



MONASH University

**The significance and future prospects of floodplains
for birds in a drying climate**

Katherine Elizabeth Selwood

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Abstract

Climate change is becoming an increasingly significant driver of biodiversity loss. Changes to climatic extremes, such as those associated with drought, may pose a more severe threat to ecosystem functioning than gradual changes in mean conditions. The duration and frequency of extreme droughts are projected to increase in many parts of the world including Australia, especially in the south of the continent. Identifying refugia that increase the capacity of biota to withstand climate extremes such as drought ('resistance') and to recover if or when adverse conditions abate ('resilience') will be critical for mitigating the effects of climate change. Locations with reliable availability of water and mesic microclimates, such as floodplains, are likely to be particularly important for supporting species persistence during drought.

In this thesis, I conducted a global meta-analysis to compare the relative effects of climate change and land-use change on demographic rates in plant and animal populations. I measured the resistance and resilience of floodplain bird assemblages to a thirteen-year drought (the 'Big Dry') in southeastern Australia. I assessed the potential of floodplains as drought refugia by comparing the resistance and resilience of birds in floodplains to those in non-floodplain zones, and assessed whether floodplains moderate the effects of aridity on bird occurrence. I investigated the importance of landscape context, the physical landscape, vegetation structure and ecological productivity in promoting the resistance of bird assemblages to prolonged drought.

In the meta-analysis, I found, on average, that climate variables had equally strong effects on demographic rates of plants and animals as did land-use change. This is significant, given that the pressures of climate change will continue to intensify in coming decades. In southeastern Australia, where climate change is

causing increased drought frequency and severity, I found that bird assemblages were severely affected by the Big Dry: a large proportion of species declined during the Big Dry, and few recovered after the drought broke. Floodplains showed potential as drought refugia because fewer species declined in floodplain zones than in non-floodplain zones, and declines in floodplains were less severe for many species. I found that floodplains moderate the effects of aridity on bird occurrence, extending the distribution of many species into more arid regions than they would otherwise be expected to occur. Vegetation productivity was the most important factor for increasing the resistance of bird assemblages to drought across the study region.

Climate change is an important driver of population viability. Drying climate conditions, such as increased drought frequency and severity, are likely to have significant effects on bird assemblages. However, the effects of drought and aridity on birds may be reduced in highly productive ecosystems such as floodplains.

Thesis including published works declaration

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 four original papers published in peer reviewed journals and one submitted publication. The core theme of the thesis is the effects of prolonged drought on bird assemblages and the potential of floodplains as drought refugia. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the student, working within the Faculty of Science under the supervision of Professor Ralph Mac Nally (Institute for Applied Ecology, University of Canberra), Associate Professor Melodie McGeoch (School of Biological Sciences, Monash University) and Dr Rohan Clarke (School of Biological Sciences, Monash University).

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research. No Monash students are listed as coauthors.

In the case of Chapters 2 to 6 my contribution to the work involved the following:

| Thesis Chapter | Publication Title | Status | Nature and % of student contribution | Coauthors |
|----------------|--|---|--|---|
| 2 | The effects of climate change and land-use change on demographic rates and population viability | Published as: Selwood et al. 2015, <i>Biological Reviews</i> , 90 (3): 837-853 | Performed literature review, wrote original manuscript and coordinated subsequent manuscript revisions (75% contribution) | M.A. McGeoch R. Mac Nally |
| 3 | A bust but no boom: responses of floodplain bird assemblages during and after prolonged drought | Published as: Selwood et al. 2015, <i>Journal of Animal Ecology</i> , 84 (6):1700-1710 | Planned and conducted analyses, wrote original manuscript and coordinated subsequent manuscript revisions (75% contribution) | R.H. Clarke S.C. Cunningham H. Lada M.A. McGeoch R. Mac Nally |
| 4 | Resistance and resilience of terrestrial birds in drying climates: do floodplains provide drought refugia? | Published as: Selwood et al. 2015, <i>Global Ecology and Biogeography</i> , 24 (7):838-848 | Planned and conducted the majority of analyses, wrote original manuscript and coordinated subsequent manuscript revisions (70% contribution) | J. R. Thomson R.H. Clarke M.A. McGeoch R. Mac Nally |
| 5 | Green tongues into the arid zone: River floodplains extend the distribution of terrestrial bird species | Published as: Selwood et al. <i>Ecosystems</i> , DOI: 10.1007/s1002 | Planned and conducted analyses, wrote original manuscript and coordinated | R.H. Clarke M.A. McGeoch R. Mac Nally |

| | | | | |
|---|--|---|--|---|
| | | 1-016-0059-y | subsequent manuscript revisions (75% contribution) | |
| 6 | High-productivity vegetation is important for lessening drought-induced declines in woodland birds | Submitted as: Selwood et al. to <i>Journal of Applied Ecology</i> , date resubmitted: 31/01/2017. Manuscript ID: JAPPL-2016-00838 | Planned and conducted analyses, wrote original manuscript and coordinated subsequent manuscript revisions (75% contribution) | M.A. McGeoch R.H. Clarke R. Mac Nally |

I have not renumbered sections of submitted or published papers.

Student signature: 

Date: 06/02/2017

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-authors' contributions to this work. In instances where I am not the responsible author I have consulted with the responsible author to agree on the respective contributions of the authors.

Main Supervisor signature: 

Date: 06/02/2017

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Chapter 1

Introduction

Introduction

Climate change as a major pressure on biodiversity

While human land-use change is recognized as the main driver of terrestrial species declines and extinctions, it is likely that climate change will equal or exceed the role of land-use change in contributing to loss of global biodiversity in coming decades (Heller and Zavaleta 2009, Bellard et al. 2012). The effects of climate change on demographic rates and population viabilities are likely to be as large as those arising from land-use change (Chapter 2, Selwood et al. 2015b). Changes to climatic extremes, such as drought, heat-waves and extreme weather events, are likely to be particularly problematic for plants and animals, and may pose a more severe threat to ecosystem functioning than gradual changes in mean conditions (Parmesan et al. 2000, Gutschick and BassiriRad 2003, Jentsch and Beierkuhnlein 2008). Extreme climatic events can have almost immediate effects on populations (McKee and Wolf 2010), and can accelerate shifts in assemblage composition and species' distributions (Jentsch et al. 2007). The frequency of both short- and long-term drought is increasing in many parts of the world, and rising temperatures are inducing more severe drying (Dai et al. 2004, Sheffield and Wood 2008, Collins et al. 2013, Kirtman et al. 2013).

The duration and frequency of extreme droughts are projected to increase in Australia, especially in the south of the continent (Collins et al. 2013, CSIRO and Bureau of Meteorology 2015). From 1997 to mid-2010, southeastern Australia experienced the 'Big Dry' (or 'Millennium Drought'), the most severe hydrological drought in the region since records commenced in the late 19th century (Leblanc et al. 2012). A sustained positive epoch for the Southern Annual Mode caused below-average rainfall during this period, especially in autumn, when rainfall intensity was

c. 25% lower than the long-term average (Verdon-Kidd and Kiem 2009, Murphy and Timbal 2008). Three consecutive El Niño events resulted in a peak in the drought between 2002 and 2004 (Verdon-Kidd and Kiem 2009). Temperatures were high throughout this period and contributed to the severity of the drying: annual maximum temperatures were c. 0.7°C degrees higher than the long-term average (Murphy and Timbal 2008). Unprecedented reductions in run-off significantly reduced inflows into the Murray-Darling River system (>35% in the south), Australia's major river basin spanning about one seventh of the continent (Chiew et al. 2011, Leblanc et al. 2012). The Big Dry was broken by the 'Big Wet' in mid-2010, two of the wettest years for Australia as a whole, and the third wettest two-year period for the Murray-Darling Basin, with extensive flooding in southern Australia (Bureau of Meteorology 2012, Timbal et al. 2015). Total rainfall during the Big Wet was about one third of the total rainfall deficiency during the Big Dry in southeastern Australia (Bureau of Meteorology 2012). The alternation of long, severe droughts and shorter, more intense rainfall periods is expected to become the norm for southeastern Australia over the next 50–70 years (Timbal et al. 2015). Climate projections indicate a drier future for southern Australia, including reductions in annual rainfall and periods of protracted more severe drying (Murphy and Timbal 2008, Delworth and Zeng 2014) and increasing temperatures that will increase evaporation (Lewis and Karoly 2014).

Drought primarily affects animal populations through two key mechanisms. First, limitations to water availability caused by reduced rainfall and run-off reduce vegetation productivity (Saatchi et al. 2013) and can lead to widespread plant mortality (Allen et al. 2010). These declines in plant productivity reduce resource availability for animals, including food (reduced availability of seeds, fruits, foliage, invertebrates), shelter (reduced vegetation cover) and nesting resources (Albright et

al. 2009) (Fig. 1). Second, xeric climate conditions, including reduced water availability for drinking, place physiological pressures on individuals (Tieleman et al. 2003, Albright et al. 2009, McKechnie and Wolf 2010). Reduced resource availability and high physiological pressures during drought may reduce survival (Mooij et al. 2002) and reproduction (Li and Brown 1999, Christman 2002, Adams 2010) or encourage individuals to disperse to locations with more favorable microclimates or higher resource availability (Gibbons et al. 1983), thereby reducing population sizes and hence population viability, and potentially leading to local extirpation (Fig. 1).

With the relief of drought conditions, increased water availability is expected to increase plant productivity, resulting in higher resource availability for animals (Hurlbert 2004), although some species, such as ground foragers may experience short-term disruptions to foraging in flood-prone landscapes. Survival and reproduction rates are expected to increase with higher vegetation productivity (Rasmussen et al. 2006) and with moderation of extreme climate conditions (Fig. 1). Increased population abundances may lead to recolonisation of suitable habitats, where local populations may have become extinct during drought.

Resistance and resilience to climate change

The ability of populations to persist under the added impost of climate change is affected by their capacity to withstand climatic extremes such as drought ('resistance') and to recover when adverse conditions abate ('resilience') (Nimmo et al. 2015). Tracking abundances or species occurrence during and after extreme climatic events provides information on the relative resistance and resilience of species (Bennett et al. 2014) (Fig. 1). More insight into population trajectories can be gained by evaluating demographic responses to climatic pressures because these

precede changes in abundance or occurrence, especially for longer-lived vertebrates (Chapter 2, Selwood et al. 2015b). Long-term studies before, during and after extreme climatic events, such as drought, are rare (Lindenmayer and Likens 2009), and so opportunities to evaluate species' resistance and resilience to climatic events are valuable for informing our understanding of the effects of climatic extremes on biota. The extent to which populations decline during extreme climatic events (e.g. drought), and subsequently recover during favorable conditions (e.g. high rainfall), are key determinants for long-term viability (Fig. 1).

Measuring the resistance and resilience of species to extreme events such as drought gives an indication of which species will be most likely to persist under changing climate conditions, and which species will be at risk. Species that are most resistant and resilient will become more dominant, while those that have limited resistance and resilience will decline and potentially become locally extirpated or even extinct (Princé and Zuckerberg 2015). Comparing the resistance and resilience between species with different ecological and life-history traits may allow us to predict which groups of species will be most at risk (e.g. small- vs large-bodied birds), and which mechanisms may mediate climate-induced declines (e.g. diet). Comparing the resistance and resilience of species or assemblages between different locations can also provide an indication of the capacity for different locations to sustain populations throughout climatic extremes such as drought.

Identifying climate refugia

Identifying landscape elements that promote the resistance and resilience of biota to climatic events will be critical for effectively prioritizing conservation resources in a changing climate (Isaac et al. 2009). Climate refugia enhance resistance and resilience

of populations to extreme climatic events by providing temporary refuges for individuals to retreat to during adverse conditions, or by acting as source areas for future recovery by supporting the survival of individuals so that populations can expand once conditions improve (Mackey et al. 2012, Davis et al. 2013, Reside et al. 2014). Refugia offer food, shelter and breeding resources that become limited in other areas of a species' range, or offer physiological relief from extreme environmental conditions. Thermal refugia, where temperatures are moderated, and hydric refugia, where water availability is greater or more consistent than other parts of a species' range, will play increasingly important roles in species persistence in regions with drying climates (Reside et al. 2014).

Landscape elements where vegetation remains relatively more productive during times of drought, and reduced rainfall, are likely to be particularly valuable for biotic persistence in a drying climate by providing more consistent (and usually higher amounts of) food, shelter and breeding resources (Mackey et al. 2012) (Fig. 1). Locations with mesic microclimate conditions are also likely to promote survival during drought, when xeric climate conditions inflict great physiological pressures (Fig. 1).

Floodplains: values and threats

Floodplains are the interface between terrestrial and freshwater ecosystems, consisting of areas that are periodically inundated by the overflow of rivers, streams or lakes, direct precipitation or groundwater (Junk et al. 1989). Flooding results in a two-way exchange of nutrients and energy between floodplain and aquatic ecosystems (Junk et al. 1989, Ballinger and Lake 2006). Nutrient and water inputs from upstream flows and access to shallow groundwater tables allow floodplain

ecosystems to support more vegetation biomass than expected given local rainfall (Naumburg et al. 2005, Ballinger and Lake 2006, Selwood et al. 2016). Floodplain microclimates are moderated by canopy cover, topography and adjacency to water bodies (Brosofske et al. 1997). The relatively higher productivity and water availability, and the moderated microclimatic conditions, compared to adjacent plain and upland ecosystems ('non-floodplain' zones) identify floodplains as good candidates for climate refugia (Capon et al. 2013, Selwood et al. 2015c) (Fig. 1).

River regulation and water extraction have modified flow and flooding regimes of river systems around the world (Malmqvist and Rundle 2002), causing the decline and degradation of floodplain ecosystems from altered flood seasonality, frequency, duration and extent (Busch and Smith 1995, González et al. 2010). The floodplain ecosystems of the Murray-Darling Basin have been much affected by human land-use (Mac Nally et al., 2011). Murray-Darling floodplains are dominated by river red gum (*Eucalyptus camaldulensis*), black box (*E. largiflorens*) or coolabah (*E. coolibah*), which are tree species that require periodic inundation to complete their life cycle (Roberts and Marston 2011, Cunningham et al. 2013). Water extraction has substantially affected the frequency, duration and seasonality of flooding of these forests, which has led to large-scale tree dieback and mortality (Horner et al. 2009) and reduced tree recruitment (Horner et al. 2016). Grazing, timber harvesting and removal of fallen wood have had negative effects on native fauna and flora (Mac Nally et al., 2011).

A drying climate in southeastern Australia has exacerbated the degrading effects of water extraction on the floodplain forests of the Murray-Darling Basin (Horner et al. 2009). There was a substantial decline in condition of the floodplain forests during the Big Dry (Cunningham et al. 2009). Rising temperatures and

declining rainfall have affected in-flows into the Murray-Darling River system, and the continuing effects of climate change will see further reductions (Cai and Cowan 2008, Horner et al. 2009).

Thesis aims

Measuring trends in biota during and after long-term droughts such as the Big Dry provides an opportunity to quantify the relative resistance and resilience of fauna. I focus on birds because their mobility allows them to respond to spatial variation in conditions and there is a greater availability of broadscale data than for other fauna. I measured the resistance and resilience of bird assemblages to the Big Dry in the Murray-Darling Basin and investigated the potential of floodplains to provide drought refugia for bird assemblages in a drying climate. I sought to answer the following questions:

1. How, and to what degree, were floodplain bird assemblages affected by the Big Dry and did they recover after the drought broke?
2. Are floodplain bird assemblages more resistant or resilient to prolonged drought compared to assemblages in non-floodplain ecosystems?
3. Do floodplains moderate the effects of aridity on bird occurrence?
4. Does vegetation structure, vegetation productivity, the physical landscape or landscape context promote the resistance of birds to prolonged drought?

The global context of this work is explored in Chapter 2. Land-use change is currently considered the main driver of biodiversity loss (Secretariat of the Convention on Biological Diversity 2010) (Fig. 1). I investigated the relative importance of climate change as a driver of biodiversity change by comparing the

relative effects of climate and land-use change on demographic rates of plant and animal populations around the world. The close connection between a pressure and a demographic-rate response means that measuring changes in demographic rates should offer a more accurate indication of the mechanisms through which the pressures associated with land-use change and climate change affect population viabilities (Chapter 2, Selwood et al. 2015b).

Changes to extreme climatic events are likely to be especially deleterious for plant and animal populations in a changing climate. Water limitations during drought reduce primary productivity and hence resource availability, and the xeric climate conditions during drought increase physiological pressures (Fig. 1). Prolonged droughts, such as the Big Dry, broken by short periods of intense rainfall, are expected to become more common in southern Australia. The extent to which animal populations can resist low resource availability and xeric climate conditions during prolonged drought, and recover after these pressures are relieved during periods of high rainfall will determine whether species will persist as droughts becomes more common and more severe (Fig. 1).

Substantial declines in bird assemblages occurred during the Big Dry in the dry upland box-ironbark forests in southeastern Australia (Mac Nally et al. 2009, Bennett et al. 2014). The occurrence of up to 62% of box-ironbark species declined during the Big Dry, and most species did not recover (Bennett et al. 2014). I complemented those assessments by measuring the resistance and resilience of bird assemblages to the Big Dry in the more mesic floodplain forests of southeastern Australia (Chapter 3, Selwood et al. 2015a). I measured changes in species occurrence during and after the Big Dry, and changes in breeding activity before and after the Big Wet as an indication of demographic resilience. I evaluated whether species

characteristics (body mass, fecundity, diet, mobility) affected the resistance or resilience of individual species.

Floodplain ecosystems have already been affected by declines in water availability due to human land-use, and this pressure is increasing as the climate dries in southeastern Australia. However, compared to non-floodplain ecosystems, floodplains have relatively higher and more stable water availability, higher vegetation productivity and more mesic microclimates and so may be more resistant and resilient to drought and drying climate conditions. These conditions may alleviate the pressures of drought on bird populations (Fig. 1). I compared trends in the occurrence of bird species in floodplains to trends in non-floodplain zones during and after the Big Dry to evaluate whether floodplains provide drought refugia for birds by supporting more resistant or more resilient bird assemblages (Chapter 4, Selwood et al. 2015c). I assessed whether floodplains moderate the effects of aridity on species occurrence by investigating whether floodplain ecosystems allow terrestrial bird species to extend into more arid regions than they otherwise would be expected to occupy (Chapter 5, Selwood et al. 2016). In Chapter 6, I conducted a broader assessment of the landscape characteristics that may affect the resistance of bird assemblages to prolonged drought, including vegetation productivity, the physical landscape, landscape context and vegetation structure.

The outcomes of this work will improve our understanding of the relative importance of climate change as a major driver of biodiversity loss and in particular, the extent to which increased drought severity and frequency will affect bird assemblages. The findings will provide an assessment of the potential of floodplains as candidates for drought refugia and will improve our understanding of the mechanisms through which landscape characteristics can improve the resistance or

resilience of birds to drought (Fig. 1). I summarize my key findings and their implications in Chapter 7, discussing the vulnerability of floodplain bird assemblages, the potential of floodplains as refugia for birds in a drying climate and the management implications of my findings.

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Chapter 2

The effects of climate change and land-use change on demographic rates and population viability

The effects of climate change and land-use change on demographic rates and population viability

Katherine E. Selwood^{1,*}, Melodie A. McGeoch¹ and Ralph Mac Nally²

¹*School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia*

²*Institute for Applied Ecology, The University of Canberra, Bruce, Australian Capital Territory 2617, Australia*

ABSTRACT

Understanding the processes that lead to species extinctions is vital for lessening pressures on biodiversity. While species diversity, presence and abundance are most commonly used to measure the effects of human pressures, demographic responses give a more proximal indication of how pressures affect population viability and contribute to extinction risk. We reviewed how demographic rates are affected by the major anthropogenic pressures, changed landscape condition caused by human land use, and climate change. We synthesized the results of 147 empirical studies to compare the relative effect size of climate and landscape condition on birth, death, immigration and emigration rates in plant and animal populations. While changed landscape condition is recognized as the major driver of species declines and losses worldwide, we found that, on average, climate variables had equally strong effects on demographic rates in plant and animal populations. This is significant given that the pressures of climate change will continue to intensify in coming decades. The effects of climate change on some populations may be underestimated because changes in climate conditions during critical windows of species life cycles may have disproportionate effects on demographic rates. The combined pressures of land-use change and climate change may result in species declines and extinctions occurring faster than otherwise predicted, particularly if their effects are multiplicative.

Key words: climate variation, extinction risk, extirpation, emigration, immigration, land-use intensification, landscape condition, mortality, natality.

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* Address for correspondence (Tel: +61 399020860; E-mail: katherine.selwood@monash.edu).

