

Changes in forest-bird assemblage structure in response to
multiple pressures: climate and vegetation change

A thesis submitted for the degree of Doctor of Philosophy

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Notice 1

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Fig.1 yellow-faced honeyeater, *Lichenostomus chrysops*



Fig.2 fragmented remanent vegetation in the box-ironbark region

Table of Contents

Abstract.....	xi
Acknowledgements	xvii
Chapter 1: General Introduction.....	1
Thesis outline.....	5
Figure 1	8
REFERENCES	9
Chapter 2: The interaction between a drying climate and land use affects forest structure and above-ground carbon storage.....	15
ABSTRACT	16
INTRODUCTION	17
METHODS	19
Vegetation characteristics.....	21
Estimation of carbon storage	21
STATISTICAL ANALYSES	23
Vegetation change	23
Environmental predictors	23
RESULTS.....	25
Overall change in vegetation	25
Change in individual vegetation characteristics	25
Vegetation characteristics.....	26
Carbon content.....	26
DISCUSSION.....	27
Forest structure	27
Carbon dynamics	28
Management	29
Overview	30
ACKNOWLEDGEMENTS.....	30
Table 1	38
Table 2.....	39
Figure 1	42
Chapter 3: Resistance and resilience to pressures: Can the abrupt end of extreme drought reverse the collapse of an avifauna?	45
ABSTRACT	46
INTRODUCTION	47

METHODS	49
Climate data	50
Bird-occurrence data	50
Fragment survey data	51
Landscape-survey data	51
Ecological traits.....	52
STATISTICAL ANALYSES	52
RESULTS	54
The Big Dry	54
The Big Wet.....	54
Long-term change	54
Consistency between survey programs	55
Species' resistance and resilience	55
Ecological traits.....	56
DISCUSSION	56
Diminished resistance and resilience	56
Resistance versus resilience	58
Ecological traits.....	58
Global implications	60
ACKNOWLEDGEMENTS	61
REFERENCES.....	62
Table 1	67
Table 2	68
Figure 1	70
Figure 2.....	70
Figure 3	70
Figure 4.....	70
Figure 5	71
Chapter 4: Climate drying amplifies the effects of fragmentation and interspecific interactions on birds.....	81
ABSTRACT.....	82
INTRODUCTION	83
METHODS	86
Climate data	86
Vegetation measurements	87

Bird surveys	87
STATISTICAL ANALYSES	89
Multivariate analyses	89
Species and guild-based analyses	89
Parameter inference	90
Responses in individual bird species to vegetation variables	90
Model-fitting and checking	91
RESULTS	92
Bird assemblage change	92
Responses of bird species to noisy miners and habitat characteristics	93
Patterns for bird guilds	94
DISCUSSION	94
Synthesis	98
ACKNOWLEDGEMENTS	99
REFERENCES	100
Table 1	106
Table 2	108
Table 3	111
Table 4	112
Figure 1	116
Chapter 5: Variation in abundance of nectarivorous birds: Does a competitive despot interfere with flower-tracking?	119
ABSTRACT	120
INTRODUCTION	122
METHODS	126
Bird surveys	126
Vegetation measurements	127
Flowering estimates	127
STATISTICAL ANALYSES	128
RESULTS	130
Flowering dynamics	130
Nectarivore dynamics	131
Nectarivore dynamics in relation to flowering	131
DISCUSSION	133
Synthesis	137

ACKNOWLEDGEMENTS	138
REFERENCES.....	139
Table 1	146
Table 2	149
Figure 1	150
Figure 2.....	150
Figure 3.....	150
Figure 4.....	151
Chapter 6: Habitat fragmentation and vegetation change alters interspecific interactions with negative consequences for the recruitment of woodland birds.....	155
ABSTRACT.....	156
INTRODUCTION	157
METHODS	160
Vegetation characteristics	160
Breeding behavior scores	161
Assemblage response variables.....	162
STATISTICAL ANALYSES	162
Assemblage response	162
Responses to predictor variables.....	163
RESULTS	165
Fragmentation effects.....	165
Vegetation characteristics	165
Effects of noisy miner	166
DISCUSSION	166
Habitat fragmentation and vegetation characteristics	167
Effects of noisy miner	168
ACKNOWLEDGEMENTS	170
REFERENCES.....	171
Table 1	178
Figure 1	180
Chapter 7: General Discussion.....	183
Conclusions.....	187
Figure 1	188
REFERENCES.....	189
Appendix 1.....	191

Abstract

Climate change is linked to negative effects on vegetation, including drought-induced vegetation dieback. Large-scale dieback leads to considerable carbon emissions and loss of ecological resources for fauna. The consequences of vegetation change for biodiversity include; reductions in breeding success, population sizes, dispersal, resistance to other pressures, and changes in species composition. Changes in species composition alter interspecific interactions, such as competition, predation, parasitism and pollination, which collectively affect assemblage dynamics and ecosystem function. Competitive species that are resistant to, or have benefited from disturbances may monopolize resources (nesting sites and food) and limit the survival and recruitment of disturbance-sensitive species.

I investigated whether and how the vegetation structure, composition and carbon content changed over a period of extended drought in a much-modified forest ecosystem. I explored if landscape configuration, management practice or soil type influenced vegetation change and identified the factors that influence the spatial and temporal distribution of bird assemblages, including climate, vegetation structure, vegetation loss/fragmentation, interspecific species interactions and resource provision. Lastly, I assessed if the recruitment of native birds is influenced by vegetation loss/fragmentation, drought-driven habitat degradation, and interspecific interactions.

Box and ironbark forests of Victoria in south-eastern Australia are an example of a highly modified, ecosystem in which the joint effects of fragmentation and climate change have not been systematically measured. These forests experienced drought stress from 1997 until 2010, in conjunction with the on-going loss, degradation and fragmentation of native vegetation by human encroachment. The study design incorporates vegetation fragments of a range of sizes, allowing the evaluation of fragmentation/habitat loss effects. I made direct comparisons of changes in avian and vegetation assemblage structure and condition over the last 15 years by revisiting sites measured previously (1997). These data, used in conjunction with observations of breeding success, provided

an opportunity to investigate the long-term interaction between vegetation change and climate-change.

Forest structure was systemically different between the two periods. Canopy cover, shrub cover and litter decreased between 1997 and 2010, while the total basal area of dead trees in all size classes increased. The effects were amplified in fragmented vegetation, probably due to greater water and heat stress. Avian assemblages changed significantly between 1997 and 2010, with many woodland bird species halving in both prevalence (proportion of sites occupied) and abundance (numbers when present). Declines were largely independent of species ecological traits (i.e. nesting, foraging, range etc.). Changes in the bird community were associated with precipitation, temperature, vegetation cover (canopy, ground and mid-storey cover) and the density of the noisy miner *Manorina melanocephala*. The reduction in canopy foliage, ground-litter and shrub cover probably has reduced food resources and nesting sites. Greater noisy miner abundance as an additive effect of fragmentation and degradation had a greater negative effect on species' breeding behavior than on-transect vegetation characteristics. Nectarivores tracked spatial and temporal variation in flowering, but this relationship was disrupted in the presence of noisy miners.

The box-ironbark region serves as an exemplar for other regions undergoing increases in the frequency and duration of extreme climatic events, such as North America, Europe, southern Africa and Asia. My work is among the first to consider interacting pressures that arise from major drivers of ecological change. The loss, fragmentation and degradation of habitat have caused declines in many native species but have facilitated increases in the abundance and distribution of other native species. Projected climate change (i.e. hotter and drier conditions) may exacerbate changes in the bird assemblage by accelerating vegetation degradation, especially in smaller fragments. I found that greater drought-driven vegetation degradation in smaller fragments facilitated the expansion of a highly competitive native, the noisy miner. The noisy miner by acting as an interference competitor (defending space) disproportionately excluded smaller-bodied birds from sites where the noisy miner occurs. This reduced the access of small-bodied birds to valuable resources (nesting and food)

which may limit their capacity to recover from adverse climate events (e.g. long drought), with long-term consequences for the persistence of small-bodied species. As climates become more extreme, similar effects to those that I report are likely to arise in other fragmented regions and for other taxa, because interspecific interactions are not limited to avifaunas, and fragmentation has been linked to altered species interactions in many regions of the world.

PART A: General Declaration

Monash University

Declaration for thesis based or partially based on conjointly published or unpublished work

General Declaration

In accordance with Monash University Doctorate Regulation 17.2 Doctor of Philosophy and Research Master's regulations the following declarations are made:

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes one original papers published in peer reviewed journals and four unpublished publications. The core theme of the thesis is the interactive impacts of climate and land use change on bird assemblages. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the Mac Nally and Clarke Lab under the supervision of Prof Ralph Mac Nally and Dr Rohan Clarke.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research. In the case of chapters 2-5 my contribution to the work involved the following:

Thesis chapter	Publication title	Publication status*	Nature and extent of candidate's contribution
2	The interaction between a drying climate and land use affects forest structure and above-ground carbon storage	Published	The candidate collected and analyzed most of the data, and was the primary author and contributor to the MS.
3	Species resistance v resilience: Can the abrupt end of extreme drought reverse the collapse of an avifauna?	In review	The candidate collected and analyzed most of the data, and was a primary author and contributor to the MS.
4	Climate drying amplifies the effects of fragmentation and interspecific interactions on birds	In review	The candidate collected all of the data, did most of the analysis and was a primary

			author and contributor to the MS.
5	Variation in abundance of nectarivorous birds: Does a competitive despot interfere with flower-tracking?	In review	The candidate collected all of the data, did most of the analysis and was a primary author and contributor to the MS.
6	Habitat fragmentation and vegetation change alters interspecific interactions with negative consequences for the recruitment of woodland birds	In review	The candidate collected all of the data, did most of the analysis and was a primary author and contributor to the MS.

I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Signed:

Date:

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Chapter 1: General Introduction

Anthropogenic climate change is expected to increase the frequency and severity of extreme climatic events, such as long-term, severe droughts and intense rains and floods (Hennessy *et al.*, 2008). An increase in the frequency of extreme events may produce a greater threat to biodiversity than a gradual deviation from mean climatic conditions because climate extremes restructure ecological assemblages (Jimenez *et al.*, 2011; Greenville *et al.*, 2012). Despite this, most ecological studies on the effects of climate change have focused on increases in mean temperature to assess range shifts (Lenoir *et al.*, 2008) and changes in life-history phenologies (Cleland *et al.*, 2007), (although see Thompson *et al.*, 2013).

Given that all inhabited continents of the world have experienced land-use change, increases in extreme climatic events will be superimposed upon already massively transformed landscapes (Opdam & Wascher, 2004; Foley *et al.*, 2005). Anthropogenic land-use change, primarily driven by the conversion of native vegetation into agricultural land, is widely recognized as the major driver of global biodiversity loss (Foley *et al.*, 2005). Although recent projections suggest climate change may surpass land-use change in the coming decades (Bellard *et al.*, 2012). It is possible, that climate change and land-use change will act synergistically so that their combined adverse effects on biota will be greater than the sum of their individual effects (Mantyka-Pringle *et al.*, 2012). Fragmented remnants of vegetation may be more vulnerable to climate change than intact vegetation due to shifts in the regional distribution of precipitation, local drying, and increased frequency and severity of fires (Brook *et al.*, 2008). Despite this, climate change and land-use change are rarely considered together in empirical studies, suggesting that current knowledge may be inadequate for effective conservation management of ecosystems threatened by multiple pressures (Mantyka-Pringle *et al.*, 2012).

The interaction of pressures may limit the ability of the biota to absorb the impacts of pressures (= resistance) and to recover following impact (= resilience) (Harrison, 1979), especially

when the frequency and duration of ‘natural’ disturbances is increasing (Hennessy *et al.*, 2008). The ability of an assemblage to return to its original state following a disturbance requires that resistance be inversely related to resilience (Herbert *et al.*, 1999; Orwin *et al.*, 2006). Such that a species with poor resistance has high resilience, while a species with high resistance has low resilience. The capacity for species to resist or recover from long-term drought, is likely to be contingent on: (1) the extent and severity of drought and the associated time lags in the replenishment of diminished resources (e.g. food and vegetation); (2) the extent of available habitat in massively altered landscapes that can accommodate resistance or recovery (Morecroft *et al.*, 2012); and (3) the ecological traits of species that enhance or reduce resistance and resilience (Smith, 2011; Chessman, 2013). Long-term, large-scale, detailed datasets that track assemblages through climatic extremes (e.g. drought) are rare, so that our knowledge of the resistance and resilience within assemblages to such events in heavily modified landscapes is limited.

The response of many species, to climate change is likely to be indirect, with the modification of habitat and asynchrony with species’ food requirements being key pressures (Bellard *et al.*, 2012). Vegetation degradation may lead to an ‘extinction spiral’, in which environmental, demographic and genetic factors interact and recruitment decreases or fails (Caughley, 1994; Ford *et al.*, 2009). Vegetation change has many effects on biodiversity, including: reductions in population sizes, breeding success, dispersal, increased vulnerability to other pressures, and changes in species composition and interspecific interactions (Mac Nally & Bennett, 1997).

Drought has been linked to adverse effects on vegetation, including dieback (Horner *et al.*, 2009; Allen *et al.*, 2010) and impaired regeneration (Suarez & Kitzberger, 2010). Forest dieback under recent severe droughts or high temperatures have been recorded in Europe (Bréda *et al.*, 2006), North America (van Mantgem *et al.*, 2009) and Australia (Cunningham *et al.*, 2009; Brouwers *et al.*, 2013), highlighting the probability that recent climate change may be causing changes in forest structure (Allen *et al.*, 2010). Climate-driven vegetation dieback may release

stored carbon, contributing to rising global atmospheric carbon dioxide (CO₂). However, the current role of CO₂ emissions from terrestrial ecosystems in the carbon cycle is not fully understood (Schaphoff *et al.*, 2006).

Vegetation change has been linked to major declines in abundance and distribution of many native species, but has facilitated the increase in abundance and distribution of others, both native and invasive alike (Carey *et al.*, 2012). Climate change, by degrading vegetation, may induce changes in interspecific interactions because these are influenced by the phenology, physiology, relative abundances, and behaviors of multiple species, which can be influenced directly by the prevailing climate (Tylianakis *et al.*, 2008). The invasion and overabundance of some species has the potential to cause further major ecological disturbance because even small shifts in the relative abundances and competitive relationships of species can significantly alter interspecific interactions and ecosystem function (Carey *et al.*, 2012). For example, habitat fragmentation, by facilitating access to forest habitat for some avian nest predators and parasites, has been linked to declines in the reproductive success of other species, potentially altering forest bird assemblages (Robinson *et al.*, 1995). The effects of altered interspecific interactions are rarely considered in studies of multiple pressures, such as climate and land-use change, probably due to their complexity and the inherent difficulty in measuring effects (Tylianakis *et al.*, 2008).

Little attention has been paid to possible population-dynamic effects of climate change, land-use change and interspecific interactions, including potential adverse effects on breeding success (Mac Nally *et al.*, 2009). Studies on the effects of human pressures typically focus on species richness or assemblage composition, but these measures do not provide an indication of the population viabilities of the constituent taxa (Korfanta *et al.*, 2012). The knowledge of which traits make species sensitive to the effects of habitat fragmentation and climate change may be useful for identifying target groups of species for conservation actions (Barbaro & van Halder, 2009).

Birds are ‘exemplars’ for investigating whether climate and land-use change interact and affect interspecific interactions. Differences in extinction risk among species will affect interspecific

interactions and the structure of assemblages (Korfanta *et al.*, 2012). Competitive species that are tolerant of, or benefit from, change may monopolize resources (nesting sites, food), limiting the persistence of disturbance-sensitive species (Brown, 2007). Such disparities in responses have potential adverse consequences on ecological services, including pollination, seed dispersal and invertebrate control performed by birds, which, in turn, may influence the on-going maintenance of vegetation (Sekercioglu, 2006). Birds are among the most mobile of animals, and many species track food resources across landscapes (Mac Nally & McGoldrick, 1997), increasing the likelihood that birds ‘experience’ and can respond to changes in landscape configuration and spatial variation in resource availability (Thomson *et al.*, 2007).

South-eastern Australia has been exposed to the interaction between land-use and climate change. Temperatures in south-eastern Australia have increased since the 1950s, with a 1 °C increase in mean daily temperature (Leblanc *et al.*, 2012). By 2070, south-eastern Australia is projected to experience a further 1–6 °C mean annual temperature increase and a 5-15% decrease in rainfall in all months (IPCC, 2007). Climate-change modelling for the region predicts substantial increases in the frequency and severity of droughts that may span a decade or more (Leblanc *et al.*, 2012). The region experienced a 13-year drought from 1997, referred to as the ‘Big Dry’, which was followed by heavy spring and summer rainfall in 2010 until early in 2012, which is now termed the ‘Big Wet’ (Leblanc *et al.*, 2012). Consistent with climate-change projections, the duration and accumulated precipitation deficit over the Big Dry was at least twice that of any other drought since instrumental records began in the 1880s (Leblanc *et al.*, 2012). The occurrence of the Big Wet was consistent with climate-change projections in which rainfall events are expected to be condensed into shorter, more intense periods (Hennessy *et al.*, 2008).

Since European settlement in Australia *c.* 225 years ago, the extent of native forest in the south-east has been halved (McAlpine *et al.*, 2009), although some bioregions have experienced as much as 97% clearance (ECC, 2001). The extensive reduction in native vegetation cover has altered surface characteristics, decreasing evapotranspiration and modified soil and atmospheric moisture

patterns (McAlpine *et al.*, 2009). The resulting changes in climate at the regional scale are likely to have further exacerbated the effects of the Big Dry (McAlpine *et al.*, 2009).

Thesis outline

The box-ironbark forests of Victoria in south-eastern Australia are a prime example of a fragmented and highly modified ecosystem in which the joint effects of fragmentation and climate change can be evaluated. The conceptual model (Fig. 1) identifies the relevance of each of my chapters to a network of interactions that arise from these two principal drivers (climate and land-use change) on terrestrial ecosystems. Victoria's box-ironbark forests have experienced significant pressure from drought from 1997 until 2010 superimposed on the pressure of vegetation loss, degradation and fragmentation (Murphy & Timbal, 2008; Mac Nally *et al.*, 2009). By revisiting sites measured previously and by gathering data in exactly the same manner, I have made a direct assessment of changes in avian and vegetation assemblage over the last 15 years. The study design of Mac Nally *et al.* (2000) incorporated fragments of a range of sizes, allowing my study to consider the effects of fragmentation/habitat loss. The long-term nature of my study provided an opportunity to investigate the nature of the interaction between land-use change and climate-change over this period (Fig. 1). These data, when used in conjunction with observations of breeding success, will allow me to estimate species' relative vulnerabilities to climate change and vegetation fragmentation, loss, and degradation. I investigated the effects of changing resource availability (e.g., nectar) and interspecific interactions on avian assemblages (Fig. 1). The breaking of the drought allowed me to assess the resilience of bird species. The main objective of this study was to investigate the factors that influence the spatial and temporal distribution of avian assemblages of box-ironbark forests. Specifically, my research sought to achieve the following aims:

1. To investigate the interaction between climate change and habitat fragmentation on the degradation of native vegetation (Fig. 1). I sought to determine whether, and how, the structure, composition and carbon content of the box-ironbark forests changed between 1997 and 2010 (the

duration of the ‘Big Dry’) and if landscape configuration, management practice or soil type influenced vegetation change (Chapter 2).

2. To determine if the avian assemblage changed over the Big Dry and if there was recovery in the Big Wet. I explored whether resistance was related to resilience to make inferences about long-term population viability of birds. Specifically, did the Big Wet reverse declines in avifauna that occurred during the Big Dry and what, if any, are the ecological traits of species that lead to higher resistance or resilience to severe drought, and do traits that confer resistance/resilience differ (Chapter 3)?
3. To investigate the link between vegetation change and avian assemblages (Fig. 1), and to determine if avifaunal changes were consistent with the changes in habitat characteristics in this much modified forest ecosystem. I sought to evaluate if changes were amplified by fragmentation or by altered species interactions (Chapter 4).
4. To investigate the link between food resources and the dynamics of consumers (Fig. 1). Nectarivores numerically dominate the box-ironbark avifauna assemblage, so I explored whether nectarivores track spatial and temporal variation in flowering (as a measureable indication of nectar availability at a large scale) and if any emerging relationship is affected by vegetation characteristics and altered competitive interspecific interactions (Chapter 5).
5. To investigate how measures of recruitment of native birds are influenced by the spatial arrangement of native vegetation, vegetation characteristics, degradation, species interactions and combinations of these factors (Chapter 6).

The outcomes of these studies will help to quantify the relationships in Fig.1. Given that these processes are global issues, my work could inform approaches to manage vegetation effectively at landscape and regional scales in other parts of the world that are experiencing, or will be subject to, increasing levels of exposure to climate extremes. The additive effects of fragmentation, degradation and climate change, which cause widespread vegetation change, which is likely to negatively affect many species while benefiting few. Highly competitive species if resistant

to vegetation change may gain a competitive edge, allowing them to monopolize resources (nesting sites and food), further limiting the success of disturbance-sensitive species (Brown, 2007).

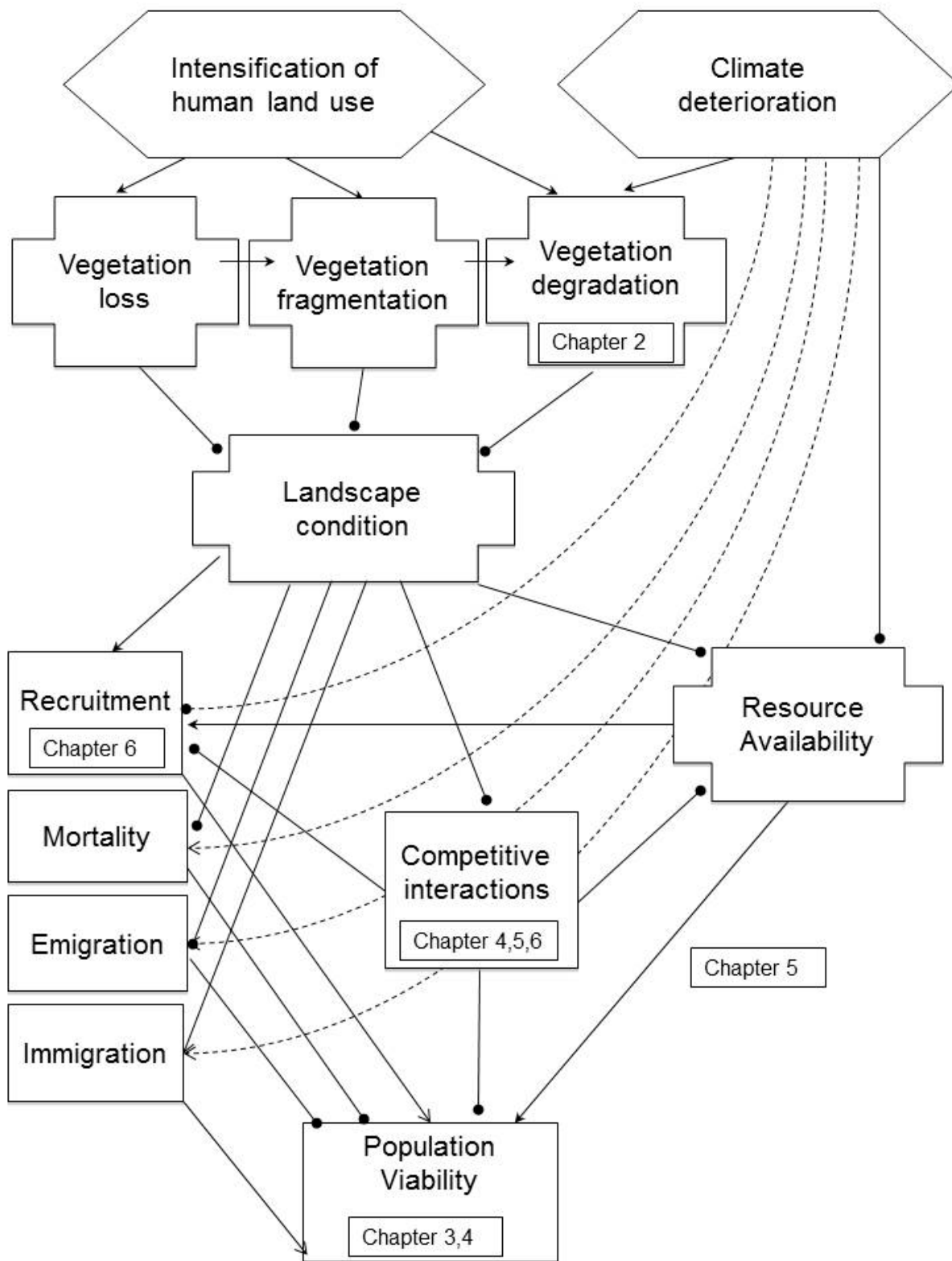


Figure 1: Conceptual model of the potential factors that may determine the spatial and temporal changes in the bird and vegetation assemblages, ↓ indicates a negative effect, ↑ indicates a positive effect and ···· not demonstrated.

REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-684.
- Barbaro, L. & van Halder, I. (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography*, **32**, 321-333.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365-377.
- Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625-644.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453-460.
- Brouwers, N., Matusick, G., Ruthrof, K., Lyons, T. & Hardy, G. (2013) Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem. *Landscape Ecology*, **28**, 69-80.
- Brown, W.P. (2007) Body mass, habitat generality, and avian community composition in forest remnants. *Journal of Biogeography*, **34**, 2168-2181.
- Carey, M.P., Sanderson, B.L., Barnas, K.A. & Olden, J.D. (2012) Native invaders – challenges for science, management, policy, and society. *Frontiers in Ecology and the Environment*, **10**, 373-381.
- Caughley, G. (1994) Directions in conservation biology *Journal of Animal Ecology*, **63**, 215-244.
- Chessman, B.C. (2013) Identifying species at risk from climate change: Traits predict the drought vulnerability of freshwater fishes. *Biological Conservation*, **160**, 40-49.

- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, **22**, 357-365.
- Cunningham, S.C., Mac Nally, R., Read, J., Baker, P.J., White, M., Thomson, J.R. & Griffioen, P. (2009) A robust technique for mapping vegetation condition across a major river system. *Ecosystems*, **12**, 207-219.
- ECC (2001) *Box-Ironbark Forests and Woodlands Investigation*. Environment Conservation Council, Melbourne.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570-574.
- Ford, H.A., Walters, J.R., Cooper, C.B., Debus, S.J.S. & Doerr, V.A.J. (2009) Extinction debt or habitat change? - Ongoing losses of woodland birds in north-eastern New South Wales, Australia. *Biological Conservation*, **142**, 3182-3190.
- Greenville, A.C., Wardle, G.M. & Dickman, C.R. (2012) Extreme climatic events drive mammal irruptions: regression analysis of 100-year trends in desert rainfall and temperature. *Ecology and Evolution*, **2**, 2645-2658.
- Harrison, G.W. (1979) Stability under environmental stress: resistance, resilience, persistence, and variability. *The American Naturalist*, **113**, 659-669.
- Hennessy, K., Fawcett, R., Kirono, D., Mpelasoka, F., Jones, D., Bathols, J., Whetton, P. & Smith, M.S. (2008) An assessment of the impact of climate change on the nature and frequency of exceptional climatic events. In. CSIRO and the Australian Bureau of Meteorology, Canberra.
- Herbert, D.A., Fownes, J.H. & Vitousek, P.M. (1999) Hurricane damage to a Hawaiian forest: nutrient supply rate affects resistance and resilience. *Ecology*, **80**, 908-920.

- Horner, G.J., Baker, P.J., Mac Nally, R., Cunningham, S.C., Thomson, J.R. & Hamilton, F. (2009) Mortality of developing floodplain forests subjected to a drying climate and water extraction. *Global Change Biology*, **15**, 2176-2186.
- IPCC (2007) Climate Change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. In: (ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), p. 996, Cambridge University Press, Cambridge.
- Jimenez, M.A., Jaksic, F.M., Armesto, J.J., Gaxiola, A., Meserve, P.L., Kelt, D.A. & Gutierrez, J.R. (2011) Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. *Ecology Letters*, **14**, 1227-1235.
- Korfanta, N.M., Newmark, W.D. & Kauffman, M.J. (2012) Long-term demographic consequences of habitat fragmentation to a tropical understory bird community. *Ecology*, **93**, 2548-2559.
- Leblanc, M., Tweed, S., Van Dijk, A. & Timbal, B. (2012) A review of historic and future hydrological changes in the Murray-Darling Basin. *Global and Planetary Change*, **80**, 226-246.
- Lenoir, J., Gégout, J.C., Marquet, P.A., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768-1771.
- Mac Nally, R. & McGoldrick, J.M. (1997) Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. *Journal of Avian Biology*, **28**, 171-183.
- Mac Nally, R. & Bennett, A.F. (1997) Species-specific predictions of the impact of habitat fragmentation: Local extinction of birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **82**, 147-155.
- Mac Nally, R., Bennett, A.F. & Horrocks, G. (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat

- fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7-29.
- Mac Nally, R., Bennett, A.F., Thomson, J.R., Radford, J.Q., Unmack, G., Horrocks, G. & Vesk, P.A. (2009) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720-730.
- Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239-1252.
- McAlpine, C.A., Syktus, J., Ryan, J.G., Deo, R.C. & McKeon, G.M. (2009) A continent under stress: interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate. *Global Change Biology*, **15**, 2206-2223.
- Morecroft, M.D., Crick, H.Q.P., Duffield, S.J. & Macgregor, N.A. (2012) Resilience to climate change: translating principles into practice. *Journal of Applied Ecology*, **49**, 547-551.
- Murphy, B. & Timbal, B. (2008) A review of recent climate variability and climate change in southeastern Australia. *International journal of climatology*, **28**, 859-879.
- Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285-297.
- Orwin, K.H., Wardle, D.A. & Greenfield, L.G. (2006) Context-dependent changes in the resistance and resilience of soil microbes to an experimental disturbance for three primary plant chronosequences. *Oikos*, **112**, 196-208.
- Robinson, S.K., Thompson, F.R., III, Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987-1990.

- Schaphoff, S., Lucht, W., Gerten, D., Sitch, S., Cramer, W. & Prentice, I. (2006) Terrestrial biosphere carbon storage under alternative climate projections. *Climatic Change*, **74**, 97-122.
- Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, **21**, 464-471.
- Smith, M.D. (2011) The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology*, **99**, 651-655.
- Suarez, M.L. & Kitzberger, T. (2010) Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. *Journal of Ecology*, **98**, 1023-1034.
- Thompson, R.M., Beardall, J., Beringer, J., Grace, M. & Sardina, P. (2013) Means and extremes: building variability into community-level climate change experiments. *Ecology Letters*, **16**, 799-806.
- Thomson, J.R., Mac Nally, R., Fleishman, E. & Horrocks, G. (2007) Predicting bird species distributions in reconstructed landscapes. *Conservation Biology*, **21**, 752-766.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351-1363.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009) Widespread increase of tree mortality rates in the western United States. *Science*, **323**, 521-524.

PART B: Suggested Declaration for Thesis Chapter

Monash University

Declaration for Thesis Chapter 2

Declaration by candidate:

In the case of Chapter 2, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The initiation, key ideas, development and writing up of the work were my responsibility. I coordinated the study and performed most of the work. I conducted most of the analysis and was the primary author of the manuscript.	60

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Shaun C. Cunningham	Contributed ideas to the work and contributed to writing of the manuscript	
Christine A. Connelly	Contributed to data collection	
Rohan H. Clarke,	Contributed to writing of the manuscript	
James R. Thomson	Support with analysis	
Ralph Mac Nally	Contributed ideas to the work and contributed to writing of the manuscript	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature		Date
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Main Supervisor's Signature		Date
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*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 2: The interaction between a drying climate and land use affects forest structure and above-ground carbon storage

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Primary Research Article

ABSTRACT

Aim Climate change has been linked to negative effects on vegetation, including drought-induced dieback. Large-scale dieback not only leads to considerable carbon emissions but often leads to loss of ecological resources. We investigated whether, and how, the structure, composition and carbon content changed over a period of extended drought (the ‘Big Dry’) in a much-modified forest ecosystem. We explored whether landscape configuration, management practice or soil type influenced vegetation change.

Location The box-ironbark forests of south-eastern Australia

Methods In 2010, we remeasured 120 forest transects that had first been measured in 1997 by using identical field methods. Vegetation structure and composition were quantified. We used allometric growth models to estimate the expected increase in above-ground carbon (AGC) storage between 1997 and 2010; these estimates were compared with observed values.

Results Forest structure was systematically different between the two periods. Canopy cover, shrub cover, and litter decreased between the 1997 and 2010 surveys, while total basal area of dead trees, dead trees in all size classes, and saplings increased between the two surveys. Climate, fragment size and their interaction were the major predictors of change in most of the measured vegetation characteristics. By comparing measured AGC in 2010 and estimates from growth models, we estimated that 5.6 ± 2.1 SE t C ha⁻¹ may have been foregone over the Big Dry.

Main conclusions Our findings add to the evidence linking climate change to negative effects on vegetation, including mortality, canopy dieback and reduced carbon sequestration. These effects may be amplified in fragmented vegetation because of greater water and heat stress. If the carbon sequestration deficit of c. 5.6 t C ha⁻¹ were to apply across the extant box-ironbark forests of Victoria (c. 255 400 ha), then 1.43 Mt of carbon sequestration may not have occurred during the Big Dry.

INTRODUCTION

Human-induced increases in atmospheric CO₂ have been linked to rising global temperatures, changes in the spatial patterns of precipitation, and increases in the frequency and severity of extreme weather events (IPCC, 2007). There is growing evidence linking climate change to adverse effects on vegetation, including dieback (Allen *et al.*, 2010) and impaired regeneration (Suarez & Kitzberger, 2010). The effects may lead to considerable shifts in the distribution of vegetation, which may induce large-scale changes in land use as natural systems respond and agriculture and other human activities are reorganized (Capon *et al.*, 2013).

Vegetation dieback and reduced tree growth may produce a net release of stored carbon (Schaphoff *et al.*, 2006). The role of emissions from terrestrial ecosystems in the carbon (C) cycle is not fully understood (Schaphoff *et al.*, 2006). There has been increasing focus on forest-based carbon storage and its relationship to biodiversity values. Forests accumulate and store carbon in soils, living biomass and fallen wood. Protecting existing and restoring structurally complex forests could result in the storage of carbon and promote biodiversity (Hatanaka *et al.*, 2011).

Dieback events caused by increases in the frequency of extreme droughts may produce large-scale changes in vegetation distribution that may be more severe than effects of gradual shifts from mean climate conditions (Hoffmann *et al.*, 2011). Forest dieback under recent severe droughts or high temperatures have been recorded in Europe (Bréda *et al.*, 2006), North America (van Mantgem *et al.*, 2009) and Australia (Brouwers *et al.*, 2013), highlighting the possibility that recent climate change may already be causing changes in forest structure (Allen *et al.*, 2010).

Since 1960, south-eastern Australia has experienced substantial warming, with a 1 °C increase in mean maximum temperature, which is consistent with global circulation models (Timbal *et al.*, 2010). From 1997, the region experienced a 13-year severe drought, ‘The Big Dry’ (Verdon-Kidd & Kiem, 2009), during which rainfall deficits were the highest recorded (Gergis *et al.*, 2011). There has been widespread clearance of forests in the south-east since European settlement in Australia, with the extent of woody vegetation halved (McAlpine *et al.*, 2009). The effects of the

Big Dry may have been exacerbated by loss of extensive tree cover, which decreases evapotranspiration and modifies atmospheric and soil moisture cycles, with flow-on effects to regional climate (McAlpine *et al.*, 2009). These processes potentially lead to further forest degradation, producing a negative climate-feedback mechanism (McAlpine *et al.*, 2009).

Land-use change resulting in the loss, fragmentation and degradation of habitat has been the most significant driver of recent biodiversity decline (Swift & Hannon, 2010). Habitat loss and fragmentation directly reduce local population sizes and increase spatial isolation, often increasing the probability of extirpation (Cushman *et al.*, 2012). In addition, fragmentation alters conditions, reducing health and seedling recruitment in many plants (Barbeta *et al.*, 2011). Fragmented vegetation may be more exposed to climate change due to regional shifts in the distribution of precipitation, local drying and increased fire frequency and severity (Brook *et al.*, 2008). Climate change may overtake land-use change as the most important negative influence on biodiversity (Mantyka-pringle *et al.*, 2012). There has been growing speculation on how climate change will affect biological populations and how it will interact with other major stressors (Mantyka-pringle *et al.*, 2012). In the Amazonian rainforests, positive feedbacks among fire, drought, forest fragmentation and climate change may already have led to irreversible changes in vegetation (Nepstad *et al.*, 2008).

The box-ironbark forests of south-eastern Australia are a prime example of a fragmented and much modified ecosystem in which the effects of fragmentation and climate change may be synergistic (Mac Nally *et al.*, 2009b). These forests generally are open woodland in character and were once widely distributed in areas now mostly used for agriculture, and there are many reports of deleterious effects on the biota of the region.

As part of the work, focused on understanding the biotic effects of land-use change in this region, detailed information on vegetation structure was collected in the late 1990s, in the early stages of the Big Dry (Mac Nally *et al.*, 2000). The availability of these data allowed us to explore

how land use (especially forest fragmentation) and climate change might interact in influencing vegetation structure.

We assessed differences in vegetation structure after the Big Dry by revisiting exactly the same sites and repeating the vegetation measures using identical field methods. Direct comparisons in such a before-after setting, spanning extended periods of time, are scarce in the literature, so these provide a rare opportunity to assess temporal changes in vegetation and the factors that influence those changes.

We expected that the Big Dry, whose occurrence is consistent with climate-change models that predict drought events of increasing duration and intensity into the 21st century, would cause widespread forest degradation. Resultant canopy dieback and tree mortality were predicted to be highest in areas with larger reductions in precipitation or larger increases in temperature (Allen *et al.*, 2010). These effects may be exacerbated in smaller remnants because of increased micro- or meso-climatic stresses, such as greater exposure to wind-throw and relatively higher evapotranspiration (Mantyka-pringle *et al.*, 2012). We asked three main questions. First, did the structure, composition and carbon content of the box-ironbark forests differ between 1997 and 2010? Second, which, if any, vegetation characteristics changed across the region over the duration of the Big Dry? Third, if there were major vegetation changes, did these differ in relation to landscape configuration, management practice or soil type?

METHODS

The box-ironbark forests of south-eastern Australia occur on the inland slopes of the Great Dividing Range, from southern Queensland to western Victoria (ECC, 2001). In the 200 yr since European settlement, the box-ironbark forests of central and northern Victoria have been reduced by 83% of their once > 3 M ha (ECC, 2001). The ecosystem has been much disturbed by human activities, including gold mining, timber felling and clearing for agriculture since European settlement, and few large (6,000–40,000 ha) remnants remain (ECC, 2001). There are many remnants scattered in

the agricultural landscape. Only 2% of the existing forest is thought to be ‘old growth’, with characteristics such as large, hollow-bearing trees. Remaining native vegetation is predominantly regrowth from wholesale clearance during in the 1850s gold rush, and on-going management for timber production has maintained the forests in a non-mature state; these woodlands are characterized by small stems that occur at high densities (ECC, 2001).

Mean annual rainfall historically ranged from 400 to 700 mm, falling mostly in winter and spring (Mac Nally *et al.*, 2000). Mean annual rainfall decreased from 537 ± 111 SD mm yr⁻¹ for 1984–1996 to 430 ± 87 mm yr⁻¹ for 1997–2009. The declines in rainfall were disproportionately large in autumn and early-winter (Verdon-Kidd & Kiem, 2009). Temperature anomalies are based on a historical baseline (1961–90), with a daily mean of 14.7 °C, a daily mean maximum of 20.6 °C and a daily mean minimum of 8.8 °C. Temperature anomalies over this period were +0.7 °C for daily mean, +0.7 °C for mean daily maximum, +0.4 °C for mean daily minimum. Between (1997–2010) mean temperature increased by 0.65 °C. Among sites between (1997–2010) cumulative temperature anomaly ranged from +0.33 °C to +0.92 °C and cumulative rainfall anomaly from –754 mm to –2023 mm. Across the domain, there was little evidence of a gradient in climate data (either from east to west or from north to south).

The spatial configuration of box-ironbark forests allows one to differentiate between the effects of fragmentation and habitat loss per se (Parker & Mac Nally, 2002). ‘Actual’ remnants of c. 10, 20, 40 and 80 ha in area were compared to replicate ‘pseudoremnants’ of notionally the same areas. Remnants have a relatively long history of isolation (> 50 yr) and are distributed around four regional centers in north-central Victoria: St Arnaud, Dunolly, Bendigo and Rushworth (Mac Nally *et al.*, 2000). Pseudoremnants were positioned within three extensive (> 10 000 ha) forest blocks in the vicinity of St Arnaud, Dunolly and Rushworth. There were 31 actual remnants (17 of 10 ha, eight 20 ha, three 40 ha and three 80 ha) and 30 pseudoremnants (twelve 10 ha, six 20 ha, six 40 ha and six 80 ha), which were each referred to as ‘sites’ (hence 61 sites containing 120 transects). To ensure representative areal coverage, survey transects were replicated within each site: (1) one

transect in each 10 ha site; (2) two in each 20 ha site; (3) three in each 40 ha site, and (4) four in each 80 ha site (Mac Nally *et al.*, 2000). Sixty-one of the 68 sites established in 1997 Mac Nally *et al.* (2000) were included in the 2010 survey; of the remainder, two 40 ha remnants and one 80 ha remnant had been largely cleared and access was no longer granted by owners at the other remnants.

Vegetation characteristics

Twenty-one vegetation variables (Table 1) were measured using exactly the same methods as were used in 1997 (Mac Nally *et al.*, 2000). To minimize potential observer differences between surveys, measurement techniques were calibrated *in situ* with G. F. B. Horrocks, who conducted the 1997 surveys. The species, diameter at breast height (DBH), and number of all trees and shrubs were recorded within an 80 × 100 m transect, as were the number of hollow-bearing trees and stumps. Trees were assigned to four size-classes; 10–39 cm DBH (small), 40–59 cm DBH (medium), 60–79 cm DBH (large) and ≥ 80 cm DBH (very large); the diameters of the latter were measured whereas the others were allocated by inspection. Trees <10 cm DBH were classified as saplings and were excluded from basal area estimates, as in the original study. An exception was the green mallee *Eucalyptus viridis*, which was included in basal area estimates because it has a multi-stemmed growth form and was considered mature regardless of stem diameter. Cover estimates were from randomly placed quadrats: two 5 × 5 m quadrats for ground-cover, two 25 × 25 m quadrats for shrub-cover, and one 10 × 50 m quadrats for fallen timber. Canopy cover was estimated at four random locations in each transect by holding a transparent grid of 30 × 20 cm, partitioned into 2 × 5 cells parallel to the ground to estimate the percentage of cells overlain by canopy.

Estimation of carbon storage

Carbon makes up c. 50% of a tree dry mass, and carbon stocks can be estimated from DBH (Grierson *et al.*, 1992). Live and dead carbon biomass at a site (t C ha⁻¹) were estimated using the allometric equation for grey box (*Eucalyptus microcarpa*), a dominant box-ironbark species within the study region (Hamilton *et al.*, 2005). The study sites within the Box-ironbark of Victoria have a relatively uniform species composition, which is dominated by three main species; *E.*

microcarpa, *E. tricarpa* and *E. leucoxylon*. All tree species in this region grow to a height of c. 25 m. The allometric equation for *E. microcarpa* was used for all species because this was the only published relationship based on trees growing in native forests within the study region and not on plantation trees in more productive regions elsewhere. This is important because climate, soils and management are major determinants of tree growth. The equation used measurements of stem cross-section as a function of volume and wood density to estimate biomass. Biomass of standing dead trees was calculated using the same allometric equations but by excluding leaves. Fallen dead timber and stump biomass was calculated using an equation developed for the river red gum (*Eucalyptus camaldulensis*), which occurs within the region; the equation converted volumetric measurements into mass (Robinson, 1997), from which C content can be calculated. The box-ironbark forest experienced wholesale clearance 150 yr ago, followed by continued selective logging of large trees up until the last decade. This repeated removal has stopped the recruitment of large trees, so that the forest cannot be considered mature. A mature tree would be at least 2 m in diameter, yet only 2 live trees were recorded across the 120 study transects that approached maturity (c. 190 cm in diameter) and no standing dead trees of this size were recorded. The majority of trees were much smaller. As such, ‘background’ mortality, due to senescence, was expected to be negligible and was excluded from estimates for biomass projections. Shrub biomass was calculated to be negligible $<0.007 \text{ t C ha}^{-1}$, and was excluded.

