitehead, G. Pardon, J. Matthews, P. McMahon & D. McIntyre (2005) Geographic patterns and correlates of the decline of granivorous birds in northern Australia. *Wildlife Research* **32**, 399-408.

Franklin, D. C. (1999) Evidence of disarray amongst granivorous bird assemblages in the savannas of northern Australia, a region of sparse human settlement. *Biological Conservation* **90**, 53-63.

Fraser, F. J. & P. J. Whitehead (2005) Predation of artificial ground nests in Australian tropical savannas: inverse edge effects. *Wildlife Research* **32**, 313-319.

Friend, G. R. & J. A. Taylor (1985) Habitat preferences of small mammals in tropical open-forest of the Northern Territory. *Australian Journal of Ecology* **10**, 173-185.

Fullagar, P. J., K. W. Lowe & S. J. J. F. Davies (1986) Intracontinental migration of Australian birds. *Acta XIX Congressus Internationalis Ornithologici*. ed. by H. Ouellet. National Museum of Natural Sciences by University of Ottawa Press, Ottawa Canada.

Garnett, S. & R. Bredl (1985) Birds in the vicinity of Edward River Settlement. Part II. Discussion, references, list of passerines. *The Sunbird* **15**, 25-40.

Garnett, S. & G. M. Crowley (1995) The decline of the Black Treecreeper *Climacteris picumnus melanota* on Cape York Peninsula. *Emu* **95**, 66-68.

Garnett, S. T. & B. W. Brook (2007) Modelling to forestall extinction of Australian tropical birds. *Journal of Ornithology* **148**, S311-S320.

Garnett, S. T., J. R. Clarkson, A. Felton, G. N. Harrington & A. N. D. Freeman (2005) Habitat and diet of the Star Finch (*Neochmia ruficauda clarescens*) in the early wet season at Princess Charlotte Bay, Cape York Peninsula, Australia. *Emu* **105**, 81-85.

Garnett, S. T. & G. M. Crowley (2002) Recovery Plan for the golden-shouldered parrot *Psephotus chrysopterygius* 2003-2007. *Report to Environment Australia*. Queensland Parks and Wildlife Service, Brisbane, Canberra.

Garnett, S. T., J. K. Szabo & G. Dutson (2010a) *The Action Plan for Australian Birds 2010* CSIRO Publishing.

Garnett, S. T. & G. Williamson (2010) Spatial and temporal variation in precipitation at the start of the rainy season in tropical Australia. *The Rangeland Journal* **32**, 215-226.

Garnett, S. T., J. C. Z. Woinarski, G. M. Crowley & A. S. Kutt (2010b) Biodiversity conservation in Australian tropical rangelands. *Wild Rangelands: Conserving Wildlife While Maintaining Livestock in Semi-Arid Ecosystems*. (ed. by J. T. du Toit, R. Kock and J. C. Deutsch), pp. 191-234. Wiley-Blackwell.

Gasner, M. R., J. Jankowski, A. L. Ciecka, K. O. Kyle & K. N. Rabenold (2010) Projecting the local impacts of climate change on a Central American montane avian community. *Biological Conservation* **143**, 1250-1258.

Gillett, N. P., A. J. Weaver, F. W. Zwiers & M. D. Flannigan (2004) Detecting the effect of climate change on Canadian forest fires. *Geophysical Research Letters* **31**, L18211.

Graham, C. H., J. Elith, R. J. Hijmans, A. Guisan, A. T. Peterson, B. A. Loiselle & G. The Nceas Predicting Species Distributions Working (2008) The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology* **45**, 239-247.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz & A. T. Peterson (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution* **19**, 497-503.

Grant, I., D. Jones, W. Wang, R. Fawcett & D. Barratt (2008) Meteorological and remotely sensed datasets for hydrological modelling: a contribution to the Australian Water Availability Project, pp. 1-4.

Green, K. (2008) Migratory bogong moths (*Agrotis infusa*) transport arsenic and concentrate it to lethal effect by estivating gregariously. *Arctic Antarctic and Alpine Research* **40**, 74-80.

Green, K. & C. M. Pickering (2002) A scenario for mammal and bird diversity in the Snowy Mountains of Australia in relation to climate change. *Mountain Biodiversity*. (ed. by C. Korner), pp. 241-249.

Griffioen, P. A. & M. F. Clarke (2002) Large-scale bird-movement patterns evident in eastern Australian atlas data. *Emu* **102**, 99-125.

Grinnell, J. (1917) Field tests of theories concerning distributional control. *The American Naturalist* **51**, 115-128.

Guisan, A., C. H. Graham, J. Elith & F. Huettmann (2007a) Sensitivity of predictive species distribution models to change in grain size. *Diversity and Distributions* **13**, 332-340.

Guisan, A. & W. Thuiller (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993-1009.

Guisan, A. & N. E. Zimmermann (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-186.

Guisan, A., N. E. Zimmermann, J. Elith, C. H. Graham, S. Phillips & A. T. Peterson (2007b) What matters for predicting the occurrences of trees: techniques, data or species' characteristics? *Ecological Monographs* **77**, 615-630.

Hannah, D., J. C. Z. Woinarski, C. P. Catterall, J. C. McCosker, N. Y. Thurgate & R. J. Fensham (2007) Impacts of clearing, fragmentation and disturbance on the bird fauna of Eucalypt savanna woodlands in central Queensland, Australia. *Austral Ecology* **32**, 261-276.

Hawke, A. (2009) The Australian Environment Act - Report of the Independent Review of the Environment Protection and Biodiversity Conservation Act 1999. Australian Government Department of hte Environment, Water, Heritage and the Arts, Canberra.