I. INTRODUCTION

Biodiversity continues to decline; of species that have been assessed for extinction risk around the world, 38% are considered to be under threat (Vié, Hilton-Taylor & Stuart, 2009). The abundances of vertebrate populations fell by one-third between 1970 and 2006, and continue to decline; 70% of assessed plant species have been classified as threatened by the IUCN (Vié *et al.*, 2009). The principal pressures causing biodiversity loss are unabated, and, in most cases, are increasing (Butchart *et al.*, 2010). Human land-use change, leading to the loss, fragmentation and degradation of native vegetation, is the predominant driver of terrestrial species decline (Sala *et al.*, 2000). Climate change has been recognized comparatively recently as a major driver, and its effect on plant and animal populations is increasing (Bellard *et al.*, 2012; Foden *et al.*, 2013).

The most widely used measure of biodiversity is species richness, although subspecies, races and genotypes are important components. However, it is the extinction of individual species, especially iconic ones, that causes most consternation among practitioners and the public, so that it is important to understand the processes leading to species extinction. While there is a relatively good understanding of the identity of the pressures acting on species, the mechanisms by which these pressures operate and interact to affect the viability of species and populations is poorly understood (Akçakaya *et al.*, 2006). Understanding the processes that ultimately cause species extinctions is critical for deciding on the most appropriate actions for conservation management (Cushman, 2006).

The effects of land-use change have been a focus for conservation biology for several decades, particularly the effects of habitat fragmentation (Fischer & Lindenmayer, 2007). The most common measures for quantifying the effects on biota are species richness, species occurrence and the abundance patterns of individual species (Debinski & Holt, 2000). Few studies on fragmentation measure demographic responses, with most studies measuring presence/absence, diversity, or abundance (McGarigal & Cushman, 2002); these are 'static' rather than dynamic measures, and so generally do not provide much information on the trajectories of change. There has been much less focus on the demographic effects of land-use change on populations, which provide indications of trajectories of change (Lampila, Mönkkönen & Desrochers, 2005).

Climate change is expected to become an equally, or more important, driver of global biodiversity loss over the next century (Heller & Zavaleta, 2009). Climate change and climatic events (e.g. drought) have already caused range shifts (Chen *et al.*, 2011), severe and long-term population declines (Sanderson *et al.*, 2006; Newton, 2008*b*) and extinctions (Thomas, Franco & Hill, 2006). While interest in the effects of climate on biodiversity has escalated in recent decades, studies on the effects of climate have predominantly focused on observed and potential shifts in species ranges (Dawson *et al.*, 2011) and changes in species phenology (Parmesan,

2006; Chambers & Keatley, 2010) and physiology (Buckley, Nufio & Kingsolver, 2013). These factors may indicate or lead to a change in the likelihood of a species' persistence, but they do not directly reveal the changes in demographic rates that determine the chances that a population will persist. Changes in the phenology, such as timing of breeding, do not in themselves indicate a deleterious effect on population viability. The population is affected when these changes alter demographic rates.

Geographic distribution is the spatial expression of demographic rates, but change in distribution is one of the last signals to be detected as a species declines (Martinez-Meyer, 2012). Focusing on shifts in species ranges misses the population-level processes leading to these shifts, including local extinctions and recolonizations, and the changes in demographic rates that lead to these. While species-distribution models may predict range expansions with climate change, demographic studies may indicate the opposite effect (Campbell *et al.*, 2012). Organisms may colonize or remain in poor-quality habitat if there is asynchrony between the cues used for habitat selection and declines in habitat suitability caused by climate change (van de Pol *et al.*, 2010), so that distributions do not necessarily inform population viability.

We refer to 'pressure' as a human-induced perturbation that negatively affects a population and that may be transient (pulse), persistent (press), or monotonically changing in magnitude (ramping) over time. We synonymize pressure with 'stressor' and 'threat'. Pressures have causative effects on demographic rates (e.g. decreased seed germination, increased nest predation), while associations between pressures and changes in species richness, species occurrence and abundance are correlative. The close connection between a pressure and a demographic-rate response means that measuring the changes in demographic rates should offer a more accurate indication of the mechanisms through which anthropogenic pressures affect population viability (Fig. 1).

Here, we review the effects of some of the major anthropogenic pressures on population viability, and we present a conceptual model to describe these relationships. We focus on the processes through which climate change and changed landscape condition induced by human land use affect population viability in terrestrial plant and animal populations. Last, we quantify these relationships by synthesizing the results of empirical studies to provide a comparison of the effects of these major pressures on population viability. For tractability, this review concentrates on terrestrial systems; different sets of pressures may predominate for freshwater (Ficke, Myrick & Hansen, 2007) and marine (Halpern *et al.*, 2008) systems. There are other pressures on biodiversity such as direct harvest (including fisheries), pollution, invasive species and disease (Mace, Masundire & Baillie, 2005). These are vast topics, so we do not consider them further; instead we focus on the influence of landscape condition and climate change as the main pressures of interest, given their pervasive influence.

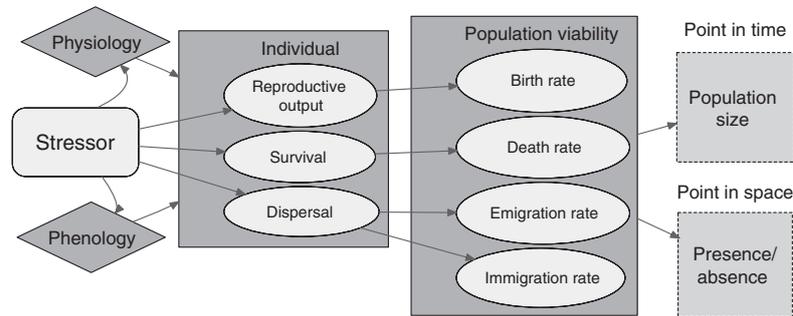


Fig. 1. A general representation of the linkages between the effects of a pressure, such as vegetation loss, and commonly used measures of populations.

(1) Factors affecting population viability

Population viability is a quantitative measure of the capacity of a population to persist, typically the probability of persistence for 100 years, which indicates the risk of extinction (Boyce, 1992). Population viability analyses often are used to quantify extinction risks for individual populations, which can include the identification of minimum viable population size (Reed *et al.*, 2003). The processes that lead to the extinction of a population arise from deleterious changes to demographic rates, which occur through changes in reproductive output, survival and dispersal of individuals in response to a pressure (Fig. 1). Population viability is based on likely changes in population size over time, with the component demographic rates contributing to changes in population size. Birth, death, immigration and emigration are the four fundamental demographic parameters that determine changes in population size (Begon, Mortimer & Thompson, 1996). The dynamics of a population can be represented by (Cohen, 1969):

$$N_{t+1} = N_t (1 + b + i - d - e),$$

where: N_t is the abundance of a population at time t , b and d are the *per capita* birth and death rates, and i and e are *per capita* immigration and emigration rates during time interval $(t+1) - t$. The effective population size will be affected by the sex ratios of individuals contributing to these demographic rates (Frankham, 1995). If one or more of these demographic rates is affected by a proximal pressure, arising from a distal driver, then this will affect the size of the population, and may decrease its viability, unless offset by changes to another demographic rate (i.e. consistently have $N_{t+1} < N_t$, Fig. 2). Once populations become small, stochastic events, inbreeding depression and genetic erosion further affect demographic rates and steepen the rate of decline in population viability (Young *et al.*, 2000; Keller & Waller, 2002). Given the direct effects on population dynamics, measuring changes in demographic rates allows us to infer likely changes to a population's viability in response to human pressures.

II. CONCEPTUAL MODEL

(1) Overview of land-use change and climate change

Changes in human land use for food and resource production and urbanization affect landscape condition through the loss and fragmentation of native vegetation (Fahrig, 1997) and the degradation of remnant vegetation (Fischer & Lindenmayer, 2007). Climate change can further degrade vegetation condition through changes to the frequency and intensity of disturbances that can affect vegetation composition, structure and function (Cunningham *et al.*, 2009; Bennett *et al.*, 2013), decrease plant growth and cause disruptions to plant–pollinator interactions (Memmott *et al.*, 2007). In some locations, increased temperature or carbon dioxide levels may enhance plant growth (Reich & Oleksyn, 2008; Wigley, Bond & Hoffman, 2010).

Barriers to movement caused by vegetation loss and fragmentation affect the movement of individuals and propagules (Cunningham, 2000a; Schtickzelle & Baguette, 2003). Vegetation loss and degradation alter microclimates, habitat quality and habitat structure, affecting conditions for survival and reproduction and modify species interactions (Mac Nally, Bennett & Horrocks, 2000). Resources for survival and reproduction are diminished in degraded and fragmented vegetation (Zanette, Doyle & Tremont, 2000).

Changes to the global climate include increased global temperature and sea levels, decreased extent of snow and ice (both sea and ice-caps) and increased prevalence and intensity of drought (IPCC, 2013). Changes to climate alter demographic rates because of the physiological responses of organisms to environmental variables such as temperature, which affect survival and reproduction (Chown *et al.*, 2010). Climate conditions affect dispersal behaviour (Altermatt, Pajunen & Ebert, 2008) and pathways (Kuparinen *et al.*, 2009). Climate-induced changes to phenology are well documented (Parmesan, 2006), and these affect demographic rates through their effects on reproduction and survival (Lehikoinen, Kilpi & Öst, 2006; Briscoe *et al.*, 2012), through mismatches in trophic relationships and species interactions (Durant *et al.*, 2007; Miller-Rushing *et al.*, 2010).

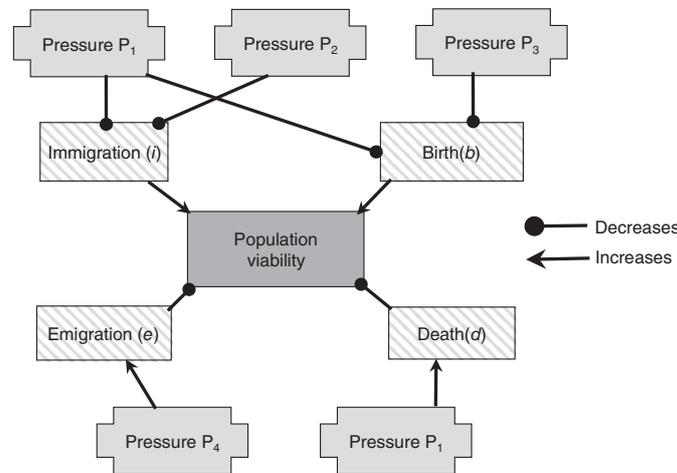


Fig. 2. A general model of the how anthropogenic pressures (P_1 – P_4) impinge on demographic rates (i , e , b , d) in complex networks of effects. The quantification of the strengths of the relationships is key to managing population viability. ‘Pressure’ refers to a human-induced perturbation that negatively affects a population and that may be transient (pulse), persistent (press), or monotonically changing in magnitude (ramping) over time (Mac Nally *et al.*, 2011). A population may be exposed to multiple pressures and the one pressure may affect multiple syntopic populations of different species. We synonymize pressure with ‘stressor’ and ‘threat’.

Demographic rates are controlled by resource availability (Skogland, 1985), such as food, which depends on climate (Previtali *et al.*, 2009; Tian *et al.*, 2010). Some populations may benefit from climate change, perhaps through an increase in survival or growth with warmer temperatures (Reich & Oleksyn, 2008). Climate-induced changes to species interactions may benefit some populations by competitor or predator release, while others may be adversely affected by, for example, weakened mutualistic relationships (Tylianakis *et al.*, 2008).

Despite the numerous mechanisms through which land-use change and climate change affect demographic rates, there has been little attention to the relationships between these pressures and demographic responses. Identifying and quantifying the pathways through which anthropogenic pressures affect population viability is important for framing management actions to contribute to population persistence.

(2) Model description

Multiple pressures need to be considered together because pressures rarely occur singly and interactions among pressures may be multiplicative rather than additive (Dawson *et al.*, 2011; Mantyka-Pringle, Martin & Rhodes, 2012). The relationships among pressures and demographic rates are shown in Fig. 2.

Depending on biological characteristics such as longevity, sexual maturity, and propensity to disperse, changes in one or more demographic rates may have a greater influence on population viability than a proportionally similar change in others (Harper, Rittenhouse & Semlitsch, 2008). For

example, long-lived species are most affected by changes in death rates because adult survivorship contributes most to population persistence (Li *et al.*, 2009).

By populating the general model of Fig. 2 with empirical information, we show how the principal human pressures (Mace *et al.*, 2005) impinge on demographic rates in plant and animal populations (Fig. 3). The model emphasizes the large roles that land-use change and climate change play in affecting population viability, which we quantify in Section III.

The loss, fragmentation and degradation of native vegetation are proximal ecological pressures stemming from land-use change, which affect demographic rates and population viability through their effects on landscape condition and resource availability. We refer to ‘landscape condition’ as the degree to which a landscape resembles its natural condition prior to substantial human disturbance or alteration, consisting of native vegetation cover, connectivity and quality. Climate change and changed landscape condition decrease resource availability, such as food, shelter, soil, nutrients, water and other resources necessary for population survival.

III. QUANTIFYING THE EFFECTS OF HUMAN PRESSURES ON DEMOGRAPHIC RATES

Here, we parameterized the strength of the linkages in the conceptual model (Fig. 3) using a representative set of literature estimates. We quantified the effects of changed landscape condition and climate variation on

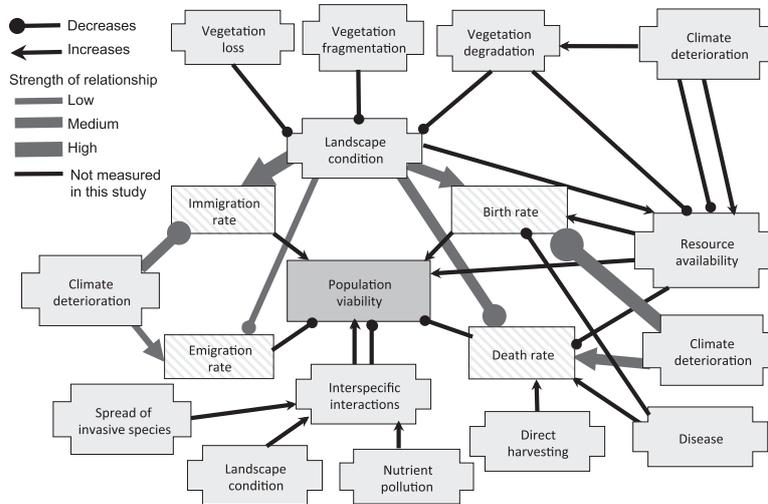


Fig. 3. Empirical application of the general model of Fig. 2 to effects on population dynamics in terrestrial landscapes; the same conventions apply. Grey arrows represent relationships reviewed here. Arrow width represents the mean effect size of the relationship for reviewed studies: low = $0.2 < r < 0.4$; medium $0.4 < r < 0.6$; high = $0.6 < r < 0.8$. No mean effect sizes were < 0.2 (very low) or > 0.8 (very high).

demographic rates, which provides an assessment of the relative importance of changed landscape condition and climate change on population viability.

(1) Literature search

We searched for papers published between 1970 and 2012 using search terms consisting of descriptors for these pressures and demographic rates under TOPIC (i.e. title, abstract and key words) in Thomson-ISI *Web of Science* (Science Citation Index Expanded) (see online supporting information, Table S1), which returned 206 papers. We examined the titles and abstracts of the papers and retained those that provided quantitative relationships between pressures arising from climate or landscape condition and demographic variables, resulting in the retention of 24 papers. A second search, including broader terms for demography (see online Table S2) was conducted to find other studies that measured variables related to demographic rates. Searching for these terms within TOPIC returned >75000 papers; a random selection of 300 of these revealed no studies that provided quantitative information on the effects of a pressure on a demographic rate. The search was restricted to titles, returning 2324 papers, of which 209 were retained. Another 60 studies were found by using the reference lists of the 233 papers found during both searches.

We examined the results of the 294 studies to obtain statistics that were appropriate for calculating the *r* correlation coefficient (Rosenthal, 1994) for relationships between demographic variables and landscape condition or climate; this was possible for 147 studies. We used the *r* correlation coefficient because of its generality and simplicity

of interpretation and consistency of meaning (Rosenthal, 1994). While *r* is most appropriate for relationships between continuous variables, it can also be calculated from pairwise comparisons (Rosenthal, 1994). We included empirical, field-based or experimental studies that directly measured the effects of variables of climate and landscape condition on demographic variables in native plant and animal populations. Only 19 studies looked specifically at *per capita* demographic rates, so we included studies that measured variables that were related to these rates, such as clutch size, fruit production, juvenile survival, and genetic differentiation.

(2) Quantification of effect sizes

Values of the correlation coefficient *r* (including linear and rank correlations: Pearson's *r*, Spearman's *r*, Kendall's τ , point-biserial *r*, and phi) range between -1 and +1, and indicate the strength of the association between variables; the sign indicates the direction of the monotonic association (De Veaux, Velleman & Bock, 2008). Where no correlation coefficient was presented, we calculated *r* following standard methods (Rosenthal, 1994; Nakagawa & Cuthill, 2007) from reported test statistics (*t*-statistic, *F*-statistic, χ^2 , ζ -score, coefficient of determination R^2 , Hedge's *d*). Where the *P*-value was the only statistic reported, we transformed these to ζ -scores using a standard normal variate (De Veaux *et al.*, 2008).

The correlation coefficient *r* for each documented relationship between a climate variable (e.g. rainfall, temperature) or landscape-condition variable (e.g. vegetation cover, patch size) and the demographic response was

obtained from all species in each study. If >1 variable related to a particular demographic rate was measured (e.g. number of eggs and number of fledglings, or number of seeds and number of seedlings), we used the variable that would contribute most to the number of adult individuals in that population, usually the more advanced life stage (e.g. number of fledglings or number of seedlings). If >1 variable related to climate (e.g. rainfall and temperature) or to landscape condition (e.g. fragment size and isolation) was measured, we included the variable that had the largest effect size on the demographic response variable. Details of included studies and their effect sizes are in Table S3. Thirty-six studies measured >1 species, demographic rate and/or driver, and so, contributed >1 datum to the analysis.

For landscape condition, values of r ranged between -1 and $+1$, with positive values being associated with a positive effect of measures such as vegetation cover or contiguity on a demographic rate. For example, if fragmentation had a negative effect on a measure of birth rates in a study, the correlation coefficient for landscape condition on birth rates for that relationship would be positive.

We did not estimate the direction of relationships between climate variables (e.g. temperature, rainfall) and demographic rates because there is difficulty in generalizing the effects of climate variables on population viability given that directional climate deviations do not uniformly affect demographic rates (Glenn *et al.*, 2011). Changes in climate depend on region, so that generalizations are not appropriate. For example, there may be increases in precipitation in some regions and decreases in others, so that decreased rainfall cannot be considered to be a consistent climate-change effect (IPCC, 2013). The effects of climate variables on demographic rates may differ among seasons (Reed & Slade, 2009) and many studies measured within-year climate measures (e.g. winter rainfall) making it inappropriate to extrapolate to general trends given the scope of this review. We considered the correlation coefficient to be an absolute value for climate variables on demographic rates when calculating an average effect size, with r ranging from 0 to 1. This provides an indication of the size of the effect that climate may have on demographic rates rather than generalizing the effects of climate variables.

We converted all r values to ζ using Fisher's transformation, which transforms r to a near-normal distribution, because the distribution of r values becomes skewed as r becomes absolutely larger (Rosenthal, 1994). We calculated the mean effect size and standard error for the effect of landscape condition and climate on demographic rates using the ζ values to gauge the size of the effect that climate and landscape condition have on demographic processes and, in the case of pressures arising from landscape condition, the direction of this effect. Means were calculated for plants and animals separately. The means and upper and lower confidence interval values (95% confidence interval) were then back-transformed to r , so that the effect size could be between 0 and 1 for the effect of climate, and between -1 and $+1$ for the effect of landscape condition (Rosenthal, 1994).

(3) Results

Most studies on climate and landscape condition were from North America and Europe (see online Table S4). Birds were the most studied animals, followed by mammals, with other groups poorly represented (see online Table S3). There were few studies on the effects of climate on plant demographic rates (see online Table S3).