The Victorian State Department of Sustainability and Environment (DSE) forestry timber resource assessment involved measurements of incremental growth within mixed-species stands for several species of *Eucalyptus* in open forest and woodlands within the box-ironbark region. We used an incremental growth rate of 0.38 cm yr^{-1} , which was calculated over a period in which rainfall was considered to be average (DSE, 1998). This figure was used to project growth from the 1997 DBH measurements to estimate potential carbon sequestration in 2010 in the absence of the Big Dry (i.e. with average growth rates). Projected carbon growth was then compared to actual live carbon in

2010 to estimate differences between expected and observed carbon storage at sites between 1997 and 2010.

STATISTICAL ANALYSES

Vegetation change

Non-metric multidimensional scaling (NMDS) was used to ordinate the vegetation data. The NMDS was based on Bray-Curtis dissimilarities to quantify differences in vegetation characteristics among transects between the two survey periods (Table 1). Vegetation data were range-standardized (subtract minimum and divide by range) and dissimilarities were calculated using the *vegdist* function in the *vegan* package of R (Oksanen *et al.*, 2010). We used the *smacofSym* function in the *smacof* package of R to fit the NMDS ordination (de Leeuw & Mair, 2009). The statistical significance of changes in vegetation characteristics between 1997 and 2010 was analyzed using the *Adonis* function of the *vegan* package. The NMDS ordination was fitted with correlation vectors for each variable using the *envfit* function of the *vegan* package to determine if any vegetation characteristics were correlated strongly with the overall vegetation change (Oksanen *et al.*, 2010).

Environmental predictors

Individual vegetation characteristics that were strongly correlated with the overall change in vegetation structure were related to potential environmental predictors. Climate characteristics, soil and management predictors were derived using Geographic Information System (GIS) (ESRI, 2010) for each site in 1997 and 2010. Climate predictors were extracted from spatial data modeled for 500 m² grids from the Bureau of Meteorology Data Library (BoM, 2012). Rainfall and temperature data were obtained from mean rainfall and temperature data from the six years prior to the surveys (1991-1996 and 2003-2009). Soil data were derived from airborne gamma ray spectrometry (Pracilio *et al.*, 2006). Gamma radiation emitted from potassium (K), uranium (U) and thorium (Th) radioisotopes in the top 30 cm of the soil are related to source elements, which are correlated with soil surface properties, such as clay content and potassium (Pracilio *et al.*, 2006). We used gamma U:Th (γ U:Th)

as an indicator of clay content, which affects water-holding capacity of soil and gamma K (γK) as a indicator of plant available potassium, which is important for plant growth and drought and heat tolerance of plants (Pracilio *et al.*, 2006). Predictors including tenure (public or private), years-since-logging and years-since-fire were collated from the DSE Corporate Spatial Data Library (DSE, 2010).

We used hierarchical Bayesian models to identify environmental factors (e.g. climate, soil type, years since fire, logging) that were predictors of individual vegetation characteristics. For each vegetation variable that showed temporal trends in the NMDS ordination (i.e. *envfit* vectors were correlated strongly with time vector), we fitted:

$$y_{ij} = (\alpha_{1997} + \delta I_{2010}) + X_{ij}(\beta_{1997,j} + \lambda_j I_{2010}) + \varepsilon_{\text{site}} + \varepsilon_{\text{transect}}$$

The model related the measured values of the response y on transect i in year j to environmental variables \mathbf{X} . The term $(\alpha_{1997} + \delta I_{2010})$ is the intercept for variable y , and consists of a value for 1997 and a deviation from that value for 2010. The term $X_{ij}(\beta_{1997,j} + \lambda_j I_{2010})$ relates the variable y to the environmental variables \mathbf{X} , allowing for time-dependent functional relationships between y and each environmental variable. There is a matrix of linear coefficients for 1997 plus an interaction matrix for the change to 2010. $\varepsilon_{\text{site}}$ is a site-based random effect, and $\varepsilon_{\text{transect}}$ is a transect-based random effect (nested within site). All random effect parameters were assigned ‘exchangeable’ (Gelman *et al.*, 1995) normal prior distributions [$\varepsilon_{\text{site}} \sim N(0, \sigma_{\text{site}}^2)$; $\varepsilon_{\text{transect}} \sim N(0, \sigma_{\text{transect}}^2)$]. Intercept parameters (α and δ) were assigned independent, uninformative normal prior distributions [$N(0, 1000)$]. Slope parameters (β and λ) were assigned uninformative, exchangeable prior distributions:

$$\beta, \lambda \sim N(0, \tau_{\beta, \lambda}); \tau_{\beta, \lambda} \sim \text{Uniform}(0, \tau_{\beta, \lambda; \text{max}}); \tau_{\beta, \lambda; \text{max}} = SD_y / 1.96.$$

where SD_y is the standard deviation of the variable y .

We used Bayesian model averaging with reversible-jump Markov chain Monte Carlo (MCMC) to estimate all model parameters and to calculate the posterior probability that each environmental variable was a predictor of the response variable (Lunn *et al.*, 2009). We fitted the model twice for each response variable: once with only linear effects, and once allowing for non-linear effects, implemented by replacing the matrix of predictor variables **X** with a basis matrix for linear splines (Lunn *et al.*, 2009). We calculated posterior probabilities that each predictor variable had linear and non-linear associations with each response variable. All models were fitted in WinBUGS 1.4, developed by the MRC Biostatistics Unit, Cambridge, UK (Spiegelhalter *et al.*, 2003) with three MCMC chains of 100 000 iterations after 20 000 iteration burns-in. Examination of MCMC chain histories and Gelman-Ruben-Brooks statistics (Brooks & Gelman, 1998) confirmed adequate MCMC mixing and convergence.

RESULTS

Overall change in vegetation

There was a distinct clustering of sites from the 1997 and 2010 surveys in the NMDS ordination (Fig. 1). There was a significant difference in vegetation characteristics between the 1997 and 2010 surveys (Adonis $P \sim 0.002$), and among the fragment size classes (Adonis $P \sim 0.001$), but there was no important interaction between survey and fragment size (Adonis $P \sim 0.915$).

Change in individual vegetation characteristics

Several vegetation characteristics were correlated strongly with the overall shift in vegetation structure and composition between the 1997 and 2010 surveys (Fig. 1). These characteristics changed systematically across the region: canopy cover, low shrub cover, high shrub cover, coarse litter load and litter depth all decreased between the 1997 and 2010 surveys (Fig. 1). Bare ground, total basal area of dead trees, basal area of dead trees in all size classes, basal area of live trees in all size classes, number of stumps, and number of live and dead saplings increased between the two

surveys (Fig. 1). All tree and shrub species were affected similarly and species relative composition remained the same between 1997 and 2010.

Vegetation characteristics

Climate, and fragment size were probable predictors of change in several vegetation characteristics in the box-ironbark forests over the study period (Table 2). In 1997, sites with higher rainfall had more live saplings and higher shrub richness (Table 3). The number of small trees and dead saplings increased relatively more at sites with higher rainfall in 2010 (Table 2). The number of hollows increased relatively more on sites with higher mean temperature (Table 2). Sites with a high soil $\gamma\text{U}:\text{Th}$ ratio, had a larger relative increase in stumps, medium and large trees compared with sites with lower soil $\gamma\text{U}:\text{Th}$ (Table 2).

Basal area of dead trees, and number of hollows and very large trees increased relatively more in remnants than in pseudoremnants (Table 2). In pseudoremnants, canopy cover and tall shrub cover decreased relatively more than in remnants, while coppices increased relatively more (Table 2). In 1997, pseudoremnants had higher canopy cover, litter depth and shrub cover than actual remnants and remnants had more coarse woody debris, and very large trees (> 80 cm) (Table 3). During the study period, years-since-fire had little effect on vegetation characteristics. In recently logged sites < 20 years, there was a larger increase in dead saplings compared with long-unlogged sites (>90 yr).

Carbon content

Live carbon in 1997 was 42.2 ± 1.4 SE t C ha⁻¹. Projected live carbon by 2010 was calculated to be 62.3 ± 2 SE t C ha⁻¹. Actual live carbon stock in 2010 was 56.7 ± 2.4 SE t C ha⁻¹, giving a mean carbon growth deficit of 5.6 ± 2.1 SE t C ha⁻¹. Higher mean rainfall was associated positively with standing live carbon (Table 2). Mean standing dead carbon increased from 3.8 ± 0.3 SE t C ha⁻¹ in 1997 to 7.5 ± 0.4 SE t C ha⁻¹ in 2010. Sites with a high soil $\gamma\text{U}:\text{Th}$ ratio had a greater increase in dead carbon.

DISCUSSION

Even under the more conservative emission scenarios, which seem increasingly unlikely, the frequency and severity of Big Dry-like droughts are predicted to increase (IPCC, 2007). In our region, reductions in precipitation seen in the Big Dry probably reflect a long-term shift to a drier climate, which is the projection for the region (Gergis *et al.*, 2011) rather than being just one, albeit severe, drought. Increases in the frequency and intensity of extreme events may produce severe effects on the biota (Thompson *et al.*, 2013); there are reports of declines in birds (Mac Nally *et al.*, 2009b), amphibians (Mac Nally *et al.*, 2009a) and freshwater invertebrates (Thomson *et al.*, 2012) in the region over this period.

Forest structure

The structure of the box-ironbark forests of central Victoria changed substantially between 1997 and 2010 following the Big Dry (Fig. 1), in which autumn and early-winter rainfall was reduced by 10–20% and there was a 0.7 °C increase in mean annual maximum temperatures across south-eastern Australia (Gergis *et al.*, 2011). There were systematic changes in vegetation characteristics that indicated that the forests were very different in character between the two periods.

Greater numbers of saplings were dead at sites with higher rainfall than at sites with lower rainfall (Table 2). This somewhat counter-intuitive result may relate to higher initial densities (in 1997) of saplings in these sites (Table 3) and intensified competition for water during the Big Dry. Saplings probably were disadvantaged relative to mature trees because of saplings' greater reliance on surface soil moisture. High stem densities induce greater competition for water and light (Dwyer *et al.*, 2010), which may leave tree stands more vulnerable to drought (Ciais *et al.*, 2005).

Dieback and regeneration partly may be related to soil properties (Fensham & Fairfax, 2007). Soil $\gamma\text{U}:\text{Th}$ is an indicator of clay content and clay soils have greater water-holding capacities than sandy soils, but once dry, such soils may not readily rehydrate (Pracilio *et al.*, 2006). Sites with higher soil $\gamma\text{U}:\text{Th}$ had greater standing dead carbon and medium and large trees (Table

2). Higher mortality can occur on favorable soils when trees have shallow root systems (Fensham & Fairfax, 2007).

There was an interaction between land use (in this case, forest fragmentation) and survey period such that increases in mortality were highest in actual remnants while reductions in canopy cover were highest in pseudofragments (Table 2). The higher mortality in fragments is consistent with global dieback trends that indicate that climate change may exacerbate water and heat stress in smaller remnants of native vegetation due to higher surface roughness and albedo of agricultural lands in which smaller remnants are embedded (McAlpine *et al.*, 2009; Allen *et al.*, 2010; Mantyka-pringle *et al.*, 2012). Reduced canopy cover, litter depth, and tall shrub cover in pseudoremnants may be due to higher initial levels in pseudoremnants than actual remnants (Table 3). The higher initial canopy cover in pseudoremnants suggests that they had experienced less water stress and, therefore, had not reduced their leaf area as much as the more exposed smaller remnants. During the chronic stress of the Big Dry, many trees within the remnants may have reduced their leaf area to the point of mortality.

Carbon dynamics

The above-ground live C biomass in 2010 was much lower than the projected value for 2010 (Table 2). Small-tree recruitment was much less in the 2010 surveys than in 1997 (Table 2). Although tree growth may be enhanced by higher temperatures, water stress probably will counter this relationship. If mortality increases and lowered growth rates occur in response to increases in the frequency and severity of drought, then forests will become net carbon emission sources, contributing to future warming through positive feedback (Chapin *et al.*, 2008).

Widespread increases in tree mortality would be a considerable source of carbon emissions, and many forests may become net carbon sources. Moreover, fewer living trees would sequester less carbon per unit area compared to previous conditions. The extant box-ironbark forests of Victoria cover c. 255 400 ha. If the carbon sequestration deficit of 5.6 ± 2.1 SE t C ha⁻¹ were to apply across this entire area, then 1.43 Mt of carbon sequestration may not have occurred during the

Big Dry. The box-ironbark forests are part of 7 Mha of 'Eucalypt Open Forest' in south-eastern Australia; much of this area was affected by the Big Dry and if our results were representative across the region, then up to 40 Mt of carbon may not have been sequestered over that severely arid period.

Without direct measures of soil and root carbon stocks and fluxes, we have no information on the dynamics of below-ground C stocks. However, root and microbial activity in the soil is reduced markedly during dry periods (Ciais *et al.*, 2005). Decreased root growth would decrease the rate of carbon accumulation in the soil while decreased microbial respiration and decomposition would reduce carbon losses from the soil, so the effects may have been marginal.

Management

The reduction in above-ground carbon sequestration and increased tree mortality suggest that the box-ironbark forests, and ones similar to them in eastern Australia and on other continents, may become poorer overall sequesters of carbon under climate change. What options are there to lessen these effects? From the perspective of landscape management, the largest relative gains might be achieved by investing in restoration activities that ameliorate the heat and water stresses experienced by remnant vegetation. Revegetating adjacent to remnants seems desirable, particularly if there are concomitant positive effects on population viabilities of the fauna and flora (Lambeck, 1997). Revegetating remnants in areas of higher precipitation and soil fertility (Vesk & Mac Nally, 2006) will be especially advantageous in generating higher growth rates of trees and more rapid carbon sequestration. Soil fertility and access to moisture promote flowering in eucalypts, which provides an important food resource for many animals (Mac Nally *et al.*, 2009b). Carbon-emission reduction schemes might be a source of revenue to influence land-holders to enact land-use change. In situ management might include thinning, which reduces mortality and results in higher carbon accumulation in floodplain forests of south-eastern Australia (Horner *et al.*, 2010). However, there is little evidence that these effects hold for drier, upland and plains forests such as the box-ironbark and its implementation is likely to damage understory plants and soil structure.

Overview

We found an increase in mortality and canopy dieback over an extended period of severe drought, which adds to evidence linking climate change to negative effects on vegetation (Allen *et al.*, 2010; Suarez & Kitzberger, 2010). Few studies have examined the importance of land-use and climate change on long-term vegetation trends, but in the few cases that have done so, disentangling which stressor is the major contributor to change has been difficult (Allen *et al.*, 2010; Mantyka-pringle *et al.*, 2012). At present, it is generally believed that habitat loss and fragmentation outweigh the effects of climate change (Mantyka-pringle *et al.*, 2012). Moreover, spatial information of environmental condition is often lacking making it difficult to determine which climate variables, including precipitation and temperature, induce forest dieback (Allen *et al.*, 2010). The spatial and temporal configuration of our study has allowed us to draw links between mortality and dieback to causal climate and landscape effects. We found less mortality in larger remnants in higher rainfall areas. Fragmented vegetation may be more susceptible to extended drought than more extensive stands of woodland because of probable greater water and heat stress in smaller fragments.

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REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-684.
- Barbeta, A., Penuelas, J., Ogaya, R. & Jump, A.S. (2011) Reduced tree health and seedling production in fragmented *Fagus sylvatica* forest patches in the Montseny Mountains (NE Spain). *Forest Ecology and Management*, **261**, 2029-2037.
- BoM (2012) *Australian climate variability & change* Available at: <http://www.bom.gov.au/cgi-bin/climate/change/timeseries.cgi> (accessed April 2012).
- Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625-644.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453-460.
- Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434-455.
- Brouwers, N., Matusick, G., Ruthrof, K., Lyons, T. & Hardy, G. (2013) Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem. *Landscape Ecology*, **28**, 69-80.
- Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D., Stewardson, M., J, R., Parsons, M. & Williams, S.E. (2013) Riparian ecosystems in the 21st Century: Hotspots for climate change adaptation? *Ecosystems*, **16**, 359-381.

- Chapin, S.F.I., Randerson, J.T., McGuire, A.D., Foley, J.A. & Field, C.B. (2008) Changing feedbacks in the climate-biosphere system. *Frontiers in Ecology and the Environment*, **6**, 313-320.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T. & Valentini, R. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529-533.
- Cushman, S., Shirk, A. & Landguth, E. (2012) Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. *Landscape Ecology*, **27**, 369-380.
- de Leeuw, J. & Mair, P. (2009) Multidimensional scaling using majorization: SMACOF in R. *Journal of Statistical Software*, **31**, 1-30.
- DSE (1998) Box-Ironbark Timber Assessment Project. In: *Bendigo Forest Management Area and Pyrenees Ranges*. Department of Natural Resources and Environment, Victoria
- DSE (2010) Victorian Spatial Data Directory, DSE, Melbourne In. Department of Sustainability and Environment, Melbourne, Victoria.
- Dwyer, J.M., Fensham, R.J., Fairfax, R.J. & Buckley, Y.M. (2010) Neighbourhood effects influence drought-induced mortality of savanna trees in Australia. *Journal of Vegetation Science*, **21**, 573-585.
- ECC (2001) *Box-Ironbark Forests and Woodlands Investigation*. Environment Conservation Council, Melbourne.
- ESRI (2010) *ArcGIS 10.0 Geographic information system*. Environmental Systems Research Institute.

- Fensham, R.J. & Fairfax, R.J. (2007) Drought-related tree death of savanna eucalypts: Species susceptibility, soil conditions and root architecture. *Journal of Vegetation Science*, **18**, 71-80.
- Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (1995) *Bayesian Data Analysis*. Chapman and Hall, London.
- Gergis, J., Gallant, A.J.E., Braganza, K., Karoly, D.J., Allen, K., Cullen, L., D'Arrigo, R., Goodwin, I., Grierson, P. & McGregor, S. (2011) On the long-term context of the 1997-2009 'Big Dry' in South-Eastern Australia: insights from a 206-year multi-proxy rainfall reconstruction. *Climatic Change*, **111**, 923-944.
- Grierson, P.F., Adams, M.A. & Attiwill, P.M. (1992) Estimates of carbon storage in the aboveground biomass of Victorias forests. *Australian Journal of Botany*, **40**, 631-640.
- Hamilton, S., Brodie, G. & O Dwyer, C. (2005) Allometric relationships for estimating biomass in grey box (*Eucalyptus microcarpa*). *Australian Forestry*, **68**, 267-273.
- Hatanaka, N., Wright, W., Loyn, R.H. & Mac Nally, R. (2011) 'Ecologically complex carbon' - linking biodiversity values, carbon storage and habitat structure in some austral temperate forests. *Global Ecology and Biogeography*, **20**, 260-271.
- Hoffmann, W.A., Marchin, R.M., Abit, P. & Lau, O.L. (2011) Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology*, **17**, 2731-2742.
- Horner, G.J., Baker, P.J., Mac Nally, R., Cunningham, S.C., Thomson, J.R. & Hamilton, F. (2009) Mortality of developing floodplain forests subjected to a drying climate and water extraction. *Global Change Biology*, **15**, 2176-2186.
- Horner, G.J., Baker, P.J., Mac Nally, R., Cunningham, S.C., Thomson, J.R. & Hamilton, F. (2010) Forest structure, habitat and carbon benefits from thinning floodplain forests: Managing early stand density makes a difference. *Forest Ecology and Management*, **259**, 286-293.
- IPCC (2007) Climate Change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. In: (ed. S.

- Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), p. 996, Cambridge University Press, Cambridge.
- Lambeck, R.J. (1997) Focal species: A multi-species umbrella for nature conservation. *Conservation Biology*, **11**, 849-856.
- Lunn, D.J., Best, N. & Whittaker, J.C. (2009) Generic reversible jump MCMC using graphical models. *Statistics and Computing*, **19**, 395-408.
- Mac Nally, R., Bennett, A.F. & Horrocks, G. (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7-29.
- Mac Nally, R., Horrocks, G., Lada, H., Lake, P.S., Thomson, J.R. & Taylor, A.C. (2009a) Distribution of anuran amphibians in massively altered landscapes in south-eastern Australia: effects of climate change in an aridifying region. *Global Ecology and Biogeography*, **18**, 575-585.
- Mac Nally, R., Bennett, A.F., Thomson, J.R., Radford, J.Q., Unmack, G., Horrocks, G. & Vesk, P.A. (2009b) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720-730.
- Mantyka-pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239-1252.
- McAlpine, C.A., Syktus, J., Ryan, J.G., Deo, R.C. & McKeon, G.M. (2009) A continent under stress: interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate. *Global Change Biology*, **15**, 2206-2223.
- Nepstad, D.C., Stickler, C.M., Soares-Filho, B. & Merry, F. (2008) Interactions among Amazon land use, forests and climate: Prospects for a near-term forest tipping point. *Philosophical Transactions: Biological Sciences*, **363**, 1737-1746.

- Oksanen, J.F., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H. & Wagner, H. (2010) *vegan: Community Ecology Package*. The Comprehensive R Archive Network.
- Parker, M. & Mac Nally, R. (2002) Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. *Biological Conservation*, **105**, 217-229.
- Pracilio, G., Adams, M.L., Smettem, K.R.J. & Harper, R.J. (2006) Determination of spatial distribution patterns of clay and plant available potassium contents in surface soils at the farm scale using high resolution gamma ray spectrometry. *Plant and Soil*, **282**, 67-82.
- Robinson, R. (1997) *Dynamics of coarse woody debris in floodplain forests: Impact of forest management and flood frequency*. Charles Sturt University, Australia.
- Schaphoff, S., Lucht, W., Gerten, D., Sitch, S., Cramer, W. & Prentice, I. (2006) Terrestrial biosphere carbon storage under alternative climate projections. *Climatic Change*, **74**, 97-122.
- Spiegelhalter, D., Thomas, A. & Best, N. (2003) WinBUGS version 1.4. Bayesian inference using Gibbs sampling. In. MRC Biostatistics Unit, Institute for Public Health, Cambridge, UK.
- Suarez, M.L. & Kitzberger, T. (2010) Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. *Journal of Ecology*, **98**, 1023-1034.
- Swift, T.L. & Hannon, S.J. (2010) Critical thresholds associated with habitat loss: A review of the concepts, evidence, and applications. *Biological Reviews*, **85**, 35-53.
- Thompson, R.M., Beardall, J., Beringer, J., Grace, M. & Sardina, P. (2013) Means and extremes: building variability into community-level climate change experiments. *Ecology Letters*, **16**, 799-806.
- Thomson, J.R., Bond, N.R., Cunningham, S.C., Metzeling, L., Reich, P., Thompson, R.M. & Mac Nally, R. (2012) The influences of climatic variation and vegetation on stream biota: lessons from the Big Dry in southeastern Australia. *Global Change Biology*, **18**, 1582-1596.

- Timbal, B., Arblaster, J., Braganza, K., Fernandez, E., Hendon, H., Murphy, B., Raupach, M., Rakich, C., Smith, K.W. & Wheeler, M. (2010) Understanding the anthropogenic nature of the observed rainfall decline across South Eastern Australia. In. Centre for Australian Weather and Climate Research (CAWCR), Australia.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009) Widespread increase of tree mortality rates in the western United States. *Science*, **323**, 521-524.
- Verdon-Kidd, D.C. & Kiem, A.S. (2009) Nature and causes of protracted droughts in southeast Australia: Comparison between the Federation, WWII, and Big Dry droughts. *Geophysical Research Letters*, **36**, 1-6.
- Vesk, P.A. & Mac Nally, R. (2006) The clock is ticking - Revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. *Agriculture Ecosystems & Environment*, **112**, 356-366.

Table 1 Vegetation characteristics used to compare differences among transects between the two survey periods, and between ‘actual’ remnants and pseudoremnants.

Abbreviation	Description
<i>Floristic variables</i>	
Shrub richness	Number of shrub species
Tree size-class distribution	Distribution of trees by size-class for each species (ha^{-1}) (DBH: 10-39 cm (small), 40-59 cm (medium), 60–79 cm (large), ≥ 80 cm (very large), and 10 - ≥ 80 cm (total). Grey box <i>Eucalyptus microcarpa</i> , red box <i>E. polyanthemos</i> , yellow box <i>E. melliodora</i> , white box <i>E. albens</i> , river red gum <i>E. camaldulensis</i> , yellow gum <i>E. leucoxylon</i> , red ironbark <i>E. tricarpa</i> , long-leaved box <i>E. goniocalyx</i> , red stringybark <i>E. macrorhyncha</i> , green mallee <i>E. viridis</i> , buloke <i>Allocasuarina luehmannii</i> , drooping sheoak <i>A. verticillata</i> , cherry ballart <i>cupressiformis</i>
Golden wattle density	Density of golden wattle <i>Acacia pycnantha</i> shrubs (ha^{-1})
<i>Structural variables</i>	
Dead trees	Total basal area of dead trees (summed over size-classes): $\text{m}^2 \text{ha}^{-1}$.
Live trees	Basal areas of tree species per size-class (DBH: 10-39 cm (small), 40-59 cm (medium), 60–79 cm (large), ≥ 80 cm (very large), and (total) ($\text{m}^2 \text{ha}^{-1}$; trees exceeding 10 cm DBH)
Live sapling density	Number of live <i>Eucalyptus</i> saplings (ha^{-1})
Dead sapling density	Number of dead <i>Eucalyptus</i> saplings (ha^{-1})
Hollows	Number of trees with hollows (ha^{-1})
Coppices	Density of coppices (ha^{-1})
Stumps	Density of stumps (ha^{-1})
All shrubs density	Density of all shrubs (ha^{-1})
Density of logs	Density of logs (ha^{-1})
Volume of logs	Fallen timber volume (fallen timber > 10 cm diameter) ($\text{m}^3 \text{ha}^{-1}$)
Canopy cover	Canopy cover (%)
‘Tall’ shrub cover	Shrubs > 2 m high (%)
‘Low’ shrub cover	Shrubs ≤ 2 m high (%)
Rock cover	Rock coverage (area of rocks $> 100 \text{ cm}^2$) (%)
Bare ground cover	Bare ground (%)
Coarse-litter cover	Cover of coarse litter (%)
Fine-litter cover	Cover of fine litter (%)
Live carbon	Total live tree carbon biomass summed across all species (t C ha^{-1})
Dead carbon	Total dead tree carbon biomass (t C ha^{-1})

Table 2 Comparison of the changes in individual vegetation characteristics with spatial environmental predictors derived from Bayesian model comparison of all possible additive models using reversible jump Markov chain Monte Carlo (MCMC). Maximum linear and non-linear posterior probabilities of inclusion (Pr) with Pr > 0.75 supporting a positive coefficient (in bold) (Table 3 shows full Pr table) and regression coefficients (β) are shown

	Fragment Size		Rainfall		Mean temperature		Logging		$\gamma_{U:Th}$		γ_k		Private	
	B	Pr	β	Pr	B	Pr	β	Pr	β	Pr	β	Pr	β	Pr
<i>Decreased overall</i>														
canopy cover	-2.59	0.87	0.26	0.46	-0.06	0.40	-0.04	0.39	-0.03	0.32	-0.83	0.54	-1.37	0.60
litter depth	-0.15	0.79	0.05	0.51	0.02	0.43	0.02	0.46	0.01	0.35	0.01	0.34	-0.09	0.58
high shrub cover	-0.89	0.87	0.19	0.47	-0.02	0.39	0.03	0.42	-0.01	0.30	-0.04	0.32	-0.01	0.46
coarse litter	3.25	0.99	-0.31	0.47	-1.01	0.65	0.14	0.41	-0.06	0.30	-0.90	0.64	0.04	0.40
<i>Increased overall</i>														
small trees	0.25	0.51	2.06	0.96	0.03	0.32	-0.52	0.72	0.00	0.21	0.02	0.26	-0.04	0.40
medium trees	-0.04	0.53	0.06	0.49	0.00	0.38	0.05	0.42	0.44	0.98	-0.05	0.37	0.06	0.46
large trees	-0.02	0.60	0.03	0.49	0.00	0.38	0.01	0.41	0.12	0.92	-0.01	0.35	0.02	0.48
very large trees	-0.18	0.99	0.02	0.45	0.02	0.41	0.03	0.44	0.01	0.31	0.00	0.30	0.00	0.45
Coppice	16.89	0.99	28.47	0.94	-1.13	0.36	-1.31	0.34	0.41	0.25	0.64	0.29	-1.15	0.39
Hollow	-2.56	0.96	9.34	0.98	4.00	0.90	0.48	0.37	-1.11	0.58	-2.38	0.85	4.13	0.84
dead basal	-4.43	0.85	13.01	0.60	10.15	0.59	7.58	0.57	4.26	0.45	-11.88	0.71	-4.72	0.51
dead saplings	1.26	0.51	10.68	0.91	1.12	0.45	-5.29	0.82	-0.14	0.33	1.90	0.51	0.06	0.43
Stump	2.58	0.75	1.90	0.58	0.51	0.41	-0.90	0.50	3.11	0.86	-0.13	0.38	0.46	0.47
dead C	0.10	0.51	1.22	0.73	0.63	0.63	0.07	0.35	0.69	0.76	-0.44	0.61	-0.14	0.43
live C	0.62	0.39	23.69	1.00	1.52	0.45	-0.31	0.40	0.24	0.22	0.13	0.19	-0.47	0.34

Table 3 Comparison of the changes in individual vegetation characteristics with spatial

environmental predictors derived from Bayesian model comparison. Maximum linear and non-linear posterior probabilities of inclusion (Pr) with $Pr > 0.75$ supporting a positive coefficient (in bold) regression coefficients

	1997								
	Fragment Size	Rainfall	Temp	Fire	Logging	$\gamma_{U:Th}$	γ_k	Public	Private
<i>Decreased overall</i>									
canopy cover	2.45	-0.13	0.06	-0.12	0.31	0.27	1.03	-0.35	0.25
litter depth	0.16	0.06	-0.01	0.04	0.01	-0.02	-0.01	0	0
low shrub cover	0.2	-0.02	0.24	0.12	-0.14	-0.06	-0.13	-1.01	0.2
high shrub cover	1.06	-0.12	-0.01	0.1	0	0.05	0.01	-0.14	0.34
coarse litter	-2.18	-0.79	0.16	-0.04	-0.06	-0.26	1.11	0.06	-0.18
<i>Increased overall</i>									
bare cover	-0.56	-0.16	0.23	0.02	0.09	-0.06	-0.37	0.55	0.02
small trees	1.13	-0.44	-0.1	0.1	-0.05	0	0.47	0.26	-0.16
medium trees	-0.01	0.17	-0.05	-0.02	0.01	-0.36	-0.36	0.1	0.07
large trees	0	0.04	-0.02	0	0	-0.09	-0.15	0.03	0.02
very large trees	-0.13	0.02	-0.01	0.01	0.01	0	-0.01	-0.03	0.11
Coppice	-0.53	1.18	0.23	0	-0.41	-0.09	0.1	0.84	-3.48
Hollow	-0.74	0.71	0.03	-0.07	0.16	-0.1	-0.25	0.36	1.33
dead small trees	-0.07	-0.08	0.48	0.22	0.55	0.83	0.56	1.57	-0.55
dead medium trees	0	0.02	0	0.02	0.03	0	-0.04	0.01	-0.01
dead large trees	0	0.03	0.01	0	0	0.01	-0.01	0.01	-0.01
dead very lg trees	0	0	0	0	0	0	-0.01	0	0
dead basal	0.06	1.19	2.96	1.72	2.5	3.65	0.73	9.22	-2.7
dead saplings	0.23	1.36	0.29	0.43	-0.53	-0.05	0.55	0.46	0.05
live sapling	0.19	2.58	0.16	-0.02	-0.86	0.05	1.22	-0.62	-0.56
Stump	0.4	-0.15	-0.47	0.34	-0.44	0.48	0.75	2.22	-0.98
shrub richness	0.17	0.36	0.1	-0.06	-0.04	0.06	0.13	-1.39	0.27
dead C	0.11	0.08	0.05	0.12	0	0.2	0.09	1.02	-0.3
live C	0.29	0.15	-0.21	0.07	-0.06	-0.4	-0.31	-0.36	1.04
	2010								
	Fragment Size	Rainfall	Temp	Fire	Logging	$\gamma_{U:Th}$	γ_k	Public	Private
<i>Decreased overall</i>									
canopy cover	-2.59	0.26	-0.06	0.13	-0.04	-0.03	-0.83	1.2	-1.37
litter depth	-0.15	0.05	0.02	0.03	0.02	0.01	0.01	0.07	-0.09
low shrub cover	-0.88	-0.34	-0.38	-0.12	0.25	0.02	-0.3	0.35	-1.28
high shrub cover	-0.89	0.19	-0.02	0.04	0.03	-0.01	-0.04	0.24	-0.01
coarse litter	3.25	-0.31	-1.01	0.16	0.14	-0.06	-0.9	-0.14	0.04
<i>Increased overall</i>									
bare cover	-0.32	0.14	0.71	-0.87	0.07	0	-0.8	0.11	0.24
small trees	0.25	2.06	0.03	0.18	-0.52	0	0.02	0.09	-0.04
medium trees	-0.04	0.06	0	0.01	0.05	0.44	-0.05	0.11	0.06
large trees	-0.02	0.03	0	0.02	0.01	0.12	-0.01	0.04	0.02
very large trees	-0.18	0.02	0.02	-0.05	0.03	0.01	0	0.03	0
Coppice	16.89	28.47	-1.13	2.1	-1.31	0.41	0.64	-1.09	-1.15
Hollow	-2.56	9.34	4	0.02	0.48	-1.11	-2.38	-0.14	4.13
dead small trees	-0.39	1.6	0.78	0.17	0.41	0.5	-0.56	2.9	-1.01
dead medium trees	-0.03	0.03	0.03	0.07	0.06	0.01	-0.05	0	-0.01
dead large trees	-0.02	0.01	0.02	0	0.01	0	-0.03	0.01	0
dead very lg trees	-0.01	0	0	0	0.01	0	-0.02	0.01	0
dead basal	-4.43	13.01	10.15	1.12	7.58	4.26	-11.88	18.95	-4.72
dead saplings	1.26	10.68	1.12	1.18	-5.29	-0.14	1.9	0.08	0.06

live sapling	0.28	-1.15	-0.34	-0.09	0.66	0.09	0.37	-0.53	-0.63
Stump	2.58	1.9	0.51	0.94	-0.9	3.11	-0.13	0.2	0.46
shrub richness	0	-0.4	0	0.04	-0.04	0.03	-0.13	-0.4	0.12
dead C	0.1	1.22	0.63	0.18	0.07	0.69	-0.44	0.5	-0.14
live C	0.62	23.69	1.52	-0.02	-0.31	0.24	0.13	1.64	-0.47

Figure legends

Figure 1 Non-metric multidimensional scaling (NMDS) ordination (stress = 0.07) of vegetation characteristics for 1997 (black) and 2010 (white), based on a Bray-Curtis dissimilarity matrix. Point size indicates the fragment size class of transects. Fitted vectors show correlations between NMDS axial scores and individual vegetation characteristics ($P < 0.001$). The length of a vector is proportional to strength of the correlation, and the direction indicates the direction of the correlation.

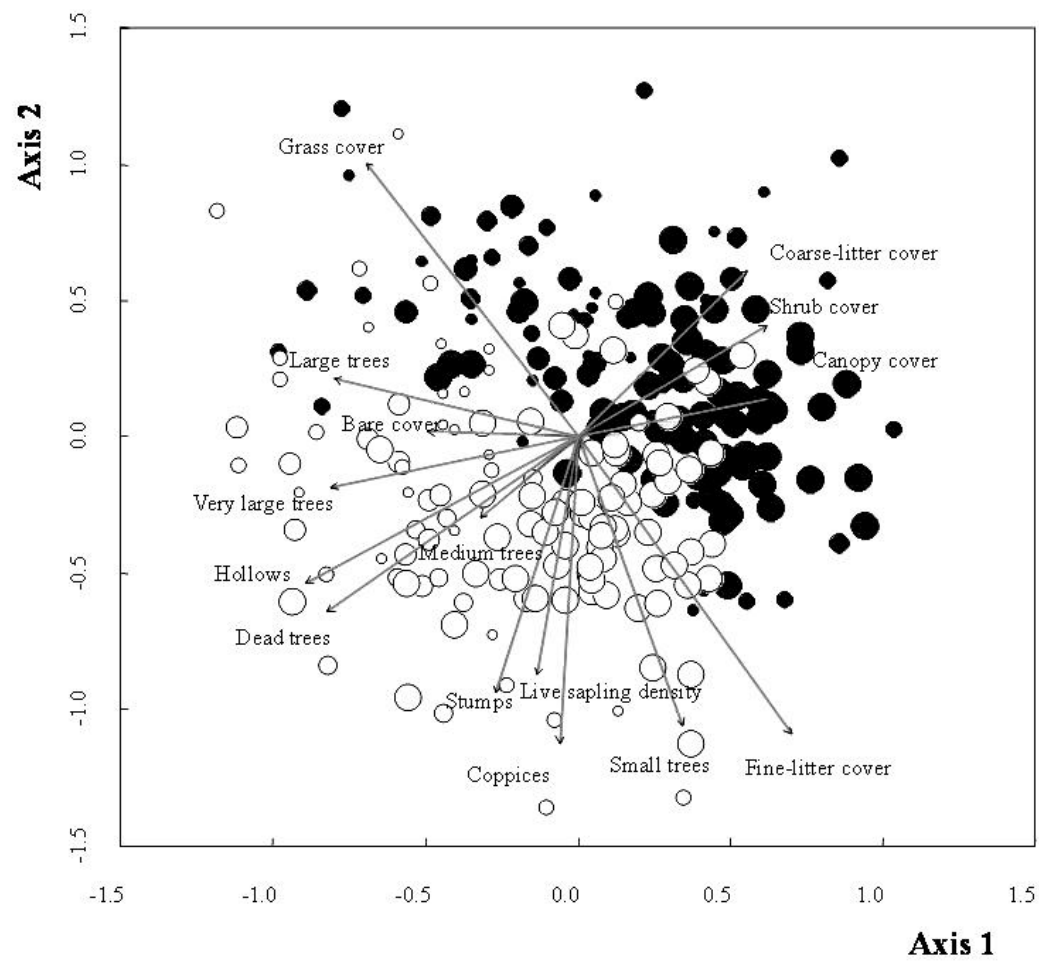


Figure 1:

PART B: Suggested Declaration for Thesis Chapter

Monash University

Declaration for Thesis Chapter 3

Declaration by candidate

In the case of Chapter 3, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The initiation, key ideas, development and writing up of the work were primarily my responsibility. I performed some of the field work (all of the regional 2010-11 data). Conducted some analysis and was the primary author of the manuscript.	50

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Dale G. Nimmo	Contributed ideas to the work and contributed to writing of the manuscript	
Rohan H. Clarke,	Contributed ideas to the work and contributed to writing of the manuscript	
Mark Hall	Contributed to data collection	
James R. Thomson	Analysis	
James Q. Radford	Contributed data	
Ralph Mac Nally	Contributed ideas to the work and contributed to writing of the manuscript	
Andrew F. Bennett	Contributed ideas to the work	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature		Date
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Main Supervisor's Signature		Date
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*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 3: Resistance and resilience to pressures: Can the abrupt end of extreme drought reverse the collapse of an avifauna?

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Keywords: climate change, land use change, fragmentation, habitat loss, Big Dry, recovery,

Primary Research Article

ABSTRACT

Aim: Extreme climatic events, such as severe droughts and intense rainfall periods, strongly affect natural populations. Climate change is expected to lead to a greater frequency and intensity of such extremes. The capacity of the biota to cope with climatic extremes may be compromised by land transformation by humans. We explored how the avifauna of a highly modified region has responded to the climatic extremes of a decade-long drought (the 'Big 'Dry'), followed by intense rainfall period (the 'Big Wet').

Location: Temperate woodlands in north-central Victoria, Australia

Methods: We used two spatially extensive, long-term, complementary datasets, both of which were repeated in three time periods: early and late in the Big Dry, and in the Big Wet. We compared species-specific changes in reporting rates (proportion of surveys that a species was present) between periods to explore the resistance and resilience of species to drought.

Results: During the Big Dry, there was a substantial decline in the reporting rates of 42-61% of species. The Big Wet led to some recovery in 21-25% of species, but 25-28% species continued to decline. More than half of the species did not recover during the Big Wet, in that their reporting rate was substantially reduced in the Big Wet compared to the onset of the Big Dry. Species' responses did not appear to be related to species' ecological traits. Species resistance to the drought was inversely related to resilience in the Big Wet for about a quarter of the species, while about three quarters of species with low resistance continued to decline in the Big Wet.

Conclusions: The weak recovery suggests that the avifauna is in significant on-going jeopardy. Declines in all species guilds suggest that a widespread mechanism is responsible for the on-going collapse. Species that declined the most during the Big Dry did not necessarily show the strongest recoveries, creating a markedly different assemblage. The extensive fragmentation and continued degradation of habitat quality are likely mechanisms leading to the on-going declines.

INTRODUCTION

As the world's climate warms, there is predicted to be a greater frequency of extreme climatic events such as long-term, severe droughts and flooding rains (IPCC, 2007). Climatic extremes restructure ecological communities (Jimenez *et al.*, 2011), and their increased frequency potentially poses a greater threat to biodiversity than gradual changes in average climatic conditions (Jentsch & Beierkuhnlein, 2008). Despite this, most ecological studies on the effects of climate change have focused solely on increases in mean temperature to assess range shifts (Lenoir *et al.*, 2008) and changes in life-history phenologies (Cleland *et al.*, 2007), although there has been some experimental assessments of assemblage-level responses to extreme events (Thompson *et al.*, 2013).

Increases in extreme climatic events most likely will occur in conjunction with a massively transformed land surface dominated by human activities (Opdam & Wascher, 2004). Land-use change is recognized as *the* major driver of global decline in terrestrial biodiversity (Fischer & Lindenmayer, 2007). Evidence suggests that fragmentation interacts with climate change (Mantyka-Pringle *et al.*, 2012), including drought (Mac Nally *et al.*, 2009; Bennett *et al.*, 2013), leading to changes in biological communities. Fragmented ecosystems may be more vulnerable to climate change due to regional shifts in the distribution of precipitation, local drying and warming (McAlpine *et al.*, 2009), and increased fire frequency and severity (Regan *et al.*, 2010). This overlap of disturbances may limit the capacity of communities to bounce back (Falkenberg *et al.*, 2013) following even 'natural' disturbances, such as drought and flood (Regan *et al.*, 2010).

The net effect on species from wide variations in climatic conditions will be determined by their ability to absorb the disturbance ('resistance'), and their capacity for recovery following the release of the disturbance ('resilience') (Harrison, 1979). The ability of an assemblage to return to its original state following a disturbance requires that resistance be inversely related to resilience (Herbert *et al.*, 1999; Orwin *et al.*, 2006) such that a species with poor resistance has high resilience and species with high resistance has low resilience, accumulating in a net effect of zero. This means

that species that decline during climatic extremes (i.e. severe drought) will need to have the capacity to recover to return to their pre-disturbance state.