Hawkins, B. A., E. E. Porter & J. A. F. Diniz (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* **84**, 1608-1623.

He, F. & S. P. Hubbell (2011) Species-area relationships always overestimate extinction rates from habitat loss. *Nature* **473**, 368-371.

Heikkinen, R. K., M. Luoto & R. Virkkala (2006) Does seasonal fine-tuning of climatic variables improve the performance of bioclimatic envelope models for migratory birds? *Diversity and Distributions* **12**, 502-510.

Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson & J.-H. Körber (2007) Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography* **16**, 754-763.

Hernandez, P. A., C. H. Graham, L. L. Master & D. L. Albert (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29**, 773-785.

Higgins, P. J. (1999) *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 4. Parrots to Dollarbird*, Oxford University Press: Melbourne.

Higgins, P. J. & S. J. J. F. Davies (1996) *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 3. Snipe to Pigeons* Oxford University Press: Melbourne.

Higgins, P. J. & J. M. Peter (2002) *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 6. Pardalotes to Shrike-thrushes*, Oxford University Press: Melbourne.

Higgins, P. J., J. M. Peter & S. J. Cowling (2006) *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 7. Boatbill to Starlings*, Oxford University Press: Melbourne.

Higgins, P. J., J. M. Peter & W. K. Steele (2001) *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 5. Tyrant-flycatchers to Chats*, Oxford University Press: Melbourne.

Hijmans, R. J. & C. H. Graham (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12**, 2272-2281.

Hilbert, D. W., M. Bradford, T. Parker & D. A. Westcott (2004) Golden bowerbird (Prionodura newtonia) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming. *Biological Conservation* **116**, 367-377.

Hobbs, J. (1988) Climatic patterns and variability in the Australian wheatbelt. *The Impact of Climate Variations on Agriculture*. (ed. by T. R. Carter and N. T. Konijn). Kluwer Academic Publishers.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham & C. D. Thomas (2008) Assisted colonization and rapid climate change. *Science* **321**, 345-346.

Hughes, L. (2003) Climate change and Australia: trends, projections and impacts. *Austral Ecology* **28**, 423-443.

Huntley, B., Y. C. Collingham, S. G. Willis & R. E. Green (2008) Potential impacts of climate change on European breeding birds. *PLoS ONE* **3**, e1439.

Huston, M. A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**, 393-401.

Hutchinson, G. E. (1957) Concluding remarks. *Cold Spring Harbour Symposia on Quantitative Biology* **22**, 415-427.

Hutchinson, M. F., D. J. Houlder, H. A. Nix & J. P. McMahon (2000) *ANUCLIM user's guide Version 5.1*. Centre for Resource and Environmental Studies, Australian National University, Canberra, Australian Capital Territory, Australia.

Intergovernmental Panel on Climate Change (2007a) Impacts, Adaptation and Vulnerability, Contribution of Working Group II to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge, UK.

Intergovernmental Panel on Climate Change (2007b) The Physical Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Isaac, J. L., J. Vanderwal, C. N. Johnson & S. E. Williams (2009) Resistance and resilience: quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Diversity and Distributions* **15**, 280-288.

IUCN (2001) IUCN Red List Categories and Criteria: Version 3.1. *IUCN*, Gland, Switzerland.

Jansen, R., R. M. Little & T. M. Crowe (1999) Implications of grazing and burning of grasslands on the sustainable use of francolins (*Francolinus* spp.) and on overall bird conservation in the highlands of Mpumalanga province, South Africa. *Biodiversity and Conservation* **8**, 587-602.

Jenni, L. & M. Kery (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**, 1467-1471.

Jetz, W. & C. Rahbek (2002) Geographic range size and determinants of avian species richness. *Science* **297**, 1548-1551.

Jetz, W., D. S. Wilcove & A. P. Dobson (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* **5**, e157.

Jiguet, F., R. Julliard, C. D. Thomas, O. Dehorter, S. E. Newson & D. Couvet (2006) Thermal range predicts bird population resilience to extreme high temperatures. *Ecology Letters* **9**, 1321-1330.

Johnson, C. N., J. L. Isaac & D. O. Fisher (2007) Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B-Biological Sciences* **274**, 341-346.

Jones, D. A., W. Wang & R. Fawcett (2007) Climate Data for the Australian Water Availability Project: Final Milestone Report. National Climate Centre, Australian Bureau of Meteorology.

Jump, A. S. & J. Peñuelas (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* **8**, 1010-1020.

Kattan, G. H. (1992) Rarity and vulnerability: The birds of the Cordillera Central of Colombia. *Conservation Biology* **6**, 64-70.

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

Kearney, M. R., B. A. Wintle & W. P. Porter (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* **3**, 203-213.

Keast, A. (1961) Bird speciation on the Australian continent. *Bulletin of the Museum of Comparative Zoology, Harvard* **123**, 305-495.

Keith, D. A., J. E. Williams & J. C. Woinarski (2002) Fire management and biodiveristy conservation: key approaches and principles. *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*. (ed. by R. A. Bradstock, J. E. Williams and A. M. Gill), pp. 199-237. Cambridge University Press.

Knapp, A. K., R. A. Matthews & O. Sarnelle (2001) Resistance and resilience of alpine lake fauna to fish introductions. *ecological Monographs* **71**, 401-421.

Krawchuk, M. A., M. A. Moritz, M.-A. Parisien, J. Van Dorn & K. Hayhoe (2009) Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE* **4**, e5102.