Landscape condition had a mean positive effect on birth rates in plant ($\bar{r}=0.3$) and animal populations ($\bar{r}=0.5$), a negative effect on death rates in animal populations ($\bar{r}=-0.6$), and a positive effect on plant dispersal and animal immigration ($\bar{r}=0.6$ for both). Landscape condition had a mean negative effect on death rates in plant populations ($\bar{r}=-0.6$) and emigration in animal populations ($\bar{r}=-0.2$), but studies were few ($N=2$ and 5) and confidence intervals overlapped zero, indicating that these effects were not significantly different from zero (Harrison, 2011) (Fig. 4A). The mean absolute effect sizes of climate on demographic rates were similar, for birth rates in plants ($\bar{r}=0.7$) and animals ($\bar{r}=0.6$), and plant ($\bar{r}=0.7$) and animal death rates ($\bar{r}=0.6$) (Fig. 4B).

There was a small mean effect size on animal emigration ($\bar{r}=0.2$), but there were only three studies, each of which reported increased measures of emigration with higher temperatures. There was just one study on animal immigration ($\bar{r}=0.6$) (Fig. 4B). There were no studies that provided statistics for calculating the effect size of climate on plant dispersal.

Studies that measured the effects of temperature and rainfall used a wide variety of temporal measures of climate (e.g. week, month, season, year, life-cycle stage), so we cannot extrapolate to responses to climate change (see online Table S5). For studies that reported an effect of rainfall, most were lower birth rates (11 of 13 studies) and increased death rates (five of eight studies) with decreasing rainfall (see online Table S5). For those assessing temperature effects, most showed a negative effect on birth rates (13 of 17 studies) and survival (five of five studies) with increasing temperatures (see online Table S5).

Landscape condition and climate appear to have substantial effects on demographic rates in plant and animal populations, with absolute effect sizes of 0.5–0.7 for all demographic rates except animal emigration (Fig. 4B). Given the large number of studies, there is good support for the positive effect of landscape condition on plant and animal birth rates and animal immigration (Fig. 4A). There were ≤ 5 studies on the effect of landscape condition on plant death rates, animal emigration and plant dispersal, but the directions of the relationships from these studies supported the conceptual model (Fig. 3).

IV. MECHANISMS AFFECTING DEMOGRAPHIC RATES

Here, we qualitatively review the mechanisms through which demographic rates in plant and animal populations are affected by changed landscape condition and climate change.

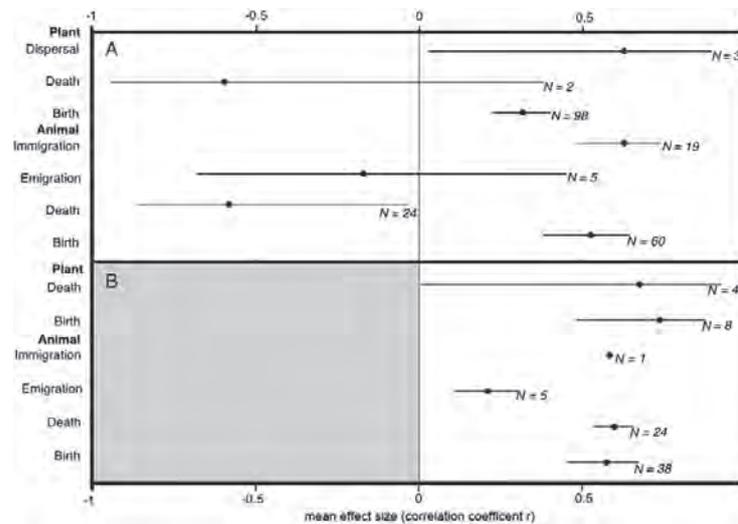


Fig. 4. (A) Mean effect sizes (\bar{r}) of landscape condition parameters and (B) mean absolute effect sizes ($\bar{|r|}$; values between 0 and 1 only) of climate parameters on measures of birth rates, death rates, immigration and dispersal in plant and animal populations. Error bars are 95% confidence intervals. The number of data points (study \times species) is shown by N .

(1) Birth rates

Our quantitative review shows strong evidence for a negative effect of changed landscape condition on birth rates in plant and animal populations. The most proximate effect on plant reproduction in changed landscapes is usually pollination limitation (Aguilar *et al.*, 2006). Changed landscape condition results in declines in native pollinator populations and reduced pollinator visitation due to isolation, which reduces fruit production and seed set (Wilcock & Neiland, 2002; Gómez *et al.*, 2010). Allee effects, including inbreeding and genetic erosion, affect mate availability and seed set and interact with pollen limitation to reduce population viability (Wagenius, Lonsdorf & Neuhauser, 2007; Young, Broadhurst & Thrall, 2012). Wind-pollination may be disrupted by fragmentation, possibly causing inbreeding (Jump & Peñuelas, 2006). Reduced seed dispersal or increased seed predation occur in modified landscapes (Benitez-Malvido, 1998; Tallmon *et al.*, 2003). Loss and degradation of vegetation alters the conditions for germination and seedling establishment, including light environments (Uriarte *et al.*, 2010), microclimatic conditions (Jacquemyn *et al.*, 2003; Werner & Gradstein, 2008), and wind erosion (Li *et al.*, 2009). Grazing by domestic stock causes trampling and herbivory of seedlings (Jansen & Robertson, 2001). These declines in plant recruitment have large effects on population viability (Bruna & Oli, 2005).

Vegetation loss and fragmentation influence birth rates in animal populations by affecting access to food resources (Mbona, Wiczakowski & Munene, 2009) and by reducing food and resource levels in vegetation remnants (Zanette *et al.*, 2000). Increased nest predation and parasitism are

common in much-modified landscapes, particularly near vegetation boundaries (Lampila *et al.*, 2005). Decreased vegetation connectivity reduces mate availability (Cooper & Walters, 2002), including through inbreeding avoidance (Boudjemadi, Lecomte & Clobert, 1999; Stow & Sunnucks, 2004). Some plant and animal populations experience higher birth rates in changed landscapes, especially those with a preference for open or edge habitat (Mac Nally *et al.*, 2012), or through decreased competition for resources such as light (Neal, Hardner & Gross, 2010).

Climate had a strong effect on birth rates, affecting rates in several ways. Most studies reported decreased birth rates with increased temperature and decreased precipitation. Global temperatures have risen, and the frequency of hot days and of heat waves is likely increasing (IPCC, 2013). Increased annual temperatures and short-term heat waves may reduce germination of plants (Chidumayo, 2008; Shevtsova *et al.*, 2009). In animals, heat stress of parents may induce declines in neonatal survival (Griffin *et al.*, 2011) and decreased fecundity (Neveu, 2009). Higher temperatures may cause heat stress in young animals, leading to lower survival rates of young (Steenhof, Kochert & McDonald, 1997). Warm and dry conditions, such as those associated with El Niño events, may harm eggs and hatchlings by altering microclimate conditions in nests (Tomillo *et al.*, 2012), although warmer temperatures may increase hatching success (Beissinger, Cook & Arendt, 2005). Warmer temperatures may enhance the breeding success and survival of young and seedlings by reducing energy needs (Nielsen & Møller, 2006; Milbau *et al.*, 2009) and reducing the occurrence of severe winters that limit reproductive success (McIntyre & Schmidt, 2012). Warming may lengthen periods suitable for breeding and result in

increased birth rates and additional generations within an annual cycle (Jönsson *et al.*, 2009; Clarke & Zani, 2012).

Lower rainfall and increased drought frequency may affect plant birth rates through decreased fruit set (Ågren, Ehrlén & Solbreck, 2008) and seedling survival (Hallett, Standish & Hobbs, 2011). Reduced food-plant productivity and food availability during periods of low rainfall, such as in El Niño events, may depress fecundity (Dunham, Erhart & Wright, 2010), prevent reproductive maturation (Lima *et al.*, 2001), and lessen offspring survival (Silllett, Holmes & Sherry, 2000). Limited water availability for lactating females may affect juvenile survival (Dunham *et al.*, 2010). Lower water levels at aquatic breeding sites may result in increased ultraviolet radiation and heat exposure, which can affect hatching success (Blaustein *et al.*, 2012), increase the vulnerability of embryos to pathogens (Kiesecker, Blaustein & Belden, 2001), and desiccate tadpoles (Pechmann *et al.*, 1991). Heavy rains or snowfalls, which are expected to increase in frequency even in areas with decreased annual precipitation (IPCC, 2013), stress gestating females (Dunham *et al.*, 2010), and increase juvenile and egg mortality (Skagen & Adams, 2012).

Phenological changes triggered by climate changes such as earlier warming, may increase self-fertilization in monoecious plants or cause mistiming in the flowering of dioecious plants (Miller-Rushing *et al.*, 2010). While earlier breeding may benefit birth rates of some species (Nielsen & Møller, 2006), advances in breeding and flowering expose flower buds (Inouye, 2000, 2008), eggs and young (Lehikoinen *et al.*, 2009) to poor or more variable weather conditions (e.g. frosts or heavy rain) if seasonal climate patterns do not advance in concert. Changed climate conditions may delay breeding so that the young may experience adverse conditions later in the season (Waite & Strickland, 2006; Senapathi *et al.*, 2011), and may inhibit breeding altogether (Pankhurst & Munday, 2011). Phenological changes in plants can cause asynchrony with pollinators, increase exposure to florivores and granivores, and increase synchrony of flowering among species competing for pollinators (Miller-Rushing *et al.*, 2010). Phenological changes to a population or its biotic resource may affect birth rates if the two do not change in synchrony. Asynchrony between food needs during breeding and food availability arises from earlier breeding (Moss, Oswald & Baines, 2001), advancement of peak prey availability (Sanz *et al.*, 2003), advanced phenology of food and larval host plants (Parmesan, 2005; Post & Forchhammer, 2008), or changed timing of food peaks (Wolf *et al.*, 2009). Climate-induced asynchronies in resource availability and resource needs during breeding have caused population extinctions (McLaughlin *et al.*, 2002). For some species, earlier warming may increase synchrony with food resources, which can increase birth rates (Vatka, Orell & Rytönen, 2011).

Spring snow cover is decreasing in the northern hemisphere (Werner, 2011). Reduction of snow cover may decrease seedling survival by permitting increased herbivory (Brodie *et al.*, 2012) and by increasing exposure to frost (Bannister *et al.*, 2005). Sea levels are rising (IPCC, 2013), and this can affect birth rates through more frequent

flooding of coastal nesting sites (van de Pol *et al.*, 2010). Physiological stress from severe weather limits reproductive success of many animals (Dunham *et al.*, 2010).

Within species, the extents to which birth rates are affected by climate changes differ depending on the elevational (Munier *et al.*, 2010; Hargrove & Rotenberry, 2011) or latitudinal (Ontiveros & Pleguezuelos, 2003; Sanz, 2003) location of populations, with some populations experiencing opposite effects of climate on birth rates in different locations (Gaston, Gilchrist & Hipfner, 2005). Climate effects on other demographic characteristics, such as death rates or sex ratios can dampen or counter positive effects (Zani, 2008; Schwanz *et al.*, 2010).

The effects of both landscape change and climate are diverse, and it is possible that there will be interactions or additive effects of these pressures on birth rates. However, while studies on variables related to birth rates were the most numerous of the demographic rates, this does not necessarily reflect the proportional importance of birth rates to population viability. In many species, rates of adult survival have a greater influence on population growth rates than do birth rates (Sæther & Bakke, 2000; Bruna, Fiske & Trager, 2009).

(2) Death rates

Although rates of survivorship in established plants usually contribute more to plant population growth rates than reproduction and seedling dynamics, there has been more focus on the effects of landscape condition on plant reproduction (Bruna *et al.*, 2009). There have been few studies on the effects of landscape condition on plant death rates, but mortality increases in many species due to transformation of native forest to plantations (Jules, 1998), and increased wind turbulence and microclimate changes near vegetation boundaries with agricultural land (Laurance *et al.*, 1998; Werner, 2011).

Elevated death rates in changed landscapes may reduce population viability for animal species (Harper *et al.*, 2008; Li *et al.*, 2009). Diminished availability of resources can contribute to higher death rates in fragmented landscapes and in small vegetation remnants (Boudjemadi *et al.*, 1999; Doherty & Grubb, 2002). Death rates may be affected by higher predation and desiccation in degraded or cleared vegetation (Rothermel & Semlitsch, 2002; Harper *et al.*, 2008), including during dispersal (Cushman, 2006). Mortality during dispersal through much-modified landscapes affects sex ratios, birth rates (Banks *et al.*, 2005) and the persistence of populations (Brooker & Brooker, 2002).

High temperatures and heat waves (Jakalanemi, 2011; Andreello *et al.*, 2012) and low rainfall and drought (Toräng, Ehrlén & Ågren, 2010) increase plant death rates through physiological stress. Drought increases susceptibility and exposure to pest species that cause mortality (Kloeppel *et al.*, 2003). Mortality of trees from increased drought occurs in many forests around the world and is expected to become more frequent (Van Mantgem & Stephenson, 2007; Horner *et al.*, 2009).

Warmer temperatures and low rainfall can accelerate water loss and energy expenditure in animals, leading to chronic stress, desiccation or hyperthermia (Grafe *et al.*, 2004; Moses, Frey & Roemer, 2012), particularly if these climate changes occur during energetically demanding phases of a species annual cycle (Grosbois *et al.*, 2006), or if temperatures approach or exceed the upper lethal limit of a species (Bale & Hayward, 2010). High temperatures increase population death rates (Grosbois *et al.*, 2006; Griffiths, Sewell & McCrea, 2010) and the frequency of catastrophic mortality events (McKechnie & Wolf, 2010). While increased temperatures may improve survival rates in some animals that experience cold stress, earlier melting of protective snow layers increases death rates by exposing animals to deleterious weather conditions, such as freezing rain and cool air temperatures (Bale & Hayward, 2010; Fisher & Davis, 2011) and increases predation risk (Lindström & Hörnfeldt, 1994). In cooler climates, elevated temperatures may increase survival rates for organisms near their lower thermal limits (Walther *et al.*, 2002; Frenot *et al.*, 2005). Asynchronies in the life cycles of predator and prey may increase the survival of the prey species, particularly if the prey is limited by predation rather than by food availability (Miller-Rushing *et al.*, 2010).

Increased frequency of high-energy weather events, such as hurricanes, storms and heavy rainfall, increase death rates in plants (Van Mantgem & Stephenson, 2007) and animals (Langtimm & Beck, 2003). Severe rain, snow or wind events cause mass mortality events (Newton, 2008a). Death rates increase with fewer food and foraging resources in the aftermath of intense weather events (Wiley & Wunderle, 1993).

Drought and much reduced rainfall can increase death rates through decreased food availability for terrestrial animals (Silleet *et al.*, 2000; Frick, Reynolds & Kunz, 2010), particularly when these occur during crucial times of breeding and survival. Climate oscillations affect food availability, and therefore death rates (Sandvik *et al.*, 2005; Morrison *et al.*, 2011).

While we have detailed several predicted and observed effects of both landscape condition and climate change on mortality, there has been relatively little research that measures the effects of these processes on death rates, and their subsequent effect on population viability. A better understanding of the effects of major anthropogenic pressures on death rates will be particularly important for those species whose population viability is most acutely affected by death rates, such as long-lived species (Sæther & Bakke, 2000).

(3) Emigration and immigration

Given that adult terrestrial plants are sedentary, emigration and immigration mostly is through the transport of seeds, fruits or vegetative propagules by animals, wind or water (Raulings *et al.*, 2011) and does not constitute the loss of an adult from the donor population *per se*. Increased isolation of plant populations and declines in seed-disperser populations (Cordeiro & Howe, 2003) inhibit biotic and abiotic seed dispersal, particularly for heavy-seeded species (Hewitt &

Kellman, 2002; McEuen & Curran, 2004), with potentially substantial effects on population viability (Hewitt & Kellman, 2002). Gene flow of plants predominantly is through the dispersal of pollen by biotic vectors and physical transmission (Ellstrand, 1992), which can be impeded by declines in landscape condition and climate change (Section IV.1).

The loss, fragmentation and degradation of native vegetation increase emigration rates and decrease immigration rates in animal populations, which affect population size and hence population viability, but the evidence for these expectations is weak (Section III). Reduced immigration can lead to skewed sex ratios (Harrison *et al.*, 2012), inbreeding (Daniels, Priddy & Walters, 2000), disruption of mating systems (Pavlova *et al.*, 2012) and mate limitations (Stow & Sunnucks, 2004), which decrease population viability.

Low emigration rates generally occur when habitat and resources are ample (Baguette, Petit & Queva, 2000). If a site is rich in resources, immigration is likely to be higher because the immigrants are attracted by the presence of numerous conspecifics (Buechner, 1987) and highly suitable habitat (for the species) increases the 'attractiveness' of sites for recolonizing individuals (Doerr, Doerr & Jenkins, 2006).

Populations in high-intensity human land-use areas or that are experiencing low resource availability are more likely to experience emigration, and, in extreme circumstances, this can cause extinction (Lin & Batzli, 2001; Mac Nally *et al.*, 2009). Individuals are more likely to emigrate if they experience low reproductive or pairing success (Bayne & Hobson, 2002; Zitske, Betts & Diamond, 2011).

Small and isolated vegetation remnants generally attract fewer immigrants (Wauters *et al.*, 1994; Holland & Bennett, 2010). Decreased dispersal success caused by death during dispersal or the inability to locate appropriate habitat in high-intensity land-use areas lowers immigration rates (Matthysen, 1999; Püttker *et al.*, 2011) and reduces population viability, even in mobile animals, such as birds (Cooper & Walters, 2002; Robles *et al.*, 2008). Measurements of genetic connectivity among populations suggest decreases in dispersal in fragmented landscapes (Vos *et al.*, 2001). These measures, when combined with direct measures of movement, have the potential to help tease out the effects of landscape condition and other pressures on immigration and emigration rates (Lowe & Allendorf, 2010).

Warmer temperatures can increase animal emigration rates (Pärn *et al.*, 2011; Franzén & Nilsson, 2012) and dispersal distances (Cormont *et al.*, 2011), but may cause disparities in dispersal between the sexes (Merckx, Karlsson & Van Dyck, 2006). Increased atmospheric instability caused by warmer temperatures induces long-distance wind dispersal of seeds (Kuparinen *et al.*, 2009) and small invertebrates (Coulson *et al.*, 2002) by increasing convective turbulent airflow. Warmer temperatures may discourage juvenile dispersal (Massot, Clobert & Ferrière, 2008) and increase dispersal mortality due to heat stress (Henry, Sim & Russello, 2012). Lower rainfall can decrease vegetation quality in high-intensity land-use areas, discouraging

emigration between fragments of native vegetation (Blaum *et al.*, 2012). Climatic events such as El Niño Southern Oscillation (ENSO) phases and consequent declines in food resources may trigger irruptive migrations of animals (Holmgren *et al.*, 2006; Lindén *et al.*, 2011).

Studies that use niche models to predict changes in species distributions predict elevational and latitudinal shifts in response to climate exposure, assuming colonization of newly suitable climate conditions (Fordham *et al.*, 2012). The structure and condition of many human-dominated landscapes are likely to impede colonization (Opdam & Wascher, 2004). Although organisms have responded to climate changes through migration and adaptation in the past, the barriers imposed by human land use and the unprecedented rate of climate change are unlikely to allow the predicted range shifts in many species to occur (Davis & Shaw, 2001). Range shifts are inhibited in much-modified landscapes, and may stall where the amount or cohesion of habitat is below thresholds necessary for population persistence (Opdam & Wascher, 2004). Fragmented vegetation may be disproportionately affected (higher mortality or die-back) by climate change (Bennett *et al.*, 2013), creating further barriers to climate-induced range shifts. Some species may be unimpeded by modified landscapes and this will affect species interactions in receiving habitats (Menéndez *et al.*, 2008). For example, landscape and climate change have increased the distribution and abundance of the despotic noisy miner (*Manorina melanocephala*) in eastern Australia. This has caused local emigration and a lack of immigration of small-bodied birds in fragmented vegetation where the species is present (Maron *et al.*, 2013).

To gauge the effects of climate change on species distributions, an understanding of the effects of climate on immigration and emigration rates and the processes of dispersal is vital, particularly in changed landscapes where these rates are already affected.

V. SYNTHESIS AND FUTURE WORK

Demographic rates are rarely the focus of studies on the effects of human pressures on native populations of plants and animals. However, these effects can be substantial and their identification enables a better understanding of the mechanisms through which pressures affect population viability. That vegetation loss, fragmentation and degradation affect demographic rates in plant and animal populations is not unexpected given the widespread declines in biodiversity that have been seen as a result of these pressures (Foley *et al.*, 2005; Butchart *et al.*, 2010). Our finding that the mean effect of climate on demographic rates is of comparable magnitude to changes in landscape condition is significant and supports recent assertions that climate change will become as, or more, important in species declines and extinctions in coming decades (e.g. Mantyka-Pringle *et al.*, 2012).