In relation to long-term drought, the capacity for species to resist or recover completely or near-completely is likely to be contingent on: (1) the extent and severity of drought and the associated time lags in the replenishment of diminished resources (e.g. food and vegetation); (2) the extent of available habitat, especially in heavily modified landscapes, that can accommodate resistance or recovery (Morecroft *et al.*, 2012); and (3) the ecological traits of species that enhance or reduce resistance and resilience, respectively (Smith, 2011; Chessman, 2013). Currently, our knowledge of the resistance and resilience of biota to extreme, long-term drought in heavily modified landscapes is limited because of a scarcity of consistent, large-scale and long-term datasets that track communities throughout the entirety of climatic extremes.

South-eastern Australia has experienced the interaction between land-use and climate change. Over the past 200 years, the region has experienced massive land transformation, primarily for agriculture (ECC, 2001). The region's biodiversity is imperiled, with major declines in several taxonomic groups (Brown *et al.*, 2008; Mac Nally *et al.*, 2009; Thomson *et al.*, 2012). The area experienced regional warming, with increases in mean annual temperature over several decades (Jones, 2012). Recently, increases in mean temperature were compounded by a long-term, severe drought - 'the Big Dry' - that commenced in 1997 and lasted until 2010 (Leblanc *et al.*, 2012). The duration and accumulated precipitation deficit over this period was at least twice that of any other drought since instrumental records began in the 1880s (Leblanc *et al.*, 2012). Climate-change scenarios project a 1–6 °C increase in mean temperature and a 5-15 % decrease in precipitation for the region by 2070 (IPCC, 2007). These observed, and projected, climate-change measures are consistent with other drying regions at similar latitudes (e.g. the North American south-west, the Mediterranean Basin, southern Africa and northern China) (IPCC, 2007).

The Big Dry and the ramping of temperature, in conjunction with land-use change, have been linked to a pronounced 'collapse' of the region's avifauna, which saw the majority of landbird

species experiencing substantial declines (Mac Nally *et al.*, 2009). This shift occurred both in and outside of protected areas, and irrespective of species' ecological traits (Mac Nally *et al.*, 2009). However, the Big Dry ended abruptly with heavy spring and summer rains between 2010 and 2012 – ‘the Big Wet’ (Leblanc *et al.*, 2012). Questions remain regarding whether the breaking of the Big Dry has offered this region’s biota a reprieve (Mac Nally *et al.*, 2014), and if the collapse of the region’s avifauna has stabilized or reversed.

Here, we use two large monitoring programs that tracked changes in the avifauna throughout an entire region during the Big Dry (Mac Nally *et al.*, 2009), and continued into the Big Wet (total span: 1995–2012). These large-scale, independent yet complementary datasets provide an opportunity to assess the extent to which the abrupt end of a severe, long-term drought can ‘unwind’ the collapse of a regional fauna in a heavily modified region. By comparing changes in the reporting rate of species (number of surveys in which a species was recorded divided by the total number of surveys) during the late Big Dry and Big Wet relative to the beginning of the Big Dry, we can ascertain changes in reporting rate at the species level (Table 1). This analysis allowed us to determine if the reporting rates of species that substantially declined during the Big Dry (i.e. low resistance) are the same species that have substantially increased during the Big Wet (i.e. high resilience)? Specifically, we asked: (1) did the Big Wet reverse the collapse of the avifauna witnessed during the Big Dry? (2) What is the relationship between the resistance and resilience of species in the Big Wet – Big Dry period? (3) Which, if any, ecological traits (i.e. nesting, foraging, range etc.) of species lead to higher resistance to severe drought and high resilience following its end, and do traits that confer resistance/resilience differ?

METHODS

The region (30000 km², central Victoria, Australia, Fig. 1) is characterized by an open canopy of moderate height (10–25 m) dominated by species of *Eucalyptus*. The understory typically consists of small shrubs and herbs such as acacias (Mimosaceae), heaths (Epacridaceae) and bush-peas

(Fabaceae). Perennial tussock grasses (*Poa* spp., *Austrodanthonia* spp.) are common. Local forest composition is dependent on soils, elevation, drainage and aspect (Mac Nally & Horrocks, 2002).

Climate data

Rainfall and temperature data were extracted from spatial data modeled for 500 m² grids from the Bureau of Meteorology Data Library (BoM, 2013). Mean annual temperature and rainfall anomalies are based on a historical baseline (1961–1990). Historically, precipitation fell mostly in winter and spring with summers being hot and dry. During the Big Dry, mean temperature increased by 0.65 °C and mean annual precipitation decreased to 430 ± 87 SD mm yr⁻¹ across the study area for 1997–2009 from 642 ± 117 SD mm yr⁻¹ for the baseline. Declines were disproportionately large in autumn and early-winter (Leblanc *et al.*, 2012). Precipitation during the Big Dry was below the Australian Bureau of Meteorology baseline for 11 of the 13 years (Fig. 2), with an accumulated deficit of almost 2.5 years of baseline average precipitation (Fig. 2).

The Big Wet replenished *c.* 1 yr of the baseline precipitation deficit accumulated in the Big Dry (BoM, 2013). Unlike previous, shorter droughts, the Big Dry was coupled with a ramping event of pronounced warming. In south-eastern Australia, consistent with global temperature rises, there have been two step-changes (in 1968 and in 1997), which has led to a total rise in mean minimum (+1.16 °C) and maximum (+1.08 °C) temperatures for the region (Jones, 2012).

Bird-occurrence data

Data were from six intensive survey periods sampled in a series of landscapes (2002–03, 2006–07 and 2011–12) (the ‘landscape program’) and in a set of fragments of native vegetation across the region (1995–97, 2004–05 and 2010–11) (the ‘fragment program’) (Table 1). The programs used a similar standard protocol for bird surveys (strip transects of area 2 ha) (Barrett *et al.*, 2003). The programs were conducted in the same region, but differed in the way transects were grouped (into ‘study landscapes’ or according to habitat fragments) and the years in which the three rounds in each program were undertaken. Each site was visited multiple times throughout the year. Birds are active throughout the year and several of the dominant eucalypts (e.g. *Eucalyptus tricarpa*) may flower

profusely in the colder months, which attracts many nectarivorous species (Mac Nally & McGoldrick, 1997). Surveys were conducted from sunrise to sunset but not if weather conditions were poor for bird activity and detection (e.g. rain, high temperature or high wind).

Fragment survey data

All fragment surveys were repeated eight times at regular intervals throughout the course of a year. Transects were spatially clustered in sites within woodland fragments and large forest blocks depending on the area of native vegetation (Mac Nally & Horrocks, 2002). We do not focus on habitat area here (our focus is on regional prevalence), but included site identity in analyses to account for spatial correlation patterns. In the 1995–97 survey, 139 sites were surveyed. In 2004–05, a subset (25 sites) of those 139 sites was resurveyed, and 40 new sites were used (Thomson et al., 2007). There were no apparent differences in the avifaunal assemblage between the original and new sites (Mac Nally, 2007). In 2010–11, 120 sites of the 139 fragment-program sites established in 1995–97 were surveyed with the other 19 being lost or access was denied.

The 1995–97 and 2004–05 surveys were conducted by G. F. B. Horrocks but the 2010–11 surveys were conducted by J. M. Bennett. To ensure that observations between the two observers were consistent, two full rounds of ‘calibration surveys’ (240 transects, both observers) were conducted prior to the commencement of the 2010–11 surveys. Differences between the observers were very few during the 2nd calibration survey round. Calibration data were excluded from analysis.

Landscape-survey data

Sites in the landscape program were arranged as ten 2-ha sites in each of twenty-four 100 km² (104 ha) ‘landscapes’ (Fig. 1) (Radford et al., 2005). Each site was visited four times, twice in the warm-season breeding period (September to December) and twice in the cooler autumn/winter period (March to July), in each of the three survey periods. Species recorded during a 20-min survey and a 10-min supplementary period were regarded as present. All of the 240 sites established in the 2002–03 survey programs were revisited in 2006–07 and in 2011–12. The landscape surveys were

conducted by the one observer (G. Cheers), with the exception of half of the 2002–03 data, which were collected by J. Radford; both were highly experienced ornithologists in this ecosystem.

Ecological traits

Species were classified into guilds (following Radford & Bennett, 2005) based on ecological traits that may lead groups of birds in the same guilds to respond similarly to change (Appendix 1). Traits used in analysis were: nesting, foraging (diet and substrate), degree of conservation concern, degree of dependence on amount of remnant vegetation in landscapes, migratory status (e.g. resident vs. migrant) and geographical range (i.e. if a species is widespread or associated with a particular environment such as mesic, semi-arid or arid environments) (Blakers *et al.*, 1984).

STATISTICAL ANALYSES

We analyzed the fragment and landscape programs individually for four reasons. First, the three rounds in each program were conducted in different sets of years. Second, the survey methods were slightly different, with the fragment program using the standard 2 ha–20 min Birds Australia 2nd-atlas method, whereas the landscape program employed an extra 10 min of observation. Third, there were different sets of observers. Last, the programs complemented each other by covering somewhat different vegetation assemblages. The fragment sites generally were located on relatively dry and infertile sites on hill-slopes, often dominated by red ironbark *E. tricarpa*. A greater proportion of sites in the landscape program were located on the plains, with more fertile soils, frequently dominated by grey box *E. microcarpa*.

Species-specific reporting rates were the response variable in all analyses. The reporting rate for a single transect i in period j (1, 2, or 3) is defined as the probability of recording a species during a single visit to that transect in period j . The mean reporting rate for period j is the expected proportion of occupied transects at any given time or, equivalently, the probability of observing a species in a single visit to a random transect. Our analyses focused on detecting changes in mean reporting rates between the three survey periods of each program. We used hierarchical Bayesian

models to estimate changes in reporting rates, while accounting for inherent spatial structures in each data set. The model was:

$$y_{i(l)j} \sim \text{Binomial}(v_{ij}, p_{ij}); \text{logit}(p_{ij}) = \alpha + \delta_l^1 \cdot I_{j>1} + \delta_l^2 \cdot I_{j=3} + \epsilon_l + \epsilon_i$$

$$\delta_l^1 \sim N(\Delta_1, \sigma_{\delta_1}^2); \delta_l^2 \sim N(\Delta_2, \sigma_{\delta_2}^2)$$

Here, $y_{i(l)j}$ is the number of times the species was recorded in transect i (within landscape / fragment l), during period j , v_{ij} is the number of surveys, and p_{ij} is the corresponding reporting rate, which was modeled on the log-odds scale as a function of: an overall mean reporting rate for the first period, α ; spatial random intercepts ϵ_l, ϵ_i ; and spatially-varying change parameters, which estimate the change in reporting rate between the first and second survey periods, δ_l^1 , and between the second and third periods, δ_l^2 . The change parameters were modeled hierarchically, with overall mean changes, Δ_1 and Δ_2 , and random variation among landscapes / fragments, $\sigma_{\delta_1}^2$ and $\sigma_{\delta_2}^2$. Note that $I_{j>1}$ is a binary indicator variable with value 1 for surveys in the second and third periods, and $I_{j=3}$ had value 1 for the third period only. Our interest was in estimating the mean changes in reporting rate during the Big Dry Δ_1 , following the Big-Wet Δ_2 , and over the full period of study, $\Delta_3 = \Delta_1 + \Delta_2$. For each species, we calculated posterior probabilities that reporting rates declined, $\text{Pr}(\Delta_n < 0)$, or increased $\text{Pr}(\Delta_n > 0)$, during each period. We considered posterior probabilities > 0.9 to be strong evidence of a change in mean reporting rate.

All models were estimated with Markov chain Monte Carlo (MCMC) sampling using WinBUGS software (Spiegelhalter et al., 2003). Mean reporting rate and change parameters were assigned independent normal prior distributions; $\alpha \sim N(0, 100)$, $\Delta_n \sim N(0, 1)$. Random intercept parameters were assigned exchangeable normal prior distributions, e.g. $\epsilon_l \sim N(0, \sigma_l^2)$, with uniform priors on the corresponding standard deviations, $\sigma_l \sim U(0, 2)$. Standard deviations for random slopes parameters σ_{δ_1} and σ_{δ_2} were assigned more constrained uniform priors, $U(0, 1)$. Posterior distributions were sampled with three independent chains of 10000 iterations each, after 5 000 iteration burn-in periods. Examination of chain histories and BGR diagnostics confirmed that adequate MCMC mixing and convergence were achieved.

The dry woodland of the study area are characteristically open with a canopy typically ≤ 20 m so that woodland birds are relatively conspicuous. We did not correct for detectability because the statistical bias introduced by such corrections is potentially large (Royle & Link, 2006; Welsh *et al.*, 2013). The analyses excluded; species found on < 5 sites, in addition to nocturnal, non-native, and aquatic species, of which there were few records

RESULTS

The Big Dry

The Big Dry had a major impact on the region's avifauna. Our analysis of changes in reporting rates from the regional survey program showed that 42% of species declined during the Big Dry (i.e. 2004-05 vs 1995-97), whereas only (6%) of species increased during that period (Fig. 3a). In the landscape survey program, 61% of species declined during the Big Dry (i.e. 2006-07 vs 2002-03), compared with only 4% of species increasing substantially (Fig. 3d).

The Big Wet

For the regional survey program, 21% of species increased relative to their reporting rates during the Big Dry. However, 28% of species declined, which included some species that had previously not declined and declining species that declined further during this period (Fig. 3b). Results from the landscape survey program were consistent with these trends. Some 25% of species showed a substantial increase in reporting rates during the Big Wet compared to the Big Dry (Fig. 3e) and 25% of species declined, despite the onset of the Big Wet (Fig. 3e).

Long-term change

Some 54% of species in the regional surveys had substantially lower reporting rates during the Big Wet compared to before the Big Dry (Fig. 3c). Only 7% of species had a substantial increase in their reporting rate over that same period. The landscape survey program indicated that 56% of species had substantially lower reporting rate during the Big Wet, compared with the initial surveys

conducted early in the Big Dry (Fig. 3f). Some 18% of species had a substantial increase in their reporting rate over that same period.

Consistency between survey programs

Widespread declines in reporting rate were recorded for 43% of species, where species declined in both the landscape and regional datasets (Table 2). Examples of widespread decliners were: fuscous honeyeater *Lichenostomus fuscus*, yellow-tufted honeyeater *L. melanops*, musk lorikeet *Glossopsitta concinna*, eastern-yellow robin *Eopsaltria australis*, restless flycatcher *Myiagra inquieta*, superb fairy-wren *Malurus cyaneus* and white-bellied cuckoo-shrike *Coracina papuensis*. Evidence of a possible, but weaker widespread decline was found for 22% species, with declines in one, but not both, programs (Table 2). Only two species, the painted buttonquail *Turnix varius* and yellow-faced honeyeater *L. chrysops*, consistently increased in both programs (Table 2). Another 7% of species showed evidence of widespread increases in one study (Table 2). A mismatch in the responses between the two sampling programs was evident for some species, including the Australian magpie *Cracticus tibicen*, brown treecreeper *Climacteris picumnus*, galah *Eolophus roseicapilla* and red wattlebird *Anthochaera carunculata*.

Species' resistance and resilience

Species that had low resistance but high resilience in both data sets were the black-faced cuckoo-strike *Coracina novaehollandiae* and jacky winter *Microeca fascians*, which declined in the initial Big Dry period and then recovered to, or exceeded, their initial reporting rate in the Big Wet. Some 76% of species detected as declining mid-way through the Big Dry and declined further by the Big Wet in both the regional and landscape surveys (Fig. 4a, b). The majority of resistant species subsequently were unchanged in the Big Wet, while 39% of species in the regional data set (Fig. 4a) and 25% in the landscape data set declined (Fig. 4b). Species that had not declined in frequency of reporting during the initial stages of the Big Dry were reported less frequently during the Big Wet in both data sets were the little eagle *Aquila morphnoides* and pied currawong *Strepera graculina*.

Ecological traits

The proportion of species responding in all periods and survey programs was largely independent of birds' ecological characteristics such as, primary habitat, foraging zone, feeding or nesting guild, broad distribution and/or level of conservation concern (Fig. 5). Marginally higher net declines were seen for aerial feeders, but there was no consistent guild effect on resilience (Fig. 5).

DISCUSSION

Predicting how the biota will respond to the increased frequency and intensity of climatic extremes that are predicted to occur with climate change is contingent upon an understanding of the species' resistance and resilience to such events. Birds in a heavily modified region generally displayed poor resistance to an extreme drought, the Big Dry, *and* poor resilience to the Big Wet. By the end of the Big Dry, there was a half to two-thirds reduction in the reporting rates of woodland bird species in the region, but only a quarter of species affected subsequently recovered during the Big Wet. Some 76% of species with low resistance to the Big Dry were still in decline after the release of pressure associated with the drought when compared to their initial reporting rates. Declining species largely were consistent between the two survey programs. Only 14% of species, mostly highly conspicuous species (e.g. large, energetic and/or vocal), showed a mismatch in response, between the regional and landscape survey programs. Reasons for these mismatches are unclear but may relate to different vegetation types sampled in the two survey programs and the temporal differences in the timing of the different surveys. Species' resistances were weakly related to resilience, and declines occurred largely irrespective of species' ecological traits.

Diminished resistance and resilience

Which factors are likely to have led to the low levels of both resistance and resilience of the avifauna to the Big Dry? First, although the drought broke, many of its effects are likely to persist. Bennett et al. (2013) documented a drought-induced decline in vegetation, including many attributes exploited by birds. The loss of canopy, litter and shrub cover as a consequence of the drought

(Bennett *et al.*, 2013) is a decline in habitat quality for many species. The regeneration of many of these vegetation attributes may take years or even decades, meaning that their recovery from drought is likely to have a time lag (Vesk *et al.*, 2008).

Second, the interaction between climate and land-use change may amplify pressures on a species. Fragments of native vegetation in human-dominated landscapes are interspersed with tracts of largely unsuitable land for woodland birds and movements between populations of species that depend on native vegetation are impeded (Opdam & Wascher, 2004). Elevated water and heat stress associated with fragmented vegetation may increase physiological stresses on birds (McAlpine *et al.*, 2009), leading to increased mortality (McKechnie & Wolf, 2010). Temperature increases affect the timing of reproduction, which may result in a mismatch between the production of nestlings and the availability of food (Stevenson & Bryant, 2000).

Third, habitat fragmentation/loss is a non-random process biased towards more productive parts of the landscape (Etter *et al.*, 2006). Consequently, larger remnants in the region occur on less fertile, drier soils (ECC, 2001). More productive parts of the landscape are likely to be pivotal in providing both opportunities for resistance by birds, through reducing the impacts of heat stress, water loss and food availability, and resilience, by acting as refuges for *in situ* resilience and resistance (Mackey *et al.*, 2012). Thus, the disproportionate loss of native vegetation from the most productive parts of landscapes may limit the potential for both resistance to the effects of climatic extremes and resilience following the relaxation of stressful events, such as prolonged drought. It is also likely that recovery is ongoing and that we have only captured the beginning of it. Given that the frequency and duration of droughts are predicted to increase, interrupted by shorter, more intense periods of precipitation (IPCC, 2007) and, the low reproductive rates of many Australian passerines (Yom-Tov, 1987), it is possible that many species have already reached a threshold from which they will not have time to recover before the start of the next dry period.

Resistance versus resilience

The relationship between resistance and resilience indicates the degree to which species (or communities) have, or can, recover following the release of a pressure. Several types of relationships between resistance and resilience have been described, including positive (Pfisterer & Schmid, 2002), neutral (Bruehlheide & Luginbühl, 2009) and negative relationships (Herbert *et al.*, 1999). In general, a strong, negative one-to-one relationship between resistance and resilience would be observed if species-level recovery were complete, in that the population had returned to its pre-disturbance abundance and extent. That is, species that declined the most - those having lowest resistance - are the same species that 'bounce back', indicative of high resilience. We found little evidence for such a relationship. There was much scatter in the resistance-resilience relationship. Some species remained unchanged throughout the entire period. Some species declined both during and following the Big Dry and others bounced back, having declined in the Big Dry. Some 14% of species at the regional scale (Fig. 4a) and 16% of species at the landscape scale (Fig. 4b) had net declines over the entire period of surveys, which indicates both low resistance and low resilience.

Ecological traits

The resistance of species to the Big Dry had little relationship to species' mobility, foraging or nesting guilds or their level of conservation concern. These results differ from other studies documenting change in avifaunas due to drought (Albright *et al.*, 2010; Jiguet *et al.*, 2011) and heat (Julliard *et al.*, 2004), which found differences attributable to species' ecological traits. That the Big Dry was an interacting ramp (temperature) and press (low rainfall) event of unprecedented severity in the instrumental records, suggests that resistance may be a function of not only a species' ecological traits but also of the intensity and type of the pressure. The lack of a trait signature in the declines points to a common mechanism. The severity of the Big Dry most likely led to a collapse in all major food resources, thereby affecting species relatively evenly regardless of their traits (Mac Nally *et al.*, 2009).

Given that extreme climatic events are likely to be interspersed by more benign periods, the duration of the latter is likely to determine the extent to which the biota is able to recover. Species that are resistant to the drought may gain a competitive edge, allowing them to rapidly expand during more benign periods and monopolize resources, which may limit the recovery of more vulnerable species (Bennett, unpublished data). Ultimately, differences in species' resistance to the extreme event and their resilience during benign periods may result in an irreversible shift in the species assemblage, which is widely predicted to be shaped by changes in species abundances, species losses (mostly specialists) and the expansion of invasive and generalist species (Jimenez *et al.*, 2011).

The primary determinants of species' resilience during benign periods are likely to be mobility (immigration) and fecundity (Dawson *et al.*, 2011). The time frames over which immigration (rapid) and recruitment (slower) are likely to influence species' resilience will differ. Itinerant nectarivores are highly mobile and move in response to changes in the spatial mosaic of flowering (Mac Nally & McGoldrick, 1997), which suggests that they may be relatively resistant if there are favorable areas to move to during droughts. At the time of the drought, flowering was much reduced, with complete failure of flowering in some years (Mac Nally *et al.*, 2009). The Big Wet led to substantial eucalypt flowering in the study region (Bennett, unpublished data). However, nectarivores did not display disproportionately high levels of resilience. Although highly mobile species can emigrate in response to fluctuations in resources, movements incur energetic costs, foregone breeding opportunities and increased mortality (Mac Nally *et al.*, 2009). Therefore, even highly mobile species may reach a condition in which recruitment in the increasingly rare good years is unlikely to 'repay' the accumulated costs associated with the more frequent dry years, resulting in an on-going decline in populations.

Resident birds, such as many smaller insectivores, have limited capacity to move in response to changes in resource availability, and their decline signals mortality without replacement (Mac Nally *et al.*, 2009). The extensive loss of canopy, litter and shrub cover during the Big Dry (Bennett

et al., 2013) most likely indicates a decline in nest-site quality (fewer sites and increased exposure) and food resources because abundances of arthropods associated with these vegetation characteristics decline during drought (Bell, 1985). Over successive years, the decline in their resource base may have severely limited insectivore recruitment to a level in which the occasional average or wet year is unlikely to compensate for recruitment failure in dry, hot years.

Global implications

Climate change and the resultant increases in frequency and intensity of extreme events have the potential to cause widespread biodiversity loss through the degradation of habitats, which may exacerbate pressures associated with land-use change due to greater heat and water stress in fragmented vegetation. Differences between species' resistance to extreme climatic events and their resilience during intermittent periods of more benign climatic conditions may reshape communities significantly. Rapid variations in climate are expected to alter assemblages to greater numbers of generalist species that are less reliant on continuous native vegetation, but our results indicate that even species with these qualities are not necessarily immune to more severe climatic extremes. Increases in the duration and frequency of Big Dry-like events may favor the few resilient species that are able to rapidly monopolize booms and busts in resources. Ultimately, this could lead to a homogenization of the bird assemblage and a loss of ecosystem services.

Even under the more optimistic emissions scenarios, which seem increasingly unlikely, the frequency and intensity of climatic extremes are set to increase in many regions of the world (IPCC, 2007). There is evidence of increases in the frequency of precipitation extremes, with extreme events documented in North America, Europe, southern Africa and Asia (Knapp *et al.*, 2008). Our system is a model for other regions undergoing rapid variations in climate. Extreme climatic events may produce some of the most dramatic effects on populations and may render populations less resistant to other drivers (e.g. invasive species) (Mantyka-Pringle *et al.*, 2012).

ACKNOWLEDGEMENTS

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REFERENCES

- Albright, T.P., Pidgeon, A.M., Rittenhouse, C.D., Clayton, M.K., Flather, C.H., Culbert, P.D., Wardlow, B.D. & Radeloff, V.C. (2010) Effects of drought on avian community structure. *Global Change Biology*, **16**, 2158-2170.
- Bell, H.L. (1985) Seasonal variation and the effects of drought on the abundance of arthropods in savanna woodland on the Northern Tablelands of New South Wales. *Australian Journal of Ecology*, **10**, 207-221.
- Bennett J.M., Cunningham S.C., Connelly C.A., Clarke R.H., Thomson J.R. & Mac Nally R (2013). The interaction between a drying climate and land use affects forest structure and above-ground carbon storage. *Global Ecology and Biogeography*, **22**, 1239-1247.
- Blakers, M., Davies, S.J.J.F. & Reilly, P.N. (1984) *Atlas of Australian Birds*. Melbourne University Press, Melbourne.
- BoM (2013) *Australian climate variability & change* Available at: <http://www.bom.gov.au/cgi-bin/climate/change/timeseries.cgi> (accessed July 2013).
- Brown, G.W., Bennett, A.F. & Potts, J.M. (2008) Regional faunal decline - reptile occurrence in fragmented rural landscapes of south-eastern Australia. *Wildlife Research*, **35**, 8-18.
- Bruehlheide, H. & Luginbühl, U. (2009) Peeking at ecosystem stability: making use of a natural disturbance experiment to analyze resistance and resilience. *Ecology*, **90**, 1314-1325.
- Chessman, B.C. (2013) Identifying species at risk from climate change: Traits predict the drought vulnerability of freshwater fishes. *Biological Conservation*, **160**, 40-49.
- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, **22**, 357-365.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53-58.
- ECC (2001) *Box-Ironbark Forests and Woodlands Investigation*. Environment Conservation Council, Melbourne.

- Etter, A., McAlpine, C., Phinn, S., Pullar, D. & Possingham, H. (2006) Characterizing a tropical deforestation wave: a dynamic spatial analysis of a deforestation hotspot in the Colombian Amazon. *Global Change Biology*, **12**, 1409-1420.
- Falkenberg, L.J., Connell, S.D. & Russell, B.D. (2013) Disrupting the effects of synergies between stressors: improved water quality dampens the effects of future CO₂ on a marine habitat. *Journal of Applied Ecology*, **50**, 51-58.
- Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265-280.
- Harrison, G.W. (1979) Stability under environmental stress: resistance, resilience, persistence, and variability. *The American Naturalist*, **113**, 659-669.
- Herbert, D.A., Fownes, J.H. & Vitousek, P.M. (1999) Hurricane damage to a Hawaiian forest: nutrient supply rate affects resistance and resilience. *Ecology*, **80**, 908-920.
- IPCC (2007) Climate Change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. In: (ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), p. 996, Cambridge University Press, Cambridge.
- Jentsch, A. & Beierkuhnlein, C. (2008) Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience*, **340**, 621-628.
- Jiguet, F., Brotons, L. & Devictor, V. (2011) Community responses to extreme climatic conditions. *Current Zoology*, **57**, 406-413.
- Jimenez, M.A., Jaksic, F.M., Armesto, J.J., Gaxiola, A., Meserve, P.L., Kelt, D.A. & Gutierrez, J.R. (2011) Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. *Ecology Letters*, **14**, 1227-1235.
- Jones, R.N. (2012) Detecting and attributing nonlinear anthropogenic regional warming in southeastern Australia. *Journal of Geophysical Research: Atmospheres*, **117**, D04105.

- Julliard, R., Jiguet, F. & Couvet, D. (2004) Evidence for the impact of global warming on the long-term population dynamics of common birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, S490-S492.
- Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., Smith, M.D., Smith, S.D., Bell, J.E., Fay, P.A., Heisler, J.L., Leavitt, S.W., Sherry, R., Smith, B. & Weng, E. (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, **58**, 811-821.
- Leblanc, M., Tweed, S., Van Dijk, A. & Timbal, B. (2012) A review of historic and future hydrological changes in the Murray-Darling Basin. *Global and Planetary Change*, **80**, 226-246.
- Lenoir, J., Gégout, J.C., Marquet, P.A., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768-1771.
- Mac Nally, R. (2007) Use of the abundance spectrum and relative-abundance distributions to analyze assemblage change in massively altered landscapes. *American Naturalist*, **170**, 319-330.
- Mac Nally, R. & McGoldrick, J.M. (1997) Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. *Journal of Avian Biology*, **28**, 171-183.
- Mac Nally, R. & Horrocks, G. (2002) Relative influences of patch, landscape and historical factors on birds in an Australian fragmented landscape. *Journal of Biogeography*, **29**, 395-410.
- Mac Nally R., Nerenberg S., Thomson J.R., Lada H. & H. C.R. (2014). Do frogs bounce, and if so, by how much? Responses to the ‘Big Wet’ following the ‘Big Dry’ in southeastern Australia *Global Ecology and Biogeography*, **23**, 223-234.
- Mac Nally, R., Bennett, A.F., Thomson, J.R., Radford, J.Q., Unmack, G., Horrocks, G. & Vesk, P.A. (2009) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720-730.

- Mackey, B., Berry, S., Hugh, S., Ferrier, S., Harwood, T.D. & Williams, K.J. (2012) Ecosystem greenspots: identifying potential drought, fire, and climate-change micro-refuges. *Ecological Applications*, **22**, 1852-1864.
- Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239-1252.
- McAlpine, C.A., Syktus, J., Ryan, J.G., Deo, R.C., McKeon, G.M., McGowan, H.A. & Phinn, S.R. (2009) A continent under stress: interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate. *Global Change Biology*, **15**, 2206-2223.
- McKechnie, A.E. & Wolf, B.O. (2010) Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, **6**, 253-256.
- Morecroft, M.D., Crick, H.Q.P., Duffield, S.J. & Macgregor, N.A. (2012) Resilience to climate change: translating principles into practice. *Journal of Applied Ecology*, **49**, 547-551.
- Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285-297.
- Orwin, K.H., Wardle, D.A. & Greenfield, L.G. (2006) Context-dependent changes in the resistance and resilience of soil microbes to an experimental disturbance for three primary plant chronosequences. *Oikos*, **112**, 196-208.
- Pfisterer, A.B. & Schmid, B. (2002) Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, **416**, 84-86.
- Radford, J.Q. & Bennett, A.F. (2005) Terrestrial avifauna of the Gippsland Plain and Strzelecki Ranges, Victoria, Australia: insights from Atlas data. *Wildlife Research*, **32**, 531-555.
- Regan, H.M., Crookston, J.B., Swab, R., Franklin, J. & Lawson, D.M. (2010) Habitat fragmentation and altered fire regime create trade-offs for an obligate seeding shrub. *Ecology*, **91**, 1114-1123.

- Royle, J.A. & Link, W.A. (2006) Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*, **87**, 835-841.
- Sekercioglu, C.H., Daily, G.C. & Ehrlich, P.R. (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 18042-18047.
- Smith, M.D. (2011) The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology*, **99**, 651-655.
- Stevenson, I.R. & Bryant, D.M. (2000) Avian phenology: Climate change and constraints on breeding. *Nature*, **406**, 366-367.
- Thompson, R.M., Beardall, J., Beringer, J., Grace, M. & Sardina, P. (2013) Means and extremes: building variability into community-level climate change experiments. *Ecology Letters*, **16**, 799-806.
- Thomson, J.R., Mac Nally, R., Fleishman, E. & Horrocks, G. (2007) Predicting bird species distributions in reconstructed landscapes. *Conservation Biology*, **21**, 752-766.
- Thomson, J.R., Bond, N.R., Cunningham, S.C., Metzeling, L., Reich, P., Thompson, R.M. & Mac Nally, R. (2012) The influences of climatic variation and vegetation on stream biota: lessons from the Big Dry in southeastern Australia. *Global Change Biology*, **18**, 1582-1596.
- Vesk, P.A., Nolan, R., Thomson, J.R., Dorrough, J.W. & Mac Nally, R. (2008) Time lags in provision of habitat resources through revegetation. *Biological Conservation*, **141**, 174-186.
- Welsh, A.H., Lindenmayer, D.B. & Donnelly, C.F. (2013) Fitting and interpreting occupancy models. *PLoS ONE*, **8**, e52015-e52015.
- Yom-Tov, Y. (1987) The Reproductive Rates Of Australian Passerines. *Australian Wildlife Research*, **14**, 319-330.

Table 1: Details of bird-occurrence studies

Program	No. sites	No. surveys/site	Years	Sources
Regional 1	139	8	1995-1997	(Mac Nally <i>et al.</i> , 2000; Mac Nally & Horrocks, 2002a)
Regional 2	65	8	2004-2005	(Thomson <i>et al.</i> , 2007)
Regional 3	120	8	2010-2011	This study
Landscape 1	240	4	2002-2003	(Radford <i>et al.</i> , 2005)
Landscape 2	300	4	2006-2007	This study
Landscape 3	300	4	2011-2012	This study

Table 2: Summary of net changes in reporting rates in the fragment- and landscape-survey programs over the entire survey period (1995–97 to 2010–11 and 2002–03 to 2011–12 respectively). Species were characterized according to ecological traits relating to their vulnerability to habitat loss and fragmentation, foraging and nesting guilds, mobility, conservation concern (Radford & Bennett, 2005) and geographic distributions (Blakers et al., 1984) (Appendix 1). Results for the fragment-survey program are shown first. ‘-’ denotes decrease; ‘0’ denotes no evidence of change; ‘+’ denotes increase (i.e. -/- = a decline in both the fragment and landscape-survey programs).

Classification	Class	total	-/-	-/0	0/-	0/0	+/0	0/+	++	-/+	+/-
Habitat	Open-country	11	3	1	3	0	0	0	0	1	3
Habitat	Open-tolerant	26	12	2	4	4	2	1	0	0	1
Habitat	Woodland-dependent	58	26	6	5	7	3	1	2	2	6
Foraging zone	Aerial	8	6	0	1	1	0	0	0	0	0
Foraging zone	Bark	4	2	0	1	0	0	0	0	0	1
Foraging zone	Canopy	31	16	3	1	1	2	0	0	2	6
Foraging zone	Ground	46	16	5	8	8	3	1	1	1	3
Foraging zone	Low shrubs	2	0	0	1	1	0	0	0	0	0
Foraging zone	Tall shrubs	4	1	1	0	0	0	1	1	0	0
Food	Frugivore	3	2	1	0	0	0	0	0	0	0
Food	Insectivore	50	21	2	7	7	4	2	0	2	5
Food	Nectarivore	16	10	2	0	0	0	0	1	0	3
Food	Raptor/vertebrate	14	5	1	3	3	1	0	0	1	0
Food	Granivore	12	3	3	2	1	0	0	1	0	2
Nesting	N/A	1	1	0	0	0	0	0	0	0	0
Nesting	Burrow	3	2	0	0	0	0	0	0	1	0
Nesting	Ground	6	3	0	1	0	0	1	1	0	0

Nesting	Hollows	18	8	3	3	2	0	0	0	0	2
Nesting	Shrub/canopy	63	27	6	7	9	4	0	1	1	8
Nesting	Parasite	4	0	0	1	0	1	1	0	1	0
Conserv. concern	No	69	29	6	10	4	4	2	1	3	10
Conserv. concern	Yes	26	12	3	2	7	1	0	1	0	0
Mobility	Migrant	18	8	1	2	2	1	2	0	1	1
Mobility	Itinerant	13	8	1	0	1	0	0	1	0	2
Mobility	Resident	64	25	7	10	8	4	0	1	2	7
Distribution	Dry	20	9	3	2	3	1	0	0	0	2
Distribution	Mesic	7	5	1	0	0	0	0	0	0	7
Distribution	Widespread	68	27	5	10	8	4	2	2	3	5
Totals	–	95	41	9	12	11	5	2	2	3	10

Figure legends

Figure 1 The location of study sites in both survey programs in the box-ironbark region of north-central Victoria, Australia (remnant vegetation is shown in grey shade). Study sites enclosed in boxes are the ‘landscapes’ of the landscape survey program.

Figure 2 Annual anomalies relative to the 1961-1990 baselines used by the Australian Bureau of Meteorology, for rainfall (mm; a) and mean maximum temperature (°C; b). Data are means from six representative stations across central Victoria, Australia (Australian Bureau of Meteorology station numbers: 81085, 81003, 81123, 81053, 88043, 88019).

Figure 3 Ranked changes in the reporting rate (log odds) of bird species derived from Bayesian logistic regression, from the regional program, (a) 1997 v 2004 (b) 2004 v 2010 and (c) 1997 v 2010, and the landscape programs; (d) 2002-3 v 2006-7, (e) 2006-7 v 2011-12, and (f) 2002-3 v 2011-12. Grey shading indicates a significant change in reporting rate (with > 90% certainty); while white indicates a non-significant change in reporting rate (< 90%).

Figure 4 Comparison of species-level coefficients for two time periods in both the regional (a) and landscape (b) survey programs. Conceptually, if recovery was complete all species would fall along the dashed ‘one-to-one’ line. Downward triangles show species that - declined from 1st to 2nd period (with > 90% certainty); upward triangles - increased from 1st to 2nd period (with > 90% certainty); circles - no substantial difference between 1st and 2nd period (< 90%); black - substantially lower in 3rd survey period than 1st (90% certainty); grey - substantially higher in 3rd survey period than 1st (90% certainty); open - no substantial difference between 1st and 3rd period (< 90%).

Figure 5 Boxplots showing the sum of species reporting rate responses within guilds between: (a) 1st and 2nd period (b) 2nd and 3rd period and (c) 1st and 3rd period (net change). The first graph for each period shows the variance components for each guild; all other plots show the estimated effects of change for each level of each guild, – indicates species unassigned to a guild.