Kutt, A. S. & A. Fisher (2011) Increased grazing and dominance of an exotic pasture (*Bothriochloa pertusa*) affects vertebrate fauna species composition, abundance and habitat in savanna woodland. *The Rangeland Journal* **33**, 49-58.

Kutt, A. S., E. P. Vanderduys, J. J. Perry & G. C. Perkins (In Review) Do miners (*Manorina* spp) affect bird assemblage in continuous, largely unmodified tropical savanna woodlands? *Austral Ecology*.

Kutt, A. S. & J. C. Z. Woinarski (2007) The effects of grazing and fire on vegetation and the vertebrate assemblage in a tropical savanna woodland in north-eastern Australia. *Journal of Tropical Ecology* **23**, 95-106.

La Sorte, F. A. & F. R. Thompson (2007) Poleward shifts in winter ranges of North American birds. *Ecology* **88**, 1803-1812.

le Roux, P. C. & M. A. McGeoch (2008) Rapid range expansion and community reorganization in response to warming. *Global Change Biology* **14**, 2950-2962.

Legge, S., S. Murphy, J. Heathcote, E. Flaxman, J. Augusteyn & M. Crossman (2008) The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. *Wildlife Research* **35**, 33-43.

Lehikoinen, A. (2011) Advanced autumn migration of sparrowhawk has increased the predation risk of long-distance migrants in Finland. *PLoS ONE* **6**, e20001.

Liedloff, A. C. & G. D. Cook (2007) Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the FLAMES simulation model. *Ecological Modelling* **201**, 269-282.

Ling, C. X., J. Huang & H. Zhang (2003) AUC: a better measure than accuracy in comparing learning algorithms. *Advances in Artificial Intelligence*. (ed. by Y. Xiang and B. Chaib-draa), pp. 329-341. Springer-Verlag, Berlin Heidelberg.

Liu, C., P. M. Berry, T. P. Dawson & R. G. Pearson (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**, 385-393.

Liu, Y., J. Stanturf & S. Goodrick (2010) Trends in global wildfire potential in a changing climate. *Forest Ecology and Management* **259**, 685-697.

Lowry, H. & A. Lill (2007) Ecological factors facilitating city-dwelling in red-rumped parrots. *Wildlife Research* **34**, 624-631.

Ludwig, J. A., D. J. Tongway, G. N. Bastin & C. D. James (2004) Monitoring ecological indicators of rangeland functional integrity and their relation to biodiversity at local to regional scales. *Austral Ecology* **29**, 108-120.

Luoto, M., J. Pöyry, R. K. Heikkinen & K. Saarinen (2005) Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Global Ecology & Biogeography* **14**, 575-584.

Mac Nally, R. (1996) A winter's tale: among-year variation in bird community structure in a southeastern Australian forest. *Australian Journal of Ecology* **21**, 280-291.

Mac Nally, R., A. F. Bennett, J. R. Thomson, J. Q. Radford, G. Unmack, G. Horrocks & P. A. Vesk (2009) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions* **15**, 720-730.

Mac Nally, R. & G. Horrocks (2000) Landscape-scale conservation of an endangered migrant: the swift parrot (*Lathamus discolor*) in its winter range. *Biological Conservation* **92**, 335-343.

Maclean, I. M. D., G. E. Austin, M. M. Rehfisch, J. Blew, O. Crowe, S. Delany, K. Devos, B. Deceuninck, K. GÜnther, K. Laursen, M. Van Roomen & J. Wahl (2008) Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology* **14**, 2489-2500.

Maclean, I. M. D. & R. J. Wilson (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences* **108**, 12337-12342.

Malcolm, J. R., C. R. Liu, R. P. Neilson, L. Hansen & L. Hannah (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* **20**, 538-548.

Manne, L. L. & S. L. Pimm (2001) Beyond eight forms of rarity: which species are threatened and which will be next? *Animal Conservation* **4**, 221-229.

Marchant, S. & P. J. Higgins (1990) Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1. Ratites to Ducks). Oxford University Press: Melbourne.

Marchant, S. & P. J. Higgins (1993) *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 2. Raptors to Lapwings*, Oxford University Press: Melbourne.

Margules, C. R., A. O. Nicholls & M. B. Usher (1994) Apparent species turnover, probability of extinction and the selection of nature reserves: a case study of the Ingleborough Limestone Pavements. *Conservation Biology* **8**, 398-409.

Marini, M., M. Barbet-Massin, L. E. Lopes & F. Jiguet (2009a) Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. *Biological Conservation* **142**, 3039-3050.

Marini, M. Â., M. Barbet-Massin, L. Esteves Lopes & F. Jiguet (2009b) Predicted climate-driven bird distribution changes and forecasted conservation conflicts in a neotropical savanna. *Conservation Biology* **23**, 1558-1567.

Maron, M., A. Lill, D. M. Watson & R. Mac Nally (2005) Temporal variation in bird assemblages: how representative is a one-year snapshot? *Austral Ecology* **30**, 383-394.

Maron, M., A. Main, M. Bowen, A. Howes, J. Kath, C. Pillette & C. A. McAlpine (2011) Relative influence of habitat modification and interspecific competition on woodland bird assemblages in eastern Australia. *Emu* **111**, 40-51.

Martin, T. G. & H. P. Possingham (2005) Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology* **42**, 400-408.

Martinez-Morales, M. A., I. Zuria, L. Chapa-Vargas, I. MacGregor-Fors, R. Ortega-Alvarez, E. Romero-Aguila & P. Carbo (2010) Current distribution and predicted geographic expansion of the Rufous-backed Robin in Mexico: a fading endemism? *Diversity and Distributions* **16**, 786-797.