The relative effects of climate on demographic rates probably are underestimates. Most studies assess

relationships between general climate measures, such as annual temperature or seasonal precipitation within average ranges of year-to-year variation. The characteristics of relationships between demographic variables and climate variations are likely to change once changes in climate fall outside the average range. The effects of climate variables on demographic rates may become greater, new effects may emerge, or the direction of relationships may change. There are likely to be critical windows of climate effects on population parameters, where climate conditions at very specific times in species life cycles are disproportionately important to population viability (Lada *et al.*, 2013). Assessing general trends in climate and demographic rates may not detect the true size of the effects on population viability that will occur if changes in climate occur during critical windows. Critical thresholds may exist, such as where temperatures exceed lethal limits (Somero, 2010). Studies that measure demographic responses to climate conditions within the average range are unlikely to detect such responses. While the studies we reviewed assumed monotonic relationships between pressures and demographic variables, physiological responses to temperature are commonly asymmetric, such that a positive response to temperature may be reversed once an optimal level is reached (Sinclair & Chown, 2003).

Climate change may introduce new pressures to otherwise viable populations, or may cause the decline of populations in changed landscapes faster than otherwise expected. Decreases in rainfall and increases in temperature probably will have deleterious effects on many populations, although some taxa almost certainly will benefit. Small populations have less capacity to evolve rapidly to changed conditions (Willi, Buskirk & Hoffmann, 2006), so climate change may have a cascading effect on the viability of populations that have been affected by changed landscape condition. Some species will have increased population viability with the amelioration of limiting climate conditions. Changes in population viability in either direction will affect species interactions, with disruptions for communities (Sorte & White, 2013). A greater focus on the relationships between climate conditions and demographic rates is needed to produce better predictions for likely impacts of climate changes on animal and plant populations. A more complete understanding of the effects on immigration and emigration must improve predictions of range shifts. Identification of the demographic rates most affected by projected climate changes will assist with better planning for climate adaptation.

Populations in changed landscapes may decline faster than expected with the added pressures arising from climate change. This is important in making predictions about population size in response to pressures such as habitat loss, including considerations of critical thresholds (Swift & Hannon, 2010), which could be reached earlier than expected with the added imposts of climate pressures and their effects may be synergistic (Mantyka-Pringle *et al.*, 2012). Landscape modification may hinder or reverse the expected

population growth in response to changed climate conditions (Warren *et al.*, 2001). Whether the effects of landscape condition and climate on demographic rates are additive or multiplicative (or for some species, opposing), is a core question.

While our review highlights some mechanisms through which the major anthropogenic pressures affect population viability, there is a clear need for more data. A more comprehensive understanding of these relationships will contribute greatly to improving the effectiveness of conservation policies and management actions. Specifically, there is a need for expanding research beyond North America and Europe, and we suggest that the most important areas for conducting this research are those that are predicted to experience the greatest changes in climate conditions. Warming is likely to occur most rapidly in the polar regions, while mid-latitude and sub-tropical dry regions are likely to be most affected by decreased precipitation (IPCC, 2013). There is a dearth of research into the effects of climate on plant demographic rates despite climate change being the most commonly cited factor in the extinction and endangerment of plant species (Mora & Zapata, 2013).

VI. CONCLUSIONS

(1) Given their intimate connection with population viability, demographic responses provide a critical indication of likely changes in extinction risk in response to human pressures.

(2) Changes in landscape condition generally have a negative effect on birth and immigration rates in plant and animal populations, and increase death and emigration rates. We predict that climate change will have a negative effect on birth and immigration rates, and a positive effect on death and emigration rates, although we did not quantitatively assess this.

(3) Despite the recognition of landscape change as the major driver of biodiversity loss, the effects of climate on demographic rates in plant and animal populations are of equivalent magnitude. This supports consideration of climate change as a major driver of population viability, of similar importance to human land-use change.

(4) A more comprehensive understanding of the rate and size of the effects of pressures on demographic rates among taxa and regions will greatly assist management attempts to arrest species declines and extinctions.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Search terms used to locate studies that measured the effect of climate and landscape condition on demographic rates.

Table S2. Search terms used to locate studies that measured the effect of climate and landscape condition on variables related to demographic rates.

Table S3. List of species used for the calculation of mean effect sizes for climate and landscape condition on population vital rates.

Table S4. Breakdown of individual studies (December 2012 and earlier) that measured demographic responses to landscape condition and climate by region and taxonomic group.

Table S5. Subset of studies (from online Table S3) that showed effects of temperature and rainfall variables on birth or death rates.

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Chapter 3

A bust but no boom: responses of floodplain bird assemblages during and after prolonged drought

A bust but no boom: responses of floodplain bird assemblages during and after prolonged drought

Katherine E. Selwood^{1*}, Rohan H. Clarke¹, Shaun C. Cunningham^{2,3}, Hania Lada³, Melodie A. McGeoch¹ and Ralph Mac Nally³

¹School of Biological Sciences, Monash University, Melbourne, Vic., 3800, Australia; ²Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Vic., 3125, Australia; and ³Institute for Applied Ecology, The University of Canberra, Bruce, ACT 2617, Australia

Summary

1. Climate change alters the frequency and severity of extreme events, such as drought. Such events will be increasingly important in shaping communities as climate change intensifies. The ability of species to withstand extreme events (resistance) and to recover once adverse conditions abate (resilience) will determine their persistence.

2. We estimated the resistance and resilience of bird species during and after a 13-year drought (the ‘Big Dry’) in floodplain forests in south-eastern Australia.

3. We conducted bird surveys at the beginning and end of the Big Dry, and after the abrupt end to the drought (the ‘Big Wet’), to evaluate species-specific changes in reporting rates among the three periods. We assessed changes in bird-breeding activity before and after the Big Wet to estimate demographic resilience based on breeding.

4. Between the start and the end of the Big Dry (1998 vs. 2009), 37 of 67 species declined substantially. Of those, only two had increased reporting rates after the Big Wet (2009 vs. 2013) that were equal to or larger than their declines, while three partially recovered. All other declining species showed low resilience: 25 showed no change in reporting rates and seven declined further. The number of breeding species and total breeding activity of all species declined after the Big Wet, and there was no change in the number of young produced.

5. The Big Dry caused widespread declines in the floodplain avifauna. Despite the drought being broken by 2 years of well-above-average rainfall and subsequent near-average rainfall, most species showed low resilience and there was little indication that overall breeding had increased. The effects of drought appeared to be pervasive for much of the floodplain avifauna, regardless of species traits (species body mass, fecundity, mobility or diet). Ecosystems such as these are likely to require active management and restoration, including reinstatement of natural flooding regimes, to improve ecological condition, to enhance resistance and resilience to extreme climate events.

Key-words: climate variability, demography, extreme events, Millennium Drought, Murray Darling Basin, population viability, rainfall, recovery

Introduction

There is strong evidence that global warming is causing latitudinal and altitudinal changes in species distributions (Parmesan & Yohe 2003), and is altering the phenology of species, which can subsequently affect demography and population viability (Miller-Rushing *et al.* 2010). Research into the effects of climate change has focused on responses

of biota to gradual shifts in climate conditions such as increasing temperature. However, extreme climatic events, such as droughts and heat waves, can have almost immediate consequences for populations (McKechnie & Wolf 2010). Extreme events can disrupt population processes and more substantially shape communities than gradual changes in mean conditions (Gutschick & BassiriRad 2003).

Drought is increasing in frequency and severity as climates change in many parts of the world, particularly in already dry regions (Hartmann *et al.* 2013). Droughts are periods when precipitation or where soil moisture is well

*Correspondence author. E-mail: katherine.selwood@monash.edu

below average, and water levels in rivers, lakes and groundwater are low (Leblanc *et al.* 2012). Severe droughts induce widespread tree mortality and declines in forest condition, which can disrupt food webs (Carnicer *et al.* 2011). Food availability is lessened, and animals are physiologically stressed, causing mortality and reduced recruitment (Selwood, McGeoch & Mac Nally 2015). The ecological effects of drought can persist if ecosystems have too little time to recover between successive droughts (Saatchi *et al.* 2013).

To persist, populations must absorb pressures ('resistance') and recover when adverse conditions abate ('resilience', Harrison 1979). The resistance and resilience of species to climate change will be influenced by the severity, geographical extent and duration of climate events, rates at which resources are replenished when extreme conditions abate, and availability of refugia (Bennett *et al.* 2014; Selwood *et al.* 2015a).

Species resistance and resilience depend on their traits (Nimmo *et al.* 2015). Important traits include the capacity for individuals to survive low food availability and high physiological stress, temporarily move to more clement locations, or to respond quickly to improved conditions. Small-bodied species may be more resilient to pressures because they reach reproductive maturation sooner (Isaac *et al.* 2009) and fare better than larger animals in warm conditions because thermoregulation of smaller animals is more efficient than in larger animals (Gardner *et al.* 2011). High fecundity may allow populations to replace quickly mortality losses and recover from population declines (Isaac *et al.* 2009), particularly for species that quickly can initiate breeding in response to rainfall (Zann *et al.* 1995). Mobility may confer resistance and resilience because nomadic and migratory species can track favourable conditions and food supply, which may enable them to better survive extremes (Mac Nally & McGoldrick 1997). Diet may affect species resistance and resilience because climate events such as drought can differentially affect food resources (Bennett *et al.* 2014).

Tracking abundance or species occurrence during and after climate events provides information on the relative resistance and resilience of species (Bennett *et al.* 2014). However, long-term studies before, during and after extreme climatic events are rare, and so estimating population trajectories can be difficult (Lindenmayer & Likens 2009). Evaluating demographic responses to the onset and release of pressures provides insight into population trajectories and the mechanisms causing population change because demographic responses precede changes in abundance or occurrence (Selwood, McGeoch & Mac Nally 2015). A population that has not increased in abundance after a pressure is relaxed but that increases in breeding activity is likely to recover if other demographic rates are unaffected.

The El Niño-Southern Oscillation, Inter-decadal Pacific Oscillation, Indian Ocean Dipole and Southern Annular Mode climate systems all appear to contribute to periodic

phases of drying in south-eastern Australia that can bring multiyear droughts (Verdon-Kidd & Kiem 2009). While droughts are relatively common in south-eastern Australia, climate change appears to be causing protracted, more severe drying (Murphy & Timbal 2008). An example of the type of severe drought that is predicted to become more common with a warming climate is the 'Big Dry' (or 'Millennium Drought') in south-eastern Australia, a 13-year (1997–mid-2010) drought associated partly with global climate change (Murphy & Timbal 2008). The Big Dry was the most severe drought in the region since records began 120 years ago (Leblanc *et al.* 2012). Significant declines in precipitation, run-off, soil moisture and groundwater occurred during this period, which substantially reduced inflows into Australia's largest river system, the Murray–Darling Basin (Leblanc *et al.* 2012). Inundation of floodplains was much reduced in extent and frequency, resulting in widespread mortality and dieback of the floodplain forests (Cunningham *et al.* 2009b). The Big Dry was broken by the 'Big Wet' in mid-2010, which was the second wettest 2-year period in Australian records (BOM 2012).

Here, we report on the resistance and resilience of woodland birds in floodplain forests of south-eastern Australia to the Big Dry. The abundance, species richness, species occurrence and breeding activity in these forests are closely linked to forest stand condition of the dominant tree species, the river red gum *Eucalyptus camaldulensis* Dehnh., whose life cycle depends on sufficient water from rainfall and flooding (Mac Nally *et al.* 2014). We conducted bird surveys at the beginning and end of the Big Dry, and after the Big Wet, from which we evaluated: (1) changes in species occurrence throughout the drought (resistance); (2) changes in species occurrence after the drought broke (resilience); and (3) changes in breeding activity between the end of the Big Dry and the Big Wet (breeding resilience). We explored whether species' biological and life-history traits (body mass, fecundity, mobility and diet) were related to their resistance and resilience to drought.

Materials and methods

STUDY AREA

The floodplains of Barmah Forest (centred on 35°53' S, 145°07' E) and Gunbower Island (centred on 35°47' S, 144°16' E) along the Murray River in south-eastern Australia consist of open forests and woodlands dominated by the river red gum (Cunningham *et al.* 2009b). The understorey consists of shrubs, sedges and grasses, and groundcover includes much fallen timber and litter (Mac Nally *et al.* 2014). The climate is temperate semi-arid, with a mean annual rainfall (for period 1961–1990) of 409–433 mm (Kerang and Mathoura State Forest weather stations; accessed 12 January 2015), and high annual evaporation (c. 1600 mm) (BOM 2015). Mean monthly maximum temperature at both locations ranges from 13 to 31 °C (BOM 2015). High flows historically flooded these forests at a mean interval of 5 years, but river

regulation has increased the interflood return time to c. 11 years, and climate projections suggest return intervals of 21 years by 2030 (Mac Nally *et al.* 2011).

STUDY SITES

This study was conducted in three survey programmes: 1998 (early Big Dry), 2009 (late Big Dry) and 2013 (post-Big Wet). The 1998 data were collected for a project on the effects of vegetation structure on avifaunas (Mac Nally *et al.* 2001), and at that time, the Big Dry was not anticipated. Fourteen sites were surveyed in 1998, seven at Gunbower Island and seven at Barmah Forest (Fig. 1). The 2009 and 2013 survey programmes were designed to measure the effects of the Big Dry, and its cessation, respectively. In 2009, 24 sites at Gunbower Island and 21 sites at Barmah Forest were surveyed (Fig. 1). In 2013, we revisited 21 of the sites at Gunbower Island that were surveyed in 2009; Barmah Forest was inaccessible in 2013 due to extensive flooding. Sites surveyed in 1998 were different to those surveyed in 2009 and 2013 but had similar geographical spread and range of forest stand conditions (Fig. 1).

BIRD SURVEYS

The three survey programmes used a similar standard protocol for bird surveys (Mac Nally *et al.* 2001, 2014). Each site was visited eight times in the 1998 survey programme and five times in the 2009 and 2013 programmes, so we used reporting rates of

species as the response variable for estimating changes over the Big Dry and Big Wet to account for differences in survey effort. Bird surveys were carried out by very experienced single observers (G. Horrocks, C. Tzaros or L. Conole in 1998, HL in 2009, KES in 2013) surveying a 2-ha area. Calibration surveys were conducted among observers to ensure consistent recording. River red gum forests consist of widely spaced, relatively short trees (20 m) with moderate foliage cover (<50%), and there is little understorey, which make bird detectability high (mean detection distance 23.9 m, Fig. S2, Supporting information). Survey areas in all three programmes were 2 ha: methods in 2013 were identical to those in 2009 (Mac Nally *et al.* 2014), but the 1998 survey sites were transects rather than circles (Mac Nally *et al.* 2001). Surveys were not conducted during rain, moderate-to-high winds or in high temperatures (>35 °C) because these conditions reduce bird activity. Sites were surveyed in randomized order in each round to avoid systematic sampling biases from diel patterns of bird activity.

BREEDING ACTIVITY

We measured bird-breeding activity in 2009 and 2013. We used breeding activity as a measure of recruitment because it can be efficiently measured for many species at many locations (Selwood, Mac Nally & Thomson 2009). For each species, we scored behaviours and other observations that provided evidence of breeding, with each activity given a score based on a consensus weighting derived from the opinions of 25 expert Australian

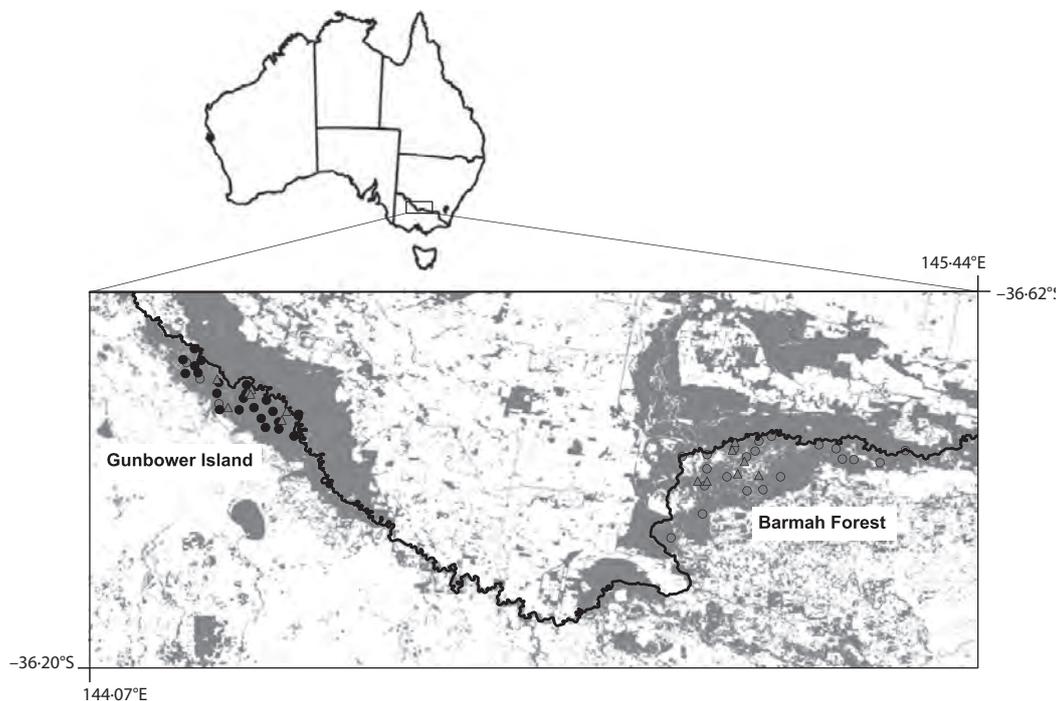


Fig. 1. Location of sites from programme one (1998, grey triangles), programme two (2009, grey circles) and both programmes two and three (2009, 2013, black circles). Light grey shading is native wooded cover.

ornithologists, which are detailed elsewhere (Mac Nally 2007a). Only the behaviour with highest score for a given nest or territory was used for analyses. For example, if courtship (weighting 3.0) and presence of juveniles (weighting 7.5) were scored for one nest, then 7.5 would be assigned. Nest locations were recorded with GPS and sketch maps. We summed breeding scores for all territories and species in each year for an overall measure of bird-breeding activity at each site ('total breeding score'). We summed the number of young produced at each site for all species in each year to estimate breeding output ('number of young'). We analysed changes in the number of breeding species by comparing the number of species at each site that showed breeding behaviour ('number of breeding species'). We assessed species-specific changes in total breeding scores for the four most common breeding bird species, which accounted for 50% of total breeding activity.

STAND CONDITION ESTIMATES

Ground measurements of forest stand condition were conducted in 2009 and 2013 in a 50 m × 50 m quadrat at the centre of each 2-ha bird survey plot in each year. A stand condition score (0–10) was calculated as the mean of three equally weighted variables: percentage live basal area, plant area index and crown extent, as defined in Cunningham *et al.* (2009b). Stand condition scores were allocated to one of five classes: good (8.1–10), declined (6.1–8), poor (4.1–6), degraded (2.1–4) and severe (0–2).

Stand condition was retrospectively estimated from spatially explicit models using historical Landsat imagery for the 1998 sites (Cunningham *et al.* 2009a,b, 2011). Available estimates of stand condition around the survey period included 1990, 2003 and 2006–2009, with stand condition during early drought (2003) considered the most representative for the 1998 survey.

TRENDS IN SPECIES REPORTING RATES

We estimated changes in individual species reporting rates during the Big Dry to estimate species resistance to drought (1998 vs. 2009), after the Big Wet (2009 vs. 2013) to estimate species resili-

ence once the drought ended, and over the entire period (1998–2013). We analysed only diurnal, terrestrial birds because raptors range too widely.