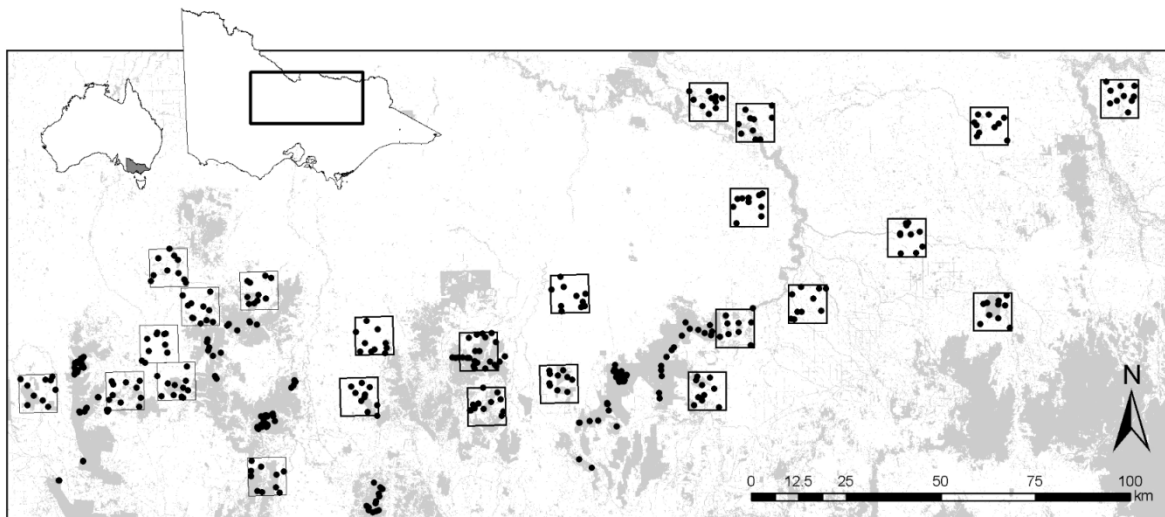


Figure 1:

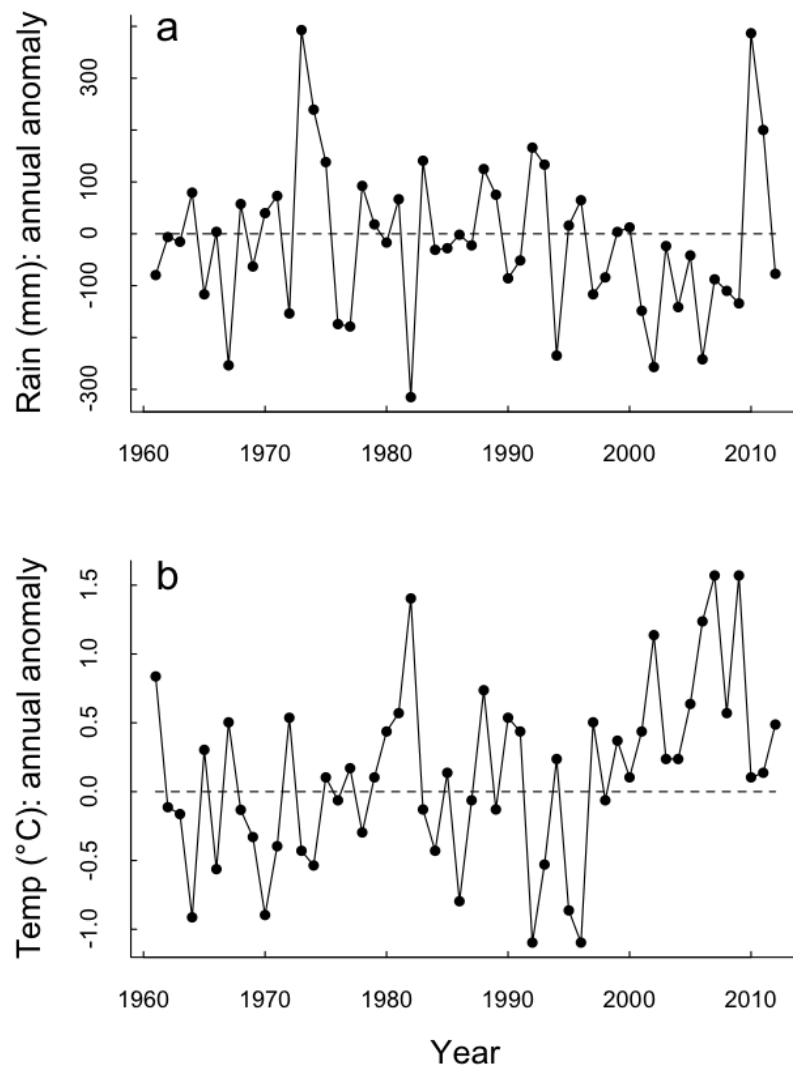


Figure 2:

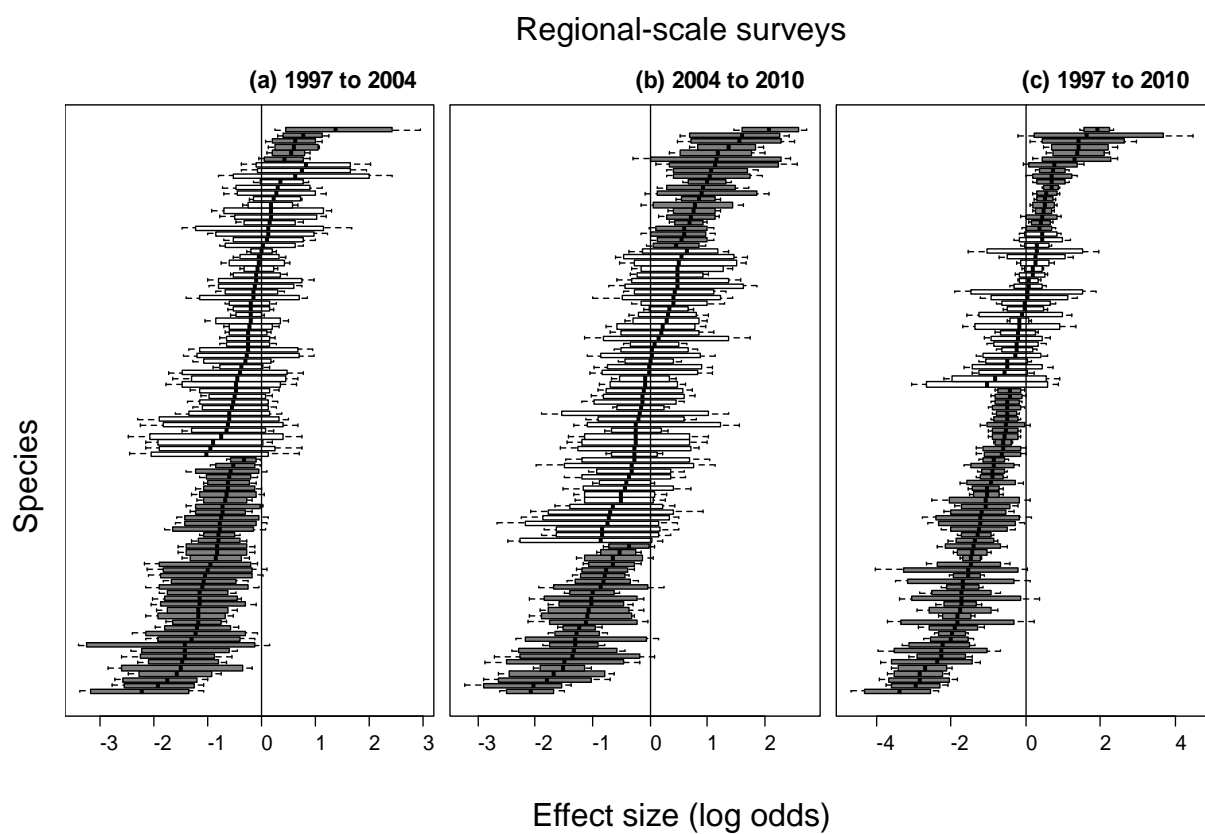


Figure 3A:

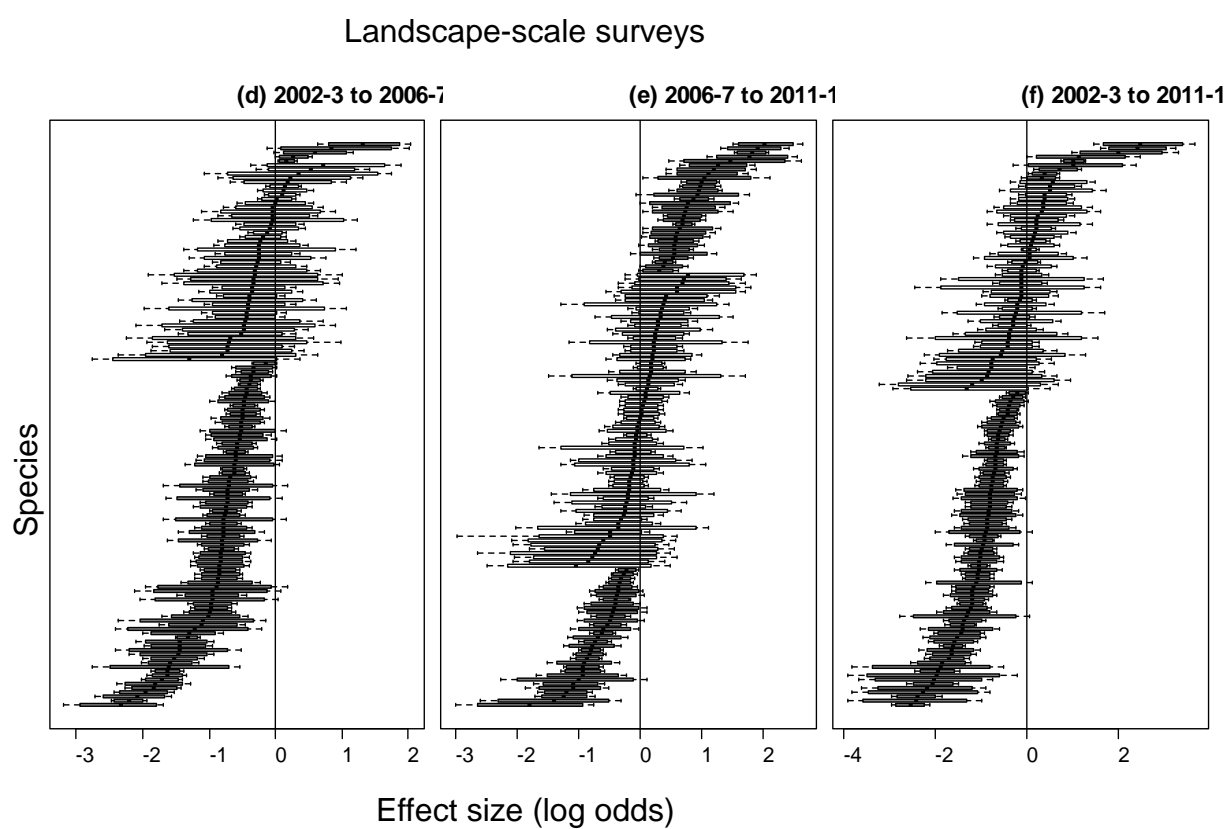


Figure 3B:

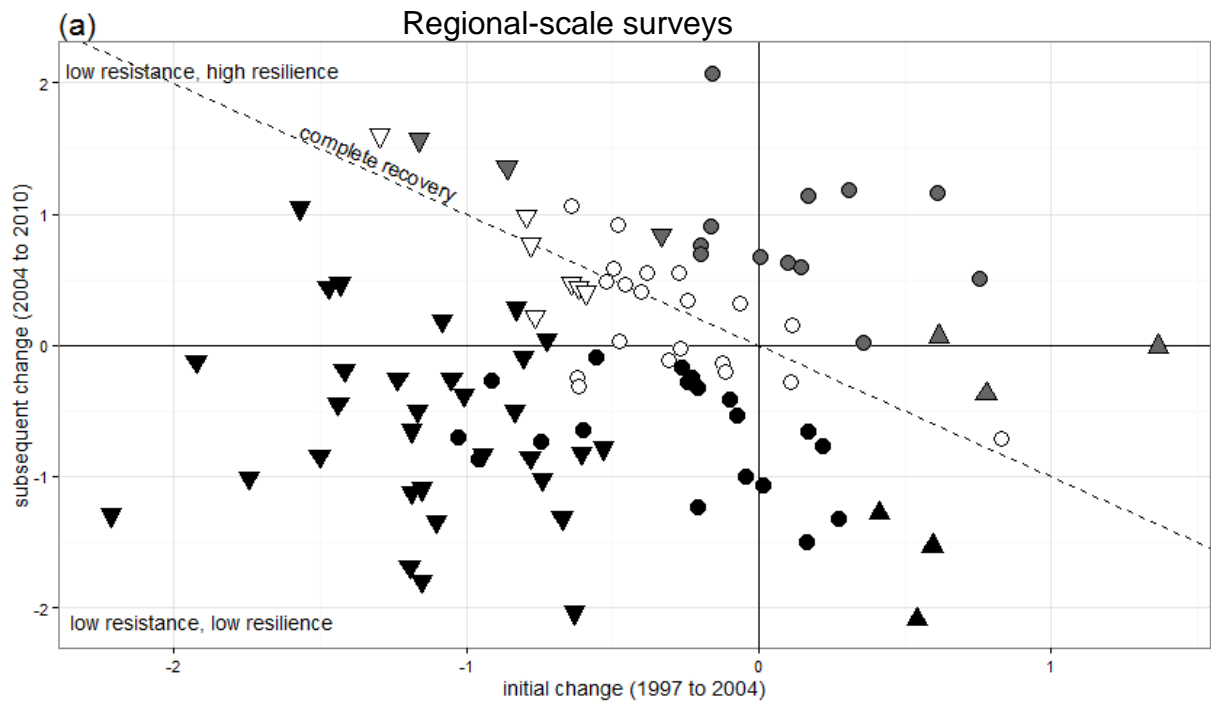


Figure 4A:

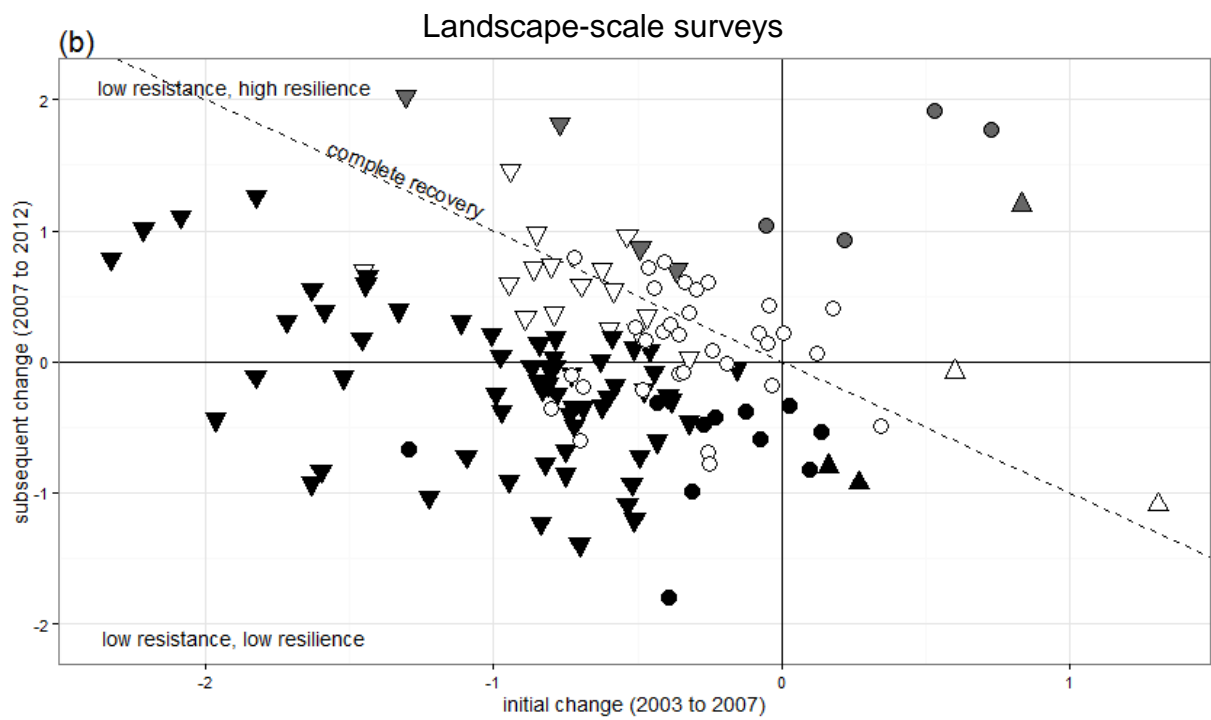


Figure 4B:

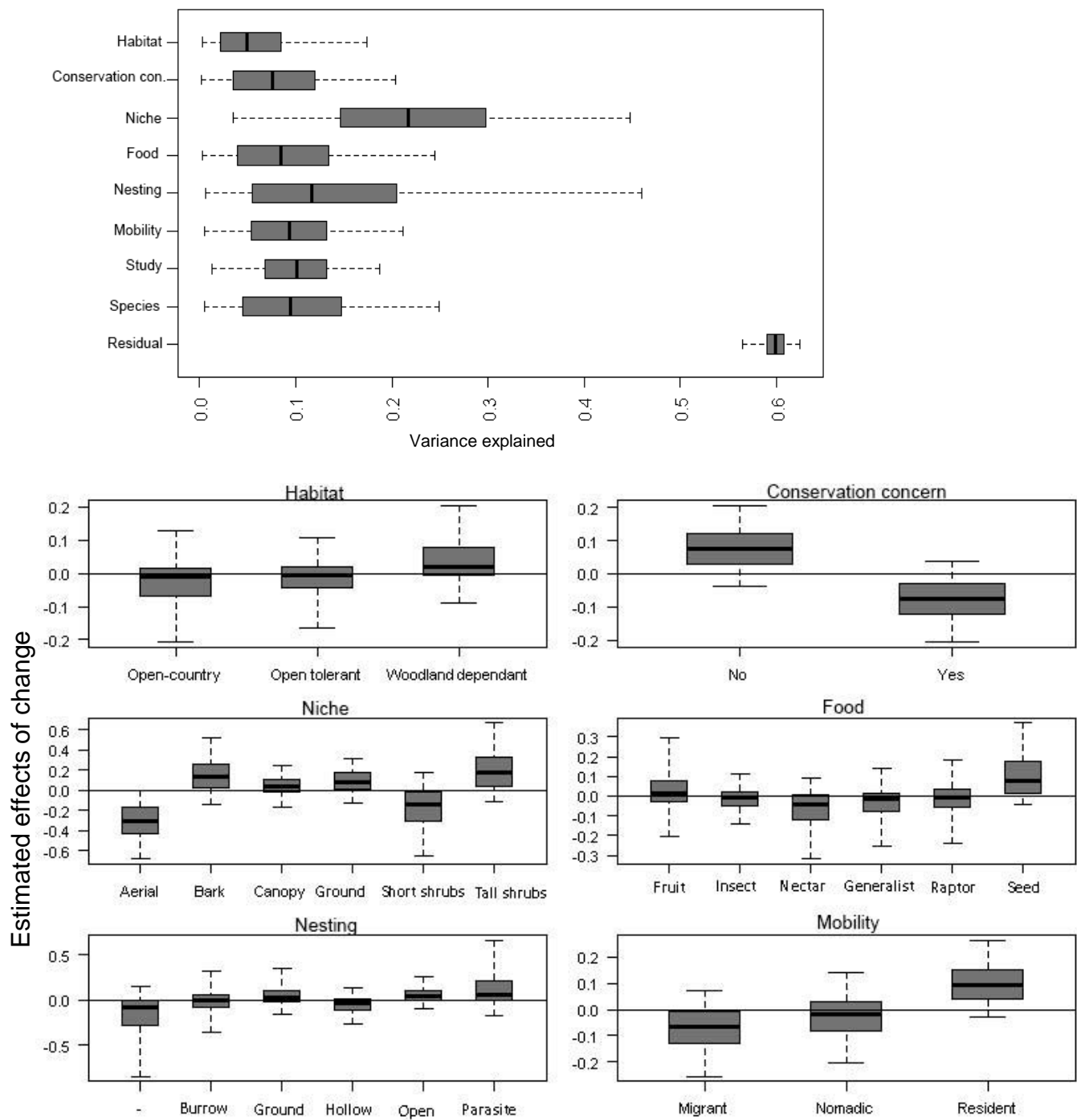


Figure 5A:

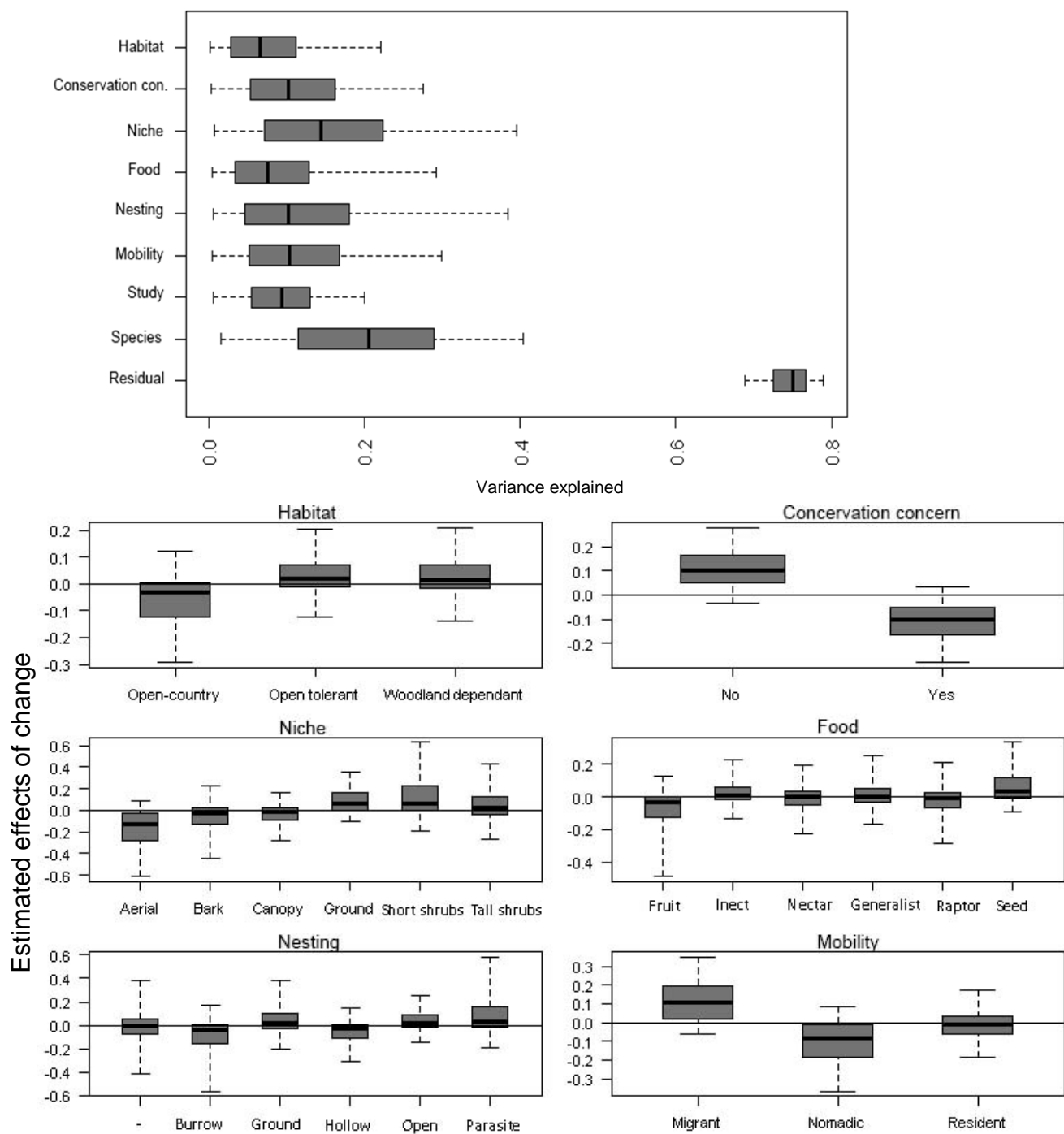


Figure 5B:

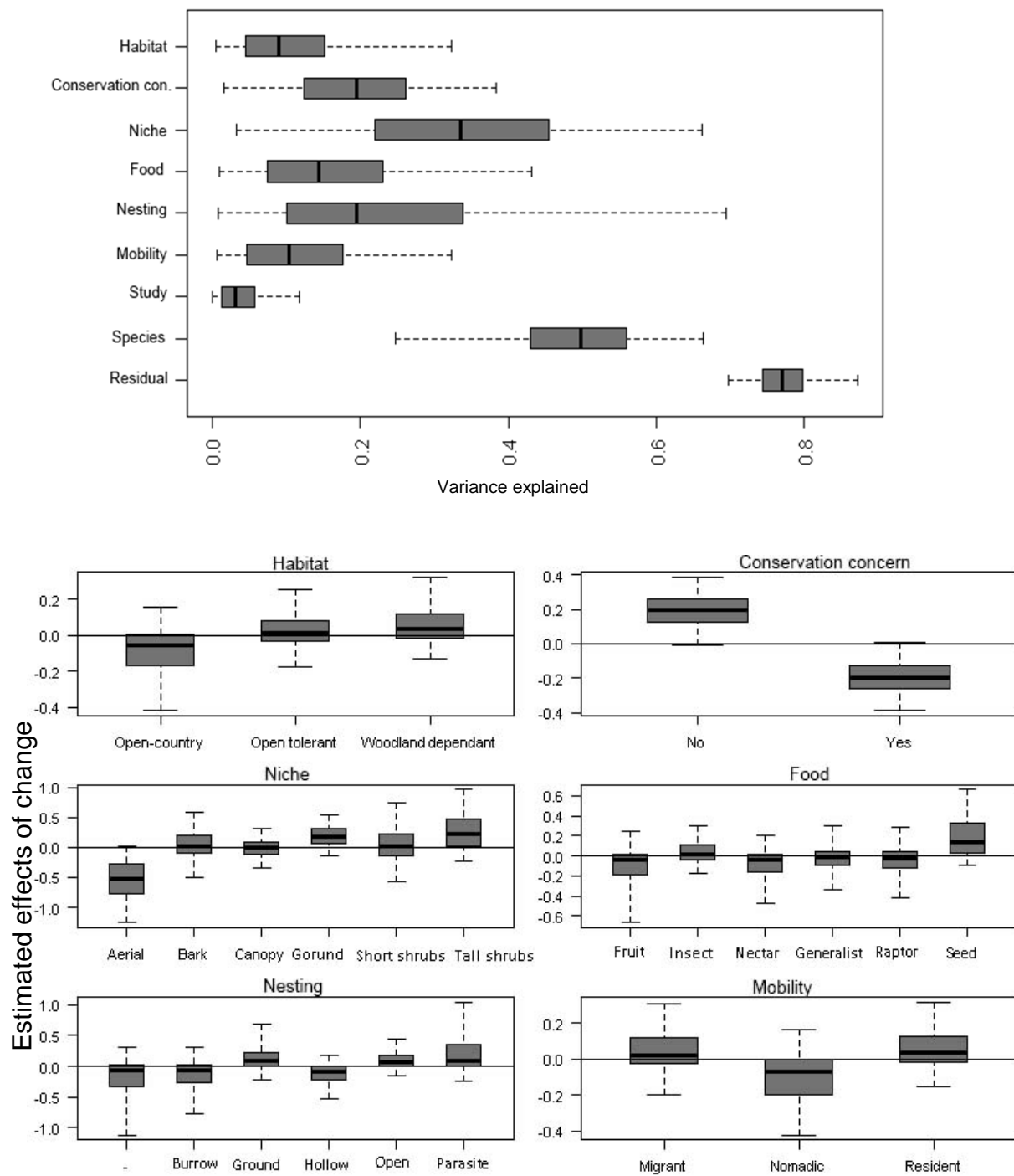


Figure 5C:

PART B: Suggested Declaration for Thesis Chapter

Monash University

Declaration for Thesis Chapter 4

Declaration by candidate

In the case of Chapter 4, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The initiation, key ideas, development and writing up of the work were my responsibility. I coordinated the study and performed most of the field work (all of the 2010-11 data), conducted most of the analysis and was the primary author of the manuscript.	65

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Rohan H. Clarke,	Contributed to writing of the manuscript	
Gregory F. B. Horrocks	Contributed 1997 data	
James R. Thomson	Support with analysis	
Ralph Mac Nally	Contributed ideas to the work and contributed to writing of the manuscript	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature		Date
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Main Supervisor's Signature		Date
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*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 4: Climate drying amplifies the effects of fragmentation and interspecific interactions on birds

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Running title: Climate, land use and competition affect birds

Keywords: climate change, despotic species, drought, interspecific competition, land-use change

ABSTRACT

Aim Climate change probably will amplify habitat fragmentation effects, including altered species interactions. We investigated whether an avifauna changed over a period of severe drought that is symptomatic of climate change and if avifaunal changes were consistent with changes in habitat characteristics in a much modified forest ecosystem. We sought to determine if changes were amplified due to fragmentation or altered species interactions.

Location The box-ironbark forests of south-eastern Australia

Methods We remeasured the avifaunas and vegetation characteristics of 120 forest transects in 2010–11 that had previously been measured in 1995–97.

Results We found a significant change in the avifauna over the prolonged drought. The magnitude of change was intensified by increased habitat degradation in smaller fragments and interspecific competition associated with increases in the abundance of a dominant avian competitor.

Main conclusions The interaction between climate and land-use change facilitated the expansion of highly aggressive species. Increases in the frequency and intensity of extreme events predicted under climate change may create a boom-bust pattern of availabilities of resources, which may favor highly competitive species that are able to monopolize remaining resources. This may lead to disproportionate declines in smaller bodied species in times of resource scarcity and hinder their recovery when conditions improve. The exclusion of smaller-bodied species by the hyper-aggressive species may lead to a homogenization of the avifauna that would affect ecosystem process, including control of insect pests, seed dispersal and pollination.

INTRODUCTION

Climate change and habitat fragmentation are processes that are likely to act synergistically so that their combined effects on biota are greater than the sum of their individual effects (Mantyka-Pringle *et al.*, 2012). Fragmented remnants of vegetation may be more vulnerable to climate change than intact remnants due to shifts in the regional distribution of precipitation, localized drying, and increased fire frequency and severity (Brook *et al.*, 2008). Despite this, climate change and habitat fragmentation are rarely considered together in empirical studies, suggesting that current knowledge may be inadequate for effective conservation management (Mantyka-Pringle *et al.*, 2012).

The response to climate change by many species is likely to be indirect with the modification of habitat and asynchrony with species' food requirements being key pressures (Bellard *et al.*, 2012). Increases in the frequency and duration of drought and heat stress from climate change have been linked to widespread vegetation dieback and distribution shifts (Allen *et al.*, 2010). Vegetation change has many effects on biodiversity, including: reductions in population sizes, breeding success, dispersal, increased vulnerability to other pressures, changes in species composition and interspecific interactions (Mac Nally & Bennett, 1997).

The effects of altered interspecific interactions are rarely considered in studies of multiple pressures, such as between climate and land-use change, probably due to their complexity and the difficulty in measuring the effect (Tylianakis *et al.*, 2008). Climate change is likely to affect interspecific interactions because these are influenced by the phenology, physiology, relative abundances, and behaviors of multiple species, which can be influenced directly by the prevailing climate (Tylianakis *et al.*, 2008). Interspecific interactions such as competition, predation, parasitism and pollination are central to communities and ecosystem function (Bellard *et al.*, 2012). One example of climate impacts on interactions is that of climate-driven phenological mismatches between plants and pollinators, which have been linked to the extinction of some plants and their pollinators (Bellard *et al.*, 2012).

Birds may be used as an ‘exemplar’ for investigating whether climate and land-use change are interacting and affecting interspecific interactions. Interspecific variation in extinction risk in birds is associated with species ecological traits, implying that demographic rates should differ among species (Öckinger *et al.*, 2010). Competitive species that are tolerant of, or benefit from, change may monopolize resources (nesting sites and food), limiting the success of disturbance-sensitive species (Brown, 2007). Such disparities in responses have consequences on ecological services, including pollination, seed dispersal and invertebrate control performed by birds which, in turn, may influence the on-going maintenance of remnant vegetation (Sekercioglu, 2006).

South-eastern Australia is a region in which climate change and land management have much affected the biota. Temperatures in south-eastern Australia have been increasing since the 1950s, with a 1 °C increase in mean daily temperature, which is consistent with the projections of global circulation models (Leblanc *et al.*, 2012). With continuing climate change, by 2070, south-eastern Australia is projected to experience a further 1–6 °C mean annual temperature increase and a 5-15 % decrease in rainfall in all months (IPCC, 2007). Climate-change modelling for the region predicts substantial increases in the frequency and severity of droughts that span a decade or more. The region experienced a 13-year drought from 1997, referred to as the ‘Big Dry’, which was followed by heavy spring and summer rainfall from 2010 until early in 2012, now termed the ‘Big Wet’ (Leblanc *et al.*, 2012). Consistent with climate change projections, the duration and accumulated precipitation deficit over the Big Dry was at least twice that of any other drought since instrumental records began in the 1880s (Leblanc *et al.*, 2012). The Big Wet was consistent with climate-change predictions where rainfall events will be condensed into shorter, more intense periods (Hennessy *et al.*, 2007).

Since European settlement in Australia *c.* 220 years ago, the extent of forest in the south-east has been halved (McAlpine *et al.*, 2009), although some bioregions have experienced as much as 97% clearance (ECC, 2001). The extensive reduction in vegetation cover has altered surface characteristics, decreasing evapotranspiration and modifying soil and atmospheric moisture patterns

(McAlpine et al., 2009). The resultant changes in climate at the regional scale are likely to have further exacerbated the effects of the Big Dry (McAlpine et al., 2009).

The Big Dry was linked to major changes in vegetation structure, with several key vegetation characteristics changing systematically; these included: increased tree mortality, increased canopy dieback, reduced vegetative ground cover and reduced shrub cover (Bennett *et al.*, 2013). These effects were more severe in fragmented vegetation. These vegetation shifts, especially, canopy dieback, are likely to affect interspecific interactions. For example, the hyperaggressive and colonial bird, the noisy miner *Manorina melanocephala*, occurs in greater abundances when canopy cover is reduced (Maron *et al.*, 2013). Noisy miners aggressively exclude other birds (especially species smaller than themselves < 63 g) and have been linked to reductions in woodland bird diversity across eastern Australia (Mac Nally *et al.*, 2012).

Bird assemblages of Victoria's box-ironbark forests, which are located in south-eastern Australia, have been under significant pressure from drought, vegetation loss, fragmentation and degradation (Mac Nally *et al.*, 2009). We predicted that bird species dependent on vegetation characteristics that had changed (i.e. canopy, ground and shrub cover) would decline disproportionately compared with other birds. These declines are expected to be exacerbated in smaller forest fragments due to higher levels of dieback associated with fragment area (Bennett *et al.*, 2013). These same structural changes in vegetation are expected to facilitate noisy miner colonization, further exacerbating avifaunal declines (Maron *et al.*, 2013). We sought to determine: (1) whether there was a shift in the bird assemblage of the box-ironbark forest between 1995–97 (our original pre-Big Dry surveys) and 2010–11 (Big Wet, post-drought surveys)? (2) If the avifaunal assemblage had changed, were these changes consistent with the changes in vegetation characteristics? And (3) whether species responses were linked to changes in climate, vegetation characteristics and the abundance of the noisy miner.

METHODS

The box-ironbark region of eastern Australia, characterized by eucalypt woodlands (mainly red ironbark *Eucalyptus tricarpa*, grey box *E. microcarpa*, and yellow gum *E. leucoxylon*), occur on the dry inland slopes of the Great Dividing Range from western Victoria to southern Queensland (ECC, 2001). The box-ironbark forests once covered > 3 Mha in central and northern Victoria. The system has been much disturbed by human activities including gold mining, timber felling and broad-scale clearing for agriculture. Only 17 % of the original area retains a cover of native forest vegetation and the few large (6 000–40 000 ha) remnants are scattered throughout the agricultural landscapes. Remnant native vegetation is predominantly regrowth from wholesale clearance during in the 1850s gold rush; these much-modified woodlands are characterized by smaller systems that occur at higher densities than the pre-disturbance structures (ECC, 2001). Only *c.* 2 % of existing forest is thought to be ‘old growth’, with characteristics such as large, hollow-bearing trees (Vesk *et al.*, 2008).

Transects were located in fragments distributed around four regional centers in north-central Victoria (St Arnaud, Dunolly, Bendigo and Rushworth) (Mac Nally *et al.*, 2000). Survey transects were replicated within each remnant to provide representative coverage for avian and vegetation surveys: (1) one transect in each 10 ha site, (2) two transects in each 20 ha site, (3) three transects in each 40 ha site, (4) four transects in each 80 ha site, and (5) 22 transects in each large remnant (Mac Nally *et al.*, 2000). There were 120 transects 17 fragments of 10 ha, eight fragments of 20 ha, three fragments of 40 ha, three fragments of 80 ha, and three large remnants (> 10 000 ha) located near to St Arnaud, Dunolly and Rushworth. Thirty-one of the 38 fragments surveyed in 1995 by Mac Nally *et al.* (2000) were included in the 2010 survey. Of the remainder, they were either cleared or access was not granted by owners.

Climate data

Historically, the average rainfall was 400–700 mm and fell mostly in winter and spring (Mac Nally *et al.*, 2000). The Australian Bureau of Meteorology (BoM) has designated the period between 1961 and 1990 a baseline against which climate variation is compared. From 1997 to 2010, there was an

increase in mean temperature of 0.65 °C relative to the BoM baseline (BoM, 2013). The mean annual rainfall of the study sites decreased from 537 ± 111 SD mm yr⁻¹ for 1984–1996 to 430 ± 87 SD mm yr⁻¹ for 1997–2009, with the declines being disproportionately large in autumn and early winter (Leblanc *et al.*, 2012). Rainfall over the Big Dry was less than the baseline for 11 of the 13 years, and the cumulative rainfall deficit was almost 2.5 years' worth of mean baseline rainfall. The Big Wet restored about a year of the Big Dry rainfall deficit (BoM, 2013). Climate predictors were extracted from spatial data modeled for 500 m² grids from the Bureau of Meteorology Data Library (BoM, 2012). Rainfall and temperature were obtained from mean rainfall and mean temperature data from the six years prior to the surveys (1991–1996 and 2003–2009).

Vegetation measurements

Twenty-one variables were measured by exact enactment of the methods used in 1995–97 (Mac Nally *et al.*, 2000). Measurements were calibrated *in situ* under the supervision of G. F. B. H, who conducted the 1997 surveys, to ensure consistency. Numbers, species and diameters at breast height (DBH) of all trees > 10 cm and the densities of shrub species were recorded within an 80 × 100 m transect, as were the densities of tree hollows, saplings and stumps. Total basal area for each tree species was calculated by assigning trees to one of four size-classes: 10–39 cm DBH (small), 40–59 cm DBH (medium), 60–79 cm DBH (large) and > 80 cm DBH (very large) (Mac Nally *et al.*, 2000). Saplings were defined as those woody stems with a DBH of < 10 cm. Cover estimates were taken at each transect using quadrats: two 25 × 25 m quadrats for shrub-cover, one 10 × 50 m quadrat for fallen timber and two 5 × 5 m quadrats for ground-cover. Canopy cover estimates were taken at four locations along each transect by viewing the canopy through a 30 × 20 cm transparent grid and estimating the percentage of cells overlain.

Bird surveys

We divided the year into a 'warm' season, from October to April, and a 'cool' season, from May to September. Eight bird surveys, four each at regular intervals in the warm and cool seasons, were carried out along strip transects of 250 × 80 m (2 ha). Methods applied in 2010–11 strictly emulated

those used in 1995–97 (Mac Nally *et al.*, 2000). Surveys were performed by a single observer proceeding along the mid-line of each transect over a 20-min period in appropriate weather conditions (i.e. surveys were not conducted in rain, high wind and/or high temperatures). Surveys were conducted from 30 min after sunrise to 30 min before sunset but not during the hottest part of the day, from 11h00 to 15h00. To avoid sampling biases, sites were visited in a randomized order.

Prior to the commencement of the field program in 2010, which was conducted by J. M. Bennett, ‘mock’ surveys were conducted to align observations with those of G. F. B. Horrocks, who conducted the 1995–97 surveys. Two full rounds of mock surveys were completed, which constituted 240 surveys. There were few differences between the two observers in the later mock-survey rounds, showing that the bird survey data would be consistent between the two programs. Data for the mock surveys were discarded.

For each transect in each survey period, we calculated the reporting rate and the abundance for each bird species. The former is the number of surveys in which a species was recorded divided by the total number of surveys (eight) and the latter is the total number of individuals summed over all eight surveys (equivalent to using the mean abundance per visit, given the equal number of visits per transect). The vegetation is open wooded vegetation with tree-heights mostly < 20 m, so birds were conspicuous and easily detected. We did not correct for detectability because the statistical biases introduced by those corrections are at least as large as not accounting for detectability (Royle & Link, 2006; Welsh *et al.*, 2013). The analyses included 105 species; non-native, nocturnal and aquatic species were not considered.

To assess whether there were trait-specific responses, species were allocated to guilds following Radford and Bennett (2005) (Table 2). Ecological traits were: foraging (diet and substrate), nesting location/method, degree of dependence or tolerance to amounts of remnant vegetation in landscapes, conservation status and general mobility (e.g. resident vs seasonal migrant) (Appendix 1).

STATISTICAL ANALYSES

Multivariate analyses

A non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities (Bray & Curtis, 1957) was used to represent bird assemblages in the two survey periods using the *smacof* package (de Leeuw & Mair, 2009) in the R statistical package (R Development Core Team, 2010). The NMDS ordination was fitted with Monte Carlo correlation vectors for predictors using the *envfit* function of the *vegan* package to determine which environmental variables might be predictors of assemblage changes between the two survey periods (Oksanen *et al.*, 2010). We used *adonis* in the *vegan* package (Oksanen *et al.*, 2010) to partition multivariate variation into temporal and spatial components and to test the statistical significance of the effect of time and habitat configuration on the bird assemblage.

Species and guild-based analyses

We used hierarchical Bayesian models to examine changes in individual species' (1) prevalences (proportion of sites ever occupied), (2) abundances (total number of individuals observed at occupied sites), and (3) reporting rates (proportion of visit that a species was present at a site) between survey periods. We used a zero-inflated Poisson model to explore changes in species prevalences (proportion of locations occupied) and local abundances when present (mean densities on transects occupied). For each species, the model was:

$$n_{ij} \sim \text{Poisson}(o_{ij}\lambda_{ij}); o_{ij} \sim \text{Bernoulli}(p_{ij})$$
$$\ln(\lambda_{ij}) = \alpha_1 + \varepsilon_{i1} + \delta_1 I_j; \text{logit}(p_{ij}) = \alpha_2 + \varepsilon_{i2} + \delta_2 I_j, \quad (1)$$

Here, n_{ij} is the abundance of the species at site i during period j (2010–11 or 1995–97), λ_{ij} is the expected abundance conditional on the species being present ($o_{ij} = 1$), and p_{ij} is the probability that the species is present. The ε_i are site specific random effects. The conditional mean abundances λ_{ij} and probabilities of local occurrence p_{ij} were modeled as functions of site-specific initial values (1995–97), $\alpha + \varepsilon_i$, plus mean proportional deviations for values in 2010–11, δ . The binary indicator

I_j equals 1 for 2010-11 and zero otherwise. The subscript ‘1’ refers to parameters relating to the in-transect abundances, while the subscript ‘2’ denotes parameters determining prevalences.

We used a binomial model for reporting rates:

$$y_{ij} \sim \text{Binomial}(r_{ij}, 8); \text{logit}(r_{ij}) = \alpha_3 + \varepsilon_{i3} + \varepsilon_i + \delta_3 I_j \quad (2)$$

In (2), the ε are fragment (patch) random effects, which were found to improve model fits for the binomial model but not for the zero-inflated model.

In all models, the α s were given uninformative, independent, normal prior distributions, $N(0, \sigma^2=100)$, while the random effects were given exchangeable normal priors $N(0, \sigma^2)$ with uniform priors on the corresponding standard deviations, $\sigma \sim U(0, 2)$. The δ s were given standard normal priors $N(0, 1)$ because proportional changes in abundance, prevalence or reporting rates exceeding e^2 is very unlikely.

Parameter inference

We calculated the posterior probabilities that the mean changes in conditional abundance δ_1 , prevalence δ_2 and reporting rate δ_3 were positive, i.e. $\Pr(\delta_n > 0)$. We considered $\Pr(\delta_n > 0) > 0.91$ to be evidence of an increase in the response variable, and $\Pr(\delta_n > 0) < 0.09$ to be evidence of a decline. Posterior probabilities exceeding 0.91 correspond to at least a 10-fold increase from prior to posterior odds in favor of an increase or decrease (prior odds are even); odds ratios ≥ 10 are considered strong evidence for one model (hypothesis) over another (Kass & Raftery, 1995). We also calculated the probability that the expected abundance at a random site, $\bar{\lambda}_j \bar{p}_j$, increased or decreased between survey periods, where $\bar{\lambda}_j = e^{(\alpha_1 + \delta_1 I_j)}$, $\bar{p}_j = e^{(\alpha_2 + \delta_2 I_j)} / (1 + e^{(\alpha_2 + \delta_2 I_j)})$.

Responses in individual bird species to vegetation variables

We added covariates to the reporting rate model and used Bayesian model selection, implemented with reversible jump Markov chain Monte Carlo MCMC; (Lunn et al. 2009), to identify transect characteristics (climate, canopy cover, noisy miner abundance etc.) that were predictors of individual bird species reporting rates. For analysis, temperature and rainfall data were combined (climate), because they were inversely correlated ($r = 0.79$) so that drier sites were also hotter. Noisy

miner abundance is correlated inversely with fragment area so we linearly regressed the abundance of noisy miners against fragment area and used residual noisy miner abundance as the corresponding covariate. The model for the linear predictor was:

$$\text{logit}(r_{ij}) = \alpha_3 + \varepsilon_{i3} + \sum_{q=1}^Q \beta_q x_{ijq} + \gamma_1 z_i + I_j \cdot (\delta_3 + \gamma_2 z_i) \quad (3)$$

In (3), the β are linear effects of Q variables x , γ_1 is a fragment area effect and γ_2 is the interaction between fragment area and survey period. We fitted the covariate model twice, once with only linear covariate effects, and once allowing for non-linear effects, by replacing the matrix of predictor variables \mathbf{X} , and fragment area z , with a basis matrix of linear splines (Thomson et al. 2010). We calculated posterior probabilities that each predictor variable had linear and non-linear associations with each species' reporting rate. Covariate coefficients, β , γ , were assigned exchangeable normal prior distributions, $\beta, \gamma \sim N(0, \sigma_{cov}^2)$, and the corresponding standard deviation was assigned a uniform prior, $\sigma_{cov} \sim U(0,1)$. Posterior model probabilities were not sensitive to reasonable variations in the upper limit placed on the prior for σ_{cov} [n.b., priors wider than $U(0,2)$ were not considered because they would imply implausible standardized coefficients on the logit scale].

Model-fitting and checking

WinBUGS 1.4 was used to fit all models (Spiegelhalter et al., 2003), with the reversible jump extension (Lunn *et al.*, 2009) used for model selection in (3). Parameters were estimated with three MCMC chains of 100 000 iterations after 20 000 iteration burns-in, which were discarded. Examination of MCMC chain histories and Gelman-Ruben-Brooks statistics (Brooks & Gelman, 1998) confirmed adequate MCMC mixing and convergence. We used posterior predictive diagnostics to assess model adequacy (Gelman *et al.*, 1996). For each model, we calculated a summed discrepancy measure $S_{obs} = \sum (observed - expected)^2 / expected$ (McCullagh & Nelder, 1989) and generated a reference distribution for the discrepancy measure, S_{sim} , based on simulated data drawn from the posterior distribution of the model. If the posterior distributions of S_{obs} and S_{sim} overlapped, such that $0.1 < Pr(S_{obs} > S_{sim}) < 0.9$, then the fitted model was acceptable. For example, for the zero-inflated Poisson model the discrepancy was $S_{obs} = \sum_{ij} (n_{ij} - o_{ij}\lambda_{ij})^2 / o_{ij}\lambda_{ij}$. The

reference distribution was estimated by drawing data from the fitted model, $\mu_{ij} \sim \text{Poisson}(o_{ij}\lambda_{ij})$ and calculating the corresponding discrepancy, $S_{sim} = \sum_{ij} (\mu_{ij} - o_{ij}\lambda_{ij})^2 / o_{ij}\lambda_{ij}$, at each MCMC iteration. We did not model species recorded at fewer than three sites.

RESULTS

Bird assemblage change

The composition of the woodland bird assemblages between 1995–97 and 2010–11 differed significantly ($P < 0.001$), as did the composition among the fragment area classes ($P < 0.001$). There was little evidence of an interaction between survey period and fragment area ($P \sim 0.932$).

Environmental predictors that were associated with the overall change in the bird community included: fragment area, mean precipitation and mean temperature, canopy cover, litter depth, basal area of small and very large trees, basal area of medium sized dead trees, number of dead and living saplings, hollows, stumps, high shrub cover, shrub richness, density of the shrub *Acacia pycnantha*, and density of the noisy miner (Fig. 1).