Mathieson, M. T. & G. C. Smith (2009) National recovery plan for the buff-breasted button-quail *Turnix olivii*. Report to Department of the Environment, Water, Heritage and the Arts, Canberra. Department of Environment and Resource Management, Brisbane.

McAlpine, C. A., R. J. Fensham & D. E. Temple-Smith (2002) Biodiversity conservation and vegetation clearing in Queensland: principles and thresholds. *The Rangeland Journal* **24**, 36-55.

McKeon, G. M., K. A. Day, S. M. Howden, J. J. Mott, D. M. Orr, E. J. Weston & W. J. Scattini (1990) Northern Australian savannas: management for pastoral production. *Journal of Biogeography* **17**, 355-372.

McKinney, M. L. (2006) How do rare species avoid extinction? A paleontological view. *The Biology of Rarity: Causes and Consequences of Rare-Common Differences*. (ed. by W. E. Kunin and K. Gaston), pp. 110-129. Chapman and Hall, London.

McMahon, J. P., M. F. Hutchinson, H. A. Nix & K. D. Ord (1995) *ANUCLIM user's guide*, Version 1. Centre for Resource and Environmental Studies, Australian National University, Canberra, Australian Capital Territory, Australia.

Menéndez, R., A. G. Megías, J. K. Hill, B. Braschler, S. G. Willis, Y. Collingham, R. Fox, D. B. Roy & C. D. Thomas (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1465-1470.

Midgley, G. F., G. O. Hughes, W. Thuiller & A. G. Rebelo (2006) Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity and Distributions* **12**, 555-562.

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press, Washington, DC and Covelo, CA.

Miller-Rushing, A. J., T. L. Lloyd-Evans, R. B. Primack & P. Satzinger (2008) Bird migration times, climate change, and changing population sizes. *Global Change Biology* **14**, 1959-1972.

Moretti, M. & C. Legg (2009) Combining plant and animal traits to assess community functional responses to disturbance. *Ecography* **32**, 299-309.

Mott, J. J., J. Williams, M. H. Andrew & A. N. Gillison (1985) Australian savanna ecosystems. *Ecology and Management of the World's Savannas*. (ed. by J. C. Tothill and J. J. Mott), pp. 56-82. Australian Academy of Science, Canberra.

Mouillot, F. & C. B. Field (2005) Fire history and the global carbon budget: a 1°× 1° fire history reconstruction for the 20th century. *Global Change Biology* **11**, 398-420.

Murphy, S. A. & S. M. Legge (2007) The gradual loss and episodic creation of Palm Cockatoo (*Probosciger aterrimus*) nest-tree in a fire- and cyclone-prone habitat. *Emu* **107**, 1-6.

Murphy, S. A., S. M. Legge, J. Heathcote & E. Mulder (2010) The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). *Wildlife Research* **37**, 145-155.

Nakicenovic, N., J. Alcamo, G. Davis, B. de Vries, J. Fenhann, S. Gaffin, K. Gregory, A. Grübler & T. Y. Jung (2000) Emissions Scenarios. *Special Report of the Intergovernmental Panel on Climate Change*. ed. by N. Nakicenovic and R. Swart, p. 570. Cambridge University Press, Cambridge.

Nature Conservation Act (1992) Reprint No. 6D. ed. by Q. P. Counsel.

Nebel, S., J. L. Porter & R. T. Kingsford (2008) Long-term trends of shorebird populations in eastern Australia and impacts of freshwater extraction. *Biological Conservation* **141**, 971-980.

Nicholls, A. O. (1998) Integrating population abundance, dynamics and distribution into broad-scale priority setting. *Conservation in a Changing World*. (ed. by G. M. Mace, A. Balmford and J. R. Ginsberg). Cambridge University Press.

Nicholls, N. & D. Collins (2006) Observed change in Australia over the past century. *Energy and Environment* **17**, 1-2.

Nix, H. (1976) Environmental control of breeding, post-breeding dispersal and migration of birds in the Australian region. *Proceedings of the 16th International Ornithological Congress*. (ed. by H. J. Frith and J. H. Calaby). Australian Academy of Science.

Noble, J. C. (1989) Fire studies in mallee (*Eucalyptus* spp.) communities of western New South Wales: the effects of fires applied in different seasons on herbage productivity and their implications for management. *Australian Journal of Ecology* **14**, 169-187.

O'Grady, J. J., D. H. Reed, B. W. Barry & R. Frankham (2004) What are the best correlates of predicted extinction risk? *Biological Conservation* **118**, 513-520.

O'Reilly, L., D. Ogada, T. M. Palmer & F. Keesing (2006) Effects of fire on bird diversity and abundance in an East African savanna. *African Journal of Ecology* **44**, 165-170.

O'Donnell, S., J. K. Webb & R. Shine (2010) Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology* **47**, 558-565.

Ogutu, J. O., H. P. Piepho, H. T. Dublin, N. Bhola & R. S. Reid (2008) Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *Journal of Animal Ecology* **77**, 814-829.

Osborne, P. E., G. M. Foody & S. Suárez-Seoane (2007) Non-stationarity and local approaches to modelling the distributions of wildlife. *Diversity and Distributions* **13**, 313-323.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* **37**, 637-669.

Parmesan, C. & G. Yohe (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37-42.

Pearson, R. G. (2006) Climate change and the migration capacity of species. *Trends in Ecology & Evolution* **21**, 111-113.

Pearson, R. G. & T. P. Dawson (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography* **12**, 361-371.

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

Perry, J. J., A. S. Kutt, S. T. Garnett, G. M. Crowley, E. P. Vanderduys & G. C. Perkins (2011b) 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.