We defined the reporting rate for a species at site *i* in period *j* (1: 1998, 2: 2009, 3: 2013) as the probability p_{ij} of observing the species during a single survey, and modelled the number of observations as a Binomial variable: $y_{ij} \sim \text{Binomial}(n_{ij}, p_{ij})$. We used a binomial model to estimate changes in reporting rates p_{ij} for each species over the Big Dry (1998 vs. 2009) and following the Big Wet (2009 vs. 2013), while accounting for the effect of yearly, site-specific forest stand condition (SC_{ij}), which affects species occurrence and abundance (Mac Nally *et al.* 2014). We used a hierarchical Bayesian model with fixed and random slope parameters to account for spatial variation in trends and in covariate effects:

$$\begin{aligned} \text{logit}(p_{ij}) &= \beta_0 + \beta_{\text{forest}}^1 D_{j>1} + \beta^2 D_{j=3} + \beta^3 SC_{ij} + \epsilon_{\text{forest}} + \epsilon_{\text{site}}; \\ \beta^n &\sim \text{Normal}(B^n, \sigma_n^2). \end{aligned}$$

Here, the reporting rate p_{ij} is modelled on the log-odds scale as a function of: an overall mean reporting rate in the first period (β_0), spatial random intercepts ϵ_{forest} , ϵ_{site} , parameters that estimate change in reporting rate between the first and second survey periods, β^1 , and between the second and third periods, β^2 , and covariate β^3 , which estimates the effect of stand condition. Parameters β^n consist of an overall mean (fixed) effect, B^n , and random variation among forests/sites σ_n^2 . Different responses to water availability have been seen in other taxa in each forest, probably due to hydrological differences in the floodplains (Lada, Mac Nally & Taylor 2008), and there were some differences in the bird assemblages in each forest (Table S1, Supporting information). Therefore, we included a random slope for forest for β^1 to allow for potentially different responses of species in each forest. We did not include a random slope for forest for β^2 because only Gunbower Island was surveyed in the third survey period, or for β^3 because the effect of stand condition on bird assemblages is consistent between the two forests (Mac Nally *et al.* 2014). The forest and site random effects were modelled as independent and identically distributed. $D_{j>1}$ is binary (late drought

Table 1. Definitions of the three life-history characteristics used for modelling species-specific responses to the drought and its cessation. Sources are listed in the order of the sequence to which they were referred to for information. HANZAB refers to species reference in Marchant & Higgins (1990); Higgins & Davies (1996); Higgins (1999); Higgins, Peter & Steele (2001); Higgins & Peter (2002); or Higgins, Peter & Cowling (2006). Mean and range of life-history traits among species are presented

| Life-history trait measure | Description | Sources | Mean and range |
|----------------------------|--|---|-----------------|
| Fecundity | Mean clutch size per female multiplied by the mean number of clutches per female per year | Passerines: Yom-Tov (1987); Non-passerines: HANZAB; Beruldsen (2003) | 4.9; 1.0–28.6 |
| Body mass | Mean adult body mass (g) | HANZAB; Baker (1997); Dunning (2007) | 153.6; 6.0–3750 |
| Mobility | 0 = resident, 1 = partial migrant (evidence of residential and migratory/nomadic populations), 2 = full migrant (all populations are migratory/nomadic). | Chan (2001); Griffioen & Clarke (2002); Blakers, Davies & Reilly (1984) | 0.7; 0–2 |
| Diet | Primary food source: Carnivore, frugivore, granivore, herbivore, insectivore, nectarivore. | HANZAB; Schodde & Tidemann (1986) | NA |

and Big Wet = 1), $D_{j=3}$ is binary with Big Wet = 1, stand condition ranges from zero to ten. We used linear combinations to estimate the marginal posterior distribution for the long-term trend in occurrence over the entire survey period, 1998–2013 ($B^1 + B^2 = B^{\text{lt}}$).

SPECIES TRAITS

We obtained information on biological and life-history traits that plausibly may influence species resistance and resilience to drought: fecundity, adult body mass, mobility and diet (Table 1). Although there are numerous other measures for estimating life-history traits, we were restricted to information that was available and consistent for all species (Table 1).

We used phylogenetic mixed models, implemented in R (R Core Team 2012) using the package MCMCglmm (Hadfield 2010) to test for an effect of species traits on species trends during the drought (B^1), Big Wet (B^2) and over the entire period (B^{lt}). We modelled fecundity (the mean number of eggs per year), adult body mass, mobility and dietary guild as fixed effects, and included a phylogeny of our species constructed from Jetz *et al.* (2012) to account for species relatedness and to estimate the phylogenetic heritability of species trends. Models were weighted by the inverse variance of the species-specific posterior distributions of species change trends. We used uninformative priors for all parameters. Posterior distributions were sampled with chains of 100 000 iterations after 15 000 iteration burn-in periods (discarded) and a thinning rate of 100. There were three independent chains for each model, and convergence was checked using the Gelman–Rubin diagnostic (Plummer *et al.* 2006).

TRENDS IN BREEDING ACTIVITY

We estimated trends in seven breeding activity response variables: total breeding score R^1 , number of young (all species) R^2 , number of breeding species R^3 , and total breeding scores for the most common breeding species: brown treecreeper (*Climacteris picumnus* Temminck & Laugier) R^4 , white-plumed honeyeater (*Lichenostomus penicillatus* Gould) R^5 , buff-rumped thornbill (*Acanthiza reguloides* Vigors & Horsfield) R^6 and white-winged chough (*Corcorax melanorhamphos* Vieillot) R^7 . Each response variable was modelled with a Gaussian distribution using a hierarchical Bayesian model:

$$R_{ij}^n = \delta_0 + \delta_1 D_{j=3} + ZSC_{ij} + \varepsilon_{site}$$

Here, the response variable at site i in year j (R_{ij}) is a function of the mean for the second period δ_0 , site random intercept ε_{site} , a change parameter δ_1 that estimates the change in the response variable R^n between the second and third period, and covariate Z , which accounts for the effect of stand condition.

MODEL FITTING

Models for estimating temporal trends in species reporting rates and breeding were fitted using integrated nested Laplace approximations using INLA (Rue, Martino & Chopin 2009, www.r-inla.org) in R (R Core Team 2012). INLA uses deterministic approximations to posterior marginal distributions for Bayesian inference (Rue, Martino & Chopin 2009). For all models, we considered a posterior probability of 0.9 as strong evidence that the

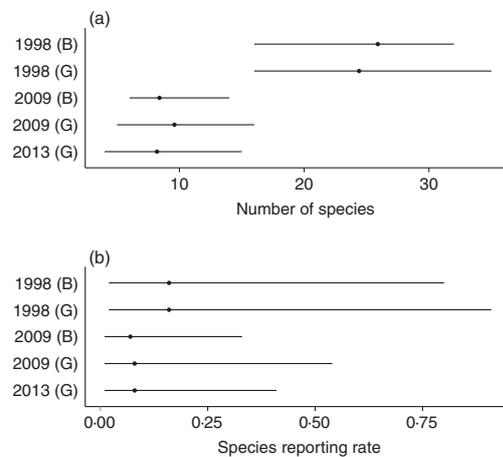


Fig. 2. Mean and range of (a) number of species recorded in one or more surveys at a site; and (b) reporting rate per species; at Barmah Forest (B) and Gunbower Island (G) in each survey year.

parameter had a positive [$\text{Pr}(\text{parameter} > 0) > 0.9$] or negative [$\text{Pr}(\text{parameter} < 0) > 0.9$] relationship to the response variable (Kass & Raftery 1995).

Results

SPECIES OCCURRENCE

Fifty-seven species were seen in 1998, 44 in 2009 and 41 in 2013; 31 species were common to all survey periods (Table S1). Species richness at each site (Fig. 2a) and the mean reporting rate per species (Fig. 2b) were highest in 1998, but were much reduced in 2009 and 2013.

TRENDS IN REPORTING RATES

Of the 67 species present in any of the three periods, there was strong evidence for declines in reporting rates for 37 species (55%) during the Big Dry, while just one species (white-winged triller *Lalage tricolour* Swainson) increased in reporting rate (Table S2, Supporting information). Just five drought declining species (14%) had increased reporting rates after the Big Wet including only two species (5%) with increases equal to or greater than their declines. The other species either declined further (eight species, 22%) or their reporting rates did not change (24 species, 65%). Over the entire period 1998–2013, 25 species (38%) declined, two increased (3%) and 40 species (60%) did not change (Table S2).

Of the 31 species that were present in all three survey programmes, reporting rates for 22 species (71%) declined during the Big Dry, with the rest showing little evidence of change (Fig. 3a). From 2009 to 2013, equal numbers of

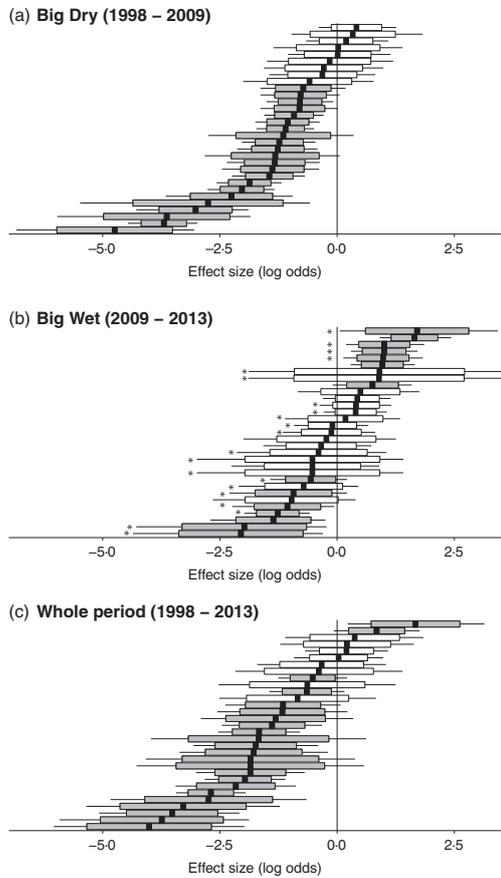


Fig. 3. Ranked changes in the reporting rate (log-odds) of bird species derived from Bayesian logistic regression between (a) 1998 vs. 2009, (b) 2009 vs. 2013 and (c) 1998 vs. 2013. Species represented are those that were present in all three survey periods. Horizontal bars show posterior distributions of change coefficients (log-odds transformed reporting rates) for each species: thick central horizontal line = posterior mean; bars extend to 80% credible intervals, lines extend to 95% CIs. Grey shading indicates a change in reporting rate with >90% certainty, white bars indicate <90% certainty. In (b), asterisks mark species that declined during the Big Dry with >90% certainty (a).

species showed declines and increases in reporting rates (7 species each, 23%), while most (17 species, 56%) did not show a change in reporting rates (Fig. 3b). Of the species that declined during the Big Dry, only five species (23%) increased in occurrence after the Big Wet, and two species (9%) had increases equal to or greater than their declines (Fig. 4). The other 17 (77%) declining species either declined further or did not change after the Big Wet (Fig. 4). Over the entire study period 1998–2013, 21 species (68%) showed overall declines, two (6%) increased and eight (26%) showed no change in reporting rates (Fig. 3c).

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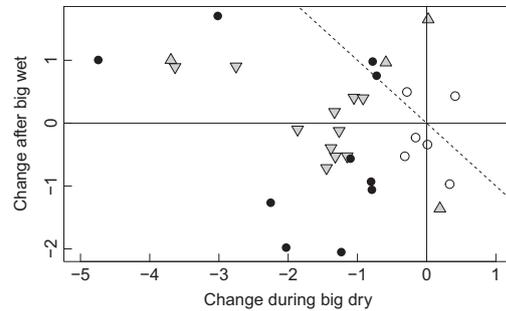


Fig. 4. Comparison of species-level coefficients for the Big Dry (1998–2009) and post-drought period (2009–2013) for species that were present in the three survey programmes. If recovery were complete, then all species would fall along the dashed 'one-to-one' line. Black circles show species that had a substantial change in reporting rates in both periods (with >90% certainty), hollow circles – no substantial change in reporting rate in either period (<90% certainty), downward triangles – substantial change during Big Dry (>90% certainty), upward triangle – substantial change during the Big Wet (>90% certainty).

SPECIES TRAITS

Species mobility appeared to have a negative effect on species trends in the post-drought period (1998–2009) and over the entire period (1998–2013), with a posterior probability of >0.90 for a negative effect in each period (Table S3, Supporting information). There was little evidence for effects of body mass, fecundity or diet on species trends in any comparison (Table S3). Phylogenetic heritability of species trends was low during the drought, post-drought period and overall (posterior mode of heritability <0.001, Table S3).

TRENDS IN BREEDING ACTIVITY

The total amount of breeding activity (R^1) among all species declined after the Big Wet ($\delta_1 = -5.66$, $\text{Pr}(\delta_1 < 0) > 0.90$), as did the number of species displaying breeding activities (R^3 ; $\delta_1 = -1.64$, $\text{Pr}(\delta_1 < 0) > 0.90$). There was no substantial increase in the number of young produced by all species (R^2 ; $\delta_1 = 0.09$, $\text{Pr}(\delta_1 > 0) < 0.90$).

Changes in breeding activity for three of the four species most commonly detected breeding paralleled the direction of their trends in reporting rates after the Big Wet: the white-plumed honeyeater (R^4) increased its breeding activity ($\delta_1 = 2.81$, $\text{Pr}(\delta_1 > 0) > 0.9$) and reporting rates (Table S2), the white-winged chough (R^7) showed no substantial change in breeding activity ($\delta_1 = 0.84$, $\text{Pr}(\delta_1 > 0) < 0.9$) or reporting rate (Table S2), and the brown tree-creeper (R^5) declined in both breeding activity ($\delta_1 = -4.61$, $\text{Pr}(\delta_1 < 0)$) and reporting rates (Table S2). Despite an increase in reporting rates (Table S2), breeding activity by the buff-rumped thornbill (R^6) declined after the Big Wet ($\delta_1 = -1.19$, $\text{Pr}(\delta_1 < 0) > 0.9$).

FOREST STAND CONDITION

Stand condition at sites surveyed in 1998 was 'good' at six sites (43%), 'declined' at seven sites (50%) and 'poor' at one site (7%). In 2009, five sites (11%) were in good condition, 24 in declined condition (53%), twelve in poor condition (27%), two (4%) in degraded condition and two in severe condition. At sites surveyed in both 2009 and 2013, the proportion of sites in good and declined conditions decreased, while the proportion in poor-to-severe condition increased (Fig. S1, Supporting information). Eleven bird species had a strong (posterior probability >0.90) positive relationship with stand condition, while eight species had strong negative relationships with stand condition (Table S2).

Discussion

RESISTANCE AND RESILIENCE

The Big Dry appeared to have had a severe effect on the floodplain forest avifauna. Many species declined during the drought (55% of species present in any period, 71% of species present in all three periods) and the magnitude of decline in most species was substantial (Fig. 3), indicating low resistance. A third of all species (31%) observed early in the drought were not seen in the late drought period, and fewer than half of these reappeared after the drought broke.

The wide geographical extent of the Big Dry (Verdon-Kidd & Kiem 2009) meant there could be no concurrent controls to allow us to infer strongly that the declines in the avifauna were caused by the drought. There seemed

to be no other major changes in conditions other than the degradation of forest stand condition (Mac Nally *et al.* 2014), for which we accounted. We would expect background population declines to be relatively low in these forests because the forests are extensive (>50 000 ha), unfragmented and relatively intact, unlike much of the other remnant vegetation in the region in which extinction debts are more likely (Ford 2011). Drought probably affected bird populations by: (1) increasing physiological pressures and (2) reducing resource availability (Fig. 5). Hot and dry climate conditions physiologically stress animals and may cause mortality or reduced fecundity, particularly if there is little free water to prevent dehydration (McKeechne & Wolf 2010). Long-term declines in water availability from reduced direct rainfall and floodplain inundation affect primary productivity and vegetation condition, decreasing food and habitat availability (Fig. 5). Declines in forest stand condition occurred in both forests during the Big Dry, with widespread loss of foliage cover and tree deaths (Mac Nally *et al.* 2014). Understorey vegetation also declined (Horner *et al.* 2012). Vegetation degradation probably resulted in lower food availability, including seed and nectar production and invertebrate abundance, and reduced availability of nesting materials and nesting sites. Reduced vegetation cover may have limited the availability of cooler microclimatic refuges for shelter during hot weather.

The proportion of birds affected and the magnitude of species declines probably were higher than our estimates because responses to the decline in stand condition were included in the change model for each species. Forest stand condition is positively associated with floodplain bird abundance, species richness and breeding activity, and condition declined in both forests during the Big Dry (Mac Nally *et al.* 2014), and again after the Big Wet at Gunbower Island sites (Fig. S1). Detectability probably increased during the Big Dry and later. These forests are relatively short (<20 m) with widely spaced trees, so that bird detectability generally is high (24 m). Given high detectability of birds in these forests, we do not expect the slight difference in bird survey method between 1998 and in 2009 and 2013 (i.e. transect vs. circular survey area) to have much affected the comparability of reporting rates in these periods. Nevertheless, the change in stand condition since 1997 (Mac Nally *et al.* 2014) led to an even more open forest structure with reduced canopy cover and foliage density. Therefore, the magnitude of declines that we report may underestimate the actual declines because detectability would have been greater in the latter two surveys (Fig. 5).

Resilience of the floodplain forest avifauna was low in the 3-year period following the break in the drought. The Big Wet in 2010–2011 was Australia's second wettest recorded 2-year period (BOM 2012), with extensive floodplain inundation (CEWO 2012). This was followed by near-average rainfall in 2012–2013 (BOM 2013, 2014), yet only five species increased in reporting rates

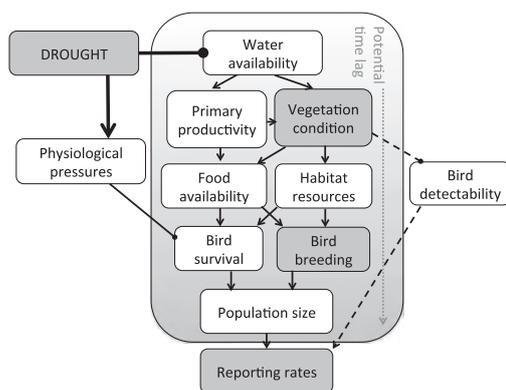


Fig. 5. Conceptual model illustrating the mechanistic pathways through which drought is likely to affect bird reporting rates. Arrows indicate relationships that promote the quantity or process to which the arrow is directed; solid circles have reducing effects. Dashed arrows indicate indirect pathways. Shaded grey boxes indicate entities that were measured in this study. Processes within the fading box are likely to experience time-lag in the direction of the grey dotted arrow.

by 2013 and just two species recovered fully by 2013. It is possible that there were time-lags in the responses of some birds to improved conditions (Fig. 5). However, we saw little recovery in bird-breeding activity between the end of the Big Dry in 2009 and the 2013. There is much less likely to be a lag in breeding activity following an improvement in conditions because demographic responses will precede changes in abundance or species occurrence (Selwood, McGeoch & Mac Nally 2015). We found declines in total breeding activity and no increases in the number of young or the number of breeding species, which suggests that lags in the recovery of reporting rates were unlikely.

Boom-and-bust patterns of flood and drought characterize arid and semi-arid Australia, and many species respond quickly to changes in resource availability (Pavey & Nano 2013). Many Australian bird species breed in response to rainfall (Keast & Marshall 1954), so we expected that breeding activity would have increased soon after the drought broke. For the four species that were assessed individually, only the white-plumed honeyeater showed an increase in breeding activity after the Big Wet, but this species appears to be tolerant of habitat modification and fragmentation (Mac Nally 2007b).

High rainfall and floodplain inundation should increase vegetative growth and primary productivity, providing more food such as nectar (Mac Nally *et al.* 2009), fruit, seeds (Cameron 2006) and invertebrates (Batzer & Wisinger 1996). However, forest stand condition had not improved in 2013 compared with 2009 (Fig. S1). The provision of vegetation resources used by birds can take years or decades to regenerate (Vesk *et al.* 2008), and mature trees killed by drought will not be replaced for decades (Horner *et al.* 2009). Lags in tree mortality may occur after drought (Bigler *et al.* 2007), and recoveries in vegetation condition after drought can be slow (Gutschick & BassiriRad 2003). If another drought were to occur prior to full recovery, then further declines in vegetation condition would be cumulative, with even fewer resources for the floodplain birds (Saatchi *et al.* 2013). The lack of resilience of the floodplain bird assemblages demonstrates that four years of average to well-above-average rainfall is inadequate to offset losses from a 13-year drought. Extended droughts broken by short but intense periods of high rainfall are projected for the region (Garnaut 2011). Although heavy rainfall can decrease breeding success and bird survival (Skagen & Adams 2012), we do not believe that the high annual rainfall in 2010 and 2011 negatively affected bird populations because there were only two days in each of 2010 and 2011 in which daily rainfall was above the long-term mean daily rainfall for that month (Gunbower Gee Tee Stud, accessed March 19 2015; BOM 2015).

While physiological pressures on individual birds may have lessened with the break in the drought, if there were subsequent increases in survival, these do not

appear to have translated into increased occurrence for most species or in breeding activity. Increasing temperatures in south-eastern Australia (Murphy & Timbal 2008) may have contributed to species declines and prevented the recovery of floodplain bird assemblages. Temperatures have remained well above average since 1995 (2012–13, BOM 2013, 2014). High temperatures increase physiological stress, which can increase mortality (McKeechne & Wolf 2010) and reduce birth rates (Steenhof, Kochert & McDonald 1997). The effects of reduced water availability during the Big Dry and ongoing high temperatures may have had a synergistic deleterious effect on the avifauna.