Between 1995–97 and 2010–11, 52 species of birds (50%) declined in reporting rate and 33 species (31%) declined in prevalence, while 26 species (25%) increased in reporting rate and 18 species (17%) increased in prevalence. Four species (4%) declined in on-site abundance when present and 30 species (29%) increased in on-site abundance. Twenty-one species declined (20%) and 20 species (19%) increased (Table 1). Together, these results suggest that many species occupied fewer sites in 2010–11, but, where species persisted, they were in equal or greater numbers to those that were recorded previously at the site. Declines were largely independent of birds' ecological characteristics, feeding or nesting guild, foraging zone, primary habitat type or broad distribution. Some of the species that declined substantially were: musk lorikeet *Glossopsitta concinna*, crested shrike-tit *Falcunculus frontatus*, restless flycatcher *Myiagra inquieta*, and eastern yellow robin *Eopsaltria australis* (Table 2).

Fifteen species increased in on-transect abundance but declined in prevalence; 12 of these species are highly mobile or flocking species. Six species were itinerant nectarivores from the honeyeater and lorikeet families, which are highly mobile and travel large distances in response to changes in nectar availability (Mac Nally *et al.*, 2009). Other highly mobile species that increased in on-transect abundance but declined in prevalence were migratory (all individuals of the population migrate) or partial-migratory (the population is part migratory and part sedentary) (Lundberg, 1988) insectivores, included the silvereye *Zosterops lateralis* and striated pardalote *Pardalotus striatus* (Table 2).

Noisy miners were found only in fragments of ≤ 20 ha in the 1995–97 surveys, but by 2010–11, the miners had moved into one 40 ha and one 80 ha fragment. In the 1995–1997 surveys, the noisy miner was the 7th most numerous species. In 2010–11 surveys, the noisy miner was the 2nd-most numerous species and the most numerous in fragmented forest remnants, with mean abundances on 10 ha and 20 ha transects (33 transects in total in both 1995–97 and 2010–11) having significantly increased from 2.9 ± 0.7 (SE) individuals in 1995–97 to 7.8 ± 1.7 (SE) ($P < 0.01$) (Table 2).

Responses of bird species to noisy miners and habitat characteristics

Noisy miner abundance and climate were the main predictors of changes in the reporting rates of individual species (Table 3 & 4). Increased abundances of the noisy miner had a predominantly negative relationship with other species, with 28 species having negative relationship. Only four species were positively associated: the eastern rosella *Platycercus eximius* musk lorikeet *Glossopsitta concinna* grey butcherbird *Cracticus torquatus* and white-winged chough *Corcorax melanorhamphos*, all of which are medium-bodied (63 to 400 g) species. Sixteen species had a negative association with change in climate and nine species, including the noisy miner, had a positive association with increases in temperature and declines in rainfall.

The interaction between survey period and fragment area was important for sixteen species. Seven species appeared to respond positively to large forest blocks in 2010, with two species of

nectarivores declining less and five species of insectivores increasing more or becoming more associated with larger forest blocks (Table 3 & 4). Six species had negative relationships with large forest blocks in 2010 (Table 3 & 4). Three medium-bodied species increased more or became more associated with smaller fragments (10 ha and 20 ha), while two small-bodied species increased more in large fragments (40 ha and 80 ha) in 2010 (Table 3 & 4).

Compared to other on-transect vegetation characteristics, mid-storey vegetation (i.e. sapling density and shrub cover) had the greatest influence on individual bird species. High shrub cover was positively associated with seven species that significantly declined in reporting rate and negatively associated with six out of seven species that significantly increased in reporting rate (Table 3 & 4). Declines in three species were associated with increases in dead trees (Table 3 & 4). Vegetation characteristics associated with silvicultural practices (i.e. high small-tree density and fallen timber) had a predominantly negative relationship with species (Table 3 & 4).

Patterns for bird guilds

Species' responses were largely independent of habitat preference (Table 1). There were greater declines in aerial feeders and in ground and burrowing nesters (Table 1). Of species considered to be of conservation concern, 48% declined in prevalence, and 32% declined in total abundance compared to 30% and 19% respectively for species not currently considered to be of conservation concern. The largest percentage increase in on-transect abundance was in species using the canopy, particularly itinerant, nectarivorous species (Table 1).

DISCUSSION

The woodland bird assemblage changed markedly between the pre- (1995–97) and post-Big Dry surveys (2010–11). These changes were attributed to observed reductions in precipitation and increases in temperatures, symptomatic of extended drought, and the resultant vegetation change that facilitated the expansion of an avian despotic species. Noisy miner abundance amplified the declines of many species in smaller fragments (where noisy miners occur), especially those species

vulnerable to noisy miner aggression (Mac Nally *et al.*, 2012). Increased noisy miner abundance was associated with the change in avian assemblage over time and was a predictor for the greatest number of declines. A higher incidence of die-back in real fragments (Bennett *et al.*, 2013) may have facilitated noisy miner invasion.

The loss, fragmentation and degradation of habitat have led to declines in abundance and distribution of many native species, but facilitated increases in abundance and distribution of others. Some of these species may become ‘native invaders’ capable of negatively affecting other species and causing ecological perturbations (Carey *et al.*, 2012). Climate change (hotter and drier conditions) may amplify these changes in assemblages by exacerbating habitat degradation, particularly in smaller fragments (Bennett *et al.*, 2013). The invasion and overabundance of native species will cause similar ecosystem dysfunction to species’ declines and extinctions because even small shifts in the relative abundance of species can significantly alter interspecific interactions and ecosystem function (Carey *et al.*, 2012). In the future, climate-change effects on competitive interactions are likely to become more frequent (Milazzo *et al.*, 2013).

During the Big Dry, about two-thirds of woodland bird species were in decline, while the fragmentation-tolerant noisy miner became more abundant (Mac Nally *et al.*, 2009). This is consistent with trends seen in Europe where declining species breed less in response to a change in climate (an extreme heat event) while species that have benefited from previous habitat disturbance had greater reproductive success (Julliard *et al.*, 2004). Noisy miners were positively associated with hotter, drier sites; the likely mechanism by which the drought benefited the noisy miner population is through the interaction between fragmentation and climate. In the box-ironbark system, noisy miners generally occupy small fragments (≤ 20 ha) and linear roadside strips of vegetation, but we found some colonization of larger fragments (≥ 80 ha). Greater vegetation degradation in fragments during the drought (Bennett *et al.*, 2013) may have facilitated noisy miner colonization. Effects are likely to worsen, because even under conservative emissions scenarios, which seem increasingly unlikely, the frequency and severity of Big Dry-like droughts are projected

to increase (IPCC, 2007) such that we expect to see further vegetation die-back in the future (Mac Nally *et al.*, 2014). The noisy miner is considered to be a slow colonizer, so its expansion is likely to continue (Maron *et al.*, 2013). Our results suggest that noisy miners are disproportionately excluding small-bodied birds and favoring medium-bodied species, which ultimately may lead to a homogenization of the bird community (Robertson *et al.*, 2013).

The increase in the noisy miner abundance and its influence over small nectarivores may exclude many species from access to nectar. Nectar-rich flowers are an important resource that was unavailable in many years during the Big Dry (Mac Nally *et al.*, 2009). Declines in canopy cover during the drought most likely reflect a reduction in this resource. Heavy spring rainfall in 2010 led to substantial eucalypt flowering in the box-ironbark forests (Bennett, unpublished data). The greatest increase in abundance and prevalence among woodland birds was in itinerant nectarivore species, most likely due to their ability to respond rapidly to flowering (Mac Nally *et al.*, 2009), leading to partial recovery or aggregation of highly mobile species in areas with richer resources. Expected increases in the frequency of droughts that are interrupted with intense periods of precipitation are likely to cause booms and busts in resource availabilities. The noisy miner expansion and its aggressive defense of space may exacerbate nectarivore declines at times of limited resource availability, and hinder recovery when nectar is more abundant.

A change in the bird assemblage, particularly the exclusion of small-bodied insectivores and nectarivores by noisy miners, is likely to have profound consequences for ecological function (Sekercioglu, 2006). Nectarivorous birds are important pollinators for many shrub and tree species (Ford, 1985). Large nectarivores frequently defend high-resource trees, while small honeyeaters move more frequently between more trees (Maron *et al.*, 2013). The exclusion of small nectarivores from sites may reduce outcrossing among plants, which may reduce seed quality and set, ultimately leading to a change in plant assemblages (Maron *et al.*, 2013). Insectivores control populations of invertebrates so that the exclusion of insectivores from smaller fragments may induce dieback

because these events have been linked to outbreaks of canopy-defoliating invertebrates (Allen *et al.*, 2010).

The underlying mechanism through which climate change appears to be affecting the avifauna assemblage is through modification of vegetation condition. The reduction in canopy foliage, ground-litter and shrub cover during the Big Dry (Bennett *et al.*, 2013), means fewer food resources and nest-sites, thereby increasing competition. Drought-induced loss of canopy cover can reduce arthropod abundance (Bell, 1985), while reduced ground litter and soil moisture during droughts may lead to fewer ground-litter invertebrates (Taylor, 2008); both factors would negatively affect insectivores. Many insectivores are resident, with limited capacity to move to alternative habitats (Mac Nally *et al.*, 2009). Declines in these resident woodland birds may indicate mortality without replacement (Ford *et al.*, 2009). The relationship between many species and mid-storey vegetation characteristics may be due to the cover provided for species that foraging in this stratum, which includes many insectivores. The relationship may partly be due to the absence of noisy miners on these sites, because noisy miners are often associated with grazed and/or degraded sites with reduced mid-storey (Eyre *et al.*, 2009). Mid-storey characteristics, such as shrub and sapling cover, may be a general indication of the ecological condition of a site. Fragmentation has been linked to reduced tree health and seed production (Barbeta *et al.*, 2011) and grazing management practices on fragments may mean tree and shrub seedlings are absent (Martin & Possingham, 2005). The negative relationship with standing dead trees and declines in some insectivores may be a symptom of the presence of noisy miners, because greater die-back was experienced in fragments where noisy miners occur.

Declines in ground and burrowing nesters (increased exposure) are likely to be due to the reductions in shrub and litter cover. These long-term changes may have led to reduced recruitment, culminating in the declines of many species. Drought has been linked to reduced clutch size and nest survival in North America (Skagen & Adams, 2012), and in our region breeding activity was much limited during the Big Dry (Mac Nally *et al.*, 2009). Australian passerines have low reproductive

rates, which increases their risk of extirpation due to events such as drought (Yom-Tov, 1987), Many species may have reached a threshold where the increasingly rare good year is unlikely to ‘repay’ the accumulated deficit of breeding failure in the more frequent dry years, leading to negative population growth rates less than replacement levels.

Global-change drivers such as climate change and species invasions may be better managed in the short-term by acting upon other drivers [e.g. habitat loss, fragmentation or degradation; (Didham *et al.*, 2007)]. In our system, the greatest gains may be made by restoring mid-storey structure or replanting adjacent to existing fragments. Increasing habitat extent and improving mid-storey structure will increase resources for birds and other taxa and limit noisy miner colonization. Investing in restoration activities that increase vegetation area may have the added benefit of ameliorating greater heat and water stresses experienced by remnant vegetation.

Synthesis

The global area affected by drought is likely to increase concurrently with greater usurpation of natural areas for human use (Capon *et al.*, 2013). Fragmentation has been linked to altered interspecific interactions in many regions around the world, demonstrating that similar effects to those that we report are likely in other fragmented regions that are experiencing drying. Altered assemblages and interspecific interactions are not limited to avifaunas (Milazzo *et al.*, 2013). Our results highlight that the interaction between climate and land-use change can have profound effects on ecosystem function not only directly, but also indirectly, by facilitating the expansion of highly competitive species. Avifaunal responses to drought probably reflect reductions in their resource base (food and vegetation) and species’ ability to compete for remaining resources. A boom-bust pattern of availabilities of resources, which would be expected to become amplified with long droughts and short intervening wet periods, may lead to disproportionate declines, and ultimately extinction, in many species, while at the same time favoring a few.

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REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-684.
- Barbeta, A., Penuelas, J., Ogaya, R. & Jump, A.S. (2011) Reduced tree health and seedling production in fragmented *Fagus sylvatica* forest patches in the Montseny Mountains (NE Spain). *Forest Ecology and Management*, **261**, 2029-2037.
- Bell, H.L. (1985) Seasonal variation and the effects of drought on the abundance of arthropods in savanna woodland on the Northern Tablelands of New South Wales. *Australian Journal of Ecology*, **10**, 207-221.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365-377.
- Bennett J.M., Cunningham S.C., Connelly C.A., Clarke R.H., Thomson J.R. & Mac Nally R (2013). The interaction between a drying climate and land use affects forest structure and above-ground carbon storage. *Global Ecology and Biogeography*, **22**, 1239-1247.
- Blakers, M., Davies, S.J.J.F. & Reilly, P.N. (1984) *Atlas of Australian Birds*. Melbourne University Press, Melbourne.
- BoM (2012) *Australian climate variability & change* Available at: <http://www.bom.gov.au/cgi-bin/climate/change/timeseries.cgi> (accessed April 2012).
- BoM (2013) *Australian climate variability & change* Available at: <http://www.bom.gov.au/cgi-bin/climate/change/timeseries.cgi> (accessed July 2013).
- Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 326-349.

- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453-460.
- Brown, W.P. (2007) Body mass, habitat generality, and avian community composition in forest remnants. *Journal of Biogeography*, **34**, 2168-2181.
- Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D., Stewardson, M., J, R., Parsons, M. & Williams, S.E. (2013) Riparian ecosystems in the 21st Century: Hotspots for climate change adaptation? *Ecosystems*, **16**, 359-381.
- Carey, M.P., Sanderson, B.L., Barnas, K.A. & Olden, J.D. (2012) Native invaders – challenges for science, management, policy, and society. *Frontiers in Ecology and the Environment*, **10**, 373-381.
- de Leeuw, J. & Mair, P. (2009) Multidimensional scaling using majorization: SMACOF in R. *Journal of Statistical Software*, **31**, 1-30.
- Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A. & Ewers, R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, **22**, 489-496.
- ECC (2001) *Box-Ironbark Forests and Woodlands Investigation*. Environment Conservation Council, Melbourne.
- Eyre, T.J., Maron, M., Mathieson, M.T. & Haseler, M. (2009) Impacts of grazing, selective logging and hyper-aggressors on diurnal bird fauna in intact forest landscapes of the Brigalow Belt, Queensland. *Austral Ecology*, **34**, 705-716.
- Ford, H.A. (1985) Nectarivory and Pollination by Birds in Southern Australia and Europe. *Oikos*, **44**, 127-131.
- Ford, H.A., Walters, J.R., Cooper, C.B., Debus, S.J.S. & Doerr, V.A.J. (2009) Extinction debt or habitat change? - Ongoing losses of woodland birds in north-eastern New South Wales, Australia. *Biological Conservation*, **142**, 3182-3190.

- Gelman, A., Meng, X.-L. & Stern, H. (1996) Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica*, **6**, 733-787.
- IPCC (2007) Climate Change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. In: (ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), p. 996, Cambridge University Press, Cambridge.
- Julliard, R., Jiguet, F. & Couvet, D. (2004) Evidence for the impact of global warming on the long-term population dynamics of common birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, S490-S492.
- Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90**, 773-795.
- Leblanc, M., Tweed, S., Van Dijk, A. & Timbal, B. (2012) A review of historic and future hydrological changes in the Murray-Darling Basin. *Global and Planetary Change*, **80**, 226-246.
- Lundberg, P. (1988) The evolution of partial migration in Birds. *Trends in Ecology & Evolution*, **3**, 172-175.
- Lunn, D.J., Best, N. & Whittaker, J.C. (2009) Generic reversible jump MCMC using graphical models. *Statistics and Computing*, **19**, 395-408.
- Mac Nally, R. & McGoldrick, J.M. (1997) Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. *Journal of Avian Biology*, **28**, 171-183.
- Mac Nally, R., Bennett, A.F. & Horrocks, G. (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7-29.

- Mac Nally, R., Bowen, M., Howes, A., McAlpine, C.A. & Maron, M. (2012) Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. *Ecology*, **93**, 668-678.
- Mac Nally R., Lada H., Cunningham S.C., Thomson J.R. & Fleishman E. (2014). Climate-change-driven deterioration of the condition of floodplain forest and the future for the avifauna. *Global Ecology and Biogeography*, **23**, 191-202.
- Mac Nally, R., Bennett, A.F., Thomson, J.R., Radford, J.Q., Unmack, G., Horrocks, G. & Vesk, P.A. (2009) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720-730.
- Mac Nally, R.C. (1995) On large-scale dynamics and community structure in forest birds: lessons from some eucalypt forests of southeastern Australia. *Philosophical Transactions Royal Society London B*, **350**, 369-379.
- Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239-1252.
- Maron, M., Grey, M.J., Catterall, C.P., Major, R.E., Oliver, D.L., Clarke, M.F., Loyn, R.H., Mac Nally, R., Davidson, I. & Thomson, J.R. (2013) Avifaunal disarray due to a single despotic species. *Diversity & Distributions*, **19**, 1468–1479,
- Martin, T.G. & Possingham, H.P. (2005) Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology*, **42**, 400-408.
- McAlpine, C.A., Syktus, J., Ryan, J.G., Deo, R.C. & McKeon, G.M. (2009) A continent under stress: interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate. *Global Change Biology*, **15**, 2206-2223.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*, 2nd ed edn. Chapman and Hall, London, UK.

- Milazzo, M., Mirto, S., Domenici, P. & Gristina, M. (2013) Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology*, **82**, 468-477.
- Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S. & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters*, **13**, 969-979.
- Oksanen, J.F., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H. & Wagner, H. (2010) *vegan: Community Ecology Package*. The Comprehensive R Archive Network.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Radford, J.Q. & Bennett, A.F. (2005) Terrestrial avifauna of the Gippsland Plain and Strzelecki Ranges, Victoria, Australia: insights from Atlas data. *Wildlife Research*, **32**, 531-555.
- Robertson, O.J., McAlpine, C., House, A. & Maron, M. (2013) Influence of interspecific competition and landscape structure on spatial homogenization of avian assemblages. *PloS one*, **8**, e65299.
- Royle, J.A. & Link, W.A. (2006) Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*, **87**, 835-841.
- Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, **21**, 464-471.
- Skagen, S.K. & Adams, A.A.Y. (2012) Weather effects on avian breeding performance and implications of climate change. *Ecological Applications*, **22**, 1131-1145.
- Taylor, S.G. (2008) Leaf litter invertebrate assemblages in box-ironbark forest: composition, size and seasonal variation in biomass. *Victorian Naturalist*, **125**, 19-27.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351-1363.

- Vesk, P.A., Nolan, R., Thomson, J.R., Dorrough, J.W. & Mac Nally, R. (2008) Time lags in provision of habitat resources through revegetation. *Biological Conservation*, **141**, 174-186.
- Welsh, A.H., Lindenmayer, D.B. & Donnelly, C.F. (2013) Fitting and interpreting occupancy models. *PLoS ONE*, **8**, e52015-e52015.
- Yom-Tov, Y. (1987) The Reproductive Rates Of Australian Passerines. *Australian Wildlife Research*, **14**, 319-330.

Table 1: Changes in prevalence, conditional abundance when present and overall expected abundance of woodland bird guilds occupying box-ironbark forests between 1995–97 and 2010–11. Species were characterized by ecological traits relating to levels of vulnerability to fragmentation and habitat loss, nesting and foraging guilds, mobility (Mac Nally, 1995) conservation concern (Radford & Bennett, 2005) and distributional range (Blakers *et al.*, 1984) (Appendix 1). Table shows % of species changed.

Classification	Class	Total	Prevalence		In-site abundance		Expected abundance		Reporting rate	
			% decline	% increase	% decline	% increase	% decline	% increase	% decline	% increase
Habitat	Open-country	13	23	0	0	23	23	23	38	31
Habitat	Open-tolerant	30	27	13	0	23	13	13	50	20
Habitat	Woodland-dependent	62	35	23	6	32	23	21	52	26
Foraging zone	Aerial	10	50	0	0	20	40	0	80	0
Foraging zone	Bark	4	25	50	25	50	25	50	50	50
Foraging zone	Canopy	32	44	25	9	56	22	28	59	34
Foraging zone	Ground	52	23	13	0	13	15	15	38	23
Foraging zone	Low shrubs	2	0	0	0	0	0	0	0	0
Foraging zone	Tall shrubs	5	20	20	0	20	20	20	60	20
Food	Frugivore	3	33	0	0	33	0	0	100	0
Food	Insectivore	52	38	23	4	29	29	23	48	29
Food	Nectarivore	18	44	17	6	56	22	22	67	28
Food	Raptor/vertebrate	16	13	6	0	6	6	6	50	13
Food	Granivore	16	13	13	6	19	6	19	25	25
Nesting	N/A	1	100	0	0	100	100	0	100	0
Nesting	Burrow	4	75	0	0	50	75	0	100	0
Nesting	Ground	9	22	11	0	0	22	11	67	22
Nesting	Hollows	20	30	10	15	25	25	10	45	10
Nesting	Shrub/canopy	67	31	21	1	33	15	25	46	31
Nesting	Parasite	4	0	25	0	0	0	0	25	25
Conserv. Concern	No	75	28	17	5	32	17	20	47	28
Conserv. Concern	Yes	30	40	17	0	20	27	17	57	17
Mobility	Migrant	20	40	15	15	15	25	5	55	20

Mobility	Itinerant	15	40	20	7	47	20	27	60	33
Mobility	Resident	70	27	17	0	29	19	21	46	24
Distribution	Dry	25	40	20	0	16	24	12	56	20
Distribution	Mesic	8	38	25	25	25	25	13	88	13
Distribution	Widespread	72	28	15	3	33	18	22	43	28
Totals	–	105	31	17	4	29	20	19	50	25

Table 2 Summary of parameter estimates for changes in prevalence, in-site abundance (if present), total abundance and total reporting rate.

Common name	Prevalence	In-site abundance	Total abundance	Total reporting rate
australasian pipit	0.28	0.66	0.48	0.73
australian magpie	1.00	0.84	1.00	1.00
australian raven	0.83	0.00	0.00	0.00
black-chinned honeyeater	1.00	0.00	0.33	0.00
black-faced cuckoo-shrike	1.00	0.97	1.00	0.99
blue-winged parrot	0.60	0.35	0.38	0.26
brown falcon	0.44	0.34	0.34	0.23
brown goshawk	0.68	0.18	0.26	0.09
brown-headed honeyeater	1.00	0.00	0.29	0.00
brown thornbill	0.61	0.75	0.77	0.31
brown treecreeper	1.00	0.98	1.00	1.00
buff-rumped thornbill	1.00	0.93	1.00	0.81
chestnut-rumped thornbill	0.41	0.37	0.35	0.35
collared sparrowhawk	0.62	0.30	0.43	0.24
common bronzewing	1.00	0.10	0.61	0.40
crested bellbird	0.26	0.63	0.51	0.46
crested pigeon	0.90	0.86	0.96	1.00
crested shrike-tit	0.26	0.00	0.00	0.00
crimson rosella	0.04	0.61	0.18	0.08
diamond firetail	0.38	0.94	0.88	0.92
dusky woodswallow	0.97	0.00	0.12	0.03
eastern rosella	0.99	0.05	0.72	0.56
eastern spinebill	0.75	0.10	0.30	0.01
eastern yellow robin	0.11	0.01	0.00	0.00
fantail cuckoo	0.58	0.49	0.54	0.61
flame robin	0.62	0.98	0.97	0.98
fuscous honeyeater	0.89	0.02	0.46	0.00
Galah	0.99	0.83	1.00	1.00
golden whistler	0.33	0.00	0.00	0.00
grey butcherbird	0.79	0.97	0.98	1.00
grey currawong	0.99	0.03	0.34	0.06
grey fantail	0.41	1.00	1.00	1.00
grey shrike-thrush	1.00	0.48	1.00	1.00
hooded robin	0.55	0.11	0.15	0.02
horsfields bronze cuckoo	0.49	0.49	0.48	0.50
jacky winter	0.71	0.86	0.90	0.90
laughing kookaburra	0.63	0.72	0.79	0.54
little corella	0.42	0.23	0.23	0.14
little eagle	0.81	0.10	0.20	0.07
little lorikeet	0.93	0.00	0.00	0.00
little raven	0.81	0.79	0.89	0.99
longbilled corella	0.60	0.33	0.38	0.38
magpie-lark	0.42	0.04	0.04	0.00

mistletoebird	0.90	0.11	0.44	0.00
musk lorikeet	0.00	0.45	0.00	0.00
noisy friar bird	0.16	0.94	0.69	0.99
noisy miner	1.00	0.79	1.00	1.00
olivebacked oriole	0.69	0.04	0.08	0.13
painted buttonquail	0.45	1.00	0.99	1.00
pallid cuckoo	0.41	0.93	0.88	0.99
peaceful dove	0.52	0.02	0.03	0.00
peregrine falcon	0.74	0.18	0.39	0.01
pied currawong	0.79	0.12	0.35	0.00
purplecrowned lorikeet	0.76	0.00	0.00	0.00
rainbow bee-eater	0.21	0.07	0.04	0.01
redcapped robin	0.70	1.00	0.99	1.00
redrumped parrot	0.47	0.49	0.47	0.13
red wattlebird	1.00	0.17	1.00	1.00
restless flycatcher	0.25	0.00	0.00	0.00
rufous songlark	0.83	0.75	0.85	0.94
rufous whistler	0.95	0.99	1.00	1.00
sacred kingfisher	0.75	0.15	0.23	0.23
scarlet robin	0.81	0.73	0.85	0.67
shining bronze cuckoo	0.84	0.21	0.47	0.01
Silvereye	0.94	0.04	0.28	0.09
southern whiteface	0.77	0.04	0.24	0.00
speckled warbler	0.79	0.00	0.01	0.00
spotted pardalote	0.98	0.00	0.00	0.00
spotted quailthrush	0.69	0.00	0.03	0.00
striated pardalote	0.94	0.00	0.02	0.00
striated thornbill	1.00	1.00	1.00	1.00
sulphurcrested cockatoo	0.27	0.18	0.12	0.01
superb fairywren	0.76	0.00	0.05	0.00
swift parrot	0.90	0.00	0.00	0.00
tree martin	0.88	0.00	0.06	0.00
varied sittella	0.98	0.86	0.98	0.92
wedgetailed eagle	0.72	0.46	0.55	0.38
Weebill	1.00	0.97	1.00	1.00
welcome swallow	0.99	0.00	0.01	0.00
whistling kite	0.58	0.19	0.22	0.07
whitebellied cuckoo-shrike	1.00	0.00	0.15	0.00
whitebrowed babbler	0.86	0.40	0.66	0.40
whitebrowed woodswallow	0.64	0.00	0.01	0.00
white-eared honeyeater	0.29	0.53	0.39	0.12
white-naped honeyeater	1.00	0.01	0.74	0.09
white-plumed honeyeater	1.00	0.19	0.98	0.02
white-throated tree-creeper	0.00	0.95	0.18	0.01
white-winged chough	0.50	0.79	0.70	0.94
white-winged triller	0.80	0.01	0.17	0.00
willie wagtail	0.68	0.63	0.71	0.45
yellow-faced honeyeater	1.00	1.00	1.00	1.00

yellow-plumed honeyeater	0.15	0.97	0.71	1.00
yellow-rumped thornbill	0.97	0.07	0.57	0.07
yellow thornbill	0.02	1.00	0.84	0.99
yellow-tufted honeyeater	1.00	0.00	0.39	0.00

Table 3: Environmental covariates associated with reporting rates of individual bird species derived from Bayesian model comparison of all possible additive models using reversible jump Markov chain Monte Carlo (MCMC). The tallies of species declining, unchanged or increasing with a positive (+) or negative (-) regression coefficient (posterior probability of a linear or non-linear association > 0.75) are shown. The effects of fragment area are relative to the 10 ha fragment sites.

	Fragment area 1997 effects				Fragment area, year interaction				Noisy miners	Climate
	large blocks				large blocks					
	20 ha	40 ha	80 ha	blocks	20 ha	40 ha	80 ha	blocks		
Declining	0	0	8	7	0	0	0	3	14	15
-	0	0	1	9	1	0	0	2	1	1
+										
No change	0	0	4	4	0	0	1	1	3	2
-	0	0	1	3	0	0	1	2	1	2
+										
Increasing	1	1	6	6	0	1	2	2	11	0
-	0	0	2	4	0	1	2	3	2	6
+										
Declining	0	3	2	1	2	1	3	1	3	5
-	1	3	1	7	3	0	0	0	1	4
+										
No change	0	1	0	2	2	4	0	0	1	0
-	0	0	1	0	0	0	2	0	0	4
+										
Increasing	0	2	0	6	2	5	1	0	0	2
-	0	0	0	1	0	2	1	0	3	5
+										

Table 4: Environmental variables associated with reporting rates of individual bird species, derived from Bayesian model comparison of all possible additive models using reversible jump Markov chain Monte Carlo (MCMC). Regression coefficients (β) and interaction (γ) are shown. Linear regression coefficients for variables with posterior probability of a linear or non-linear association exceeding 0.75 are bolded.

	Fragment Size	Fragment Size, Year Interaction	Noisy Miners	Climate	Canopy	Litter depth	Low shrub cover	High shrub cover	Fallen Timber	Small tree density	Very large tree density	Dead basal	Sapling Density
<i>Decreaser</i>													
australian raven	-0.75	0.01	0.04	0.04	-0.05	0.20	0.03	-0.01	-0.42	-0.02	-0.01	-0.06	0.00
black-chinned honeyeater	0.58	0.00	-0.45	-0.03	-0.01	0.25	-0.04	0.18	0.04	-0.03	-0.11	-0.07	-0.09
brown-headed honeyeater	0.47	0.11	-0.11	-0.35	0.08	-0.03	-0.05	0.02	-0.01	0.11	-0.19	0.04	0.06
crested shrike-tit	-0.33	-0.02	-0.74	-0.03	0.07	0.05	0.03	0.15	-0.09	-0.03	0.12	-0.08	-0.01
crimson rosella	0.74	-0.60	0.02	-0.28	-0.04	0.02	0.01	0.00	0.16	-0.01	0.14	0.01	0.10
dusky woodswallow	-0.19	-0.18	-0.68	0.12	0.01	0.12	0.00	0.26	-0.02	-0.01	0.09	0.01	-0.05
eastern spinebill	0.07	0.08	-0.07	-0.89	0.03	0.04	-0.06	-0.06	-0.19	0.24	-0.11	-0.11	0.28
eastern yellow robin	0.26	0.11	-0.46	-0.10	0.31	0.07	0.21	0.01	-0.03	-0.02	0.01	0.03	-0.14
fuscous honeyeater	1.56	0.16	-0.61	-0.06	-0.01	0.12	-0.02	0.26	0.04	0.03	0.26	-0.09	-0.22
grey currawong	0.57	0.01	0.06	-0.28	-0.01	0.00	0.01	-0.05	-0.16	0.16	-0.18	-0.11	0.01
little lorikeet	0.09	-0.20	-0.03	-0.08	-0.04	0.37	-0.16	0.11	0.00	-0.10	0.05	-0.37	-0.23
magpie-lark	-2.20	0.10	-0.23	0.06	0.06	-0.18	0.02	-0.15	-0.17	-0.09	-0.17	-0.66	-0.29
musk lorikeet	-0.20	-0.04	0.08	0.04	0.01	0.00	0.01	0.03	-0.01	0.03	0.04	-0.01	-0.09
peaceful dove	-0.64	0.10	-0.79	0.03	-0.03	-0.08	0.04	0.27	-0.14	-0.18	-0.22	-0.06	0.02
purple-crowned lorikeet	-0.13	-0.03	-0.07	-0.29	-0.04	0.17	-0.01	0.31	0.08	-0.01	0.03	-0.13	-0.17
restless flycatcher	-0.76	0.38	-1.12	-0.17	0.31	-0.08	0.02	0.00	-0.20	-0.21	-0.04	0.03	-0.15
shining bronze cuckoo	0.03	0.00	-0.03	-0.48	-0.06	-0.01	-0.05	0.02	-0.02	0.08	-0.06	-0.01	-0.03
speckled warbler	0.19	-0.04	-0.12	-0.53	-0.12	-0.05	0.23	0.00	-0.04	-0.09	-0.10	0.00	0.52
spotted pardalote	0.51	-0.01	-0.06	-0.32	0.05	-0.04	-0.01	0.01	-0.02	0.10	-0.02	0.05	0.35
spotted quail-thrush	0.91	-0.27	-0.02	-0.40	-0.03	-0.10	0.04	-0.02	0.02	-0.02	-0.26	-0.03	0.23
striated pardalote	-0.01	0.06	-0.04	-0.03	0.01	-0.01	-0.11	0.01	0.01	-0.05	0.02	-0.12	-0.05

sulphur-crested cockatoo	0.02	-0.06	0.01	-0.08	-0.07	0.04	0.01	0.26	0.15	-0.08	0.03	-0.02	0.05
superb fairywren	0.06	-0.49	-1.03	-0.12	0.05	0.10	0.69	-0.05	0.03	-0.64	0.00	0.00	-0.05
tree martin	-1.21	0.26	-1.00	-0.20	0.33	0.23	-0.15	0.03	-0.07	-0.14	-0.11	0.04	-0.05
welcome swallow	-1.37	-0.05	-0.32	-0.09	0.01	0.02	0.04	-0.02	-0.08	-0.07	-0.05	-0.40	-0.01
white-browed woodswallow	0.14	-0.03	-0.07	-0.09	0.00	0.09	0.08	-0.04	-0.07	-0.09	0.07	-0.14	-0.01
white-naped honeyeater	0.38	0.39	-0.07	-0.10	0.10	0.01	-0.01	0.24	-0.02	0.02	0.00	-0.01	-0.25
white-plumed honeyeater	-2.82	-0.21	-1.51	0.11	0.39	-0.19	0.09	-0.27	-0.60	-0.19	0.05	0.06	-0.01
white-throated treecreeper	0.88	0.75	-0.40	-0.23	0.02	0.03	0.05	-0.13	-0.02	0.08	-0.14	0.02	0.37
yellow-tufted honeyeater	1.37	-0.51	-1.02	-0.05	0.09	0.28	0.03	0.33	0.10	0.10	0.31	0.13	-0.81
<i>Neutral</i>													
brown falcon	-0.72	-0.16	0.10	-0.31	-0.02	-0.02	0.05	-0.11	-0.13	-0.17	-0.02	-0.16	0.00
brown thornbill	0.88	0.58	-0.27	-0.33	-0.19	-0.36	0.13	-0.17	-0.04	-0.25	-0.05	-0.05	0.35
buff-rumped thornbill	1.04	0.88	-0.28	-0.45	0.02	-0.04	-0.01	-0.59	-0.31	0.03	-0.19	0.04	0.51
common bronzewing	-0.12	-0.18	-0.05	0.03	0.01	-0.05	0.23	0.11	-0.04	-0.21	0.28	0.12	0.04
eastern rosella	-0.38	-0.42	0.37	0.17	0.13	0.07	0.03	0.00	-0.06	-0.26	0.03	-0.01	-0.02
jacky winter	-0.28	0.26	-1.13	0.10	0.16	-1.08	-0.25	-0.33	0.05	-0.08	0.01	-0.29	-0.04
laughing kookaburra	-0.97	0.42	0.00	0.00	0.00	-0.03	-0.02	-0.35	-0.77	0.00	0.03	-0.02	-0.01
long-billed corella	-0.38	-0.05	-0.08	0.01	0.05	0.03	-0.05	-0.05	-0.11	-0.14	0.39	-0.29	-0.27
red-rumped parrot	-2.08	-0.01	-0.43	0.17	0.02	-0.01	0.00	-0.03	0.02	-0.12	0.01	0.03	-0.01
sacred kingfisher	0.02	-0.16	-0.15	-0.04	0.16	0.02	0.02	-0.03	-0.13	-0.11	0.04	0.04	0.29
scarlet robin	0.42	0.19	-0.06	-0.04	-0.02	0.03	0.00	-0.17	-0.07	0.01	-0.01	-0.04	0.05
white-eared honeyeater	1.20	0.49	-0.10	-0.26	-0.10	-0.03	0.31	0.02	-0.22	-0.03	-0.12	0.04	0.50
willie wagtail	-1.34	0.02	-0.91	0.02	0.04	-0.15	-0.02	-0.08	-0.13	-0.28	0.01	0.05	0.02
<i>Increases</i>													
australian magpie	-1.57	0.08	0.00	0.19	0.04	-0.05	0.00	-0.01	-0.07	-0.02	-0.05	-0.01	-0.13
black-faced cuckoo-shrike	-0.37	0.25	-0.32	0.02	0.03	-0.01	-0.02	0.03	-0.06	-0.01	-0.01	-0.02	-0.15
brown treecreeper	-0.02	-0.01	-2.01	0.08	0.18	0.09	0.00	0.02	0.00	-0.21	0.23	-0.02	-0.03
crested pigeon	-0.84	-0.18	-0.14	0.66	0.07	-0.11	0.11	-0.05	-0.15	-0.57	0.02	-0.01	-0.11
Galah	-0.74	-0.02	0.06	0.12	0.00	0.03	0.00	0.00	0.00	-0.64	0.00	-0.02	-0.04
grey butcherbird	-0.57	-0.04	0.79	0.11	0.01	-0.19	-0.02	-0.14	-0.03	0.52	0.00	-0.01	0.02

grey fantail	0.30	0.07	-0.10	-0.06	0.04	-0.01	0.09	-0.32	-0.04	0.01	-0.08	-0.02	0.20
grey shrike-thrush	0.05	0.09	-1.01	0.04	0.01	0.02	0.01	0.19	0.08	0.03	0.05	0.08	0.00
little raven	-0.99	-0.47	0.01	0.04	0.00	0.03	0.02	-0.14	-0.02	-0.04	-0.26	-0.02	-0.37
noisy miner	-3.78	0.23	N/A	1.09	-0.07	-0.07	0.08	-0.05	-0.03	-0.41	-0.12	-0.23	-0.20
red-capped robin	0.16	0.25	-0.17	0.01	-0.02	0.02	-0.03	-0.14	-0.07	0.21	0.03	0.10	0.42
red wattlebird	0.10	-0.01	-0.40	0.04	0.02	0.01	0.11	-0.02	-0.02	-0.07	0.01	0.01	-0.01
rufous whistler	0.10	0.68	-0.39	0.06	-0.03	-0.19	-0.02	-0.24	0.00	0.01	0.00	-0.01	0.09
striated thornbill	0.72	0.74	-0.18	-0.03	-0.02	-0.10	-0.01	-0.34	-0.04	0.24	-0.01	0.04	0.56
varied sittella	0.33	0.49	-0.30	-0.09	0.17	-0.38	-0.04	-0.57	0.01	0.11	-0.13	0.00	0.03
Weebill	1.14	0.47	-0.18	-0.16	0.05	-0.10	0.01	-0.38	-0.03	0.19	-0.27	0.08	0.51
white-winged chough	-0.26	0.00	0.12	0.01	0.00	0.01	-0.07	0.01	-0.01	-0.02	0.00	-0.11	-0.02
yellow-faced honeyeater	0.52	0.02	-0.26	-0.08	-0.17	-0.23	-0.01	-0.29	-0.17	0.00	-0.03	0.11	0.16

Figure legends

Figure 1 Non-metric multidimensional scaling (NMDS) ordination (stress = 0.05) of the woodland bird community that occupied box-ironbark forests in 1995–97 (filled circles) and 2010–11 (open circles), based on a Bray-Curtis dissimilarity matrix. The point sizes indicate the fragment area class (very small = 10 ha, small = 20 ha, medium = 40 ha, and large = 80 ha). Fitted vectors show correlations between NMDS axial scores and individual vegetation characteristics ($P < 0.05$). The bearing indicates the direction of the correlation whilst the length of any vector is proportional to strength of the correlation.

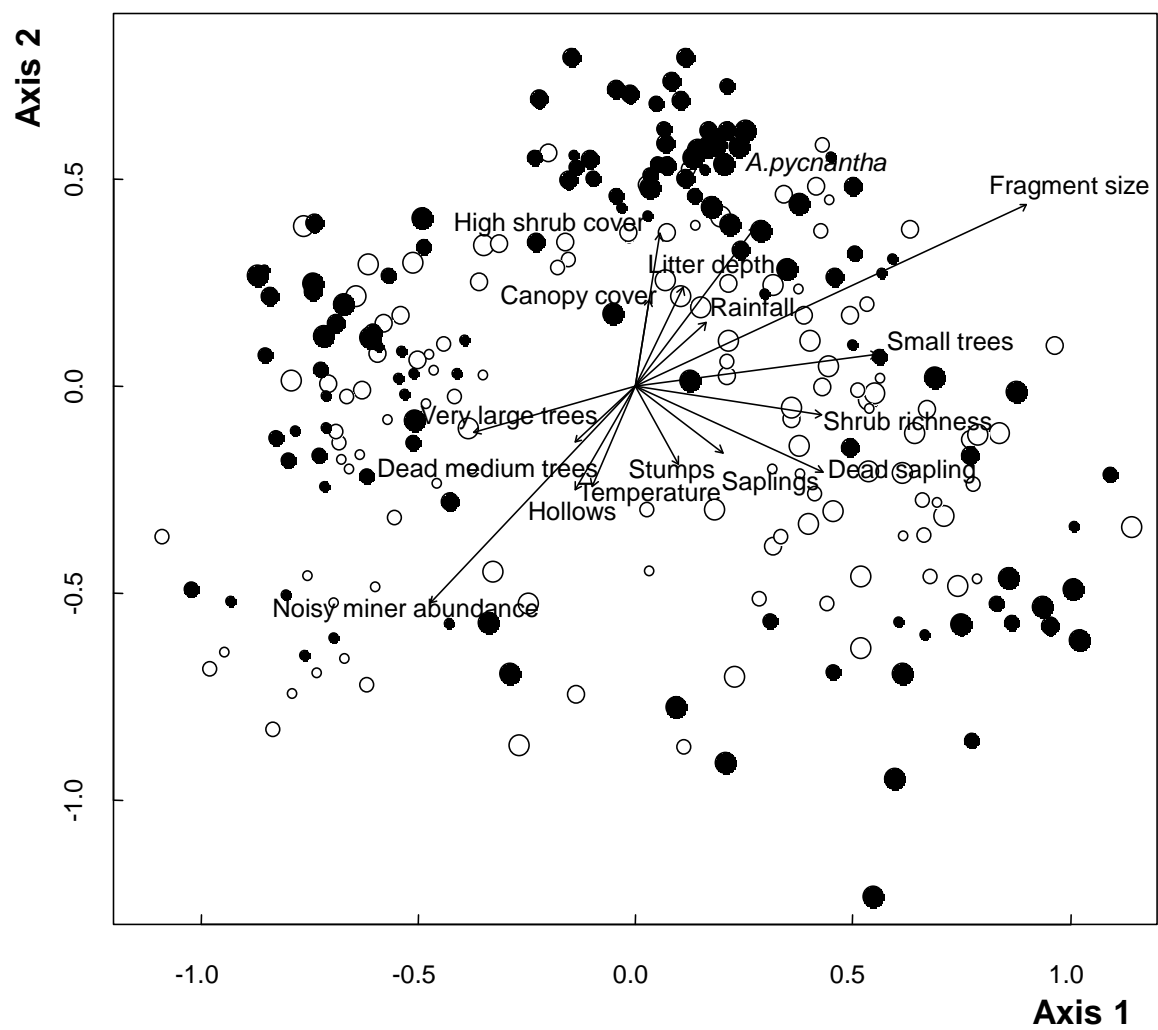


Figure 1:

PART B: Suggested Declaration for Thesis Chapter

Monash University

Declaration for Thesis Chapter 5

Declaration by candidate

In the case of Chapter 5, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The initiation, key ideas, development and writing up of the work were my responsibility. I coordinated the study and performed all of the field work. I conducted the analysis and was the primary author of the manuscript.	70

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Rohan H. Clarke,	Contributed to writing of the manuscript	
James R. Thomson	Support with analysis	
Ralph Mac Nally	Conceived the research and contributed to writing of the manuscript	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature		Date
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Main Supervisor's Signature		Date
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*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.