Petrie, S. A. & K. H. Rogers (2004) Nutrient-reserve dynamics of semiarid-breeding White-faced Whistling Ducks: a north-temperate contrast. *Canadian Journal of Zoology* **82**, 1082-1090.

Phillips, S. J., R. P. Anderson & R. E. Schapire (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**, 231-259.

Phillips, S. J. & M. Dudik (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**, 161-175.

Phillips, S. J., M. Dudik & R. E. Schapire (2004) A maximum entropy approach to species distribution modeling. *Proceedings of the 21st International Conference on Machine Learning*.

Pimm, S. L. (1984) The complexity and stability of ecosystems. *Nature* **307**, 321-326.

Pitman, A. J., G. T. Narisma & J. McAneney (2007) The impact of climate change on the risk of forest and grassland fires in Australia. *Climatic Change* **84**, 383-401.

Porter, W. P., S. Budaraju, W. E. Stewart & N. Ramankutty (2000) Calculating climate effects on birds and mammals: impacts on biodiversity, conversation, population parameters, and global community structure. *American Zoologist* **40**, 597-630.

Pounds, J. A., M. P. L. Fogden & J. H. Campbell (1999) Biological response to climate change on a tropical mountain. *Nature* **398**, 611-615.

Prates-Clark, C. D. C., S. S. Saatchi & D. Agosti (2008) Predicting geographical distribution models of high-value timber trees in the Amazon Basin using remotely sensed data. *Ecological Modelling* **211**, 309-323.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling & K. A. Wilson (2007) Conservation planning in a changing world. *Trends in Ecology & Evolution* **22**, 583-592.

Price, B., A. S. Kutt & C. A. McAlpine (2010) The importance of fine-scale savanna heterogeneity for reptiles and small mammals. *Biological Conservation* **143**, 2504-2513.

Price, B., C. A. McAlpine, A. S. Kutt, S. R. Phinn, D. V. Pullar & J. A. Ludwig (2009) Continuum or discrete patch landscape models for savanna birds? Towards a pluralistic approach. *Ecography* **32**, 745-756.

Price, O. & D. M. J. S. Bowman (1994) Fire-stick forestry: a matrix model in support of skilful fire management of *Callitris intratropica* R. T. Baker by north Australian Aborigenes. *Journal of Biogeography* **21**, 573-580.

Price, O. F., J. C. Z. Woinarski & D. Robinson (1999) Very large area requirements for frugivorous birds in monsoon rainforests of the Northern Territory, Australia. *Biological Conservation* **91**, 169-180.

Pulliam, H. R. (2000) On the relationship between niche and distribution. *Ecology Letters* **3**, 349-361.

Rabe-Hesketh, S., A. Pickles & A. Skrondal (2003) Correcting for covariate measurement error in logistic regression using nonparametric maximum likelihood estimation. *Statistical Modelling* **3**, 215-232.

Rabinowitz, D. (1981) Seven forms of rarity. *The Biological Aspects of Rare Plant Conservation*. (ed. by H. Synge), pp. 205-217. John Wiley and Sons Ltd.

Raupach, M. R., G. Marland, P. Ciais, C. Le Quéré, J. G. Canadell, G. Klepper & C. B. Field (2007) Global and regional drivers of accelerating CO2 emissions. *Proceedings of the National Academy of Sciences* **104**, 10288-10293.

Reid, J. (2003) What's the link, if any, between recent changes in distribution of Australian birds and greenhouse climate change? *Climate Change Impacts on Biodiversity in Australia: Outcomes of a Workshop Sponsored by the Biological Diversity Advisory Committee, 1-2 October 2002*. ed. by M. Howden, L. Hughes, M. Dunlopet al, pp. 37-39. CSIRO Sustainable Ecosystems, Canberra.

Reside, A. E., J. VanDerWal & A. S. Kutt (In prep) Assessing vulnerability to climate change: a comprehensive examination of Australian tropical savanna birds.

Reside, A. E., J. VanDerWal & A. S. Kutt (In Review) Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios. *Ecology and Evolution*.

Reside, A. E., J. VanDerWal, A. S. Kutt, I. Watson & S. E. Williams (2011a) Fire regime shifts affect bird species distributions. *Diversity and Distributions*, 1-13.

Reside, A. E., J. J. VanDerWal, A. S. Kutt & G. C. Perkins (2010) Weather, not climate, defines distributions of vagile bird species. *PLoS ONE* **5**, e13569.

Reside, A. E., I. Watson, J. VanDerWal & A. S. Kutt (2011b) Incorporating low-resolution historic species location data decreases performance of distribution models. *Ecological Modelling*, DOI:10.1016/j.ecolmodel.2011.1006.1015.

Ridpath, M. G. (1985) Ecology in the wet-dry tropics: how different? *Proceedings of the Ecological Society of Australia* **13**, 3-20.

Ritchie, E. G. & E. E. Bolitho (2008) Australia's savanna herbivores: bioclimatic distributions and an assessment of the potential impact of regional climate change. *Physiological and Biochemical Zoology* **81**, 880-890.

Root, T. (1988) Energy constraints on avian distributions and abundances. *Ecology* **69**, 330-339.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig & J. A. Pounds (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57-60.

Roques, K. G., T. G. O'Connor & A. R. Watkinson (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**, 268-280.

Roshier, D. A., M. Asmus & M. Klaasen (2008) What drives long-distance movements in the nomadic Grey Teal *Anas gracilis* in Australia? *Ibis* **150**, 474-484.