SPECIES TRAITS

Mobility seemed not to affect species resistance during the drought. Mobility would be unlikely to promote resistance in the Big Dry if more resources or more suitable habitats were not within migration distance. The Big Dry was geographically widespread, with most of south-eastern Australia subject to severe rainfall deficiencies (Verdon-Kidd & Kiem 2009). There were documented bird declines in upland forests (Stevens & Watson 2013; Bennett *et al.* 2014), and in the wider Murray–Darling Basin region (Selwood *et al.* 2015a). The effects of the Big Dry probably were more severe in non-floodplain systems, and so resource availability was unlikely to have been greater elsewhere in the region (Selwood *et al.* 2015a). Mobility appeared to have a negative effect on the response of species to the Big Wet and so, on trends over the entire period. Rather than indicating a lack of resilience, this may indicate that more mobile species were able to track booms in resource availability in the wider region in response to increased rainfall so that their occurrence in the study area became more sporadic in this wetter period.

Species body mass, fecundity and diet did not appear to affect the relative resistance or resilience of species. High physiological stresses and resource pressures during drought may have exceeded survival thresholds for so many species that there was little differentiation in species resistance based on body mass. There may have been so few breeding adults remaining that there could be little differentiation in resilience between species with different reproductive potentials. It is likely that the drought caused pervasive declines in food types because resistance and resilience did not differ among dietary guilds. Other life-history attributes may be better predictors of resilience and resistance in this system, although other studies on the effects of the Big Dry on woodland birds found little effect of species ecological traits such as nesting and foraging guilds (Bennett *et al.* 2014; Selwood *et al.* 2015a). The change in environmental conditions during the Big Dry probably was so severe that they negated potential effects of species traits that might occur under less severe changes in conditions.

FUTURE PROSPECTS

The avifauna may eventually recover if the floodplain vegetation recovers from the effects of the drought. There is evidence of some recovery of floodplain forests following the Big Wet, with the extent of forest in good condition increasing by 5% of the total area of the Murray River floodplain (Cunningham *et al.* 2014). However, the onset of another drought may halt or reverse recoveries in bird populations. The effects of severe climatic events such as drought can be persistent when systems do not have sufficient time to recover between events (Saatchi *et al.* 2013). The frequency of droughts in south-eastern Australia is predicted to increase with climate change (Mpelasoka *et al.* 2008), so that drought pressures on bird assemblages are likely to intensify in coming decades. The effects of other climate pressures such as increased temperature and hence higher evapotranspiration, coupled with human pressures such as water extraction and timber-harvesting, may be additively detrimental for birds (Mac Nally *et al.* 2011).

As the frequency and severity of drought is projected to increase in many parts of the world (Hartmann *et al.* 2013), our work highlights some of the potential effects that prolonged drought will have on bird assemblages. Increased drought frequency alongside other climate pressures will alter the structure and composition of animal assemblages. More resistant and resilient species will become more dominant, while less resistant and resilient species will decline, potentially to local extirpation or extinction (Princé & Zuckerman 2015). Maintaining and, more problematically, restoring the condition of ecosystems may improve the resistance and resilience of species to extreme climate events. More intact ecosystems are likely to be more resistant and resilient to pressures than those that are in poor initial condition (Whitford, Rapport & deSoysa 1999). Drought-induced vegetation degradation can be more severe in smaller remnants (Bennett *et al.* 2013), so that the maintenance and restoration of landscape cover may dampen the effects of drought.

In floodplain forests, a reinstatement of more natural flooding regimes would greatly improve forest condition (Mac Nally *et al.* 2011), which may increase resistance, resilience and the potential to function as drought refugia (Selwood *et al.* 2015a). Although some environmental water allocations have increased in many parts of the world, including North America, Australia and South Africa (Hughes & Rood 2003), reduced precipitation and competing demands for water from a growing human population will impose limits to the extent to which natural regimes can be reinstated (Horner *et al.* 2012). Development of optimal temporal and spatial environmental watering regimes that maximize the extent of floodplain forest in good condition will likely improve the resistance and resilience of terrestrial floodplain biota.

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Data accessibility

Species occurrence and breeding data are deposited in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.276d6> (Selwood *et al.* 2015b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Lists of bird species by survey period

Table S2. Changes in reporting rates and effects of stand condition for all species observed in the 1998, 2009 or 2013 survey programmes

Table S3. Parameter estimates for the effects of species traits on species trends and estimates of the phylogenetic heritability

Fig. S1. Proportion of sites at Gunbower Island with forest stands in severe, degraded, poor, declined or good condition in 2009 and 2013.

Fig. S2. Detection distances for bird observations in 2009 and 2013.

Chapter 4

**Resistance and resilience of terrestrial birds in drying
climates: do floodplains provide drought refugia?**



RESEARCH
PAPER

Resistance and resilience of terrestrial birds in drying climates: do floodplains provide drought refugia?

Katherine E. Selwood^{1*}, James R. Thomson², Rohan H. Clarke¹,
Melodie A. McGeoch¹ and Ralph Mac Nally²

¹School of Biological Sciences, Monash University, Clayton, Vic. 3800, Australia,

²Institute for Applied Ecology, The University of Canberra, Bruce, ACT 2617, Australia

ABSTRACT

Aim Climate refugia will become increasingly important for biota as climate change causes an increased frequency and intensity of extreme events, such as drought. Floodplains are potential drought refugia because they have cooler and more mesic microclimates than adjacent areas, and greater water availability through shallower groundwater and flooding. We explored the role of floodplains as drought refugia by estimating the resistance and resilience of terrestrial birds over a 13-year drought (the ‘Big Dry’) and for 4 years following the break in the drought in floodplain and non-floodplain zones.

Location Murray–Darling Basin, Australia.

Methods We used Atlas of Australian Birds survey data from more than 39,000 surveys at over 28,000 sites to estimate trends in reporting rates in floodplain and non-floodplain zones for 144 bird species during extended drought (1998–2009) and in the post-drought period (2010–13).

Results There was greater resistance to drought in floodplain zones: fewer species declined in floodplain zones (19%) than in non-floodplain zones (29%) during the Big Dry, and more species had elevated reporting rates (13% vs. 8%). More species showed a recovery in reporting rates in non-floodplain zones (40.3%) than in floodplain zones (15.3%) during the post-drought period, which was expected because declines during the Big Dry were more common in non-floodplain zones. There was some evidence for limitations in the resilience of floodplain avifauna, with only 17.9% of species that declined in floodplain zones during the drought subsequently recovering.

Conclusions Floodplains appear to enhance resistance to drought for many bird species, and are likely to be particularly important as refugia in areas with an arid climate. However, their role in resilience is less clear. Floodplain ecosystems require long-term management to relieve pressures and to restore their ecological condition so that their role as drought refugia is maintained or enhanced.

Keywords

Aridity, climate change, climate refuge, climate refugia, climate variability, extreme events, Millennium Drought, recovery, riparian zone.

*Correspondence: Katherine E. Selwood, School of Biological Sciences, Monash University, Clayton, Vic. 3800, Australia.
E-mail: katherine.selwood@monash.edu

INTRODUCTION

Climate change has emerged as a key driver of loss of global biodiversity loss (Bellard *et al.*, 2012). Among the pressures associated with climate change is the increased frequency and severity

of drought – the global area affected by drought has increased (IPCC, 2014). The frequency of both short- and long-term drought is projected to increase world-wide and rising temperatures induce more severe drying (IPCC, 2014). Rainfall is likely to be concentrated into more intense events (IPCC, 2014).

Severe climate conditions have physiological effects on biota and affect resource availability, which increase extinction risk (Selwood *et al.*, 2014). Hot and dry conditions are physiologically stressful for individuals (Silllett *et al.*, 2000) and drought conditions degrade habitats through mortality and dieback of vegetation and decreased primary production (Allen *et al.*, 2010), especially in landscapes modified by the fragmentation and loss of native vegetation (Bennett *et al.*, 2013). These effects can be persistent, especially when systems do not have sufficient time to recover between severe climatic events (Saatchi *et al.*, 2013; Mac Nally *et al.*, 2014).

For a population to persist it must absorb pressures such as drought ('resistance') and recover fully if conditions improve ('resilience') (Harrison, 1979). Refugia enhance resistance and resilience of biota to extreme climate events by providing temporary habitat refuges for individuals to retreat to during adverse conditions or by acting as source areas for future generations by supporting the survival of individuals so that populations that can expand if conditions improve (Mackey *et al.*, 2012). Refugia offer food, shelter and breeding resources that become limited in other areas of a species' range, or offer physiological relief from extreme environmental conditions (Mackey *et al.*, 2012). Thermal refugia, where temperatures are moderated, and hydric refugia, where water availability is greater or more reliable than other parts of a species range, will play increasingly important roles in species persistence as climate pressures intensify (Reside *et al.*, 2014). Increased frequency and severity of drought, reduced rainfall and increased evaporation with higher temperatures are likely to have particularly severe effects on biota in arid and semi-arid regions, given that these systems are primarily water limited (Weltzin *et al.*, 2003).

Riparian areas and floodplains are likely to be crucial areas for adaptation to climate change because they have cooler and more mesic microclimatic conditions than do adjacent areas (Capon *et al.*, 2013) and access to water through flooding and shallower groundwater (Mac Nally *et al.*, 2011). Nutrient and water subsidies provided by floodwaters mean floodplains are often more productive than adjacent areas (Ballinger & Lake, 2006). While riparian areas and floodplains support higher species abundance, higher species richness and provide seasonal habitat for terrestrial bird species (Sabo *et al.*, 2005), their potential as climate refugia has not been evaluated.

While their microclimatic conditions and water availability make intact floodplains good candidates for climate refugia, a number of factors may limit their potential. The fertile and moist soils and flat topography mean that floodplains are preferred for human use, so they are often highly disturbed environments (Tockner & Stanford, 2002), which may hamper ecological recovery once droughts break (Whitford *et al.*, 1999). The high level of exposure and sensitivity of floodplain ecosystems to the effects of climate may cause them to be disproportionately affected by climate changes and extreme climatic events (Capon *et al.*, 2013). Floods are critical to the life cycle of many floodplain flora and fauna, so they may be severely affected by reduced flooding frequency with increased

drought duration, particularly given that water regulation for human land use has already reduced the frequency and extent of floodplain inundation in many locations (Capon *et al.*, 2013).

South-eastern Australia experienced a prolonged drought from 1997 to 2010, known as the 'Big Dry' (or Millennium Drought), which was at least partly associated with global climate change (Verdon-Kidd & Kiem, 2009; Chiew *et al.*, 2011). There were unprecedented decreases in recorded rainfall run-off during this time, which significantly reduced inflows into the Murray–Darling River Basin, which is Australia's largest catchment and most important agricultural region (Chiew *et al.*, 2011). The Big Dry was broken by the 'Big Wet' in mid-2010 to 2012, which was the wettest 2-year period in Australian records (Bureau of Meteorology (Australia), 2012). The increasing pressures of climate, along with vegetation loss and modification and water regulation and extraction for human land use, have degraded vegetation and caused large-scale faunal declines in the region (Mac Nally *et al.*, 2009; Bennett *et al.*, 2014). While the effects of these pressures have been observed in upland and floodplain ecosystems (Bennett *et al.*, 2014; Mac Nally *et al.*, 2014), the relative severity of these effects on different ecosystems is less clear.

Species with temporal declines in occurrence during the Big Dry would be considered to have low resistance to drought, while those with positive or stable temporal trends would be considered to be drought resistant. Species that declined during the drought but had positive temporal trends in the post-drought period have resilience, while those that had declined but did not recover substantially have low resilience. Here, we estimated the temporal trends in reporting rates of terrestrial birds during the Big Dry and following the onset of the Big Wet in floodplain and non-floodplain areas. We compared trends in occurrence for individual species in floodplain zones with their trends in non-floodplain zones to assess whether floodplains enhanced resistance or resilience to drought. We refer to a positive difference in trends between zones (faster increase in occurrence, slower decrease in occurrence, or increase versus decrease) as being 'more positive' (which, in some cases, means 'less negative') (see Fig. 1). A more positive temporal trend in floodplain zones compared with non-floodplain zones indicates that floodplains enhanced species resistance (Big Dry temporal trends) or resilience (post-drought temporal trends).

A more positive temporal trend in one zone compared with another can be caused by (1) the movement of individuals from one zone (increased emigration rates) to another (increased immigration rates), or (2) greater population viability in one zone compared with another due to higher birth rates or lower death rates. We do not distinguish between these two mechanisms in our study because we did not measure population demographic rates, but both cases indicate a potential refugial role of a zone in enhancing resistance (Big Dry) or resilience (post-drought).

We related temporal trends to species ecological traits to assess whether guilds differed in resistance or resilience to

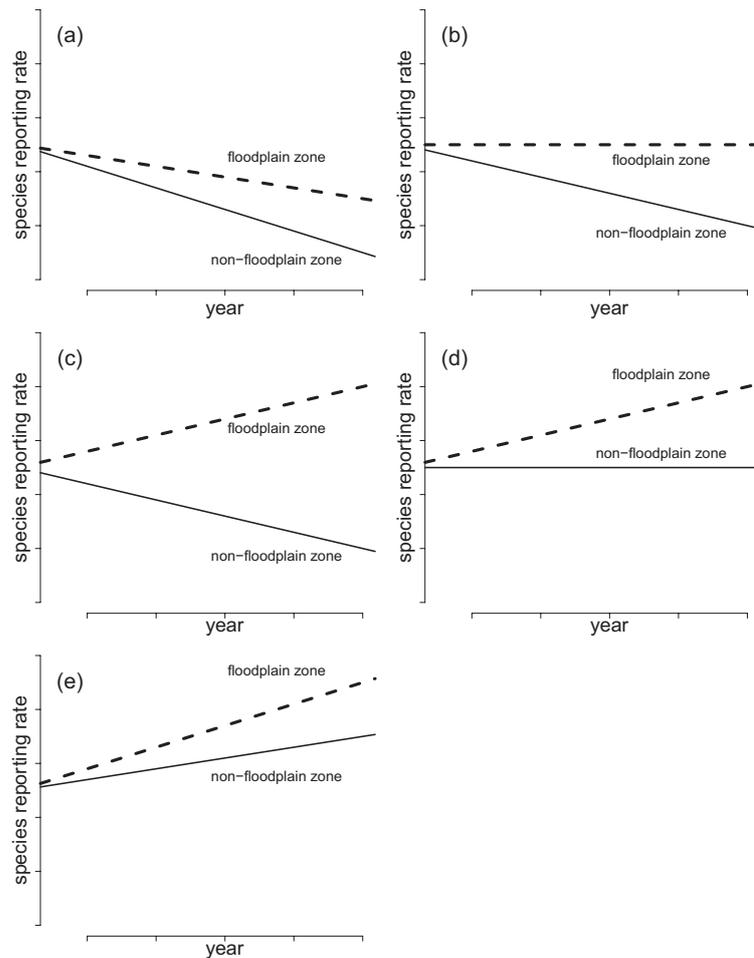


Figure 1 Illustration of the outcomes that result in more positive temporal trends in reporting rates of a species in floodplain zones (dashed lines) compared with non-floodplain zones during the Big Dry or post-drought period. Dashed lines represent the species temporal trend in reporting rates in floodplain zones while solid lines represent the trend in reporting rates in non-floodplain zones: (a) trends in both zones are negative, but decline is slower in floodplains; (b) negative trend in non-floodplain zone, but stable trend in floodplain zone; (c) negative trend in non-floodplain zone, positive trend in floodplain zone; (d) stable trend in non-floodplain zone, positive trend in floodplain zone; (e) positive trends in both zones, but faster increase in reporting rates in floodplain zone.

drought in either zone, or whether floodplains provide refugia for certain guilds. We assessed whether landscape aridity affected the proportion of species that declined in floodplain and non-floodplain zones to investigate whether bird assemblages in drier climates had lower resistance to drought.

METHODS

Study region

The Murray–Darling Basin (MDB) covers 14% of the Australian mainland (Fig. 2). It consists of *c.* 6 million hectares of active floodplains (1 in ≤ 10 year flood-return period) interspersed among upland ecosystems (Mac Nally *et al.*, 2011). The mean annual rainfall is between 300 and 800 mm, with high evaporation (Bureau of Meteorology (Australia), 2014). Rainfall deficits occurred across most of the MDB throughout the Big Dry, and were especially severe in the south (Chiew *et al.*, 2011).

Water regulation and extraction have substantially modified the riparian and floodplain systems of the MDB through

changed seasonality of river flows and reduced frequency and duration of flooding (Horner *et al.*, 2009). The region has been subjected to extensive vegetation loss and fragmentation over the last two centuries and much of the remaining floodplain forest has experienced long-term timber extraction, grazing and forest dieback from reduced flooding and groundwater salinity (Cunningham *et al.*, 2011).

Bird data

We used bird survey data from BirdLife Australia’s Atlas of Australian Birds (Barrett *et al.*, 2003) for January 1998 to December 2013. All standard 2-ha/20-min surveys within the MDB were used, which consisted of 39,180 surveys from 28,037 sites (Fig. 2). We focused on native terrestrial birds, so we excluded non-native species and obligate coastal and wetland birds from analyses. We included species that were observed in 10 or more surveys in floodplain and non-floodplain areas to compare trends for species that occurred in both major topographic areas. We tested several thresholds for the minimum number of

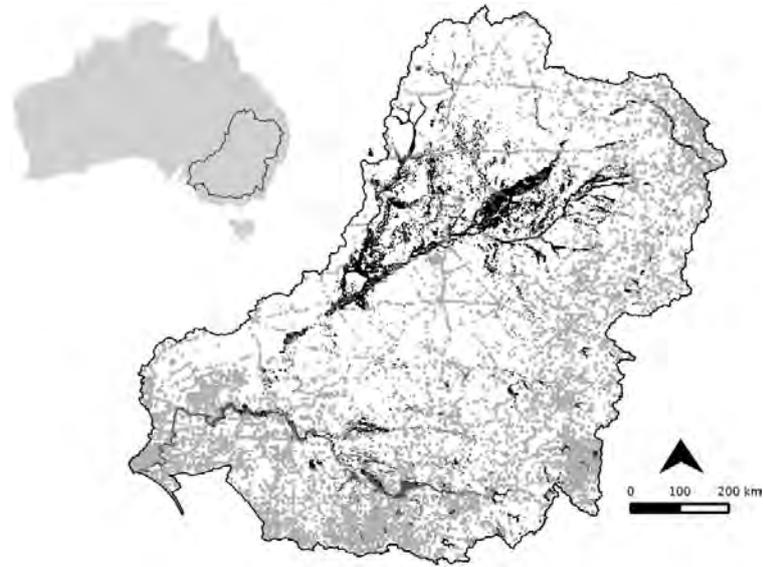


Figure 2 Distribution of active floodplain (1 in ≤ 10 year flood return period) in the Murray–Darling Basin, Australia (black) overlaid with site locations for surveys used in this study (grey).

floodplain surveys in which a species was present (≥ 10 to ≥ 100 , intervals of five), but the choice of threshold had little discernible effect on the proportion of species showing substantial temporal trends in floodplains (Appendix S3). Therefore we used the lowest threshold (≥ 10) to avoid overlooking trends for uncommon species; 144 terrestrial bird species were analysed (Appendix S1 in Supporting Information).

Landscape and climate data

We used QGIS 2.0 (QGIS Development Team, 2013) and R (R Core Team, 2012) with the packages ‘raster’ (Hijmans & van Etten, 2013) and ‘maptools’ (Bivand & Lewin-Koh, 2013) to obtain information about each survey site using coordinates from the Atlas of Australian Birds data. We classified all survey sites as either (1) floodplain topographic zone (active floodplain, 1 in ≤ 10 year flood-return period) or (2) non-floodplain topographic zone (all other areas). We gathered information on the landscape context of sites (flood-return period, landscape vegetation cover, vegetation type, rainfall isohyet band) from multiple sources (Table 1). Annual site-specific climate deviations in maximum and minimum temperatures and total rainfall were obtained using spatial data modelled for 500-m grids by the Bureau of Meteorology (Bureau of Meteorology (Australia), 2014).

Statistical analysis

We estimated temporal trends in reporting rates for periods (1) during the Big Dry to estimate species resistance to drought (1998–2009) and (2) during the post-drought period (2010–13) to estimate species resilience once the drought ended. We estimated Big Dry and post-drought trends in floodplain and

non-floodplain areas to assess the resistance and resilience of populations in each topographic zone. Specifically, we tested for differences in temporal trends between floodplain and non-floodplain zones using species trends in non-floodplain zones as the reference trend. We related temporal trends to species ecological traits to assess whether some guilds were more or less resistant or resilient to drought in either zone. We assessed whether the effects of drought were greater in arid regions by relating the trend in the proportion of species that declined in a catchment during the drought to mean catchment aridity, and whether such trends were consistent in the floodplain and non-floodplain zones.