Chapter 5: Variation in abundance of nectarivorous birds: Does a competitive despot interfere with flower-tracking?

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Running title: interspecific competition disrupts resource-tracking by birds

Keywords: interspecific interactions, eucalyptus, nectar, noisy miner, resource tracking, seasonal movements.

Primary Research Article

ABSTRACT

Aim: Adaptive resource tracking in space and time may be disrupted by the modification of resources and competitors. Major global change drivers (e.g. land-use change) have induced declines in many native species while facilitating only a few. Given that many resources are predicted to become increasingly scarce under the joint effects of climate and land-use change, disturbance-tolerant species that are able to defend high-value resources may further limit the persistence of disturbance-sensitive species. We sought to determine which nectarivorous birds track variation in flowering and if relationships between nectarivores and flowering are affected by on-transect vegetation structure or the occurrence of a native, hyper-aggressive species, the noisy miner *Manorina melanocephala*, which has become more prevalent.

Location: Temperate woodlands in north-central Victoria, Australia

Methods: We measured eucalypt flowering and nectarivore bird biomass and abundance over the course of a year; we measured vegetation structure on the same forest transects.

Results: Nectarivores tracked spatial and some temporal variation in flowering, but this relationship was disrupted by noisy miners. Where present, the noisy miner excluded small-bodied nectarivores (< 63 g) from fragments, limiting the ability of this numerically dominant component of the avifauna to gain access to flowering resources.

Conclusions: Altered patterns of interspecific competition due to vegetation fragmentation and climate-induced degradation may have led to changes in the distribution of small nectarivore species that is a departure from the ‘ideal free distribution’ model. Interactions between noisy miners and small-bodied nectarivores appear to be best described by the ‘ideal despotic distribution’ model in which noisy miners exclude smaller competitors and monopolize local resources. Increases in the severity and frequency of extreme climatic events (e.g. long droughts) predicted under climate change may create a boom-bust pattern of availabilities of resources. The apparent insensitivity of noisy miners to such variation in flowering resource availability and their influence on the ability of small nectarivores to access resources may lead to disproportionate declines in smaller-bodied

nectarivorous species. Reduced tracking of flowering by nectarivores has the potential to disrupt ecosystem services (e.g. pollination, seed dispersal) and may have long-term consequences for the persistence of fragmented vegetation adding further pressure to forest-dependent biota.

INTRODUCTION

Resource availability is a key determinant of the distribution of species (Morris 2003). Models such as the ‘ideal free distribution’ (IFD) predict that population densities will be distributed in space among habitat patches in proportion to the amount of resources available in each patch, so that spatial variation in resource availability will be matched by their consumers (Fretwell & Lucas 1969). Several studies have found that population densities are greater within habitat patches with greater food resources (Crampton *et al.* 2011; Blendinger *et al.* 2012), but a perfect match between resources and consumers is rarely seen because species cannot have a perfect knowledge of the distribution of resources (Jones *et al.* 2006).

A limitation of the IFD model is that it fails to account for interspecific interactions, yet species do not forage in isolation (Morris 2003). Interspecific interactions have been incorporated into density-dependent habitat selection theory in two sets of models. Isodar models predict species densities according to attributes of habitat quality (Morris 1988) based on IFD. Isobar models predict the densities at which two species can coexist in a two-habitat system (Rosenzweig 1981) according to the ‘ideal despotic distribution’ (IDD). The IDD asserts that when there are competitive differences between species, the dominant species will influence the habitat choices of subordinate species (Fretwell 1972). Despotic habitat selection occurs when a dominant species, usually one with a larger body mass than that of subordinates, occupies the more productive habitats to the exclusion of subordinate species. This mechanism has been documented in birds in the Amazon (Robinson & Terborgh 1995) and Australia (Mac Nally & Timewell 2005), desert rodents in the Americas (Brown & Maurer 1986) and coastal fish in the Mediterranean (Milazzo *et al.* 2013).

Most, if not all, ecological systems are characterized by dynamic resources (e.g. varying seasonally or annually), examples of which include pulses in nectar availability and seed production, insect irruptions, and phytoplankton blooms (Letnic & Dickman 2010). A consequence of the IFD model is that inter-annual and seasonal variation in vegetation characteristics should

affect the spatial distribution of consumer species, where individuals alter their distribution in accordance with seasonal changes in the relative quality (e.g. food availability) of patches (Jones *et al.* 2006). Spatio-temporal variation in population densities due to seasonal changes in habitat quality may intensify species interactions causing populations to shift along a ‘free’ to ‘despotic’ continuum (Haché *et al.* 2012).

Understanding how animals distribute themselves in space and time according to the availability of resources is of fundamental importance in conservation biology because adaptive tracking may be disturbed by multiple anthropogenic drivers. Drivers of ecological change may alter ecosystems either directly or through the alteration of resources, competitors or consumers (Carey *et al.* 2012). Habitat change has been linked to major declines in the abundance and distribution of many native species, but has facilitated the increase in abundance and distribution of others (Carey *et al.* 2012). Invasions of exotics and irruptions of native taxa due to human actions have the potential to cause major ecological disturbances because even small shifts in the relative abundance of species can much alter interspecific interactions and ecosystem function (Carey *et al.* 2012). For example, habitat fragmentation, by facilitating access to forest habitat by some avian nest predators and parasites, has been linked to decreases in reproductive success that could ultimately alter forest bird assemblages (Robinson *et al.* 1995). Climate change has been linked to intensified interspecific interactions in sympatric coastal fishes in the Mediterranean (Milazzo *et al.* 2013). Climate change is likely to amplify changed species interactions, such as phenology, relative abundances, physiology, and behaviours of multiple species, because these are influenced by many factors that themselves are sensitive to prevailing climate (Bellard *et al.* 2012). Adaptive resource tracking may be disturbed by land-use change, climate change and altered interactions all of which act at different spatial and temporal scales (Lehouck *et al.* 2009).

Birds are ideal for studying the influence of interspecific interactions on consumer-resource dynamics. Food resources for birds vary spatially (e.g. among habitat patches), temporally (e.g. among seasons and years) and spatio-temporally (e.g. seasonal variations between patches)

(Crampton *et al.* 2011). Birds are among the most mobile of animals, increasing the likelihood that they experience and can monitor variation in resource availability in landscapes (Thomson *et al.* 2007). Bird dynamics have been defined in relation to the availability of food resources such as fruit (Blendinger *et al.* 2012), insects (Epanchin *et al.* 2009) and nectar (Symes *et al.* 2008; Hart *et al.* 2011). Birds provide key ecological services, including seed dispersal, pollination and invertebrate pest control, so changes in bird assemblages may have a negative effect on the long-term persistence of fragmented native vegetation (Sekercioglu 2006). Extinction risk in birds, as with other taxa, is associated with species' ecological traits, suggesting that demographic rates should differ among species, which may affect interspecific interactions and assemblage structure (Korfanta *et al.* 2012). Disturbance-tolerant, competitive species that have been unaffected, or have gained an advantage from past disturbances, may monopolize resources and competitively exclude other disturbance-sensitive species (Brown 2007).

Since the early 19th century, when Europeans first colonized the inland areas of south-eastern Australia, there has been widespread forest clearance, with the extent of woodland and forest vegetation having been halved (McAlpine *et al.* 2009). The region experienced a 13 year-drought from 1997 ('the Big Dry'), which was linked to major changes in vegetation structure, with die-back amplified in fragmented vegetation (Bennett *et al.* 2013). The effects of the drought superimposed upon landscape change have been linked to major declines in forest and woodland birds (Mac Nally *et al.* 2009).

One species, the hyper-aggressive noisy miner *Manorina melanocephala*, appears to have benefited from land-use change because of its preference for edges and small (≤ 20 ha) habitat fragments (Maron *et al.* 2011). Vegetation change in the Big Dry, particularly canopy die-back, was linked to further increases in the abundance and occurrence of this species (J.M.B unpublished data). The noisy miner is a cooperative breeder, typically forming large colonies that collectively defend space by aggressive mobbing to the exclusion or severe reduction of almost all smaller bird species (< 63 g) (Mac Nally *et al.* 2012). Noisy miners, by restricting the access of other nectarivores to

food and space, reduce the movement options of these species. Such actions may limit pollination outcrossing, reducing seed set and quality and ultimately leading to changes in plant assemblages (Maron *et al.* 2013).

In the box-ironbark forests of south-eastern Australia, the avifauna is numerically dominated by nectarivorous birds (Mac Nally *et al.* 2009). We expected that nectarivore abundance and biomass would track the dynamics of flowering, but that the presence of noisy miners may limit resource tracking by nectarivores smaller than the noisy miner. Noisy miners have a preference for fragments with reduced shrub and canopy cover (Maron *et al.* 2013), so that a more dense vegetation structure may affect interspecific competition in this system. Despite the known link between vegetation structure and interspecific competition, vegetation structure has not been accounted for in most previous studies (Crampton *et al.* 2011). We used both nectarivore biomass and abundance because, while abundance is good indication of the number of birds, biomass provides an indication of the capacity of a site to support birds (e.g. one 76 g musk lorikeet *Glossopsitta concinna* cannot be treated as equivalent to one 16 g fuscous honeyeater *Lichenostomus fuscus*). We sought to determine: (1) how closely do nectarivores track variation in flowering? (2) do noisy miners influence the dynamics of small nectarivores with regard to flower tracking? (3) if detected, is flower tracking by nectarivores or the noisy miner's influence on flower tracking modified by vegetation structure?

METHODS

The box-ironbark study region is a forest-agricultural mosaic in north-central Victoria, Australia (30 000 km²). Since European settlement, the region has been much modified by gold mining, timber felling and agriculture, reducing the vegetation cover to 17% of its original extent with just a few large (6 000–40 000 ha) remnants remaining. The box-ironbark woodlands and forests occur on the dry inland slopes of the Great Dividing Range. The canopy is characterized by box and ironbark *Eucalyptus*, predominantly grey box *Eucalyptus microcarpa*, red ironbark, *E. tricarpa* and yellow gum *E. leucoxylon*. Vegetation is mostly regrowth, with only *c.* 2% of *extant* vegetation considered to be old growth, with characteristics such as large, hollow-bearing trees (Vesk *et al.* 2008). Historically, mean annual rainfall ranged from 400–700 mm, falling mostly in winter and spring. Summers in the region are dry and hot (Mac Nally *et al.* 2000).

Study sites were distributed in forest fragments around four localities in north-central Victoria: St Arnaud, Dunolly, Bendigo and Rushworth. To ensure representative coverage of fragments, transects were randomly placed and replicated within fragments based on forest area; (1) one transect in each 10 ha fragment, (2) two transects in each 20 ha fragment, (3) three transects in each 40 ha fragment, (4) four transects in each 80 ha fragment and (5) 22 transects in each > 6 000 ha forest block (Mac Nally *et al.* 2000). Transects within large forest blocks were clustered within fixed areas that were notionally of the same size as fragments, so that there were 30 clusters in large forest blocks (12 of 10 ha, six of 20 ha, six of 40 ha and six of 80 ha) and 31 fragments (17 of 10 ha, eight of 20 ha, three of 40 ha and three of 80 ha), with 120 transects in total. Other work (Mac Nally *et al.* 2000) has used the design to investigate the interaction between the effects of habitat area and fragmentation, but we do not focus on this question here.

Bird surveys

Eight survey rounds were conducted from mid-2010 until mid-2011 by the one observer (J.M. Bennett). For each survey, the observer proceeding along the mid-line of a 250 × 80 m (2 ha) strip transect for 20 min. Surveys were conducted from 30 min after sunrise to 30 min before sunset, but

only in fair weather (i.e. surveys were not conducted in rain, high wind, or high temperatures) and not during the hottest part of the day (11h00 to 15h00). Survey rounds were conducted at regular intervals throughout the year. Sites were visited in a randomized order to avoid systematic temporal biases (Mac Nally *et al.* 2000).

We calculated the total abundance and biomass of nectarivore species, as recognized by Radford and Bennett (2005), for each transect in each survey round. Biomass was calculated by multiplying the abundance for that species by the average body masses for the species (Marchant & Higgins 1990).

Vegetation measurements

Vegetation characteristics were measured along the first 100 m of each bird survey transect (giving 80×100 m vegetation transects). The abundances of tree and shrub species were recorded, as were the numbers of mistletoe plants, hollows, saplings (woody stems with diameter at breast height [DBH] of < 10 cm) and stumps. Trees were assigned to one of four size-classes: 10-39 cm DBH (small), 40-59 cm DBH (medium), 60-79 cm DBH (large) and > 80 cm DBH (very large) to calculate the total basal area for each tree species (Mac Nally *et al.* 2000). Ground and mid-storey cover estimates were taken using quadrats randomly placed along the transect: two 5×5 m quadrats for ground-cover, one 10×50 m quadrat for fallen timber and two 25×25 m quadrats for shrub-cover at each transect. Transect-level canopy cover estimates were made at four random locations along each transect by viewing the canopy through a 30×20 cm transparent viewing grid and estimating the percentage of cells overlain by canopy; the average of the four values was used.

Flowering estimates

The collection of nectar to directly measure production of this resource was not possible because the canopy height of box-ironbark species usually exceed 10 m, so flowering, which is related to nectar production, was measured (Timewell & Mac Nally 2004). Data collection coincided with the timing of bird surveys and was conducted by J.M. Bennett. The canopy diameter of a random subset of each tree species in each size class was estimated from ground level. Foliage cover was then

estimated by holding the viewing grid directly under each tree. To estimate a canopy volume per tree species in each size class, the canopy was first treated as though a sphere and then multiplied by the proportion of foliage cover. To calculate flowering for each transect the following equation was used:

$$I_f = \sum_{trees} V_i L_i F_i C_i,$$

where: V_i is the estimated canopy volume for tree i , L_i is the foliage cover, F_i is proportion of trees in flower and C_i proportion of canopy in flower (for flowering trees in each species and size class). The sum of all tree species in all size classes within a transect constituted the flowering index for that transect.

STATISTICAL ANALYSES

Preliminary analyses indicated strong interactions between nectarivore body size, noisy miner density and landscape context. Therefore, we treated the abundances of small (smaller than the noisy miner, < 63 g), large nectarivores (greater than the noisy miner, > 63 g) and noisy miners as separate response variables, and analysed data from the large forest blocks (30 clusters of transects, 240 surveys) and 31 fragments (248 surveys) separately.

We used Bayesian multi-level analysis of variance (ANOVA) (Gelman 2005; Qian & Shen 2007) to partition variation in nectar availability and nectarivore abundance and biomass [$\log(y+1)$ transformed] into spatial and temporal components, and to examine the relationship between nectarivores and flowering at multiple spatial and temporal scales. Bayesian multilevel ANOVA involves the use of hierarchical regression models to partition variation in response variables among sources of variation (Gelman 2005; Qian & Shen 2007). The basic model was:

$$y_i = \alpha + \sum_{s=1}^S \beta_{li}^s + \varepsilon_i. \quad (1)$$

Here, α is the grand mean, the β s are linear coefficients corresponding to group level effects (deviations from conditional means) within each of S sources of variation (factors), and ε_i is the residual error. β_{li}^s is the coefficient for level l (e.g. Bendigo) of factor s (e.g. region) relevant to

datum i . The coefficients within each source s were drawn from exchangeable normal prior distributions, $\beta_i^s \sim \text{Normal}(0, \sigma_s^2)$, with the corresponding standard deviations assigned flat uniform priors, $\sigma_s \sim \text{Uniform}(0, A)$, where A was $\gg \text{SD}(y)$. The variance component for factor s is estimated from σ_s^2 (the ‘supra-population’ variance) or by the variance of the coefficients, $\text{var}(\beta^s)$ (the ‘finite-population’ variance, Gelman 2005). We used the latter because it is more stable for factors with few sampled levels, although the two measures converge for factors with many levels.

Our models included three spatial components *transect*, *fragment or cluster*, and *region*, one temporal component, *month*, and three spatio-temporal interaction terms, *transect* \times *month*, *fragment/cluster* \times *month*, *region* \times *month*. To examine the association between nectarivore biomass and flowering, we included spatial and temporal components of flower score as covariates in models of nectarivore abundance/biomass. The spatial flowering covariate was the mean flowering score at a transect over all visits (\bar{n}_s). The temporal flowering covariate was the deviation from the transect-specific mean in each survey ($n'_{sm} = n_{sm} - \bar{n}_s$). We assessed how much variation in nectarivore abundance was explained by flowering at each spatial and temporal scale by comparing the variance components in models with and without flowering covariates. We used Bayesian model selection, implemented with reversible-jump Markov chain Monte Carlo (MCMC) methods (Lunn *et al.* 2009; Thomson *et al.* 2010), to assess the influence of vegetation structure, fragment size (fragment data) and the abundance of noisy miners (fragment data only: miners were absent from large blocks) on nectarivore abundance and biomass. Bayesian model selection uses Bayes factors (ratios of marginal likelihoods) to weight model structures (combinations of variables), and yields model-averaged regression coefficients and posterior probabilities that each candidate covariate has a non-zero association with the response [$\text{Pr}(\gamma \neq 0)$] (Wintle *et al.* 2003; Thomson *et al.* 2007).

The full model relating nectarivore abundance (biomass) to flowering score and other covariates was:

$$y_i = \alpha + \sum_{s=1}^S \beta_{i_s}^s + \beta_1^f \cdot \bar{n}_{s_i} + \beta_2^f \cdot n'_{sm_i} + \sum_{j=1}^Q \gamma_j x_{ij} + \varepsilon_i. \quad (2)$$

In (2), the β^f are associated with the linear coefficients of the spatial and temporal components of flowering and γ_s are model averaged linear coefficients associated with Q additional candidate covariates; the other parameters are defined in (1). Candidate covariates included interactions between flowering n_{sm} and selected habitat variables (fragment size, noisy miner abundance and some structural vegetation variables, e.g. $n_{sm} \times \text{noisy miner}$). If an interaction were found, the interaction was decomposed into spatial ($\overline{n_s} \times \text{noisy miner}$), and temporal ($n'_{sm} \times \text{noisy miner}$) components.

All models were estimated using MCMC methods in WinBUGS software version 1.4 (Lunn *et al.* 2000) using the reversible-jump add on (Lunn, Best & Whittaker 2009) for model selection and spline fitting. Parameter posterior distributions were sampled with three independent chains of 50 000 iterations each, after 20 000 iteration burns-in were discarded. Examination of chain histories and convergence diagnostics were used to check that adequate MCMC mixing and convergence were achieved. We used the observed measurements of bird counts to calculate abundance and biomass because accounting for detection error produces biases that are at least as great as the methods used to account for detectability (Welsh *et al.* 2013).

RESULTS

Flowering dynamics

In large forest blocks, 32% of the total variation in flowering index was attributed to monthly variation within transects, reflecting a relatively consistent temporal pattern across all transects, with maximum flowering in August through to October, and little flowering outside of that period (Fig. 3). Flowering was more variable in fragments, with a large fragment \times month component (41%) reflecting greater variation in the timing of peak flowering among fragments (Fig. 4 and Table 1).

Nectarivore dynamics

Sixteen species of nectarivore were recorded (12 honeyeaters, family Meliphagidae, three lorikeets and one parrot, all family Psittacidae). The most common species were the fuscous honeyeater (19.1%), noisy miner (18.6%) and white-plumed honeyeater *Lichenostomus penicillatus* (17.8%). Transect biomass was dominated by the larger nectarivores, especially the red wattlebird *Anthochaera carunculata* (42.0%), noisy miner (24.7%) and musk lorikeet (10.8%). Fragments were numerically dominated by the noisy miner and white-plumed honeyeater, which contributed 31.6% and 29.6% respectively to the total nectarivore abundance in fragments. Forest blocks were numerically dominated by the fuscous honeyeater and the red wattlebird which contributed 39.7% and 24.9% respectively of the total nectarivore abundance in forest blocks.

Spatial and temporal variation in nectarivore abundance and biomass were highly correlated, so we report only on abundance. In both forest blocks and fragments, the majority (>50%) of variation in small nectarivore abundance was spatial, with more larger scale (among location and fragments) variation in fragments and more smaller scale (among transects) variation within large blocks. There was no consistent temporal variation (<2% for month) in small nectarivore abundances, and little spatio-temporal variation at larger spatial scales (month \times cluster/fragment, month \times region, Table 1). Temporal and spatio-temporal sources of variation were relatively more important for large nectarivores, particularly in fragments, where there was some consistent temporal pattern within all transects, and considerable spatio-temporal variation at fragment and region scales (Table 1).

The large components of residual variation (~30- 50%, Table 1) indicate relatively high variation in the short-term (monthly) within transects, especially for large nectarivores within large blocks. Note that an unknown fraction of residual variation is sampling error.

Nectarivore dynamics in relation to flowering

In large forest blocks, a strongly positive association between the mean abundance of small nectarivores and mean flowering index (posterior mean β_1^f [95% credible interval] = 0.85

[0.27,1.50]) explained 10% of the total variation, including 50% and 44% of among region and among cluster variation, respectively (Fig. 1A, Table 1). Number of small trees (-0.18 [-0.47,0.00], $\Pr(\gamma \neq 0) = 0.84$) explained another 5% of variance in small nectarivores (Table 2). The spatial relationships between large nectarivores and mean flowering was much weaker ($\beta_1^f = 0.14 [-0.09, 0.37]$), and explained <5% of the total variation (Fig. 1B, Table 1). Temporal variation in abundance was not associated with temporal variation in flowering for small ($\beta_2^f = 0.06 [-0.05, 0.16]$, Fig. 1C) or for large ($\beta_2^f = 0.05 [-0.04, 0.14]$, Fig. 1D) nectarivores in large blocks.

In fragments, noisy miners density was the dominant predictor of the abundance of small nectarivores (*noisy miner* coefficient = -0.53 [-0.76, -0.30], $\Pr(\gamma \neq 0) = 1$), with small nectarivores largely absent from transects with high noisy miners densities, regardless of flowering activity (Fig. 2A). There was no consistent relationship between small nectarivore abundance and flowering among ($\beta_1^f = 0.03 [-0.30, 0.39]$) or within ($\beta_2^f = 0.03 [0.04, 0.11]$) fragment transects (Fig. 2A, 2C). However, there was some evidence of interactions between noisy miner density and flowering in fragments, ($\overline{n_s} \times \text{noisy miner}$ interaction coefficient = -0.11 [-0.38, 0.04], $\Pr(\gamma \neq 0) = 0.62$), suggesting that the response of small nectarivores to flowering in miner-free fragments may be similar to their response in large blocks. The combined data (fragment and large block) yielded a much stronger noisy miner \times flowering interaction term ($\overline{n_s} \times \text{noisy miner}$ interaction coefficient = -0.37 [-0.66, 0.00], $\Pr(\gamma \neq 0) = 0.94$) and a positive small nectarivore-flowering relationship overall (0.50 [0.11, 0.90]). Note that there was no relationship between noisy miner densities and flowering index among ($\beta_1^f = -0.04 [-1.06, 1.06]$) or within ($\beta_2^f = 0.06 [0.09, 0.22]$) fragment transects.

The abundance of large nectarivores in fragments was positively associated with both spatial ($\beta_1^f = 0.36 [0.16, 0.56]$) and temporal variation in flowering ($\beta_2^f = 0.25 [0.12, 0.40]$). Flowering explained 20% of the total variation in large nectarivore abundance in fragments, including 31%, 45% and 23% of the among-fragment, location \times month and fragment \times month variation, respectively (Table 1). Fragment area (-0.18 [-0.34,0.00], $\Pr(\gamma \neq 0) = 0.93$) and the number of very

large trees (-0.17 [-0.31,0.00], $\Pr(\gamma \neq 0) = 0.94$) together explained another 14% of variation in large nectarivore abundances (Table 2).

DISCUSSION

Flowering had a distinct temporal pattern, with most flowering occurring in the austral winter and spring, although there was some flowering in all months. Variation in nectarivore biomass and abundance was related to flowering, which supported the Ideal Free Distribution IFD model. Small nectarivores tracked spatial variation in flowering only in large forest blocks, where noisy miners were absent. Large nectarivores tracked spatial and temporal variation in flowering but only in fragments.

The strong spatial and temporal variation in large nectarivore abundance in fragments demonstrated marked seasonal differences in biomass and abundance of large nectarivorous species, between fragments and between regions, although the movements of individual birds are not known. Temporal variation in nectarivore abundance and biomass among all transects was a small component of total nectarivore variation, indicating that there was little *net* migration into or out of the study area. The small temporal changes in nectarivore abundance and biomass that were observed may have been at least partly explained by differences in demographic processes among sites (e.g. mortality and reproduction) (DeAngelis *et al.* 2011).

The abundance of large nectarivores was positively associated with both spatial and temporal variation in flowering in fragments, indicating that large nectarivores track flowering in space and time. This result is consistent with previous reports that many nectarivores in this region are itinerant (Mac Nally 1995), moving in response to changes in the spatial-temporal mosaic of flowering (Mac Nally & McGoldrick 1997). The spatial relationship between mean flowering and mean abundance was stronger than the temporal relationship within transects, indicating that birds may not be tracking flowering at all sites. The relatively weak temporal tracking by large nectarivores, and absence of temporal tracking by small nectarivores, may indicate that nectar was non-limiting in the

region at the time of the study (2010-11); flowering was recorded in all months and animals have less reason to move when food is non-limiting in their current location (DeAngelis *et al.* 2011).

Itinerant nectarivores may travel large distances and even leave a region at times of nectar scarcity (Mac Nally *et al.* 2009). Flowering was much reduced during the Big Dry (drought from 1997 to 2009) with complete failure in some years (Mac Nally *et al.* 2009). Flowering failure probably caused a mass exodus of the red wattlebird and musk lorikeet from the region. A large increase in the abundance of the musk lorikeet 120 km away in urban Melbourne occurred concurrently, although one cannot say whether the same birds had moved there (Fitzsimons *et al.* 2003). A similar pattern was observed for two small nectarivores, the fuscous honeyeater and yellow-tufted honeyeater *Lichenostomus melanops*, where abundances declined in winter 2007 in the study region and these species were reported beyond their usual geographical range, into southwestern Victoria (Mac Nally *et al.* 2009). During the Big Dry, about two-thirds of bird species, independent of their ecological traits, had declined, which was attributed to a resource bottleneck (Mac Nally *et al.* 2009). The Big Dry broke in 2010 with heavy spring and summer rainfall (BoM 2012), which probably led to the high flowering rates recorded during our study because precipitation induces flowering (Williams & Middleton 2008). Given the recent avifaunal collapse in the Big Dry (Mac Nally *et al.* 2009), this profusion of flowering may have constituted an oversupply of nectar at the time of this study.

There are greater energetic costs from flying among patches compared to foraging within a patch (Brown *et al.* 1978). Larger birds have greater energy needs, which may increase their need to track (Brown *et al.* 1978) the greater flowering resources associated with fragments. Small nectarivores probably track variation in flowering at a smaller scale (i.e. within transects). Small-bodied birds can survive on smaller quantities of nectar but use energy reserves more rapidly while not feeding (e.g. flying over unsuitable vegetation) than large-bodied birds (Brown *et al.* 1978). Therefore, agricultural lands may act as a greater barrier to small-bodied nectarivore species than large-bodied species.

The IFD model assumes that individuals have a perfect knowledge of food availability throughout their environment and are able to move freely without incurring major costs (Fretwell & Lucas 1969). Individual birds cannot have full knowledge of all resources in the landscape, or at larger scales. There are considerable costs with movements beyond well-known areas, including decreased foraging efficiency, increased predation risk (Kennedy & Gray 1997) and foregone breeding opportunities. Such movements, if repeated over a number of years, may lead to a decline in regional populations (Mac Nally *et al.* 2009). Consumers should only move to a new patch if the increase in performance (energy intake and growth) at the new site outweighs all costs of getting there (Fretwell 1972). Given the potential costs of moving, individuals may move in resources at their present location to a point where they can no longer support themselves rather than to gain access to greater resources *per se*.

Interspecific interactions pose another constraint because territorial and competitive behaviour may prevent species from using a site (Kennedy & Gray 1997). Noisy miners appeared to be a major constraint on the distribution of small nectarivores among fragment transects, consistent with recent reports (Mac Nally *et al.* 2012; Maron *et al.* 2013). Small nectarivore abundance was related spatially to flowering in large forest blocks that lack noisy miners, and possibly among fragment transects that lack noisy miners. The later relationship was weak and very uncertain, possibly because of small sample size (35 fragment transects that were noisy-miner free), or because of direct fragmentation effects that limit the capacity of small nectarivores to track resources.

Noisy miners are interference competitors (Schoener 1986) that limit the ability of other species, especially small-bodied species, to gain access to resources. The apparent absence of a relationship between noisy miners and flowering was not unexpected because noisy miners form relatively sedentary colonies and rely comparatively little on nectar (Maron *et al.* 2013). Fretwell (1972) contended that individuals are more competitive when closer to the centre of their territories, so that smaller territories will be better defended. In creating small patches of native vegetation that are easily defended, the process of fragmentation probably facilitated the expansion of the noisy

miner, which may have led to a change in the distribution of nectarivore species that is nearer to the expectations of the IDD model (Fretwell 1972) than to those of the IFD model (Fretwell & Lucas 1969)

By preventing unimpeded movements of small nectarivores in response to variation in nectar, the noisy miner may have wider consequences for ecological function (Sekericioglu 2006; Hoehn *et al.* 2008). In eucalypt forests, many trees and shrubs are bird-pollinated (Ford 1985) so fewer small-nectarivore movements may limit plant outcrossing, leading to reduced seed quality and set and, ultimately, induce changes in plant assemblages, which may limit the long-term viability of fragmented vegetation assemblages (Maron *et al.* 2013). By excluding small nectarivores from fragments, the noisy miner may decrease plant functional diversity, which also may lessen seed set (Hoehn *et al.* 2008).

Contrary to our expectations, vegetation characteristics did not modulate the effects of the noisy miner. Vegetation structure appeared to be important for nectarivores, but was less so than the effects of flowering and variation in abundance of the noisy miner. The strong spatial and temporal tracking in fragments highlighted the importance of fragmented vegetation in this system. Large, mature trees generally are confined to vegetation fragments because of a long history of intensive silvicultural practises in forest blocks (Vesk & Mac Nally 2006). Mature large trees provide greater nectar (Vesk & Mac Nally 2006), so their presence in a fragment probably would be attractive for all nectarivores. Large trees provide other important resources for many birds, including tree hollows for nesting (Vesk & Mac Nally 2006). Smaller vegetation fragments generally occur in the more fertile, wetter parts of the landscape, where more intense flowering and more rapid tree growth are likely (Vesk & Mac Nally 2006). The strong association between noisy miners and vegetation fragments may lead to small honeyeaters being displaced into less productive areas while being denied access to the greater resources associated with large, mature trees, possibly leading to reduced long-term persistence (Montague-Drake *et al.* 2011).

In our region, as in many regions around the world, climate change is expected to lead to an increase in the frequency and intensity of prolonged droughts, which are punctuated by intense, short periods of precipitation (Hennessy *et al.* 2008). Nectar production is positively associated with precipitation (Williams & Middleton 2008) and such a climate regime probably would result in extended periods of nectar scarcity, with short periods when nectar is abundant. The apparent immunity of noisy miners to this pattern of precipitation and resource availability (Maron *et al.* 2013), and the influence of the noisy miner on the ability of small nectarivores to acquire food resources may mean the long-term outlook for many small-nectarivore species is grim.

Synthesis

Flowering strongly influenced the spatio-temporal dynamics of nectarivorous birds, but this relationship was modulated by the despotic noisy miner. Altered competition as a consequence of fragmentation and degradation probably led to a change in the distribution of small nectarivore species that departed from the Ideal Free Distribution model and is now best described by the Ideal Despotic Distribution model (Fretwell & Lucas 1969). Altered assemblages and interspecific interactions arising from a change in climate are not limited to birds (Milazzo *et al.* 2013), and fragmentation has been linked to altered species interactions in many regions of the world (Tylianakis *et al.* 2008). Therefore, similar effects to those that we report almost will certainly arise in other fragmented regions and in other taxa. By limiting access to increasingly variable resources, noisy miners may reduce the capacity of smaller nectarivores to recover from adverse climate events (e.g. extended drought) and other disturbances, threatening the long-term persistence of many small bird species. Reduced access to nectar sources for nectarivores may also disrupt ecosystem services (e.g. pollination, seed dispersal) and have long-term consequences for the persistence of fragmented vegetation, further imperilling dependent fauna.

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REFERENCES

- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365-377.
- Bennett, J.M., Cunningham, S.C., Connelly, C.A., Clarke, R.H., Thomson, J.R. & Mac Nally R (2013) The interaction between a drying climate and land use affects forest structure and above-ground carbon storage. *Global Ecology and Biogeography*, **22**, 1239-1247.
- Blendinger, P.G., Ruggera, R.A., Núñez Montellano, M.G., Macchi, L., Zelaya, P.V., Álvarez, M.E., Martín, E., Acosta, O.O., Sánchez, R. & Haedo, J. (2012) Fine-tuning the fruit-tracking hypothesis: spatiotemporal links between fruit availability and fruit consumption by birds in Andean mountain forests. *Journal of Animal Ecology*, **81**, 1298-1310.
- BoM (2012) Australian climate variability & change Bureau of Meteorology, Melbourne.
- Brown, J.H., Calder, W.A. & Kodric-Brown, A. (1978) Correlates and consequences of body size in nectar-feeding birds. *American Zoologist*, **18**, 687-738.
- Brown, J.H. & Maurer, B.A. (1986) Body size, ecological dominance and Cope's rule. *Nature*, **324**, 248-250.
- Brown, W.P. (2007) Body mass, habitat generality, and avian community composition in forest remnants. *Journal of Biogeography*, **34**, 2168-2181.
- Carey, M.P., Sanderson, B.L., Barnas, K.A. & Olden, J.D. (2012) Native invaders – challenges for science, management, policy, and society. *Frontiers in Ecology and the Environment*, **10**, 373-381.
- Crampton, L.H., Longland, W.S., Murphy, D.D. & Sedinger, J.S. (2011) Food abundance determines distribution and density of a frugivorous bird across seasons. *Oikos*, **120**, 65-76.
- DeAngelis, D.L., Wolkowicz, G.S.K., Lou, Y., Jiang, Y., Novak, M., Svanbäck, R., Araújo, M.S., Jo, Y. & Cleary, E.A. (2011) The effect of travel loss on evolutionarily stable distributions of populations in space. *The American Naturalist*, **178**, 15-29.

- Epanchin, P.N., Knapp, R.A. & Lawler, S.P. (2009) Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. *Ecology*, **91**, 2406-2415.
- Fitzsimons, J.A., Palmer, G.C., Antos, M.A. & White, J.G. (2003) Refugees and residents: densities and habitat preferences of lorikeets in urban Melbourne. *Australian Field Ornithology*, **20**, 2-7.
- Ford, H.A. (1985) Nectarivory and Pollination by Birds in Southern Australia and Europe. *Oikos*, **44**, 127-131.
- Fretwell, S. & Lucas, H., Jr. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16-36.
- Fretwell, S.D. (1972) *Populations in a seasonal environment*. Princeton University Press.
- Gelman, A. (2005) Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis*, **1**, 1-19.
- Haché, S., Villard, M.-A. & Bayne, E.M. (2012) Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology*, **94**, 861-869.
- Hart, P.J., Woodworth, B.L., Camp, R.J., Turner, K., McClure, K., Goodall, K., Henneman, C., Spiegel, C., LeBrun, J., Tweed, E. & Samuel, M. (2011) Temporal variation in bird and resource abundance across an elevational gradient in Hawaii (variación temporal de la abundancia de aves y recursos en un gradiente altitudinal en Hawai). *The Auk*, **128**, 113-126.
- Hennessy, K., Fawcett, R., Kirono, D., Mpelasoka, F., Jones, D., Bathols, J., Whetton, P. & Smith, M.S. (2008) An assessment of the impact of climate change on the nature and frequency of exceptional climatic events. CSIRO and the Australian Bureau of Meteorology, Canberra.
- Hoehn, P., Tschardtke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2283-2291.
- Jones, O.R., Pilkington, J.G. & Crawley, M.J. (2006) Distribution of a naturally fluctuating ungulate population among heterogeneous plant communities: ideal and free? *Journal of Animal Ecology*, **75**, 1387-1392.

- Kennedy, M. & Gray, R.D. (1997) Habitat choice, habitat matching and the effect of travel distance. *Behaviour*, **134**, 905-920.
- Korfanta, N.M., Newmark, W.D. & Kauffman, M.J. (2012) Long-term demographic consequences of habitat fragmentation to a tropical understory bird community. *Ecology*, **93**, 2548-2559.
- Lehouck, V., Spanhove, T., Vangestel, C., Cordeiro, N.J. & Lens, L. (2009) Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? *Ecography*, **32**, 789-799.
- Letnic, M. & Dickman, C.R. (2010) Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews*, **85**, 501-521.
- Lunn, D., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325-337.
- Lunn, D.J., Best, N. & Whittaker, J.C. (2009) Generic reversible jump MCMC using graphical models. *Statistics and Computing*, **19**, 395-408.
- Mac Nally, R., Bennett, A.F. & Horrocks, G. (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7-29.
- Mac Nally, R., Bennett, A.F., Thomson, J.R., Radford, J.Q., Unmack, G., Horrocks, G. & Vesk, P.A. (2009) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720-730.
- Mac Nally, R., Bowen, M., Howes, A., McAlpine, C.A. & Maron, M. (2012) Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. *Ecology*, **93**, 668-678.
- Mac Nally, R. & McGoldrick, J.M. (1997) Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. *Journal of Avian Biology*, **28**, 171-183.

- Mac Nally, R. & Timewell, C.A.R. (2005) Resource availability controls bird-assemblage composition through interspecific aggression. *Auk*, **122**, 1097-1111.
- Mac Nally, R.C. (1995) A protocol for classifying regional dynamics, exemplified by using woodland birds in southeastern Australia. *Australian Journal of Ecology*, **20**, 442-454.
- Marchant, S. & Higgins, P.J. (1990) *Handbook of Australian, New Zealand and Antarctic birds*. Oxford University Press, Melbourne.
- Maron, M., Grey, M.J., Catterall, C.P., Major, R.E., Oliver, D.L., Clarke, M.F., Loyn, R.H., Mac Nally, R., Davidson, I. & Thomson, J.R. (2013) Avifaunal disarray due to a single despotic species. *Diversity & Distributions*, **19**, 1468-1479.
- Maron, M., Main, A., Bowen, M., Howes, A., Kath, J., Pillette, C. & McAlpine, C.A. (2011) Relative influence of habitat modification and interspecific competition on woodland bird assemblages in eastern Australia. *Emu*, **111**, 40-51.
- McAlpine, C.A., Syktus, J., Ryan, J.G., Deo, R.C. & McKeon, G.M. (2009) A continent under stress: interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate. *Global Change Biology*, **15**, 2206-2223.
- Milazzo, M., Mirto, S., Domenici, P. & Gristina, M. (2013) Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology*, **82**, 468-477.
- Montague-Drake, R., Lindenmayer, D., Cunningham, R. & Stein, J. (2011) A reverse keystone species affects the landscape distribution of woodland avifauna: a case study using the Noisy Miner (*Manorina melanocephala*) and other Australian birds. *Landscape Ecology*, **26**, 1383-1394.
- Morris, D. (1988) Habitat-dependent population regulation and community structure. *Evolutionary Ecology*, **2**, 253-269.
- Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1-13.

- Qian, S.S. & Shen, Z. (2007) Ecological applications of multilevel analysis of variance. *Ecology*, **88**, 2489-2495.
- Radford, J.Q. & Bennett, A.F. (2005) Terrestrial avifauna of the Gippsland Plain and Strzelecki Ranges, Victoria, Australia: insights from Atlas data. *Wildlife Research*, **32**, 531-555.
- Robinson, S.K. & Terborgh, J. (1995) Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology*, **64**, 1-11.
- Robinson, S.K., Thompson, F.R., III, Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987-1990.
- Rosenzweig, M.L. (1981) A Theory of Habitat Selection. *Ecology*, **62**, 327-335.
- Schoener, T.W. (1986) Mechanistic approaches to community ecology: a new reductionism. *American Zoologist*, **26**, 81-106.
- Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, **21**, 464-471.
- Symes, C., Nicolson, S. & McKechnie, A. (2008) Response of avian nectarivores to the flowering of *Aloe marlothii*: a nectar oasis during dry South African winters. *Journal of Ornithology*, **149**, 13-22.
- Thomson, J.R., Kimmerer, W.J., Brown, L.R., Newman, K.B., Mac Nally, R., Bennett, W.A., Feyrer, F. & Fleishman, E. (2010) Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications*, **20**, 1431-1448.
- Thomson, J.R., Mac Nally, R., Fleishman, E. & Horrocks, G. (2007) Predicting bird species distributions in reconstructed landscapes. *Conservation Biology*, **21**, 752-766.
- Timewell, C.A.R. & Mac Nally, R. (2004) Diurnal foraging-mode shifts and food availability in nectarivore assemblages during winter. *Austral Ecology*, **29**, 264-277.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351-1363.

- Vesk, P.A. & Mac Nally, R. (2006) The clock is ticking - Revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. *Agriculture Ecosystems & Environment*, **112**, 356-366.
- Vesk, P.A., Nolan, R., Thomson, J.R., Dorrough, J.W. & Mac Nally, R. (2008) Time lags in provision of habitat resources through revegetation. *Biological Conservation*, **141**, 174-186.
- Welsh, A.H., Lindenmayer, D.B. & Donnelly, C.F. (2013) Fitting and interpreting occupancy models. *PloS one*, **8**, e52015-e52015.
- Williams, S.E. & Middleton, J. (2008) Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions*, **14**, 69-77.
- Wintle, B.A., McCarthy, M.A., Volinsky, C.T. & Kavanagh, R.P. (2003) The use of bayesian model averaging to better represent uncertainty in ecological models. *Conservation Biology*, **17**, 1579-1590.

Table 1: Spatial and temporal components of variation in flowering index, small nectarivore abundance, and large nectarivore abundance. Variance = posterior median (95% CI) of ‘finite population’ variance (Gelman 2005) for each component of variation in model with no covariates (model 1); % = % of total variation attributable to each component; Residual Variance = posterior median (95% CI) of ‘finite population’ residual variance for each component in a model with covariates (flowering, and interactions with noise miner density or vegetation, as indicated); % exp = percentage of variance explained by covariates within each component.