Rowley, I. (1975) *Bird Life*, Collins: Sydney.

Rowley, I. & E. Russell (1993) The purple-crowned fairy-wren *Malurus coronatus*. II. Breeding biology, social organization, demography and management. *Emu* **93**, 235-250.

Rowley, I. & E. Russell (2002) A population study of the blue-breasted fairy-wren, *Malurus pulcherrimus*, at Dryandra, Western Australia. *Emu* **102**, 127-135.

Rubel, F. & M. Kottek (2010) Observed and projected climate shifts 1901-2100 depicted by world maps of the Köppen-Geiger climate classification. *Meteorologische Zeitschrift* **19**, 135-141.

Russell-Smith, J. (2002) Pre-contact Aboriginal, and contemporary fire regimes of the savanna landscapes of northern Australia: patterns, changes and ecological processes. *Australian Fire Regimes: Contemporary Patterns (April 1998-March 2000) and Changes Since European Settlement*. ed. by J. Russell-Smith, R. Craig, A. M. Gill, R. Smith and J. Williams. Australia State of the Environment Second Technical Paper Series (Biodiversity), Department of the Environment and Heritage, Canberra.

Russell-Smith, J. & D. M. J. S. Bowman (1992) Conservation of monsoon rainforest isolates in the Northern Territory, Australia. *Biological Conservation* **59**, 51-63.

Sarkar, S., R. L. Pressey, D. P. Faith, C. R. Margules, T. Fuller, D. M. Stoms, A. Moffett, K. A. Wilson, K. J. Williams, P. H. Williams & S. Andelman (2006) Biodiversity conservation planning tools: present status and challenges for the future. *Annual Review of Environment and Resources* **31**, 123-159.

Schodde, R. (1981) Bird communities of the Australian mallee: composition, derivation, distribution, structure and seasonal cycles. *Mediterranean-type shrublands*. (ed. by F. di Castri, D. W. Goodall and R. L. Specht), pp. 387-415. Elsevier Scientific, New York.

Schodde, R. (1982) Origin, adaptation and evolution of birds in arid Australia. *Evolution of the Flora and Fauna of Arid Australia*. (ed. by W. R. Barker and P. J. M. Greenslade). Peacock Publications, Frewville.

Schröter, D., C. Polsky & A. G. Patt (2005) Assessing vulnerabilities to the effects of global change: an eight step approach. *Mitigation and Adaptation Strategies for Global Change* **10**, 573-596.

Schwinning, S., O. E. Sala, M. E. Loik & J. R. Ehleringer (2004) Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* **141**, 191-193.

Secretariat of the Convention on Biological Diversity (2010) Global Biodiversity Outlook 3, p. 94, Montréal.

Şekercioğlu, Ç. H. (2007) Conservation ecology: area trumps mobility in fragment bird extinctions. *Current Biology* **17**, R283-R286.

Şekercioğlu, Ç. H., G. C. Daily & P. R. Ehrlich (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 18042-18047.

Sharp, B. R. & R. J. Whittaker (2003) The irreversible cattle-driven transformation of a seasonally flooded Australian savanna. *Journal of Biogeography* **30**, 783-802.

Shoo, L. P., C. Storlie, J. Vanderwal, J. Little & S. E. Williams (2011) Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Global Change Biology* **17**, 186-193.

Shoo, L. P., S. E. Williams & J. M. Hero (2005) Climate warming and the rainforest birds of the Australian wet tropics: using abundance data as a sensitive predictor of change in total population size. *Biological Conservation* **125**, 335-343.

Sirami, C., C. Seymour, G. Midgley & P. Barnard (2009) The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Diversity and Distributions* **15**, 948-957.

Smit, B., O. Pilifosova, I. Burton, B. Challenger, S. Huq, R. J. T. Klein, G. Yohe, N. Adger, T. Downing, E. Harvey, S. Kane, M. Parry, M. Skinner, J. Smith & J. Wandel (2001) Adaptation to climate change in the context of sustainable development and equity. *Climate Change 2001: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* . ed. by J. J. McCarthy, O. F. Canziani, N. A. Leary, D. J. Dokken and K. S. White. Cambridge University Press, Cambridge, UK.

Smithers, B. V., D. R. Peck, A. K. Krockenberger & B. C. Congdon (2003) Elevated sea-surface temperature, reduced provisioning and reproductive failure of wedge-tailed shearwaters (*Puffinus pacificus*) in the southern Great Barrier Reef, Australia. *Marine and Freshwater Research* **54**, 973-977.

Smyth, A. K. & C. D. James (2004) Characteristics of Australia's rangelands and key design issues for monitoring biodiversity. *Austral Ecology* **29**, 3-15.

Sparks, T. H., F. Bairlein, J. G. Bojarinova, O. Hüppop, E. A. Lehikoinen, K. Rainio, L. V. Sokolov & D. Walker (2005) Examining the total arrival distribution of migratory birds. *Global Change Biology* **11**, 22-30.

Stephens, S. L. & L. W. Ruth (2005) Federal forest-fire policy in the United States. *Ecological Applications* **15**, 532-542.

Stewart, J. B., R. V. Smart, S. C. Barry & S. M. Veitch (2001) 1996/97 Land Use of Australia - Final Report for Project BRR5. ed. by C. National Land and Water Resources Audit.

Stockwell, D. R. B. & A. T. Peterson (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**, 1-13.

Swets, J. (1988) Measuring the accuracy of diagnostic systems. *Science* **240**, 1285-1293.

Tassicker, A. L., A. S. Kutt, E. Vanderduys & S. Mangru (2006) The effects of vegetation structure on the birds in a tropical savanna woodland in north-eastern Australia. *Rangeland Journal* **28**, 139-152.