We used a suite of variables that might influence species occurrence and abundance when estimating temporal trends (Table 1). The annual site-specific reporting rate of noisy miners (*Manorina melanocephala* Latham) was included as a covariate because this behaviourally hyper-aggressive species has a profound effect on bird assemblages in south-eastern Australia (Thomson *et al.*, 2015). Vegetation type at survey locations and the percentage cover of vegetation in the surrounding landscape were included to account for species–habitat associations and for the effects of landscape context (Thomson *et al.*, 2009). We included floodplain status (floodplain versus non-floodplain) as a binary indicator to account for potential species preferences for topographic zone. Annual site-specific temperature and rainfall anomalies were used as covariates because short-term variability is an important determinant of bird distribution and abundance (Reside *et al.*, 2010).

Big Dry and post-drought trends

We defined the reporting rate for a species at site i in year j as the probability p_{ij} of observing the species during a single survey,

Table 1 Description of covariates and random error components used to estimate species temporal trends during the Big Dry and post-drought periods in non-floodplain and floodplain zones.

| Variable name | Description and source |
|-------------------------------------|---|
| Covariates | |
| 1. Floodplain | 1 = floodplain (1-in-10 year flood return period under current conditions), 0 = non-floodplain from Chen <i>et al.</i> (2012) |
| 2. Landscape vegetation cover | Percentage cover of native forest and woodland (NVIS categories 1–15; Department of Environment (Australia), 2012) in a 1-km radius from site |
| 3. Vegetation type | Category of land cover (NVIS; Department of Environment (Australia), 2012): forests and woodlands, low vegetation, cleared/modified vegetation or naturally non-vegetated |
| 4. Noisy miner reporting rate | Proportion of surveys in year <i>j</i> that noisy miner was present |
| 5. Deviation of maximum temperature | Deviation of the mean maximum daily temperature for the survey year from the long-term mean (1961–90) (Bureau of Meteorology (Australia), 2014) |
| 6. Deviation of minimum temperature | Deviation of the mean maximum daily temperature for the survey year from the long-term mean (1961–90) (Bureau of Meteorology (Australia), 2014) |
| 7. Deviation of annual rainfall | Deviation of annual total rainfall for the survey year from the long-term (1961–90) (Bureau of Meteorology (Australia), 2014) |
| Random error components | |
| 1. Year | Year of survey |
| 2. Catchment | River basin identification (Geoscience Australia, 2004) |
| 3. Rainfall isohyet band | 200 mm mean rainfall isohyet (Bureau of Meteorology (Australia), 2014) |
| 4. Site | Unique identification for survey location |

NVIS, National Vegetation Information System.

and modelled the number of observations as a binomial variable: $y_{ij} \sim \text{binomial}(n_{ij}, p_{ij})$. We used a logistic model to estimate temporal trends in reporting rates p_{ij} for each species over the Big Dry (1998–2009) and in the post-drought period (2010–13) in floodplain and non-floodplain zones, while accounting for possible effects of spatial and spatio-temporal covariates (Table 1). We used a hierarchical Bayesian model with fixed and random slope parameters to account for spatial variation in trends and in covariate effects. Random slope models allow for variation in variable effects among groups, in this case, among river catchments. The model was:

$$\text{logit}(p_{ij}) = \beta_0 + \gamma_{c(ij)} \times \text{year}_j + \sum_{p=1}^p \beta_{c(ij)}^{(p+4)} X_{pi} + \epsilon_{ij};$$

$$\gamma_{c(ij)} = D_j(\beta_{c(ij)}^1 + F_i\beta_{c(ij)}^2) + (1 - D_j)(\beta_{c(ij)}^3 + F_i\beta_{c(ij)}^4);$$

$$\beta_c^n \sim N(B^n, \sigma_n^2); \quad \epsilon_{ij} = \epsilon_j^1 + \epsilon_{c(ij)}^2 + \epsilon_{r(ij)}^3 + \epsilon^4.$$

Here, the estimated temporal trend for catchment *c*, $\gamma_{c(ij)}$, depends on the period ($D_j = 1$ for drought, 0 wet) and whether the site is on a floodplain ($F_i = 1$) or not ($F_i = 0$). The catchment-specific trend parameters ($\beta_c^1, \dots, \beta_c^4$) and *p* covariate effects ($\beta_c^5, \dots, \beta_c^{p+4}$) comprise overall mean (fixed) effects, B^n , and random variation with variance σ_n^2 . The random error components (ϵ_{ij}): year (ϵ^1), catchment (ϵ^2), rainfall isohyet band (ϵ^3) and site (ϵ^4). The year random effect was modelled with a first-order autoregressive model and the catchment, rainfall isohyet band and site random effects were modelled as independent and

identically distributed. We fitted the model with (model 1) and without (model 2) time-varying climate covariates (Table 1, covariates 5–7) to check whether temporal trends in species reporting rates were confounded by trends in annual climate variables.

We used linear combinations to estimate the marginal posterior distributions for annual trends in floodplains for the Big Dry ($B^{\text{fp-dry}} = B^1 + B^2$) and post-drought ($B^{\text{fp-post}} = B^3 + B^4$), catchment-specific trends in floodplains and non-floodplain zones for each period and differences in annual trends between the Big Dry and post-drought in non-floodplain zones ($\Delta_{\text{non}} = B^1 - B^2$) and in floodplain zones ($\Delta_{\text{fp}} = B^{\text{fp-dry}} - B^{\text{fp-post}}$).

Ecological traits

We classified species by traits that might influence their response to environmental change to investigate whether particular traits might explain species relative resistance and resilience to drought (Bennett *et al.*, 2014). We tested whether the estimated temporal trends of a particular species during drought in non-floodplain or floodplain zones (i.e. resistance) or post-drought in non-floodplain or floodplain zones (i.e. resilience) from model 1 were related to ecological traits. Species traits were classified according to Radford & Bennett (2005) and included: habitat preference (open country, open-tolerant or woodland dependent), woodland habitat type (generalist, dry, mallee, upland, riverine, non-woodland), conservation status (of conservation concern: yes or no), foraging substrate (aerial, bark, canopy, ground, low shrubs, tall shrubs), feeding guild (frugivore, insectivore, nectarivore, raptor/feeds

on vertebrates, granivore) and nesting substrate (burrow, ground, hollow, shrub/canopy, parasitic). We used a random effects model to partition the variation in species mean estimated trends in the Big Dry and post-drought among species ecological traits. The proportion of variation explained by each ecological trait was calculated from the posterior modes of the random effects variance parameters (Gelman, 2005). The model was run separately for Big Dry trends in non-floodplain and floodplain zones (B^1 , B^{fp_dry} respectively) and post-drought trends in non-floodplain and floodplain zones (B^3 , B^{fp_wet}), using the posterior mean parameter estimates from model 1 assuming Gaussian distributions. We tested whether the difference in species trends between floodplain and non-floodplain zones during the drought (B^2) or post-drought (B^4) period was dependent on ecological traits using the same model.

Effects of drought along an aridity gradient

To assess whether arid landscapes experienced a greater proportion of species declines during drought, we tested whether there was a relationship between the proportion of species declining in each zone within a catchment during the Big Dry and the aridity of that catchment (at the catchment geometric centroid). We used the United Nations Environment Program aridity index (Ezcurra, 2006) $AI = P/ET$, where P is mean annual precipitation and ET is mean annual potential evapotranspiration, so that lower values of AI indicate higher aridity. We tested this relationship for trends in both floodplain and non-floodplain zones using a beta regression model:

$$d_c \sim \text{beta}(\mu\phi, -\mu\phi + \phi); \text{logit}(\mu) = \delta AI + \epsilon_{\text{catchment}}$$

Here, d_c is the proportion of species present in a catchment c that showed strong evidence of a decline during the drought (floodplain or non-floodplain topographic zone), and δAI is the effect of aridity. μ is the mean response, and ϕ is a dispersion parameter. We included catchment as a random effect ($\epsilon_{\text{catchment}}$). We ran the model separately for the proportion of species exhibiting declines in non-floodplain topographic zones ($d_{c_non_floodplain}$) and the proportion exhibiting declines in floodplain topographic zones ($d_{c_floodplain}$). We modelled the aridity (AI) with a nonlinear spline model. The relationship between aridity and d_c (for both $d_{c_non_floodplain}$ and $d_{c_floodplain}$) was found to be linear so we subsequently fitted a linear model to estimate δ .

Model fitting

All models were fitted using integrated nested Laplace approximations (INLA) using the INLA package (Rue *et al.*, 2009, <http://www.r-inla.org>) in R (R Core Team, 2012). INLA uses deterministic approximations to posterior marginal distributions for Bayesian inference, which makes it an accurate and computationally efficient solution for large datasets (Rue *et al.*, 2009). We considered a posterior probability of $\text{Pr}(\text{parameter} > 0) > 0.9$ as strong evidence that that parameter

had a positive relationship to the response variable, and a posterior probability of $\text{Pr}(\text{parameter} < 0) > 0.9$ as strong evidence for a negative relationship (Kass & Raftery, 1995).

RESULTS

Big Dry and post-drought temporal trends

The inclusion of climate covariates (model 1) did not affect estimates of temporal trends for most species, with little change in estimates of temporal trends if the annual climate measures were omitted (model 2) and there were no strong monotonic temporal trends in climate variables in the Big Dry or post-drought period (Appendix S4). There was greater evidence of temporal trends for more species using model 1, so the inclusion of climate covariates probably accounted for short-term variability in reporting rates that improved the precision of longer term (residual) estimates of temporal trends. We used temporal trend estimates from model 1 and model 2 in secondary analyses of trends, but the results did not differ, so we only report results for model 1.

Fewer species declined in floodplain zones (19.4%, 28 species, Fig. 3a) than in non-floodplain zones (28.5%, 41 species, Fig. 3b) during the drought (Table 2). Fewer species in non-floodplain zones had increasing reporting rates (8.3%, 12 species, Fig. 3a) than in floodplains during the drought (12.5%, 18 species, Fig. 3b) (Table 2). There was strong evidence for a more positive temporal trend in floodplain zones (see Fig. 1) during the drought for 24.3% of species (35 species, Table 2), while during the post-drought period only 7.6% (11 species, Table 2) had more positive trends in floodplains (Fig. 3c). Of species with more positive trends in floodplain zones during the

Table 2 Numbers of species with positive trends [$\text{Pr}(B^i) > 0 > 0.9$], negative trends [$\text{Pr}(B^i) < 0 > 0.9$] and little evidence of change in trends during the Big Dry, after the Big Dry ceased (post-drought) and differences between reporting rates during and after the Big Dry in non-floodplain zones (NFP) and floodplain zones (FP). Percentage of the total number of species is in brackets.

| | Positive | Negative | Little evidence of change |
|--|------------|------------|---------------------------|
| Big Dry | | | |
| NFP | 12 (8.3%) | 41 (28.5%) | 91 (63.2%) |
| FP | 18 (12.5%) | 28 (19.4%) | 98 (68.1%) |
| FP > NFP | 35 (24.3%) | 27 (18.8%) | 82 (56.9%) |
| Post-drought | | | |
| NFP | 58 (40.3%) | 13 (9.0%) | 73 (50.7%) |
| FP | 22 (15.3%) | 12 (8.3%) | 110 (76.4%) |
| FP > NFP | 11 (7.6%) | 35 (24.3%) | 98 (68.1%) |
| Big Dry versus post-drought | | | |
| $\Delta\text{NFP} (\Delta_{\text{non}})$ | 54 (37.5%) | 9 (6.3%) | 81 (56.3%) |
| $\Delta\text{FP} (\Delta_{\text{fp}})$ | 24 (16.7%) | 14 (9.7%) | 106 (73.6%) |

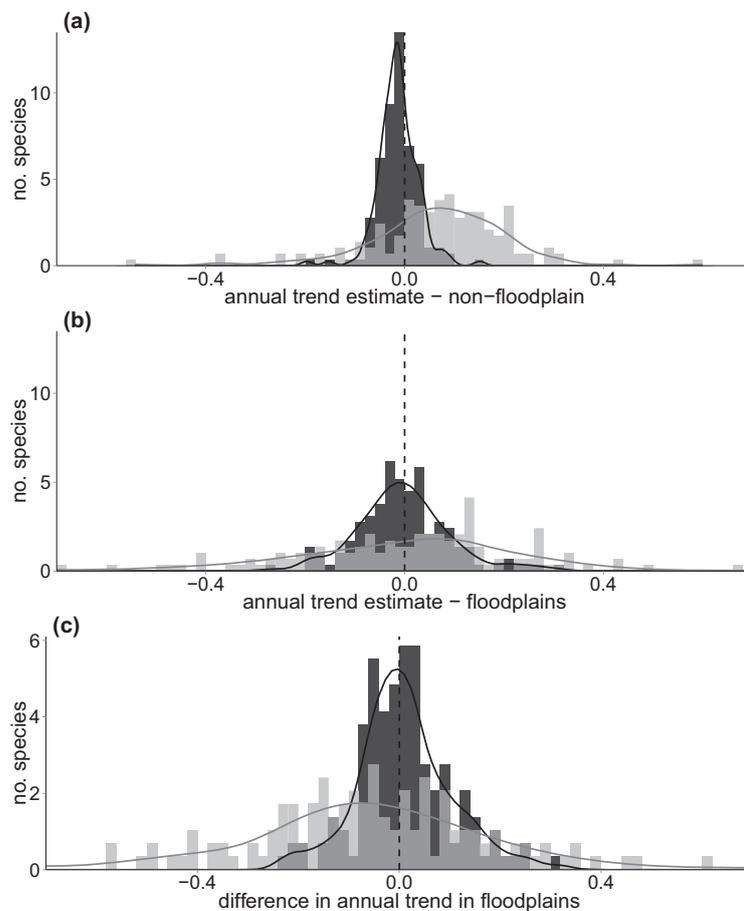


Figure 3 Frequency distribution of the slope estimates for temporal trends of 144 species during the Big Dry (dark grey) and post-drought (light grey) periods in (a) non-floodplain zones and (b) floodplain zones, and (c) the difference in annual trends between floodplain and non-floodplain zones in each period.

Big Dry, eleven declined in non-floodplain areas during the drought, while either increasing (three species) or remaining stable (eight species) in floodplain zones (Appendix S1, Fig. 1b,c). Another eleven species had stable trends in non-floodplain zones but positive trends in floodplain zones (Fig. 1d), and one species increased in occurrence in both zones but more strongly in floodplains (Fig. 1e). Eight other species had strong evidence for more positive trends in floodplain zones during the Big Dry (five species with opposing trends and two species with stronger positive trends), but posterior probabilities for the temporal trends in each zone were < 0.90 , indicating that trends in occurrence were still relatively stable in both zones.

The number of species with a negative difference in trends between floodplain and non-floodplain zones did not change much; during the drought 18.8% (27 species, Table 2) had more positive temporal trends in non-floodplain zones than in floodplains and after the drought 23.4% (35 species, Table 2) had lower annual trends in floodplain zones.

In the post-drought period, 40.3% of species (58 species) had positive trends in reporting rates in non-floodplain zones, while 15.3% (22 species) had positive trends in floodplain zones. The

proportion of species declining in the post-drought period was similar in both zones (Table 2, Fig. 3). In non-floodplain zones, 37.5% of species (54 species) had increased annual trends (i.e. weaker declines, stronger increases, or a shift from a negative to a positive trend) in the post-drought period compared with the Big Dry, while in floodplain zones only 16.7% of species (24 species) had increased annual trends in the post-drought period (Table 2). After the Big Dry broke, 46.3% of species (19 of 41 species) that had declined during the drought in non-floodplain zones had positive annual trends, but in floodplain zones only 17.9% of species (five of 28 species) that had declined during the drought increased in reporting rates (Appendix S1).

Ecological traits

Ecological traits explained little variation in species-specific temporal trends during the Big Dry and post-drought in non-floodplain and floodplain zones, or in the deviation in trends between non-floodplain and floodplain topographic zones during either period (Appendix S3). No single trait category accounted for $> 4.5\%$ of variation in trends during the Big Dry,

and no category accounted for > 1.5% of variation in trends in the post-drought period. Ecological traits explained almost no variation in the difference in trends between floodplain and non-floodplain zones in either period (< 0.01 per trait category).

Catchment-specific drought trends

A higher proportion of species declined in non-floodplain zones during the drought in more arid catchments [$\delta = -0.667$, $\text{Pr}(\delta < 0) > 0.9$], suggesting that the effect of drought on birds was more intense in more arid areas. There was little evidence for an effect of aridity on the proportion of species declining in floodplain zones across the same catchments [$\delta = 0.227$, $\text{Pr}(\delta > 0) < 0.9$].

DISCUSSION

The Big Dry from 1997–2009 led to the decline of many bird species in the study region, and these effects were for all ecological guilds. Annual variation in temperature or rainfall did not explain species declines, suggesting that the succession of dry years had cumulative effects on populations. Resource availability probably declined, with drought-induced degradation of native vegetation occurring in both floodplain and non-floodplain zones in the study region, including tree mortality, extensive loss of canopy, declines in litter and shrub cover (Horner *et al.*, 2009; Bennett *et al.*, 2013) and reduced food availability (Mac Nally *et al.*, 2009). Physiological stress would have been high (Sillett *et al.*, 2000). These adverse conditions could have led to high mortality rates (Sillett *et al.*, 2000), reduced recruitment (Selwood *et al.*, 2009), reduced immigration and increased emigration (Selwood *et al.*, 2014), resulting in lower reporting rates.

Floodplains appeared to provide several species with increased resistance to drought. During the Big Dry, fewer species declined in floodplains compared with non-floodplain zones (19.4% vs. 28.5%), more species increased (12.5% vs. 8.3%) and about a quarter of species had more positive trends. Although there was minimal inundation of the MDB floodplains during the drought (Chiew *et al.*, 2011), residual groundwater and higher nutrient availability (Ballinger & Lake, 2006) may have buffered floodplain vegetation from declines in productivity and condition. Relative differences in habitat quality can emerge during drought, with gullies and lowland areas having greater vegetation cover and better vegetation condition than the drier plains and uplands (Lunney *et al.*, 1991). Floodplain vegetation, particularly adjacent to watercourses, may provide microclimatic buffers to high temperatures and low rainfall (Capon *et al.*, 2013), thereby reducing physiological stress on birds.

Of those species with more positive trends in floodplain zones during the drought, 11 species declined in non-floodplain zones while remaining stable or increasing in floodplain zones, indicating that floodplains buffered these declining species from drought-induced declines (Fig. 1b,c). The white-naped

honeyeater (*Melithreptus lunatus* Vieillot), grey currawong (*Strepera versicolor* Latham) and golden whistler (*Pachycephala pectoralis* Latham) appeared to use the floodplain forests as a drought refuge, with higher reporting rates in floodplains during the Big Dry but reduced rates in non-floodplain zones, suggesting movement of individuals into floodplain zones or differential reproduction or mortality *in situ*. There were more species (24.3% vs. 7.6%) with more positive trends in reporting rates in floodplain zones during the Big Dry than afterwards, indicating that differences in resource availability or abiotic conditions between floodplain and non-floodplain zones diminished once the drought broke.

In non-floodplain zones, the effects of drought on the avifauna were stronger in arid catchments, which had a higher proportion of declining species. Productivity in arid systems is primarily limited by water availability (Weltzin *et al.*, 2003). Drought has a stronger effect on vegetation productivity and condition in more arid regions (Weltzin *et al.*, 2003), and drought-induced vegetation die-off is common (Allen *et al.*, 2010), with flow-on effects for the avifauna (Albright *et al.*, 2009). There is likely to have been a more pronounced decline in resource availability for birds in arid regions compared with more mesic areas from the rainfall deficits during the Big Dry. Extreme climate conditions and degradation of vegetation during the drought may have resulted in the contraction of species distributions away from arid and semi-arid areas to more mesic areas.

Floodplains have greater vegetation biomass than local rainfall could otherwise support due to access to water through groundwater reserves and intermittent flooding (Horner *et al.*, 2009), which is particularly evident in arid regions (Naumburg *et al.*, 2005). The absence of a positive relationship between the number of declining species and catchment aridity in floodplain zones may reflect less variability in water availability, and so vegetation condition, along the aridity gradient. Floodplains may have provided a mesic refuge in arid areas during the Big Dry, which might explain the pattern of decreasing declines of floodplain species with increasing catchment aridity.