	Flowering index		Small nectarivores				Large nectarivores			
<i>Fragments</i>	Variance	%	Variance	%	Residual Variance (flowering)	%	Residual Variance (flowering, noisy miner)	%	Variance	%
Region	0.04 (0.00, 0.25)	2	0.15 (0.00, 0.64)	10	0.15 (0.00, 0.59)	0	0.21 (0.01, 0.54)	-40	0.01 (0.00, 0.07)	1
Fragment	0.29 (0.12, 0.50)	16	0.70 (0.35, 1.02)	45	0.73 (0.39, 1.08)	-4	0.14 (0.00, 0.45)	80	0.16 (0.09, 0.26)	18
Transect	0.04 (0.00, 0.11)	2	0.14 (0.06, 0.31)	9	0.14 (0.06, 0.31)	0	0.17 (0.08, 0.32)	-21	0.01 (0.00, 0.04)	1
Month	0.16 (0.01, 0.38)	9	0.01 (0.00, 0.05)	1	0.02 (0.00, 0.05)	-100	0.02 (0.00, 0.05)	-100	0.07 (0.00, 0.18)	8
Region*Month	0.20 (0.06, 0.45)	11	0.02 (0.00, 0.07)	1	0.02 (0.00, 0.07)	0	0.02 (0.00, 0.07)	0	0.11 (0.04, 0.21)	13
Fragment*Month	0.77 (0.62, 0.95)	41	0.05 (0.00, 0.14)	3	0.06 (0.00, 0.14)	-20	0.05 (0.00, 0.14)	0	0.22 (0.14, 0.30)	25
Residual	0.36 (0.30, 0.43)	19	0.47 (0.41, 0.54)	30	0.47 (0.41, 0.54)	0	0.47 (0.40, 0.54)	0	0.30 (0.26, 0.36)	34
Total	1.91 (1.64, 2.34)	100	1.56 (0.82, 2.76)	100	1.58 (1.29, 2.18)	-1	1.08 (0.49, 2.11)	31	0.89 (0.77, 1.08)	100
<i>Forest blocks</i>	Variance	%	Variance	%	Residual Variance (flowering)	%	Residual Variance (flowering, small trees)	%	Variance	%
Region	0.00 (0.00, 0.03)	0	0.02 (0.00, 0.23)	1	0.01 (0.00, 0.15)	50	0.02 (0.00, 0.18)	0	0.04 (0.00, 0.14)	6
Cluster	0.01 (0.00, 0.06)	1	0.34 (0.07, 0.67)	23	0.19 (0.01, 0.46)	44	0.20 (0.01, 0.49)	41	0.07 (0.02, 0.12)	11
Transect	0.09 (0.05, 0.15)	8	0.46 (0.31, 0.70)	31	0.47 (0.31, 0.68)	-2	0.39 (0.24, 0.63)	15	0.02 (0.00, 0.06)	3
Month	0.35 (0.20, 0.49)	32	0.02 (0.00, 0.10)	1	0.02 (0.00, 0.08)	0	0.02 (0.00, 0.08)	0	0.05 (0.00, 0.13)	8
									0.04 (0.00, 0.11)	20

Region Month	0.04 (0.00, 0.12)	4	0.06 (0.01, 0.13)	4	0.05 (0.01, 0.12)	17	0.05 (0.01, 0.11)	17	0.07 (0.03, 0.15)	11	0.07 (0.03, 0.14)	0
Cluster Month	0.13 (0.06, 0.20)	12	0.08 (0.01, 0.16)	5	0.07 (0.01, 0.15)	12	0.06 (0.00, 0.15)	25	0.05 (0.00, 0.09)	8	0.05 (0.01, 0.10)	0
Residual	0.47 (0.42, 0.53)	43	0.51 (0.45, 0.58)	34	0.51 (0.46, 0.58)	0	0.52 (0.46, 0.59)	-2	0.34 (0.31, 0.39)	54	0.34 (0.31, 0.39)	0
Total	1.10 (0.96, 1.28)	100	1.52 (1.30, 1.93)	100	1.33 (0.80, 2.23)	10	1.26 (0.72, 2.23)	15	0.65 (0.56, 0.81)	100	0.62 (0.37, 1.07)	2

Figure legends

Figure 1 Tracking of flowering by small (A, C) and large (B, D) nectarivores within large forest blocks, separated into spatial (between transect, A, B) and temporal (between months within transects, C, D) components. Top panels show mean abundances of small (A) and large (B) nectarivores per transect as a function of mean flowering index. Lower panels show abundance anomalies (monthly departures from the overall mean abundance at each transect) for small (C) and large (D) nectarivores against flowering anomaly (monthly departure from the overall mean flowering score at each transect). Estimated linear relationships are shown as posterior means (solid black line), 75% credible intervals (dark grey band, solid lines) and 95% credible intervals (light grey band, dashed line). Note that plotted abundances are $\log(count+1)$.

Figure 2 Tracking of flowering by small (A, C) and large (B, D) nectarivores within woodland fragments (<100 ha), separated into spatial (between transect, A, B) and temporal (between months within transects, C, D) components (see Fig 1). Symbol size is proportional to fragment size (10, 20, 40 or 80 ha). Symbol shading is proportional the density of noisy miners at the time of the survey (C, D) or averaged over all surveys (A, B): open symbols indicate the absence of noisy miners. In panel A, the two fitted lines show fitted relationships between small nectarivore abundance and flowering in the absence of noisy miners (“no miners”) and at the mean density of miners when present (“miners”). Note that the 95% CI’s for mean miner line are not shown for clarity, but include the possibility of a positive slope (standardized coefficient 95%CI = [-1.1, 0.4]).

Figure 3 Boxplot of flowering score in fragments (dark grey) and large blocks (light grey) in each month.

Figure 4 Flowering score by transect for (A) large blocks and (B) fragments. Each line is a transect.

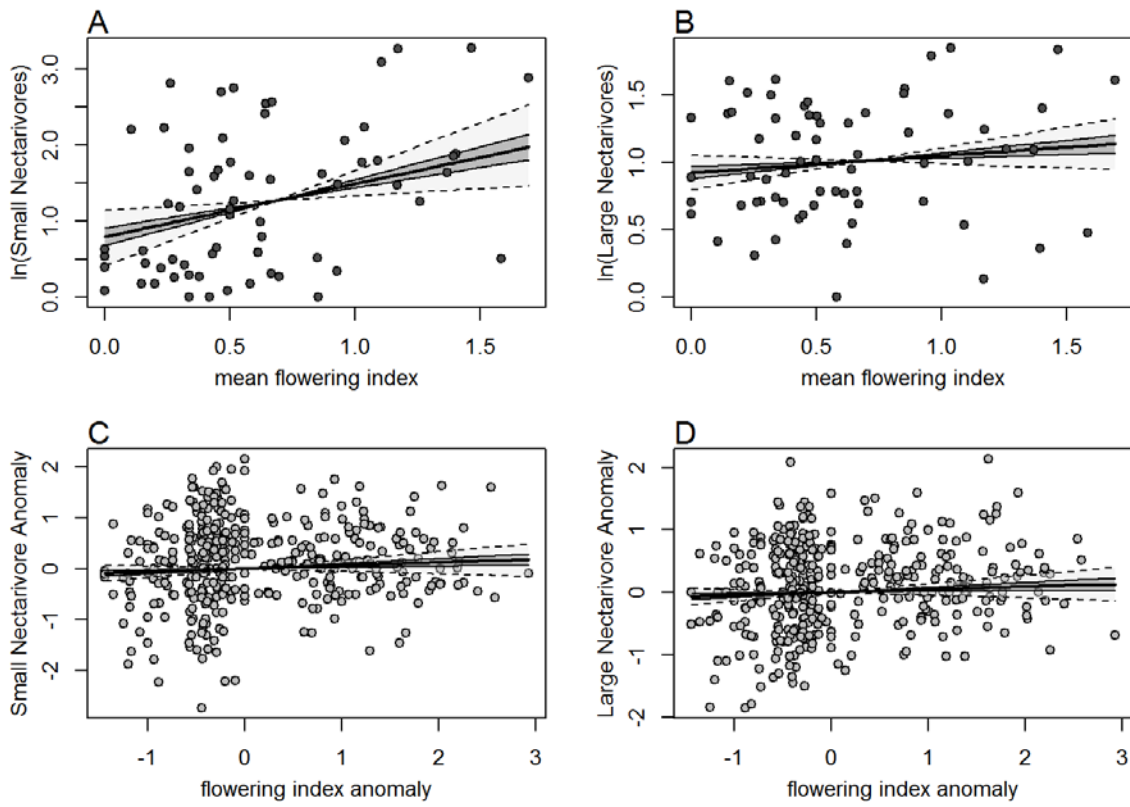


Figure 1:

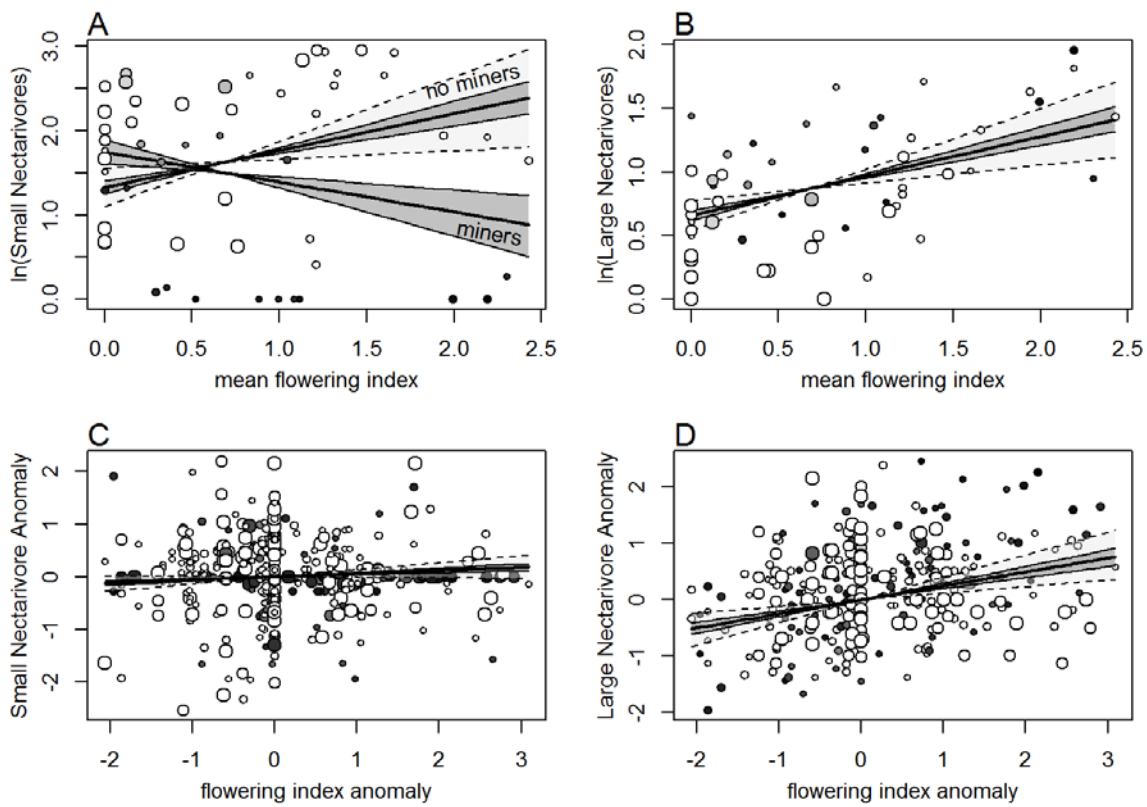


Figure 2:

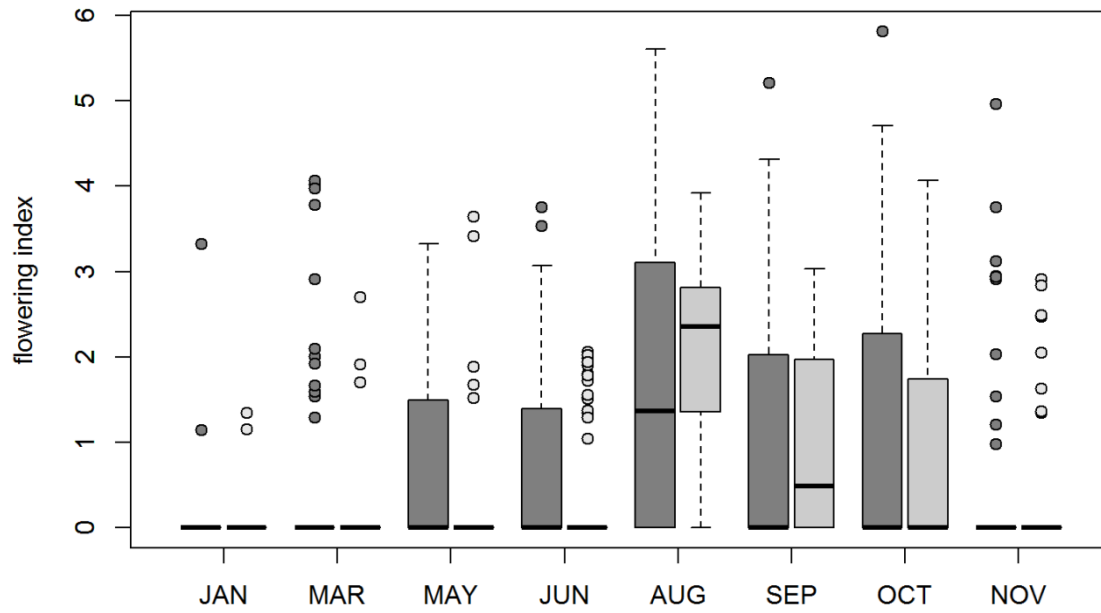


Figure 3:

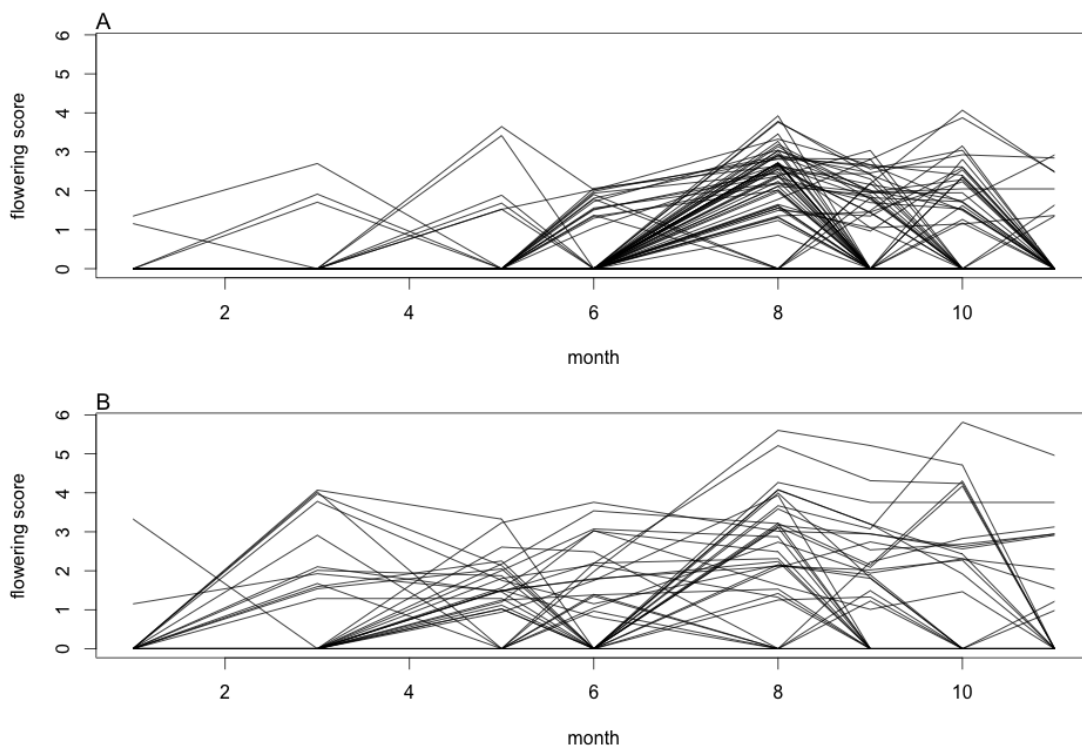


Figure 4:

PART B: Suggested Declaration for Thesis Chapter

Monash University

Declaration for Thesis Chapter 6

Declaration by candidate

In the case of Chapter 6, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The initiation, key ideas, development and writing up of the work were my responsibility. I coordinated the study and performed all of the field work. I conducted most of the analysis, and was the primary author of the manuscript.	70

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Rohan H. Clarke,	Contributed to writing of the manuscript	
James R. Thomson	Support with analysis	
Ralph Mac Nally	Contributed ideas to the work and contributed to writing of the manuscript	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature		Date
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Main Supervisor's Signature		Date
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*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 6: Habitat fragmentation and vegetation change alters interspecific interactions with negative consequences for the recruitment of woodland birds

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Running title: Drought, land use and competition affect bird recruitment

Keywords: climate change, despotic species, drought, interspecific competition, land use change

Primary Research Article

ABSTRACT

Aim Climate change may amplify the adverse effects of fragmentation by affecting interspecific species interactions. Increased competition may reduce the ability of vulnerable species to require resources (breeding sites and food), which may reduce recruitment and long-term viability of native species. We assessed how measures of recruitment of native birds were influenced by area of native vegetation, vegetation characteristics, vegetation change, as an indication of degradation, and the occurrence of an increasingly prevalent native competitor (the noisy miner *Manorina melanocephala*).

Location Inland-slope forests of south-eastern Australia

Methods We recorded avian breeding behavior on 120 forest transects in 2010–11. We remeasured vegetation characteristics that had previously been measured in 1995–97 (to assess vegetation degradation).

Results Vegetation area and abundance of noisy miner had a greater effect on species breeding behavior than did on-transect vegetation characteristics and vegetation degradation. Higher abundances of the noisy miner reduced breeding activities of species with a body mass smaller than noisy miners (< 63 g), while breeding increased in many species with body mass larger than noisy miners. Recruitment measures for the noisy miner were positively associated with smaller fragments and greater vegetation change indicating that fragmentation and vegetation degradation have facilitated noisy miner recruitment.

Main conclusions The interaction between climate change, fragmentation and vegetation degradation may lead to increased effects of interspecific competition in fragments of native vegetation, with potential adverse effects on the viability of many species. The spread and increasing abundance of a hyperaggressive native species suggests that species assemblages will be increasingly disrupted by the interacting effects of climate change, fragmentation, degradation and interspecific interactions.

INTRODUCTION

Human-induced climate change, driven by elevated greenhouse gas emissions has been linked to increasing global temperatures, changes in the spatial patterns of precipitation, and increases in the severity and frequency of extreme climatic events such as droughts and flooding rains (IPCC, 2007). Increases in extreme climatic events arising from global warming, including drought and heat stress, have been linked to widespread vegetation dieback and distribution shifts (Allen *et al.*, 2010) and these changes may be amplified in fragmented systems (Bennett *et al.*, 2013). Fragmented remnant vegetation may become more degraded than intact remnant vegetation with climate change due to shifts in the regional distribution of precipitation and localized drying and warming (McAlpine *et al.*, 2009).

Vegetation change has many effects on biota, such as reductions in breeding success, population sizes, dispersal, and changes in species composition (Mac Nally & Bennett, 1997). Changes in assemblage composition occur from species having different responses to habitat change, which arise from species having different ecological traits (Öckinger *et al.*, 2010). Different species composition affect interspecific interactions, such as competition, predation, parasitism and pollination, which influence assemblage dynamics and ecosystem function (Ewers & Didham, 2006). Despite extensive evidence that habitat attributes and interspecific interactions structure species assemblages, biotic interactions are poorly integrated into biogeographical knowledge due to the difficulties in measuring interaction strengths that vary substantially in space and time (Brown, 2007; Tylianakis *et al.*, 2008).

Studies on the effects of human pressures typically focus on impacts on species richness or assemblage composition, but these measures do not provide an indication of the population viabilities of the constituent taxa (Korfanta *et al.*, 2012). The ‘gold standard’ would be to conduct a full demographic analysis at the appropriate spatial scale for the taxa of interest, including species-specific measurements of recruitment, mortality, emigration and immigration. This probably is infeasible for even one species let alone an assemblage of perhaps dozens of taxa, so a compromise

is to move to a subset of measures that relate to recruitment as an advance on ‘standing crop’ measures, such as abundance (Mac Nally, 2007; Selwood *et al.*, 2009).

Our focus is on birds for several reasons. Birds are among the most mobile of fauna, increasing the likelihood that birds are more rapidly exposed to changes in landscape configuration and spatial variation in resource availability than other taxa (Thomson *et al.*, 2007). Birds also have the capacity to drive vegetation change by controlling invertebrate populations, pollinating, and dispersing seeds, which have important long term effects on vegetation (Sekercioglu, 2006). In birds, as with other taxa, extinction risk is associated with species’ life-history traits, suggesting that variation in demographic rates should occur among species (Öckinger *et al.*, 2010) and ultimately this may affect interspecific interactions that structure assemblages (Korfanta *et al.*, 2012). Competitive species that are tolerant of, or benefit from, disturbances may monopolize resources (nesting sites and food) and limit the survival and recruitment of disturbance-sensitive species (Brown, 2007).

The box-ironbark forests in south-eastern Australia, where this study was conducted, have been exposed to the interaction between climate change and land-use. There has been widespread clearance of forests in south-eastern Australia since European settlement in the 19th century, with the extent of woody vegetation halved (McAlpine *et al.*, 2009). Temperatures in south-eastern Australia have increased over several decades (Leblanc *et al.*, 2012). Increases in temperature were compounded by a long-term, severe drought, ‘the Big Dry’ that commenced in 1997 and lasted until it was broken by heavy spring and summer precipitation between 2010 and 2012 - ‘the Big Wet’ (Leblanc *et al.*, 2012). The accumulated precipitation deficit over the Big Dry and its duration (1997- early 2010) were unprecedented since instrumental records began in the 1880s (Leblanc *et al.*, 2012).

The Big Dry, which is consistent with climate-change scenarios that predict an increase in the frequency and intensity of extreme events such as long-term, severe droughts, appeared to be responsible for major changes in vegetation structure (Bennett *et al.*, 2013). The extensive loss of

canopy, litter and shrub cover and greater tree mortality as a consequence of the drought (Bennett *et al.*, 2013) is a decline in habitat quality for many species and hence the overall change in vegetation condition can be used as a measure of habitat degradation. Projected and observed changes in climate in our region are consistent with other drying regions (e.g. the North American south-west, the Mediterranean Basin, Southern Africa and China) (IPCC, 2007), so that our results potentially have wide relevance elsewhere in the world.

We assessed how measures of recruitment of native birds were influenced by the area of available habitat (native vegetation), drought-driven habitat degradation, and the occurrence of the native bird (the noisy miner *Manorina melanocephala*), a hyper-competitive species that has become more prevalent in the inland woodlands of eastern Australia since the 1990s (Maron *et al.*, 2013). While habitat loss, fragmentation and degradation have been linked to substantial declines in many forest and woodland birds (Ford, 2011), the noisy miner has benefited from land-use change because it seems to prefer forest edges and small (≤ 20 ha) remnants (Maron *et al.*, 2011). The noisy miner can form large colonies and breeds cooperatively (Dow, 1977). Its mobbing behavior excludes other bird species (especially species smaller than itself) from vegetation under control of the colony, substantially altering the structure of woodland bird assemblages, which has led to its classification as a ‘despot’ (Mac Nally *et al.*, 2012). The vegetation degradation seen during the Big Dry was expected to facilitate noisy miner recruitment and colonization because the noisy miner occurs in greater abundances when canopy cover and shrub cover are reduced (Maron *et al.*, 2013).

We assessed how measures of recruitment of native birds were influenced by the area of native vegetation, drought-driven habitat degradation, and the occurrence of the noisy miner. We expected that vegetation fragmentation, degradation and altered interspecific interactions attributable to interference competition from the noisy miner may act together to affect recruitment. We used breeding activity as a measure of recruitment because it can be measured for multiple species at many locations. We sought to determine: (1) does habitat fragmentation/loss or vegetation characteristics account for variation in breeding of individual species (including noisy miners)? and

(2) do vegetation degradation, fragmentation/loss and noisy miner abundance interact with one-another to reduce breeding behaviors of woodland birds?

METHODS

The box-ironbark forests of eastern and south-eastern Australia occur on the western slopes of the Great Dividing Range, from southern Queensland to western Victoria (ECC, 2001). In the central Victorian region, upon which we report, mean annual rainfall ranged from 400–700 mm, falling mostly in winter and spring; summers are hot and dry (Mac Nally *et al.*, 2000). Since European settlement in the 19th century, the system has been much disturbed by agriculture, timber production and gold mining (ECC, 2001). The box-ironbark forests of central and northern Victoria once covered > 3 Mha, but now only c. 17% of the original extent remains (ECC, 2001). Of the remaining forest, only c. 2% is considered to be ‘old growth’, with characteristics such as large, hollow-bearing trees (Vesk *et al.*, 2008). Few large (6 000–40 000 ha) remnants of forest remain, predominantly on areas of low-fertility, shallow soils. These forest blocks are regrowth generally, characterized by high densities of small stems (ECC, 2001).

Transects (80 x 250 m) were located in remnant vegetation with a relatively long history of isolation (> 50 yr), distributed around four regional centers in central Victoria (St Arnaud, Dunolly, Bendigo and Rushworth) (Mac Nally *et al.*, 2000). Transects were randomly placed and replicated within each remnant to provide representative coverage for vegetation and avian surveys: (1) one transect in each of the seventeen 10 ha fragments, (2) two transects in each of the eight 20 ha fragments, (3) three transects in each of the three 40 ha fragments, (4) four transects in each of the three 80 ha fragments, and (5) 22 transects in each of the three large remnants (>6 000 ha), which we refer to as ‘blocks’, giving 120 transects in total (Mac Nally *et al.*, 2000).

Vegetation characteristics

Twenty-one vegetation variables were measured for each transect using exactly the same methods as were used in 1997 (Mac Nally *et al.* 2000). We measured the number of stumps and hollow-bearing

trees and the species and abundance of all shrubs and trees. Trees > 10 cm in diameter were classified into four size classes using diameter at breast height (DBH; c. 130 cm above ground): 10-39 cm (small), 40-59 cm (medium), 60-79 cm (large) and > 80 cm (very large) (Mac Nally et al. 2000). Saplings were regarded as trees < 10 cm DBH. Cover estimates were taken using randomly placed quadrats: one 10 × 50 m quadrat for fallen timber, two 25 × 25 m quadrats for shrub-cover and two 5 × 5 m quadrats for ground cover. Estimates of canopy cover were made at four random locations using a 30 × 20 cm transparent grid, held overhead parallel to the ground. Where necessary, we averaged values over the multiple quadrat measurements.

Breeding behavior scores

During the peak breeding period from July to mid-November, six rounds of avian breeding surveys were conducted at regular intervals on c. 63% of transects per year in both 2010 and 2011. Surveys were conducted on 72 transects in 2010, and 88 transects in 2011. Forty transects were surveyed in both years to evaluate between-year consistency. Surveys were conducted within 2 wk of each other at each transect to contend with potentially short intervals between hatching and fledging of some bird species. Surveys were conducted from dawn to dusk, excluding times when bird activity is low (e.g. the hottest part of the day 11h00 – 15h00, or during poor weather conditions, such as high wind, high temperatures, or rain). To minimize sampling biases, transects were visited in a randomized order by the same observer (J. M. Bennett). Nest locations were registered spatially using GPS for each transect to relocate nests during subsequent visits. Each transect was surveyed for evidence of breeding activity for 40 min. The observer proceeded along the mid-line of the transect for 20 min conducting a census and then actively searched for nests for 20 min over the entire 2 ha area. A scoring system based on a consensus rank importance of breeding behaviors in relation to the production of young was used to measure breeding activity (Mac Nally 2007). Behaviors that indicated breeding success, such as feeding of fledglings, were given a high score, and behaviors that indicated preparedness to breed but not actual production of young, such as the collection of nesting material, were given a lower score (Mac Nally 2007). For a given nest (or

territory) of a species on a transect, only the highest scored behavior was used in analysis; for example if an adult was seen on a nest (a score of 6) and then later young were being feed outside that nest (a score of 9) then a score of 9 would be given overall.

Assemblage response variables

To investigate the effects of noisy miners and habitat characteristics on the breeding bird assemblage, three assemblage-level response variables were calculated, excluding data for noisy miners: (1) the total breeding score, which was the combined maximum scores of the breeding activities by all species at each transect over the six visits; (2) the minimum realized reproductive success, which is the total number of fledged young on each transect over the six visits, which was an indicator of recruitment into the free-living life stage; and (3) the number of breeding species, which was the number of species displaying any breeding behavior on a transect over the six visits.

STATISTICAL ANALYSES

Assemblage response

The vegan package in R was used for all assemblage-level analyses (R Development Core Team, 2010). To identify differences in the breeding bird assemblage among transects and survey years, a non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities of the total breeding scores per species on a transect (Bray & Curtis, 1957) was produced using the *smacof* function (de Leeuw & Mair, 2009). Despite the difference in spring rainfall patterns between the 2010 and 2011, the NMDS revealed an almost complete overlap in the species assemblage between the survey years. Furthermore, the total breeding score at a transect (paired *t*-test = 0.72, *P* = 0.48, d.f.=39), so the means were used for those transects surveyed in both 2010 and 2011.

Bray-Curtis dissimilarities (Bray & Curtis, 1957) were calculated to quantify differences in vegetation characteristics among transects between 1995-1997 (pre-Big Dry) and 2010 (immediately post-Big Dry) surveys. The vegetation changes seen during the Big Dry were driven by declines in canopy, shrub and litter cover and increased tree mortality, which are important resources for birds

and hence greater vegetation change is an indication of vegetation degradation for most birds.

Vegetation data were range-standardized (subtract minimum and divide by range) and dissimilarities were calculated (Oksanen *et al.*, 2010). To identify predictors (in-transect vegetation composition, vegetation change, fragment area and noisy miner abundance) associated with differences in the overall breeding bird assemblage, the NMDS ordination was fitted with correlation vectors for each predictor using the *vegan envfit* function. We used the *adonis* function to test whether the breeding bird assemblage was different between fragments of different areas (Oksanen *et al.*, 2010).

Responses to predictor variables

We used hierarchical Bayesian models to identify characteristics (e.g. fragment area, canopy cover, degradation, noisy miner abundance etc.) that were predictors of the five response variables: the individual breeding scores for each species (for species recorded on more than 1 transect), number of breeding species, total breeding score, minimum realized reproductive success and the number of species exhibiting breeding behavior. We used Bayesian model selection implemented with reversible jump Markov chain Monte Carlo (MCMC) (Lunn *et al.*, 2009). Given that mean noisy miner abundance is correlated strongly with fragment size, we used the residuals of a linear regression of noisy miners against fragment size as a potential predictor. We fitted both linear and nonlinear models to all response variables. The linear model was:

$$y_i \sim \text{Normal}(\mu_i, \sigma^2); \mu_i = \alpha + \sum_{q=1}^Q \beta_q x_{iq} + \gamma_i,$$

and the non-linear model was:

$$y_i \sim \text{Normal}(\mu_i, \sigma^2); \mu_i = \alpha + \sum_{q=1}^Q \sum_{s=1}^S \beta_{qs} x_{iqs} + \gamma_i.$$

Here, the β are linear coefficients corresponding to Q variables in \mathbf{X} , α is the grand intercept term, γ_i is a transect-level random intercept (accounting for spatial autocorrelation of transects with (pseudo)fragments), and σ^2 is the residual error. In the nonlinear spline model, the matrix of predictor variables \mathbf{X} was replaced with a basis matrix of S ($= 5$) linear spline segments (Thomson *et al.*, 2010). This formulation allowed us to calculate the posterior probability that each predictor

variable had linear or non-linear associations with response variables. Tilde (\sim) means ‘is distributed as’.

In all models, the residual error variance was assigned an uninformative prior [$1/\sigma^2 \sim \text{Gamma}(0.001, 0.001)$], linear coefficients and fragment random effects were assigned exchangeable normal prior distributions, $\beta \sim N(0, \sigma_{cov}^2)$; $\gamma \sim N(0, \sigma_{frag}^2)$, with uniform prior distributions on the corresponding standard deviations, $\sigma_{cov} \sim U(0, A)$; $\sigma_{frag} \sim U(0, 2A)$. Note that σ_{cov} determines the plausible effect sizes and, therefore, the effective penalty for additional free parameters in Bayesian model selection; a (hyper) prior on σ_{cov} reflects uncertainty about effect sizes (cf. use of point estimates implicit in conventional information criteria). Posterior model probabilities were not sensitive to reasonable and plausible variations in the upper limit A ; we present results for $A = \text{SD}(y)/2$, but $A = \text{SD}(y)/4$, $\text{SD}(y)$ and $2 \text{SD}(y)$ produced indistinguishable results for all response variables.

All models were fitted using WinBUGS 1.4 (Spiegelhalter *et al.*, 2003) with the reversible jump extension for model selection (Lunn *et al.*, 2009). Parameters were estimated with three MCMC chains of 100 000 iterations after 20 000 iteration burns-in (results discarded). Adequate MCMC mixing and convergence were confirmed by examining MCMC chain histories and Gelman-Ruben-Brooks statistics (Brooks & Gelman, 1998). Posterior predictive diagnostics were used to assess model adequacy (Gelman *et al.*, 1996). For each model, we calculated a summed discrepancy measure $S_{obs} = \sum (\text{observed} - \text{expected})^2 / \text{expected}$ (McCullagh & Nelder, 1989) and generated a reference distribution for the discrepancy measure, S_{sim} , based on simulated data drawn from the posterior distribution of the model. If the posterior distributions of S_{obs} and S_{sim} overlapped, such that $0.1 < \Pr(S_{obs} > S_{sim}) < 0.9$, then the fitted model was regarded as acceptable (i.e. capable of generating the observed data).

RESULTS

Sixty-three of the observed 104 bird species were recorded as exhibiting breeding behavior. The five species exhibiting the most activity were: red wattlebird *Anthochaera carunculata* (9.8% of the total breeding activity), noisy miner (9.5%), white-winged chough *Corcorax melanorhamphos* (8.9%), white-plumed honeyeater *Lichenostomus penicillatus* (6.3%) and fuscous honeyeater *L. fuscus* (5.7%). The highest summed observed fledgling abundance for a species over the duration of the study was 17, for the noisy miner.

Fragmentation effects

There was a clustering of transects that corresponded to the size of the fragment (total area) in which the transect was located in the NMDS ordination (Fig. 1). Fragment area was associated with changes in the breeding bird assemblage (Fig. 1). There was a significant difference between the assemblage of birds breeding in the blocks and fragments (Adonis $P \sim 0.001$), and among the fragment area classes (Adonis $P \sim 0.001$), with an important interaction between these factors (Adonis $P \sim 0.001$). The species exhibiting the most breeding behavior of all species in fragments were: noisy miner (17.8%), white-plumed honeyeater (11.6%), white-winged chough (7.2%) and Australian magpie *Cracticus tibicen* (6.7%). In the blocks, breeding behavior was dominated by red-wattlebird (16%), fuscous honeyeater (11.4%) and white-winged chough (10.9%).

Fragment area was a stronger predictor of breeding behavior in species than vegetation characteristics (Table 1). Breeding activity in two insectivorous species the white-browed babbler *Pomatostomus superciliosus* and the dusky woodswallow *Artamus cyanopterus* was greatest in larger fragments (40 ha and 80 ha). Breeding activity in three species, the red-rumped parrot *Psephotus haematonotus*, the white-plumed honeyeater and the noisy miner, was significantly lower in larger remnants (80 ha fragments and blocks) (Table 1).

Vegetation characteristics

Vegetation characteristics that probably affected the breeding bird assemblage included tall-shrub cover and high shrub richness, number of saplings, basal areas of small trees, number of very large

trees and number of dead trees and number of hollows and coppices (Fig. 1). Transects with high densities of small trees and high loads of coarse litter had fewer fledglings (Table 1). Standing dead trees were positively associated with increased number of fledglings and higher richness of breeding species (Table 1). The total breeding score on a transect was not well predicted by any environmental variable (Table 1). Several vegetation characteristics were important predictors for species, with some species responding positively to greater: canopy cover, litter cover, tall-shrub cover, coarse litter, fallen timber, small tree basal area, vegetation change, and sapling density (Table 1). Very large trees were an important predictor for two species that responded differently (one negative and one positive). Low sapling cover was negatively correlation with one species (Table 1). The number of noisy miner fledglings was positively correlated with greater vegetation change between 1995-97 and 2010-11, the number of very large trees and greater leaf litter (Table 1). More litter cover was positively correlated with total breeding behavior of noisy miner (Table 1). Higher densities of small trees, tall-shrub and canopy cover were negatively related to the number of noisy miner fledglings (Table 1).

Effects of noisy miner

Noisy miner abundance was a possible driver of change in the breeding bird assemblage (Fig. 1); it was the strongest on-transect environmental predictor of breeding behavior in species (Table 1). For three species, the Australian magpie, musk lorikeet *Glossopsitta concinna* and white-winged chough, breeding activity increased with higher abundances of noisy miners. The breeding activities of two honeyeaters, the black-chinned honeyeater and the white-plumed honeyeater, were negatively associated with greater noisy miner abundance. The number of breeding species was reduced on transects with greater noisy miner abundances (Table 1).

DISCUSSION

The interactive effects of habitat loss/fragmentation and interspecific competition had a greater influence on breeding activity than in-transect vegetation characteristics. The breeding bird

assemblage was markedly different in large forest blocks compared to smaller fragments. There was evidence that the hyper-aggressive noisy miner reduced breeding behavior in small-bodied (< 63 g) birds and increased breeding behavior in medium to large-bodied birds in fragmented vegetation where the noisy miner occurred. The additive effect of fragmentation and climate-driven habitat degradation are the likely drivers for this effect because we found measures of noisy miner recruitment to be positively associated with these processes. In-transect vegetation structure and characteristics were important for many species, but were secondary in determining the apparent attractiveness of areas for breeding birds compared to noisy miner abundance and fragmentation effects. This interaction between climate, fragmentation, degradation and altered species interactions may be responsible for the decline in the regional bird assemblages and wider declines in the woodland bird species (Mac Nally *et al.*, 2009).

Habitat fragmentation and vegetation characteristics

In-transect vegetation characteristics such as greater canopy and mid-storey cover and fallen timber loads features usually associated with continuous forests (Vesk *et al.*, 2008), were positively associated with breeding behavior for many birds. Fallen timber is associated with increased invertebrate abundance, an important food resource for birds, while also providing shelter (Selwood *et al.*, 2009). We found a positive relationship between the volume of fallen timber and breeding activity in the black-chinned honeyeater. A positive relationship between fallen timber and breeding activity in honeyeater species has been reported previously (Selwood *et al.*, 2009). Tree thinning has been proposed to provide ecological benefits by opening the canopy, particularly in dense forest blocks (Horner *et al.*, 2010), which may explain the positive relationship between logs and the black-chinned honeyeater, which is a canopy feeder and nester. However, more fallen timber and high densities of smaller trees, which are associated with silviculture, negatively affected the numbers of fledglings. In North America, changes in vegetation structure due to silviculture alter species assemblages and lower nest success in birds (King & DeGraaf, 2000).

Nectar production is associated with higher canopy cover, which was a predictor of breeding behavior in two species including the musk lorikeet, a nectarivorous canopy feeder. Middle- and ground-level habitat features were predictors of breeding behavior in many species, supporting claims that these features provide valuable resources for birds and should be considered for restoration activities (Yen *et al.*, 2011). The positive relationship between increased sapling and tall-shrub density and breeding behavior in many species may be due to an increase in ground cover, which is important for many ground-foraging insectivores, and is an increase in potential nesting sites (Yen *et al.*, 2011). Fragmentation has been linked to reduced seed production and health in trees (Barbeta *et al.*, 2011) and tree and shrub seedlings may be missing from smaller fragments due to grazing, which has negative effects on breeding birds and on nesting success (Martin & Possingham, 2005; Perlut & Strong, 2011).

Vegetation characteristics associated with mature forests, such as very large trees and standing dead trees, were important for many species. More fledglings were associated with increased standing dead trees, which are an important source of nesting hollows, and are required by many species for breeding (Söderström, 2009). Large trees in mature forests often provide more nectar, diverse and abundant invertebrate assemblages, large overhanging branches for nesting and perching, decorticating bark, and tree hollows (Vesk & Mac Nally, 2006). However, in our system, large trees occur in small fragments amidst agricultural land uses, due to silviculture practices in blocks (Vesk & Mac Nally, 2006).

Effects of noisy miner

Noisy miners have been linked to a shift in bird assemblages towards medium-size taxa by disproportionately excluding small-bodied birds (Robertson *et al.*, 2013). Aggressive exclusion apparently can also lead to reduced breeding activity of smaller species, even those from the same family (Meliphagidae; e.g. black-chinned and white-plumed honeyeaters). The presence of noisy miners may benefit the recruitment of medium-bodied species, although the mechanism is unclear. Three medium-bodied species, the Australian magpie, white-winged chough and musk lorikeet, bred

more in transects occupied by noisy miners. These three species are ecologically dissimilar to the noisy miner and probably are large enough to withstand the miners' aggression. It is possible that the three medium-bodied species may profit from the presence and aggression of the noisy miner, perhaps through mutual territorial defense, which seems to occur between pied flycatchers *Ficedula hypoleuca* and titmice *Baeolophus bicolor* in Europe (Forsman et al., 2002).

The great mobility of birds (relative to other terrestrial taxa) may make birds relatively immune to dispersal barriers arising from habitat fragmentation compared with other terrestrial taxa (Amos et al., 2014). However, when a despotic competitor, such as the noisy miner, benefits from the fragmentation process and from vegetation degradation associated with climate change, then dispersal may be much impaired for the small-bodied species subject to the aggression of the noisy miner. The effects of the noisy miner may limit out-crossing and 'rescue effects' (Brown & Kodric-Brown, 1977).

Global implications

Global land-use change has led to the decline of many native species, but has facilitated the expansion of others, and some of these advantaged species may be capable of exerting strong negative effects on other species (Carey *et al.*, 2012). Climate change (hotter and drier conditions) may amplify these changes in assemblages by exacerbating habitat degradation, particularly in smaller fragments (Bennett *et al.*, 2013). The expansion and overabundance of native species is just as much a sign of ecosystem dysfunction as species' declines and extinctions because even small shifts in the relative abundance of species can significantly alter outcomes of interspecific interactions and ecosystem function (Carey *et al.*, 2012). There is much potential for similar effects to those we report to occur in many parts of the world because the anthropogenic pressures that we have dealt with are typical of those affecting most terrestrial systems. The interaction between climate and land-use change can cause profound ecosystem disruption both directly and indirectly by facilitating the expansion of a strongly interacting native species, such as noisy miners.

Managing for the effects of one human-induced driver (e.g. invasive species) most certainly will require management of other drivers (Tylianakis *et al.*, 2008). Our results support this idea because noisy miners, as with many other invaders, have benefited from increases in edge vegetation arising from fragmentation (Ewers & Didham, 2006). Restoring vegetation adjacent to existing fragments may reduce the influence of noisy miners. Increasing vegetation area has other benefits for biota, such as increasing resources and reducing degradation (Bennett *et al.*, 2013). Replanting in areas of higher precipitation and soil fertility may accelerate improvements in conditions by promoting tree growth and flowering, which provide food resources for birds and other taxa (Mac Nally *et al.*, 2009).

Altered interspecific competition arising from habitat fragmentation and degradation may exert the greatest negative influence on breeding behavior, adversely affecting species persistence. Studies that do not account for interspecific interactions as a consequence of habitat change are likely to underestimate or unable to explain the total effects on assemblages. Our system may be an exemplar for fragmented systems elsewhere in the world, because fragmentation has been linked to altered species composition around the world. Under climate change and increased land-use pressures, the area of degraded habitat is likely to increase worldwide, which is likely to exacerbate adverse biotic effects. The expansion of a native despot highlights the likelihood that, even in the absence of exotic species, species assemblages will continued to be disrupted by the interacting and cascading effects of climate change, habitat degradation and interspecific interactions.

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REFERENCES

- Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D.D., Hogg E.H., Gonzalez P., Fensham R., Zhang Z., Castro J., Demidova N., Lim J.H., Allard G., Running S.W., Semerci A. & Cobb N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-684.
- Amos J.N., Harrisson K.A., Radford J.Q., White M., Newell G., Mac Nally R., Sunnucks P. & Pavlova A. (2014). Species- and sex-specific connectivity effects of habitat fragmentation in a suite of woodland birds. *Ecology*, 10.1890/13-1328.1.
- Barbeta A., Penuelas J., Ogaya R. & Jump A.S. (2011). Reduced tree health and seedling production in fragmented *Fagus sylvatica* forest patches in the Montseny Mountains (NE Spain). *Forest Ecology and Management*, **261**, 2029-2037.
- Battin J. (2004). When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations. *Conservation Biology*, **18**, 1482-1491.
- Bennett J.M., Cunningham S.C., Connelly C.A., Clarke R.H., Thomson J.R. & Mac Nally R (2013). The interaction between a drying climate and land use affects forest structure and above-ground carbon storage. *Global Ecology and Biogeography*, **22**, 1239-1247.
- Bray J.R. & Curtis J.T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 326-349.
- Brooks S.P. & Gelman A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434-455.
- Brown J.H. & Kodric-Brown A. (1977). Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology*, **58**, 445-449.
- Brown W.P. (2007). Body mass, habitat generality, and avian community composition in forest remnants. *Journal of Biogeography*, **34**, 2168-2181.