TEEB (2009) The global biodiversity crisis and related policy challenge. *The Economics of Ecosystems and Biodiversity for National and International Policy Makers*. ed. by P. ten Brink. Institute for European Environmental Policy (IEEP).

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, M. F. Alan Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips & S. E. Williams (2004) Extinction risk from climate change. *Nature* **427**, 145-148.

Thomas, C. D. & J. J. Lennon (1999) Birds extend their ranges northwards. *Nature* **399**, 213-213.

Tingley, M. W., W. B. Monahan, S. R. Beissinger & C. Moritz (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences* **106**, 19637-19643.

Traill, L. W., P. Whitehead & B. W. Brook (2009) How will climate change affect plant-herbivore interactions? A tropical waterbird case study. *Emu* **109**, 126-134.

Turner, I., B. L., R. E. Kasperson, P. A. Matson, J. J. McCarthy, R. W. Corell, L. Christensen, N. Eckley, J. X. Kasperson, A. Luers, M. L. Martello, C. Polsky, A. Pulsipher & A. Schiller (2003) A framework for vulnerability analysis in sustainability science. *PNAS* **100**, 8074-8079.

Uys, R. G., W. J. Bond & T. M. Everson (2004) The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* **118**, 489-499.

Valentine, L. E., L. Schwarzkopf, C. N. Johnson & A. C. Grice (2007) Burning season influences the response of bird assemblages to fire in tropical savannas. *Biological Conservation* **137**, 90-101.

Van Der Jeugd, H. P., G. Eichhorn, K. E. Litvin, J. Stahl, K. Larsson, A. J. Van Der Graaf & R. H. Drent (2009) Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology* **15**, 1057-1071.

VanDerWal, J., L. Beaumont, N. E. Zimmermann & P. Lorch (2011) Package 'climates': methods for working with weather and climate, www.rforge.net/climates/.

VanDerWal, J., L. P. Shoo, C. Graham & S. E. William (2009a) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling* **220**, 589-594.

VanDerWal, J., L. P. Shoo, C. N. Johnson & S. E. Williams (2009b) Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist* **174**, 282-291.

Visser, M. E., C. Both & M. M. Lambrechts (2004) Global Climate Change Leads to Mistimed Avian Reproduction. *Advances in Ecological Research: Birds and Climate Change*. (ed. by A. P. Moller, W. Fiedler and P. Berthold), pp. 89-110. Elsevier Academic Press.

Visser, M. E., A. C. Perdeck, J. H. van Balen & C. Both (2009) Climate change leads to decreasing bird migration distances. *Global Change Biology* **15**, 1859-1865.

Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen & C. M. Lessells (1998) Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 1867-1870.

Walker, J. & A. N. Gillison (1982) Australian savannas. *Dynamics of Savanna Ecosystems*. (ed. by B. Huntley and B. Walker), pp. 5-24. Springer-Verlag, Heidelberg.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg & F. Bairlein (2002) Ecological responses to recent climate change. *Nature* **416**, 389-395.

Ward, D. P. & A. S. Kutt (2009) Rangeland biodiversity assessment using fine scale on-ground survey, time series of remotely sensed ground cover and climate data: an Australian savanna case study. *Landscape Ecology* **24**, 495-507.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D. Moss & C. D. Thomas (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65-69.

Watterson, I., P. H. Whetton, A. Moise, B. Timbal, S. Power, J. Arblaster & K. McInnes (2007) Regional climate change predictions. *Climate Change in Australia, Technical Report*. CSIRO, Australian Bureau of Meteorology.

Weaver, C. M. (1982) Breeding habitats and status of the golden-shouldered parrot *Psephotus chrysopterygius*, in Queensland. *Emu* **82**, 2-6.

Webb, T. J. & K. J. Gaston (2000) Geographic range size and evolutionary age in birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**, 1843-1850.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan & T. W. Swetnam (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science* **313**, 940-943.

Whetton, P. H., K. L. McInnes, R. N. Jones, K. J. Hennessy, R. Suppiah, C. M. Page, J. Bathols & P. J. Durack (2005) Australian climate change projections for impact assessment and policy application: A review. Climate Impact Group, CSIRO Marine and Atmospheric Research.

Wiens, J. A. (1974) Climatic instability and the "Ecological Saturation" of bird communities in North American grasslands. *The Condor* **76**, 385-400.

Wiens, J. A. (1976) Population responses to patchy environments. *Annual Review Ecology, Evolution and Systematics* **7**, 81-120.

Wilbanks, T. J. & R. W. Kates (1999) Global change in local places: how scale matters. *Climatic Change* **43**, 601-628.

Williams, A. A. J., D. J. Karoly & N. Tapper (2001) The sensitivity of Australian fire danger to climate change. *Climatic Change* **49**, 171-191.

Williams, J. W., S. T. Jackson & J. E. Kutzbacht (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 5738-5742.

Williams, R. J., R. A. Bradstock, G. J. Cary, N. J. Enright, A. M. Gill, A. C. Leidloff, C. Lucas, R. J. Whelan, A. N. Andersen, D. M. J. S. Bowman, P. J. Clarke, G. D. Cook, K. J. Hennessy & A. York (2009a) Interactions between climate change, fire regimes and biodiversity in Australia – a preliminary assessment. Report to the Department of Climate Change and Department of the Environment, Water, Heritage and the Arts, Canberra.

Williams, R. J., J. Carter, G. A. Duff, J. C. Z. Woinarski, G. D. Cook & S. L. Farrer (2005) Carbon accounting, land management, science and policy uncertainty in Australian savanna landscapes: introduction and overview. *Australian Journal of Botany* **53**, 583-588.

Williams, R. J., A. D. Griffiths & G. E. Allan (2002) Fire regimes and biodiversity in the savannas of northern Australia. *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*. (ed. by R. A. Bradstock, J. E. Williams and A. M. Gill), pp. 281-304. Cambridge University Press.

Williams, S. E., E. E. Bolitho & S. Fox (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**, 1887-1892.

Williams, S. E. & J. Middleton (2008) Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions* **14**, 69-77.

Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann & G. Langham (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* **6**, e325.

Williams, S. E., Y. M. Williams, J. VanDerWal, J. L. Isaac, L. P. Shoo & C. N. Johnson (2009b) Ecological specialization and population size in a biodiversity hotspot: how rare species avoid extinction. *Proceedings of the National Academy of Sciences* **106**, 19737–19741.

Woinarski, J. (2006) Predictors of nomadism in Australian birds: a re-analysis of Allen and Saunders (2002). *Ecosystems* **9**, 689-693.

Woinarski, J. C., G. Connors & D. C. Franklin (2000a) Thinking honeyeater: nectar maps for the Northern Territory, Australia. *Pacific Conservation Biology* **6**, 61-80.

Woinarski, J. C. Z. (1990) Effects of fire on the bird communities of tropical woodlands and open forests in northern Australia. *Australian Journal of Ecology* **15**, 1-22.

Woinarski, J. C. Z. (1993a) Australian tropical savannas, their avifauna, conservation status and threats. *Birds and their habitats: status and conservation in Queensland*. (ed. by C. P. Catterall, P. V. Driscoll, K. Hulsman, D. Muir and A. Taplin), pp. 45-63. Queensland Ornithological Society, Brisbane.

Woinarski, J. C. Z. (1993b) A cut-and-paste community - birds of the monsoon rainforests in Kakadu National Park, Northern Territory. *Emu* **93**, 100-120.

Woinarski, J. C. Z. (2000) The conservation status of rodents in the monsoonal tropics of the Northern Territory. *Wildlife Research* **27**, 421-435.

Woinarski, J. C. Z., M. Armstrong, K. Brennan, A. Fisher, A. D. Griffiths, B. Hill, D. J. Milne, C. Palmer, S. Ward, M. Watson, S. Winderlich & S. Young (2010) Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research* **37**, 116-126.

Woinarski, J. C. Z. & A. J. Ash (2002) Responses of vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. *Austral Ecology* **27**, 311-323.

Woinarski, J. C. Z., C. Brock, M. Armstrong, C. Hempel, D. Cheal & K. Brennan (2000b) Bird distribution in riparian vegetation in the extensive natural landscape of Australia's tropical savanna: a broad-scale survey and analysis of a distributional data base. *Journal of Biogeography* **27**, 843-868.

Woinarski, J. C. Z., C. Brock, A. Fisher, D. Milne & B. Oliver (1999) Response of birds and reptiles to fire regimes on pastoral land in the Victoria River District, Northern Territory. *Rangeland Journal* **21**, 24-38.

Woinarski, J. C. Z. & C. P. Catterall (2004) Historical changes in the bird fauna at Coomooboolaroo, northeastern Australia, from the early years of pastoral settlement (1873) to 1999. *Biological Conservation* **116**, 379-401.

Woinarski, J. C. Z., S. Legge, J. A. Fitzsimons, B. J. Traill, A. A. Burbidge, A. Fisher, R. S. C. Firth, I. J. Gordon, A. D. Griffiths, C. N. Johnson, N. L. McKenzie, C. Palmer, I. Radford, B. Rankmore, E. G. Ritchie, S. Ward & M. Ziembicki (2011) The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters*, DOI: 10.1111/j.1755-1263X.2011.00164.x.

Woinarski, J. C. Z., J. C. McCosker, G. Gordon, B. Lawrie, C. James, J. Augusteyn, L. Slater & T. Danvers (2006) Monitoring change in the vertebrate fauna of central Queensland, Australia, over a period of broad-scale vegetation clearance, 1973-2002. *Wildlife Research* **33**, 263-274.

Woinarski, J. C. Z., D. J. Milne & G. Wanganeen (2001) Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecology* **26**, 360-370.

Woinarski, J. C. Z., J. Risler & L. Kean (2004) Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* **29**, 156-176.

Woinarski, J. C. Z., P. J. Whitehead, D. M. J. S. Bowman & J. Russell-Smith (1992) Conservation of mobile species in a variable environment: the problem of reserve design in the Northern Territory, Australia. *Global Ecology and Biogeography Letters* **2**, 1-10.

Woinarski, J. C. Z., R. J. Williams, O. Price & B. Rankmore (2005) Landscapes without boundaries: wildlife and their environments in northern Australia. *Wildlife Research* **32**, 377-388.

Yu, J. & F. S. Dobson (2000) Seven forms of rarity in mammals. *Journal of biogeography* **27**, 131-139.

Ziembicki, M. & J. Woinarski (2007) Monitoring continental movement patterns of the Australian Bustard *Ardeotis australis* through community-based surveys and remote sensing. *Pacific Conservation Biology* **13**, 128-142.

Zimmermann, N. E., N. G. Yoccoz, T. C. Edwards, E. S. Meier, W. Thuiller, A. Guisan, D. R. Schmatz & P. B. Pearman (2009) Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences* **106**, 19723-19728.

Zuckerberg, B., A. M. Woods & W. F. Porter (2009) Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* **15**, 1866-1883.