- Burke D.M. & Nol E. (2000). Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications*, **10**, 1749-1761.
- Catterall C.P., Cousin J.A., Piper S. & Johnson G. (2010). Long-term dynamics of bird diversity in forest and suburb: decay, turnover or homogenization? *Diversity and Distributions*, **16**, 559-570.
- Caughley G. (1994). Directions in conservation biology *Journal of Animal Ecology*, **63**, 215-244.
- Darling E.S. & Côté I.M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters*, **11**, 1278-1286.
- de Leeuw J. & Mair P. (2009). Multidimensional scaling using majorization: SMACOF in R. *Journal of Statistical Software*, **31**, 1-30.
- Dow D. (1977). Indiscriminate interspecific aggression leading to almost sole occupancy of space by a single species of bird. *Emu*, **77**, 115-121.
- ECC (2001). *Box-Ironbark Forests and Woodlands Investigation*. Environment Conservation Council, Melbourne.
- Ewers R.M. & Didham R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117-142.
- Eyre T.J., Maron M., Mathieson M.T. & Haseler M. (2009). Impacts of grazing, selective logging and hyper-aggressors on diurnal bird fauna in intact forest landscapes of the Brigalow Belt, Queensland. *Austral Ecology*, **34**, 705-716.
- Forsman J.T., Seppänen J.-T. & Mönkkönen M. (2002). Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**, 1619-1623.
- Gelman A., Meng X.-L. & Stern H. (1996). Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica*, **6**, 733-787.
- IPCC (2007). Climate Change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. (ed.

- Solomon S, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller) Cambridge University Press, Cambridge, p. 996.
- Keith D.A., Rodríguez J.P., Rodríguez-Clark K.M., Nicholson E., Aapala K., Alonso A., Asmussen M., Bachman S., Basset A., Barrow E.G., Benson J.S., Bishop M.J., Bonifacio R., Brooks T.M., Burgman M.A., Comer P., Comín F.A., Essl F., Faber-Langendoen D., Fairweather P.G., Holdaway R.J., Jennings M., Kingsford R.T., Lester R.E., Mac Nally R., McCarthy M.A., Moat J., Oliveira-Miranda M.A., Pisanu P., Poulin B., Regan T.J., Riecken U., Spalding M.D. & Zambrano-Martínez S. (2013). Scientific Foundations for an IUCN Red List of Ecosystems. *PLoS ONE*, **8**, e62111.
- Korfanta N.M., Newmark W.D. & Kauffman M.J. (2012). Long-term demographic consequences of habitat fragmentation to a tropical understory bird community. *Ecology*, **93**, 2548-2559.
- Leblanc M., Tweed S., Van Dijk A. & Timbal B. (2012). A review of historic and future hydrological changes in the Murray-Darling Basin. *Global and Planetary Change*, **80**, 226-246.
- Lindenmayer D.B., Possingham H.P., Lacy R.C., McCarthy M.A. & Pope M.L. (2003). How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecology Letters*, **6**, 41-47.
- Lunn D.J., Best N. & Whittaker J.C. (2009). Generic reversible jump MCMC using graphical models. *Statistics and Computing*, **19**, 395-408.
- Mac Nally R. (2007). Consensus weightings of evidence for inferring breeding success in broad-scale bird studies. *Austral Ecology*, **32**, 479-484.
- Mac Nally R., Baker P.J., Cunningham S.C., Horner G.J. & Thomson J.R. (2011). Dynamics of Murray-Darling floodplain forests under multiple water stressors - The past, present and future of an Australian icon. *Water Resources Research*, **47**, W00G05.
- Mac Nally R., Bennett A.F. & Horrocks G. (2000). Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation

- on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7-29.
- Mac Nally R., Bennett A.F., Thomson J.R., Radford J.Q., Unmack G., Horrocks G. & Vesk P.A. (2009). Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720-730.
- Mac Nally R., Bowen M., Howes A., McAlpine C.A. & Maron M. (2012). Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. *Ecology*, **93**, 668-678.
- Mantyka-Pringle C.S., Martin T.G. & Rhodes J.R. (2012). Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239-1252.
- Maron M., Grey M.J., Catterall C.P., Major R.E., Oliver D.L., Clarke M.F., Loyn R.H., Mac Nally R., Davidson I. & Thomson J.R. (2013). Avifaunal disarray due to a single despotic species. *Diversity & Distributions*, **19**, 1468-1479.
- McAlpine C.A., Syktus J., Ryan J.G., Deo R.C. & McKeon G.M. (2009). A continent under stress: interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate. *Global Change Biology*, **15**, 2206-2223.
- McCullagh P. & Nelder J.A. (1989). *Generalized linear models*. 2nd ed edn. Chapman and Hall, London, UK.
- Öckinger E., Schweiger O., Crist T.O., Debinski D.M., Krauss J., Kuussaari M., Petersen J.D., Pöyry J., Settele J., Summerville K.S. & Bommarco R. (2010). Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters*, **13**, 969-979.
- Oksanen J.F., Blanchet G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P.M., Stevens H.H. & Wagner H. (2010). *vegan: Community Ecology Package*. In. The Comprehensive R Archive Network.

- Perlut N.G. & Strong A.M. (2011). Grassland birds and rotational-grazing in the northeast: Breeding ecology, survival and management opportunities. *The Journal of Wildlife Management*, **75**, 715-720.
- R Development Core Team (2010). R: A Language and Environment for Statistical Computing. In. R Foundation for Statistical Computing Vienna, Austria. <http://www.R-project.org>.
- Robertson O.J., McAlpine C., House A. & Maron M. (2013). Influence of interspecific competition and landscape structure on spatial homogenization of avian assemblages. *PloS one*, **8**, e65299.
- Sekercioglu C.H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, **21**, 464-471.
- Selwood K., Mac Nally R. & Thomson J.R. (2009). Native bird breeding in a chronosequence of revegetated sites. *Oecologia*, **159**, 435-446.
- Selwood K., McGeoch M. & Mac Nally R. (in review). The effects of climate deterioration and land-use change on demographic rates and population viability.
- Söderström B. (2009). Effects of different levels of green- and dead-tree retention on hemi-boreal forest bird communities in Sweden. *Forest Ecology and Management*, **257**, 215-222.
- Spiegelhalter D., Thomas A. & Best N. (2003). WinBUGS version 1.4. Bayesian inference using Gibbs sampling. In. MRC Biostatistics Unit, Institute for Public Health Cambridge, UK.
- Thomson J.R., Kimmerer W.J., Brown L.R., Newman K.B., Mac Nally R., Bennett W.A., Feyrer F. & Fleishman E. (2010). Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications*, **20**, 1431-1448.
- Thomson J.R., Mac Nally R., Fleishman E. & Horrocks G. (2007). Predicting bird species distributions in reconstructed landscapes. *Conservation Biology*, **21**, 752-766.
- Tylianakis J.M., Didham R.K., Bascompte J. & Wardle D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351-1363.

- Vesk P.A. & Mac Nally R. (2006). The clock is ticking - Revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. *Agriculture Ecosystems & Environment*, **112**, 356-366.
- Vesk P.A., Nolan R., Thomson J.R., Dorrough J.W. & Mac Nally R. (2008). Time lags in provision of habitat resources through revegetation. *Biological Conservation*, **141**, 174-186.
- Yen J.D.L., Thomson J.R., Vesk P.A. & Mac Nally R. (2011). To what are woodland birds responding? Inference on relative importance of in-site habitat variables using several ensemble habitat modelling techniques. *Ecography*, **34**, 946-954.

Table 1: Associations between bird breeding response variables and candidate predictor variables, derived from Bayesian model averaging of all possible additive models using reversible jump Markov chain Monte Carlo (MCMC). Values are model-averaged linear coefficients (i.e. weighted averages over all models considered, where weights are posterior model probabilities). Bold values indicate posterior probability of non-zero linear coefficient > 0.75 . Non-linear (NL) indicates posterior probability of a non-linear relationship > 0.75 and $\text{Pr}(\text{linear}) < 0.75$ (i.e. a strongly non-linear relationship). Only important predictors are shown. *Excludes data for the noisy miner.

Common names/size classes	Noisy miner	Coarse Litter	Fallen Timber	Canopy cover	Fine Litter	Short shrub	Tall shrub	Small trees	Very			Dead trees	Saplings	Vegetation Change	Fragment area	
									large trees	large trees	large trees				40 ha	80 ha >10 000 ha
<i>Small-bodied < 63 g</i>																
black-chinned honeyeater	NL	0.00	0.05	0.00	0.00	0.00	NL	NL	-0.03	0.00	0.00	-0.02	0.00	0.00	0.00	0.01
dusky woodswallow	-0.05	0.07	-0.01	0.00	0.01	-0.03	-0.12	-0.11	0.09	0.09	0.54	0.23	NL	0.89	-0.23	
hooded robin	-0.02	0.00	0.00	0.03	0.00	0.00	-0.01	0.01	0.13	-0.03	0.00	-0.01	-0.01	0.10	-0.01	
red-capped robin	0.00	0.00	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	0.05	0.00	-0.01	0.02	0.00	
red-rumped parrot	-0.03	0.00	-0.01	0.00	-0.01	-0.02	-0.01	-0.01	0.00	0.01	0.00	0.00	0.07	-0.01	-0.14	
scarlet robin	0.00	0.00	0.01	-0.02	-0.01	0.00	0.03	NL	-0.01	-0.01	0.00	0.01	-0.01	0.00	0.04	
white-bellied cuckoo-shrike	0.00	0.01	0.05	0.08	0.00	0.00	-0.02	-0.01	-0.05	-0.03	0.03	-0.01	-0.01	0.00	0.02	
white-browed babbler	-0.03	0.00	-0.01	-0.02	-0.01	-0.01	-0.01	0.00	0.03	0.02	0.02	0.11	0.78	1.39	-0.12	
white-plumed honeyeater	-0.61	-0.04	-0.11	0.00	-0.03	-0.03	0.00	-0.18	-0.09	0.13	0.01	-0.40	0.07	NL	-2.53	
yellow-tufted honeyeater	-0.07	-0.04	-0.01	-0.01	-0.02	0.02	0.41	0.03	0.01	0.11	-0.03	0.05	-0.01	0.20	-0.08	
<i>Medium-large bodied 63-400 g</i>																
australian magpie	1.06	-0.10	0.03	0.29	-0.10	-0.24	-0.03	-0.27	0.12	0.03	-0.07	-0.21	0.14	-0.16	-0.57	
musk lorikeet	0.13	0.00	-0.02	0.10	0.11	0.02	-0.01	-0.02	0.01	0.00	-0.05	0.00	-0.01	-0.01	-0.03	
white-winged chough	0.41	0.01	-0.01	0.02	0.22	-0.03	-0.17	-0.01	-0.05	-0.05	-0.02	-0.16	0.06	-0.07	0.00	
noisy miner	NA	-0.01	-0.01	-0.05	NL	-0.05	-0.05	-0.32	0.12	0.00	-0.03	0.53	-1.12	NL	-4.19	
<i>Very large-bodied > 400 g</i>																
little eagle	0.00	0.11	0.05	-0.01	-0.01	0.00	-0.01	0.00	0.00	0.00	-0.01	-0.01	0.00	0.00	0.02	
little raven	0.01	-0.02	0.01	-0.02	NL	-0.25	0.00	-0.01	0.02	-0.01	0.01	0.00	-0.03	-0.02	-0.12	
sulphur-crested cockatoo	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NL	0.00	0.00	0.01	
<i>Response Variables</i>																

total transect score*	-0.63	-0.30	-0.32	0.07	0.04	-0.37	-0.13	-0.80	-0.04	0.24	-0.23	0.18	0.07	0.60	-0.14
minimum realized*	-0.10	NL	-0.03	0.01	-0.01	-0.02	0.00	-0.24	-0.03	0.20	-0.03	0.06	-0.01	0.11	0.00
minimum realized noisy miner	NA	-0.01	-0.01	NL	0.13	0.04	NL	-0.06	0.08	0.01	-0.01	NL	-0.03	-0.04	-0.11
number of Breeding species*	-0.29	-0.02	-0.06	0.04	0.07	-0.04	-0.04	-0.13	0.01	0.03	-0.01	0.03	0.02	0.13	-0.19

Figure 1 Non-metric multidimensional scaling ordination (stress = 0.09) of the woodland bird community that were detected breeding is based on Bray-Curtis dissimilarities. Black points are forest blocks (>6 000 ha) and clear points are fragments, the point sizes indicate the fragment area (very small = 10 ha, small = 20 ha, medium = 40 ha, large = 80 ha). Fitted vectors show correlations between NMDS axial scores and individual vegetation characteristics ($P < 0.05$). Arrow directions indicate the direction of the correlation while the vector length is proportional to strength (R^2) of the correlation.

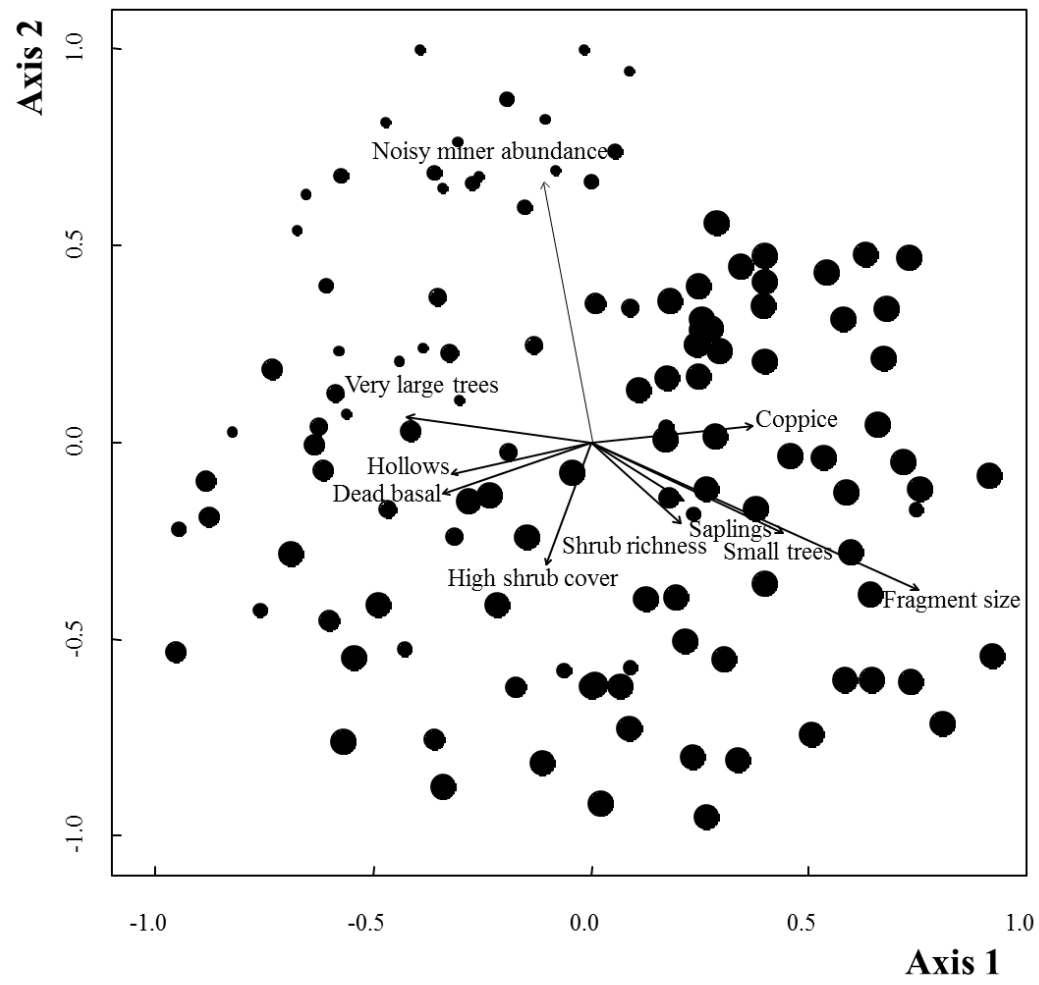


Figure 1:

Chapter 7: General Discussion

Climate change and the projected increases in frequency and intensity of extreme events have the potential to cause widespread native biodiversity decline. The effects of climate change, greater heat and water stress associated with fragmented vegetation, will most likely accelerate habitat degradation. The global area affected by drought is likely to increase concurrently with greater usurpation of natural areas for human use (Capon *et al.*, 2013), suggesting that the effects demonstrated in this thesis most likely will be widespread. Extreme climatic events may produce some of the most dramatic effects on populations and may render many populations even less resistant than previously thought to other global change drivers, such as land-use change (Mantyka-Pringle *et al.*, 2012).

I found an increase in tree mortality and canopy dieback between the pre- (1995–97) and post-Big Dry (2010–11) surveys (Chapter 2; Bennett *et al.*, 2013), which adds to a growing body of evidence linking climate change to adverse effects on vegetation (Allen *et al.*, 2010; Suarez & Kitzberger, 2010). Few studies have examined the importance of land-use and climate change on long-term vegetation trends, so disentangling which of the pressures is the major driver of change has been difficult (Allen *et al.*, 2010; Mantyka-Pringle *et al.*, 2012). Moreover, spatial information of environmental condition is often lacking, making it difficult to determine which climate drivers, precipitation or temperature, induce forest dieback (Allen *et al.*, 2010). The spatial and temporal configuration of my study allowed me to draw links between the mortality of shrub and trees and canopy dieback to causal climate and landscape effects. I found greater mortality in small fragments in lower rainfall areas, which supports the hypothesis that fragmented systems may be more vulnerable to climate change than more intact woodland (Fig. 1) .

There was a concurrent marked change in the woodland bird assemblage over the same period (Chapter 3). These changes in the avifauna were attributed to reductions in precipitation and increases in temperatures, symptomatic of an extended ‘hot’ drought (Fig. 1). Declines were of all

species guilds, supporting the idea that a broad mechanism was responsible for the collapse (Chapter 3). There appeared to be relatively minor rates of recovery in the Big Wet because most species' declines were ongoing (Chapter 3). Species that declined the most did not necessarily show stronger resilience (Chapter 3). Differences between species resistance to extreme climatic events and their resilience during intermittent periods of more benign climatic conditions will reshape assemblages. Rapid variations in climate are expected to push assemblages towards having more generalist, open-tolerant species (Jiguet *et al.*, 2007). However, my results indicate that even species with these qualities are not immune to climate change, given their low resistance (Chapter 3). It is possible that recovery is ongoing (particularly for less mobile species) and I have only captured the beginning of it, as surveys were completed soon after the Big Wet.

An important mechanism through which climate change appears to be affecting the avifauna assemblage is through modification of vegetation condition (Fig. 1). Avifaunal responses to drought probably reflect reductions in the resource base (food and vegetation) and species' ability to compete for remaining resources (Fig. 1). A boom-bust pattern in the availability of resources, which may be amplified with long droughts and short intervening wet periods, may lead to disproportionate declines, and ultimately to extirpation of many species, while favoring relatively few.

The loss, fragmentation and degradation of habitat have led to declines in abundance and distribution of many native species but have facilitated increases in the abundance and distribution of other native species. Projected climate change (hotter and drier conditions) may exacerbate these changes in bird assemblages by accelerating vegetation degradation, especially in smaller fragments (Chapter 2; Bennett *et al.*, 2013). Some species may become 'native invaders', capable of negatively affecting other species and causing ecological perturbations (Carey *et al.*, 2012). The invasion and overabundance of a behaviorally- or ecologically-dominant native species may cause similar ecosystem dysfunction to those generated by species' declines and extinctions because even small shifts in the relative abundance of species can significantly alter interspecific interactions and

ecosystem function (Carey *et al.*, 2012). I found that the interaction between climate and land-use change in which vegetation degradation was greater in smaller fragments may have facilitated the increase of a highly aggressive species, the noisy miner *Manorina melanocephala* (Fig. 1).

The elevated abundance of noisy miner was associated with the declines of many species in smaller fragments, especially those species with a body size smaller than the noisy miner (< 63 g) (Chapter 4, 5 & 6). The noisy miner, by aggressively defending space, excluded smaller-bodied species from sites limiting those species access to resources, such as food and nesting sites (Fig. 1). This may lead to disproportionate declines in smaller bodied species in times of resource scarcity, hindering their recovery if and when conditions improve.

Such an outcome may lead to a homogenization of the avifauna that would affect ecosystem processes, including control of insect pests, pollination and seed dispersal. In the long-term, this may lead to loss of the fragmented vegetation. Insectivores control populations of invertebrates so that the exclusion of insectivores from smaller fragments may exacerbate dieback because these events have been linked to outbreaks of canopy-defoliating invertebrates (Allen *et al.*, 2010). I found that resource availability (flowering) had a major influence on the dynamics of the nectarivorous bird assemblage, but this relationship was impaired by the noisy miner (Chapter 5; Fig. 1). The hyper-aggression of the noisy miner may have led to a change in distribution of small-bodied species, which has shifted from the Ideal Free Distribution (where resources availability is the key determinant of the distribution of species) to an Ideal Despotic Distribution (where a highly competitive species, determines the distribution of other species, particularly those small in body-mass) (Fretwell, 1972). In eucalypt forests, many trees and shrubs are bird-pollinated (Ford, 1985), so that a marked reduction in the ability of the assemblage to track resources (moving among fewer sites) is likely to limit plants' outcrossing, which may reduce seed quality and set. The noisy miner by excluding small nectarivores from fragments may decrease plant functional diversity, which also may lessen seed set (Hoehn *et al.*, 2008). A reduction in seed quality and set may ultimately lead to a change in plant assemblages (Maron *et al.*, 2013).

Global change drivers such as climate change and species invasions may be better managed in the short-term by targeting other drivers [e.g. habitat loss, fragmentation or degradation (Didham *et al.*, 2007)]. In the system considered here, the greatest gains may be made by replanting adjacent to existing fragments. Investing in restoration activities that increase vegetation extent may ameliorate the elevated heat and water stress that is experienced by remnant vegetation, while also increasing habitat extent. Such actions would have the added benefits of increasing resources for birds and other taxa while limiting opportunities for colonization by the noisy miner.

The knowledge gained from my study has allowed me to propose a model to explain the interactive effects of climate change and land-use change on the vegetation and bird assemblage (Fig. 1). Although the model was developed using insight gained from the box-ironbark system, it is potentially applicable to other fragmented regions experiencing rapid variations in climate. The thicknesses of the arrows in the model (Fig. 1) indicate the strength of the effect in my study. I found that climate change is probably interacting with fragmentation, so that vegetation die-back and decline have been faster in smaller fragments (Fig. 1). It is likely that climate change is accelerating vegetation degradation in fragmented vegetation because of greater heat and water stress experienced by fragments (Fig. 1). A mechanism by which climate change is affecting woodland birds is through the degradation of habitats (Fig. 1). The Big Dry led to a significant alteration of the bird assemblage. The effects were predominately negative with major declines in the abundance and distribution of many native species, although a few species appeared to have benefited (Fig 1). The increased vegetation degradation in small fragments may have exacerbated bird species' declines by facilitating the expansion of a highly competitive species (Fig. 1). This may have increased competition for limited and important resources such as breeding sites and food, which, in the long-term, may be the major constraint of the capacity of avifauna to persist and maintain viable populations in increasingly turbulent climate futures (Fig. 1).

Conclusions

There is evidence of increases in the frequency of precipitation extremes, such as extreme events, which have been documented in North America, Europe, southern Africa and Asia (Knapp *et al.*, 2008). Hence, the box-ironbark region serves as an exemplar for other regions undergoing rapid variation in climate. As a model, my work is among the first to consider interacting pressures that arise from major drivers of ecological change. The interaction between climate and land-use change profoundly affected the bird assemblage not only directly, but also indirectly, by facilitating the expansion of highly competitive species. Altered assemblages and interspecific interactions are not limited to avifaunas (Milazzo *et al.*, 2013), and fragmentation has been linked to altered species interactions in many regions of the world (Tylianakis *et al.*, 2008). Therefore, similar effects to those that I report are likely to arise in other fragmented regions and for other taxa, as climates become more extreme.

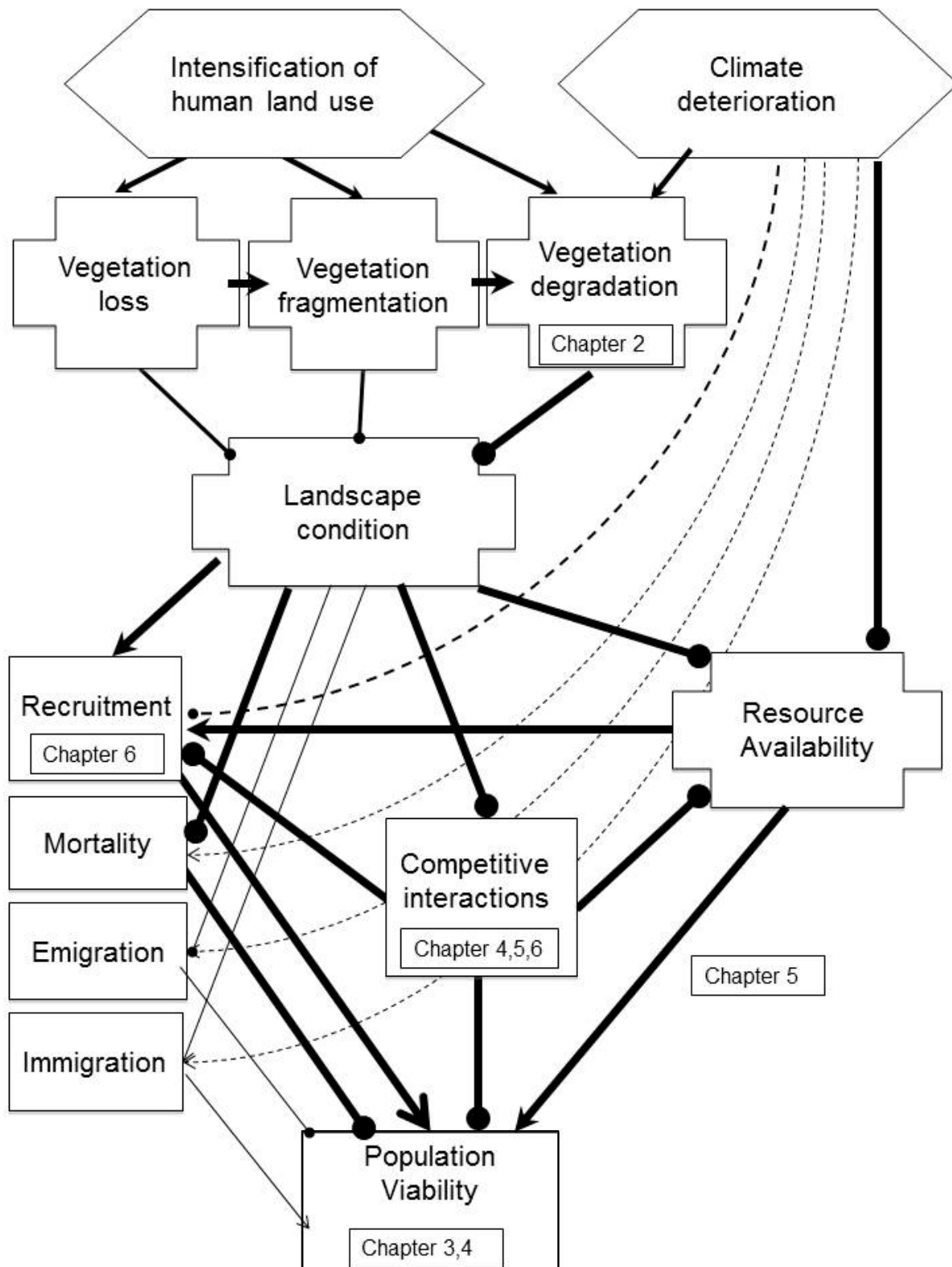


Figure 1: Conceptual model of the potential factors that may determine the spatial and temporal changes in the bird and vegetation assemblages, \bullet indicates a negative effect, \uparrow indicates a positive effect and \cdots not demonstrated (thicker lines = most important).

REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-684.
- Bennett, J.M., Cunningham, S.C., Connelly, C.A., Clarke, R.H., Thomson, J.R. & Mac Nally R (2013) The interaction between a drying climate and land use affects forest structure and above-ground carbon storage. *Global Ecology and Biogeography*, **22**, 1239-1247.
- Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D., Stewardson, M., J, R., Parsons, M. & Williams, S.E. (2013) Riparian ecosystems in the 21st Century: Hotspots for climate change adaptation? *Ecosystems*, **16**, 359-381.
- Carey, M.P., Sanderson, B.L., Barnas, K.A. & Olden, J.D. (2012) Native invaders – challenges for science, management, policy, and society. *Frontiers in Ecology and the Environment*, **10**, 373-381.
- Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A. & Ewers, R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, **22**, 489-496.
- Ford, H.A. (1985) Nectarivory and Pollination by Birds in Southern Australia and Europe. *Oikos*, **44**, 127-131.
- Fretwell, S.D. (1972) *Populations in a seasonal environment*. Princeton University Press.
- Hoehn, P., Tschardtke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2283-2291.

- Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E. & Couvet, D. (2007) Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology*, **13**, 1672-1684.
- Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., Smith, M.D., Smith, S.D., Bell, J.E., Fay, P.A., Heisler, J.L., Leavitt, S.W., Sherry, R., Smith, B. & Weng, E. (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, **58**, 811-821.
- Mac Nally, R. & McGoldrick, J.M. (1997) Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. *Journal of Avian Biology*, **28**, 171-183.
- Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239-1252.
- Maron, M., Grey, M.J., Catterall, C.P., Major, R.E., Oliver, D.L., Clarke, M.F., Loyn, R.H., Mac Nally, R., Davidson, I. & Thomson, J.R. (2013) Avifaunal disarray due to a single despotic species. *Diversity & Distributions*, **19**, 1468-1479.
- Milazzo, M., Mirto, S., Domenici, P. & Gristina, M. (2013) Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology*, **82**, 468-477.
- Suarez, M.L. & Kitzberger, T. (2010) Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. *Journal of Ecology*, **98**, 1023-1034.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351-1363.

Appendix 1. Bird species, classified into guilds (following Radford & Bennett, 2005) and geographical range (following Blakers *et al.*, 1984), excluding species found on < 5 sites, nocturnal, non-native, and aquatic species. Species only recorded at the landscape study indicated by * and regional study indicated by †.

Species common name	Habitat	Cons. status	Niche	Diet	Nesting	Mobility	Distribution
apostlebird*	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Dry
australian hobby	Open tolerant	No	Aerial	Raptor	Open	Resident	Widespread
australian magpie	Open-country	No	Ground	Insectivore	Open	Resident	Widespread
australian raven	Open-country	No	Ground	Predator	Open	Resident	Widespread
azure kingfisher*	Woodland dependent	Yes	Ground	Predator	Burrow	Resident	Mesic
black falcon	Open-country	Yes	Aerial	Raptor	Open	Resident	Dry
black-chinned honeyeater	Woodland dependent	Yes	Canopy Low	Nectarivore	Open	Nomadic	Dry
black-eared cuckoo*	Woodland dependent	No	shrubs	Insectivore	Parasite	Migrant	Dry
black-faced cuckoo-shrike	Open tolerant	No	Canopy	Insectivore	Open	Nomadic	Widespread
black-shouldered kite*	Open-country	No	Ground	Raptor	Open	Resident	Widespread
blue-faced honeyeater*	Woodland dependent	No	Canopy	Nectarivore	Open	Nomadic	Widespread
blue-winged parrot†	Open tolerant	No	Ground	Granivore	Hollow	Migrant	Widespread
brown falcon	Open-country	No	Ground	Raptor	Open	Resident	Widespread
brown goshawk	Open tolerant	No	Ground	Raptor	Open	Resident	Widespread
brown quail*	Woodland dependent	Yes	Ground	Granivore	Ground	Resident	Widespread
brown songlark*	Open-country	No	Ground Low	Insectivore	Ground	Migrant	Widespread
brown thornbill	Woodland dependent	No	shrubs	Insectivore	Open	Resident	Widespread
brown treecreeper	Woodland dependent	No	Bark	Insectivore	Hollow	Resident	Dry
brown-headed honeyeater	Woodland dependent	No	Canopy	Nectarivore	Open	Nomadic	Widespread
buff-rumped thornbill	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Widespread
bush stone-curlew	Woodland dependent	Yes	Ground	Predator	Ground	Resident	Dry
chestnut-rumped heathwren	Woodland dependent	Yes	Ground	Insectivore	Ground	Resident	Mesic
chestnut-rumped thornbill	Woodland dependent	Yes	Ground Low	Insectivore	Hollow	Resident	Dry
clamorous reed warbler*	Open-country	No	shrubs	Insectivore	Ground	Migrant	Widespread
cockatiel	Open tolerant	No	Ground	Granivore	Hollow	Nomadic	Dry
collared sparrowhawk	Open tolerant	No	Aerial	Raptor	Open	Resident	Widespread
common bronzewing	Woodland dependent	No	Ground	Granivore	Open	Resident	Widespread
crested bellbird	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Dry
crested pigeon	Open-country	No	Ground	Granivore	Open	Nomadic	Widespread
crested shrike-tit	Woodland dependent	Yes	Bark	Insectivore	Open	Resident	Widespread
crimson rosella	Woodland dependent	No	Canopy	Granivore	Hollow	Resident	Mesic
diamond dove†	Woodland dependent	Yes	Ground	Granivore	Open	Resident	Dry
diamond firetail	Woodland dependent	Yes	Ground	Granivore	Open	Resident	Dry
dollarbird*	Woodland dependent	No	Aerial	Insectivore	Hollow	Migrant	Dry
dusky woodswallow	Woodland dependent	No	Aerial	Insectivore	Open	Resident	Widespread
eastern rosella	Open tolerant	No	Ground Tall	Granivore	Hollow	Resident	Widespread
eastern spinebill	Woodland dependent	No	shrubs	Nectarivore	Open	Nomadic	Widespread
eastern yellow robin	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Mesic
emu	Open tolerant	Yes	Ground	Frugivore	Ground	Nomadic	Widespread
fairy martin	Open-country	No	Aerial Tall	Insectivore	Burrow	Migrant	Widespread
fan-tailed cuckoo	Woodland dependent	No	shrubs	Insectivore	Parasite	Migrant	Widespread
flame robin	Open tolerant	Yes	Ground	Insectivore	Open	Migrant	Widespread
fuscous honeyeater	Woodland dependent	No	Canopy	Nectarivore	Open	Nomadic	Dry

galah	Open-country	No	Ground Tall	Granivore	Hollow	Resident	Widespread
gilbert's whistler*	Woodland dependent	Yes	shrubs Tall	Insectivore	Open	Resident	Dry
golden whistler	Woodland dependent	No	shrubs	Insectivore	Open	Migrant	Widespread
grey butcherbird	Open tolerant	No	Ground	Predator	Open	Resident	Widespread
grey currawong	Open tolerant	No	Ground	Predator	Open	Resident	Widespread
grey fantail	Woodland dependent	No	Canopy	Insectivore	Open	Resident	Widespread
grey shrike-thrush	Woodland dependent	No	Canopy	Insectivore	Open	Resident	Widespread
grey-crowned babbler*	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Dry
hooded robin	Woodland dependent	Yes	Ground Low	Insectivore	Open	Resident	Dry
horsfield's bronze-cuckoo	Woodland dependent	No	shrubs	Insectivore	Parasite	Migrant	Widespread
jacky winter	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Dry
laughing kookaburra	Open tolerant	No	Ground	Predator	Hollow	Resident	Widespread
leaden flycatcher	Woodland dependent	No	Aerial	Insectivore	Open	Migrant	Mesic
little button-quail [†]	Open-country	Yes	Ground	Granivore	Ground	Resident	Dry
little corella	Open-country	No	Ground	Granivore	Hollow	Resident	Widespread
little eagle	Open tolerant	No	Ground	Raptor	Open	Resident	Widespread
little friarbird*	Woodland dependent	No	Canopy Low	Nectarivore	Open	Migrant	Dry
little grassbird*	Open-country	No	shrubs	Insectivore	Open	Migrant	Widespread
little lorikeet	Woodland dependent	Yes	Canopy	Nectarivore	Hollow	Nomadic	Widespread
little raven	Open-country	No	Ground	Predator	Open	Resident	Widespread
long-billed corella	Open-country	No	Ground	Granivore	Hollow	Resident	Widespread
magpie-lark	Open-country	No	Ground	Insectivore	Ground	Resident	Widespread
masked lapwing*	Open-country	No	Ground	Insectivore	Ground	Resident	Widespread
masked woodswallow	Open tolerant	No	Aerial	Insectivore	Open	Migrant	Dry
mistletoebird	Woodland dependent	No	Canopy	Frugivore	Open	Resident	Widespread
musk lorikeet	Woodland dependent	No	Canopy	Nectarivore	Hollow	Nomadic	Widespread
nankeen kestrel	Open-country	No	Ground Tall	Raptor	Open	Resident	Widespread
new holland honeyeater*	Open tolerant	No	shrubs	Nectarivore	Open	Resident	Widespread
noisy friarbird	Woodland dependent	No	Canopy	Nectarivore	Open	Migrant	Widespread
noisy miner	Open tolerant	No	Canopy	Nectarivore	Open	Resident	Widespread
olive-backed oriole	Woodland dependent	No	Canopy	Insectivore	Open	Migrant	Widespread
painted button-quail	Woodland dependent	Yes	Ground	Granivore	Ground	Resident	Widespread
painted honeyeater*	Woodland dependent	Yes	Canopy	Frugivore	Open	Nomadic	Dry
pallid cuckoo	Open tolerant	No	Ground	Insectivore	Parasite	Migrant	Widespread
peaceful dove	Woodland dependent	Yes	Ground	Granivore	Open	Resident	Dry
peregrine falcon	Open tolerant	No	Aerial	Raptor	Open	Resident	Widespread
piebald butcherbird*	Open tolerant	No	Ground	Predator	Open	Migrant	Dry
piebald currawong	Woodland dependent	No	Canopy	Predator	Open	Migrant	Mesic
purple-crowned lorikeet	Woodland dependent	No	Canopy	Nectarivore	Hollow	Nomadic	Dry
rainbow bee-eater	Open tolerant	No	Aerial	Insectivore	Burrow	Migrant	Dry
red wattlebird	Woodland dependent	No	Canopy	Nectarivore	Open	Nomadic	Widespread
red-browed finch*	Woodland dependent	Yes	Ground	Granivore	Open	Resident	Mesic
red-capped robin	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Dry
red-rumped parrot	Open tolerant	No	Ground	Granivore	Hollow	Resident	Widespread
restless flycatcher	Open tolerant	Yes	Ground	Insectivore	Open	Resident	Dry
richard's pipit	Open-country	No	Ground	Insectivore	Ground	Resident	Widespread
rufous songlark	Open tolerant	No	Ground	Insectivore	Ground	Migrant	Widespread
rufous whistler	Woodland dependent	No	Canopy	Insectivore	Open	Resident	Widespread
sacred kingfisher	Woodland dependent	Yes	Ground	Predator	Hollow	Migrant	Widespread
scarlet robin	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Widespread
shining bronze-cuckoo	Woodland dependent	No	Canopy	Insectivore	Parasite	Migrant	Widespread
silveryeye	Open tolerant	No	Canopy	Frugivore	Open	Migrant	Widespread
singing bushlark	Open-country	No	Ground	Insectivore	Ground	Resident	Widespread
southern whiteface*	Woodland dependent	Yes	Ground	Insectivore	Hollow	Resident	Dry

speckled warbler	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Dry
spotted harrier*	Open-country	No	Ground	Raptor	Open	Resident	Dry
spotted pardalote	Woodland dependent	No	Canopy	Insectivore	Burrow	Resident	Widespread
spotted quail-thrush	Woodland dependent	Yes	Ground	Insectivore	Ground	Resident	Mesic
striated pardalote	Open tolerant	No	Canopy	Insectivore	Hollow	Resident	Widespread
striated thornbill	Woodland dependent	No	Canopy	Insectivore	Open	Resident	Mesic
stubble quail*	Open-country	No	Ground	Granivore	Ground	Nomadic	Widespread
sulphur-crested cockatoo	Open tolerant	No	Ground	Granivore	Hollow	Resident	Widespread
superb fairy-wren	Woodland dependent	No	Ground	Insectivore	Open	Resident	Widespread
superb parrot*	Woodland dependent	Yes	Ground	Granivore	Hollow	Resident	Dry
swamp harrier*	Open-country	No	Ground	Raptor	Open	Resident	Widespread
swift parrot	Woodland dependent	Yes	Canopy	Nectarivore	-	Migrant	Widespread
tree martin	Woodland dependent	No	Aerial	Insectivore	Hollow	Resident	Widespread
turquoise parrot*	Woodland dependent	Yes	Ground	Granivore	Hollow	Resident	Widespread
varied sittella	Woodland dependent	Yes	Bark	Insectivore	Open	Resident	Widespread
wedge-tailed eagle	Open tolerant	No	Ground	Raptor	Open	Resident	Widespread
weebill	Woodland dependent	No	Canopy	Insectivore	Open	Resident	Dry
welcome swallow	Open-country	No	Aerial	Insectivore	Burrow	Resident	Widespread
			Tall				
western gerygone*	Woodland dependent	Yes	shrubs	Insectivore	Open	Migrant	Dry
whistling kite	Open tolerant	No	Ground	Raptor	Open	Resident	Widespread
white-backed swallow*	Open tolerant	No	Aerial	Insectivore	Burrow	Nomadic	Dry
white-bellied cuckoo-shrike	Woodland dependent	Yes	Canopy	Insectivore	Open	Resident	Widespread
white-breasted woodswallow*	Open tolerant	No	Aerial	Insectivore	Open	Migrant	Widespread
white-browed babbler	Woodland dependent	Yes	Ground	Insectivore	Open	Resident	Dry
			Low				
white-browed scrubwren*	Woodland dependent	No	shrubs	Insectivore	Open	Resident	Mesic
white-browed woodswallow	Open tolerant	No	Aerial	Insectivore	Open	Migrant	Dry
white-eared honeyeater	Woodland dependent	No	Canopy	Nectarivore	Open	Resident	Widespread
white-fronted chat*	Open-country	No	Ground	Insectivore	Open	Nomadic	Widespread
white-naped honeyeater	Woodland dependent	No	Canopy	Nectarivore	Open	Migrant	Mesic
white-plumed honeyeater	Woodland dependent	No	Canopy	Nectarivore	Open	Resident	Widespread
white-throated treecreeper	Woodland dependent	No	Bark	Insectivore	Hollow	Resident	Mesic
white-winged chough	Woodland dependent	No	Ground	Insectivore	Open	Resident	Widespread
white-winged triller	Woodland dependent	Yes	Canopy	Insectivore	Open	Migrant	Widespread
willie wagtail	Open tolerant	No	Ground	Insectivore	Open	Resident	Widespread
yellow rosella*	Woodland dependent	No	Ground	Granivore	Hollow	Resident	Dry
yellow thornbill	Woodland dependent	No	Canopy	Insectivore	Open	Resident	Widespread
			Tall				
yellow-faced honeyeater	Woodland dependent	No	shrubs	Nectarivore	Open	Nomadic	Widespread
yellow-plumed honeyeater	Woodland dependent	No	Canopy	Nectarivore	Open	Nomadic	Dry
yellow-rumped thornbill	Open tolerant	No	Ground	Insectivore	Open	Resident	Widespread
yellow-tufted honeyeater	Woodland dependent	No	Canopy	Nectarivore	Open	Nomadic	Dry
zebra finch*	Open-country	No	Ground	Granivore	Open	Resident	Dry