While floodplains appeared to enhance the resistance of the avifauna to drought, their role in resilience was less clear. Few species showed more positive trends in floodplains compared with non-floodplain zones after the drought. More than twice as many species had increased reporting rates in non-floodplain zones than in floodplains. This does not necessarily indicate lower resilience in floodplain zones because fewer species had declined in floodplain zones than in non-floodplain zones during the drought. Fewer and less severe declines in bird occurrence on floodplains leave less capacity for the birds to recover. If floodplain vegetation were less affected by the drought than non-floodplain vegetation, it is likely that increased rainfall during the Big Wet had a proportionately greater effect on primary production and general vegetation condition in non-floodplain than in floodplain topographic zones, so that recoveries in bird occurrence would be more likely.

For some species, the breaking of the Big Dry may have triggered dispersal of birds from floodplain refugia into

non-floodplain zones as populations recovered, resulting in increased reporting rates in non-floodplain zones but corresponding declines in floodplain zones as populations expanded from the floodplain refugia. It is not possible to gauge from our study whether there was such differential dispersal because we have no data for banded or tracked individuals.

There was evidence for limited resilience of floodplain avifauna. Only a small proportion of species that declined in floodplain areas during the drought subsequently recovered (17.9%). Extensive flooding occurred in the MDB floodplains during the Big Wet (Commonwealth Environmental Water Office (Australia), 2013), but there may have been a lag in the effects of these floods on the productivity and condition of floodplain vegetation, or the floods may have been insufficient to induce recovery in vegetation productivity or condition. Regeneration of floodplain forests may take many decades following widespread mortality caused by drying (Horner *et al.*, 2009). Many floodplains of the MDB have been degraded by changed flooding regimes, soil salinity, grazing and timber extraction (Mac Nally *et al.*, 2011), which may limit their ability to recover from drought (Whitford *et al.*, 1999).

Reduced precipitation and drought have resulted in widespread increases in tree mortality rates and declines in the condition of forest stands (Allen *et al.*, 2010), with consequent effects on fauna (Bennett *et al.*, 2014). The frequency of intense droughts is expected to increase in many parts of the world (IPCC, 2014). The effects of drought can cascade, especially if ecosystems do not have sufficient time to recover fully between droughts (Saatchi *et al.*, 2013). Climate change amplifies the pressure on biota already affected by land-use change (Mantyka-Pringle *et al.*, 2012) and the need for climate change refugia is becoming increasingly important, especially in more arid landscapes. There is a need for thermal and hydric refugia (Reside *et al.*, 2014) and areas that remain relatively more productive during severe climatic events (Mackey *et al.*, 2012). Floodplain ecosystems meet these criteria, and we have demonstrated their potential to assist avifauna to resist drought. Our findings demonstrate that floodplains should be priority areas for protection and restoration, and be managed so that pressures are mitigated. To increase the resilience of these ecosystems, multidecadal active environmental management is required so that the regeneration of forest structure can occur where water over-extraction has caused mortality through lack of inundation (Horner *et al.*, 2009).

While floodplains may act as important climate refugia, floodplain ecosystems are among the most threatened in the world (Tockner & Stanford, 2002). Large areas of floodplain have been developed for agriculture and for urbanization, especially in Europe and Asia, where 60–99% of riparian zones have been transformed for human land use (Tockner & Stanford, 2002). Water extraction and river regulation have altered the extent, duration and frequency of floodplain inundation, resulting in changes to floodplain vegetation condition and structure, and biotic composition (Tockner & Stanford, 2002; Hughes & Rood, 2003). The geographical extent of floodplain zones has been reduced (Tockner & Stanford, 2002). There have recently

been provisions of water for water-dependent ecosystems through environmental water allocations, including in North America, Australia and South Africa (Hughes & Rood, 2003). These flows need to be managed to sustain not only water-dependent biota but also terrestrial biota that rely on floodplains, especially during drought. Floodplain ecosystems require long-term management to relieve pressures and restore their ecological condition so that their resilience is improved and their potential as drought refugia is fully realized.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Residual annual trends in bird reporting rates.

Appendix S2 Percentages of variation explained by species ecological traits.

Appendix S3 Proportions of species showing strong evidence of a temporal trend in floodplains as a function of number of records.

Appendix S4 Boxplots of site-specific deviations in mean maximum temperature, mean minimum temperature and total annual rainfall per year of study.

BIOSKETCH

Katherine Selwood is a graduate student interested in the effects of climate change on species assemblages and population viability, and the importance of climate refugia. She is the lead author of a recent meta-analysis that showed that the relative effects of land-use change and climate change on demographic parameters are of similar magnitude.

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Chapter 5

**Green tongues into the arid zone: river floodplains extend
the distribution of terrestrial bird species**

Green Tongues into the Arid Zone: River Floodplains Extend the Distribution of Terrestrial Bird Species

Katherine E. Selwood ^{1*}, Rohan H. Clarke,¹ Melodie A. McGeoch,¹ and
Ralph Mac Nally²

¹School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia; ²Institute for Applied Ecology, The University of
Canberra, Bruce, Australian Capital Territory 2617, Australia

ABSTRACT

Floodplain and riparian ecosystems have cooler, wetter microclimatic conditions, higher water availability and greater vegetation biomass than adjacent terrestrial zones. Given these conditions, we investigated whether floodplain ecosystems allow terrestrial bird species to extend into more arid regions than they otherwise would be expected to occupy. We evaluated associations between aridity and the occurrence of 130 species using bird survey data from 2998 sites along the two major river corridors in the Murray–Darling Basin, Australia. We compared the effects of aridity on species occurrence in non-floodplain and floodplain ecosystems to test whether floodplains moderate the effect of aridity. Aridity had a negative effect on the occurrence of 58 species (45%) in non-floodplain ecosystems, especially species dependent on forest and woodland habitats. Of these 58 species, the negative effects of aridity were moderated in floodplain ecosystems for 22 (38%) species: 12 showed no association with

aridity in floodplain ecosystems and the adverse effects of aridity on species occurrence were less pronounced in floodplain ecosystems compared to non-floodplain ecosystems for ten species. Greater vegetation greenness indicated that floodplain vegetation was more productive than vegetation in non-floodplain ecosystems. Floodplain ecosystems allow many terrestrial species to occur in more arid regions than they otherwise would be expected to occupy. This may be due to higher vegetation productivity, cooler microclimates or connectivity of floodplain vegetation. Although floodplain and riparian ecosystems will become increasingly important for terrestrial species persistence as climate change increases drying in many parts of the world, many are also likely to be highly affected by reduced water availability.

Key words: aridity gradient; birds; climate change; climate refugia; regional diversity; riparian.

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*Corresponding author; e-mail: Katherine.selwood@monash.edu

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INTRODUCTION

Floodplain and riparian ecosystems offer multiple values for aquatic and water-dependent biota. Floodplains are vital in providing habitat for at least some life stages of many water-dependent species

(Junk and others 1989; Museth and others 2011) and riparian vegetation condition positively affects aquatic communities by maintaining water quality and natural in-stream ecosystem processes (Death and Collier 2010; Giling and others 2014). However, the importance of floodplain and riparian ecosystems for non-aquatic biota (for example, terrestrial vertebrates) is not so well known. Our limited understanding of the reliance of terrestrial biota on floodplain and riparian ecosystems is likely to have underestimated the adverse ecological effects of river regulation, the benefits of natural flooding regimes (Ballinger and Lake 2006) and the value of floodplain and riparian vegetation for terrestrial biota, particularly in drying climates (Capon and others 2013).

We define floodplain ecosystems as the interface between terrestrial and aquatic zones, consisting of terrestrial vegetation in stream channels, adjacent to water bodies and on floodplains, dominated by plant species that require periodic flooding to complete their life cycle (Naiman and others 1993). Access to water tables and flooding allow floodplain ecosystems to support more vegetation biomass than one would expect given local rainfall (Naumburg and others 2005) and to maintain more consistent production during drought (Selwood and others 2015b). Floodplain microclimates are moderated by canopy cover, topography and adjacency to water bodies (Brososke and others 1997). The contrast in vegetation and microclimate between mesic floodplains and non-floodplain ecosystems is likely to be greater in more arid climates, where water availability is limited and temperatures are high, although the degree to which floodplain ecosystems differ from adjacent ecosystems depends on flood intermittency and groundwater depth (Stromberg and others 2006; Brand and others 2011).

Abundances of terrestrial fauna often are higher in floodplain ecosystems than in adjacent plains and upland areas and floodplain ecosystems provide seasonal habitat and drought refuges for birds (Woinarski and others 2000; Tischler and others 2013; Smith 2015). Although floodplain and riparian ecosystems sometimes have higher faunal species richness than adjacent habitats (Mac Nally and others 2000; Smith 2015), these ecosystems predominantly increase regional species richness by harbouring substantially different species assemblages (Sabo and others 2005; Pavey and Nano 2009). The contrast between faunal assemblages in floodplain and adjacent ecosystems is greater in xeric areas compared to mesic and humid locations (Sabo and others 2005). This greater contrast be-

tween floodplain and adjacent faunal assemblages in more arid regions may occur because floodplain ecosystems facilitate the occurrence of some species into more arid climates than they could otherwise occur, leading to differences between typical arid zone assemblages and more mesic assemblages in floodplain habitat.

Here, we explored whether floodplains moderate the effects of aridity on species occurrence to facilitate the occurrence of species in more arid climate zones than they otherwise would be expected to occupy. Our focal region includes the forests and woodlands in the river corridors of Australia's largest river system, the Murray–Darling Basin. Floodplain forest and woodland occurs throughout the region, forming an extensive network of vegetation on floodplains and along rivers that is interspersed among terrestrial ecosystems ranging from humid to arid (United Nations Environment Program 1997; Bureau of Meteorology (Australia) 2015a).

Terrestrial bird assemblages in floodplain and adjacent zones are more differentiated from each other in regions with low mean annual rainfall (Tzaros 2001). Therefore, we evaluated changes in the occurrence of bird species along the two major river corridors (the Murray and Darling river bioregions) to see whether the effects of aridity on species occurrence differed between non-floodplain and floodplain ecosystems. Evidence for a reduced negative effect of aridity on species occurrence in floodplain ecosystems compared to non-floodplain ecosystems suggests a moderating effect of floodplains on the effects of aridity, allowing species to occur in more xeric regions (Figure 1). We explored whether floodplain vegetation was more productive than other vegetation. Finally, we linked species associations with aridity with species ecological traits to assess whether different guilds (foraging, nesting, diet, habitat, movement dynamics, body size) were more likely to be affected by aridity and whether species within particular guilds differed in their likelihood to have their distributions extended by floodplains.

METHODS

Study Region

The study region consists of bioregions along the two major river corridors of the Murray–Darling Basin, which include the alluvial fans and plains of the Murray and Darling Rivers and their major tributaries (Figure 2). Vegetation in the Murray River corridor consists of *Eucalyptus* spp. forest and woodlands, saltbush shrublands and extensive

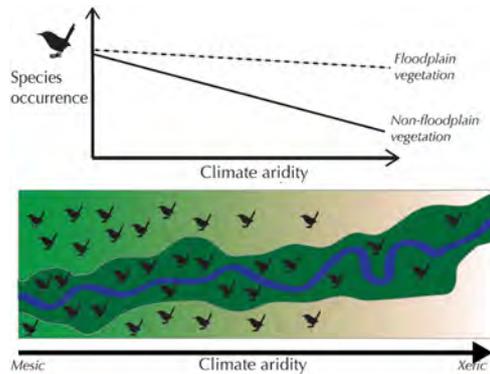


Figure 1. Illustration of how differences in associations between species occurrence and aridity in non-floodplain ecosystems *versus* floodplain ecosystems can indicate the facilitation of species occurrence in more arid regions by floodplains. A moderating effect of floodplains on the association between species occurrence and aridity (= less negative in floodplain ecosystems than in non-floodplain ecosystems) indicates that floodplains may carry species into more arid regions.

grassland and swamp communities (Environment Australia 2000). The Darling River corridor primarily consists of woodlands and open woodlands dominated by *Eucalyptus* spp. (Environment Australia 2000; Breckwoldt and others 2004). The floodplain zones of these corridors are primarily dominated by river red gum (*Eucalyptus camaldulensis*), black box (*E. largiflorens*) or coolabah (*E. coolabah*) forests and woodlands, which are tree species that require periodic inundation to complete their life cycle (Roberts and Marston 2011; Cunningham and others 2013). Mean annual rainfall for most of the region ranges from 200 to 800 mm, increasing generally from west to east along each river (Figure 1; Bureau of Meteorology (Australia) 2015a) and the aridity of the region ranges from humid to arid (United Nations Environment Program 1997; Bureau of Meteorology (Australia) 2015a).

Bird Data

We used bird survey data from BirdLife Australia's New Atlas of Australian Birds (Barrett and others 2003), from 01-Jan-1998 to 31-Dec-2013. All standard 2-ha/20-min surveys in native vegetation (Department of the Environment 2014) within the study region were used, which consisted of 2998 sites that were surveyed at least once (mean number of surveys = 2.3; standard deviation = 4.8),

including 1547 sites within floodplain vegetation. We focused on native terrestrial birds, excluding non-native species and obligate wetland birds from the analyses. We also excluded birds of prey because they range over areas substantially greater than 2 ha. We included species that were observed in at least ten surveys (130 species) in floodplain and non-floodplain zones to allow comparisons in species occurrence between these two zones; previously, we have shown that applying a lower limit of ten produces similar results to more severe limits up to 100 occupied sites (Selwood and others 2015b).

Spatial Data

We used QGIS 2.0 (QGIS Development Team 2013) and R (R Core Team 2015) with the packages 'raster' (Hijmans and van Etten 2013) and 'maptools' (Bivand and Lewin-Koh 2013) to obtain information about each survey site using coordinates from the Atlas of Australian Birds data. We classified all survey sites as (1) floodplain ecosystems or (2) non-floodplain ecosystems (all other native vegetation). We defined floodplain ecosystems as sites located in communities dominated by river red gum, black box or coolabah, with spatial information on occurrence from (Cunningham and others 2013). Although shrublands and grasslands are present on some floodplains in the drier parts of the Murray–Darling Basin, we focus here on the more mesic woodland and forested floodplain communities. We obtained information on the vegetation community type of each site (nested within floodplain and non-floodplain ecosystem type) to control for species' vegetation associations (Department of the Environment 2012). Information on precipitation and potential evapotranspiration at each site was obtained from spatial data modelled for 500-m grids by the Bureau of Meteorology (Bureau of Meteorology (Australia) 2015a). The aridity of each site was calculated using the inverse of the United Nations Environment Program aridity index (Ezcurra 2006), $A = ET/P$. Here, P is mean annual precipitation and ET is mean annual potential evapotranspiration so that higher values of A indicate higher aridity. We obtained information on native vegetation cover in the landscape surrounding sites from a digital map of native vegetation cover (Department of the Environment 2014).

Vegetation Greenness

We tested whether floodplain vegetation was likely to be more productive than non-floodplain vegetation by comparing the Normalized Difference

Vegetation Index (NDVI) at surveyed sites. NDVI is a measure of vegetation greenness that provides an estimate of photosynthetic activity (Wang and others 2004). We used mean annual estimates of NDVI calculated from bands 1 and 2 of the MODIS Terra satellite 250-m imagery NASA (Atlas of Living Australia and Bureau of Rural Sciences 2015). We tested whether NDVI was higher in floodplains compared to non-floodplain ecosystems, and included aridity as a covariate in the model to account for the effects of climate on vegetation productivity. Our model was:

$$\text{NDVI}_i = \delta_0 + \delta_1 F_i + \delta_2 A_i + \epsilon_V$$

Here, F is binary (1 = floodplain ecosystem, 0 = non-floodplain ecosystem), A_i is the aridity at site i and ϵ_V is the random effect of specific vegetation community type, nested within F (Department of

the Environment 2012). The δ s are regression parameters.

Species Occurrence

We evaluated the occurrence of individual species in the Murray River and Darling River bioregions to test whether individual species occurrence decreased with increasing aridity (A) in non-floodplain ecosystems, and whether this negative association was less, or absent, in floodplain ecosystems (Figure 1). We estimated the probability p_i of observing the species during a single survey at site i , and modelled the number of observations as a Binomial variable: $y_i \sim \text{Binomial}(n_i, p_i)$, where n_i was the number of surveys conducted at a site.

For each species, the model was

$$\text{logit}(p_i) = \beta_0 + \gamma_{c[i]} A_i + \beta_{3,c[i]} F_i + \beta_{4,c[i]} V_i + \beta_{5,c[i]} C_i + \epsilon_i;$$

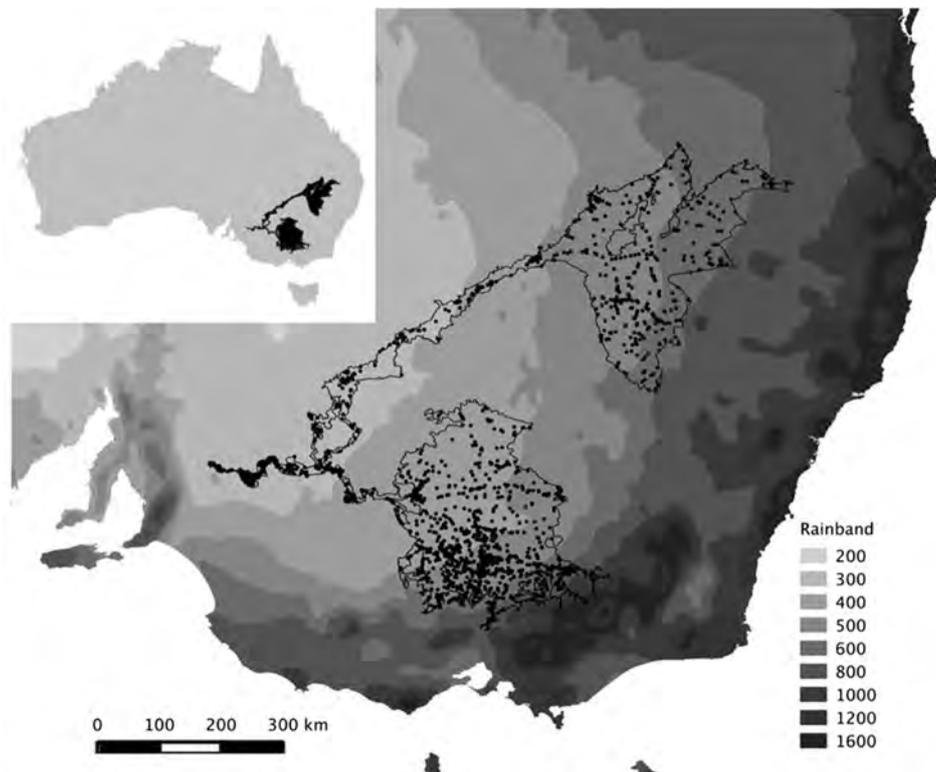


Figure 2. Location of the study region (*black shaded region* in inset map) and study sites (*black dots* on enlarged map) along the Murray and Darling River corridors. The study region consists of the Riverina and Darling River Plains bioregions as classified by Department of the Environment (2012b). Rainfall isohyet bands are shaded in *grey scale* with darker colours indicating higher rainfall; *legend* indicates maximum rainfall per band.

Table 1. Species Traits and Guild Categories Used to Compare Species Responses to Aridity

| Trait | Guilds |
|--------------------|--|
| Body mass | Mean adult body mass category: small (≤ 20 g), medium (>20 – 50 g), large (>50 – 200 g), very large (>200 g). Source: Dunning (2007), Lislevand and others (2007) |
| Nesting | Primary nesting substrate: Terrestrial vegetation, ground, hollow, ledge, brood parasite, aquatic vegetation |
| Foraging | Primary foraging substrate: aerial, bark, canopy, ground, shrub |
| Diet | Primary food source: carnivore, frugivore, granivore, nectarivore or insectivore |
| Habitat preference | Forests and woodlands ('forest'), open country including farmland ('open'), low native vegetation ('shrub'), habitat adjacent to water ('water') |
| Movement dynamics | Resident (local movements only), migrant (moves out of a region seasonally), itinerant (moves within a region seasonally) |

Unless specified, source for information was species reference in Marchant and Higgins (1990); Higgins and Davies (1996); Higgins (1999); Higgins and others (2001); Higgins and Peter (2002); or Higgins and others (2006).

$$\gamma_{c[i]} = \beta_{1,c[i]} + \beta_{2,c[i]}F_i;$$

$$\beta_{n,c} \sim N(B_n, \sigma_n^2); \epsilon_i = \epsilon_{1,c[i]} + \epsilon_{2,i}$$

Here, the estimated effect of the aridity for site i nested within river corridor c (Murray or Darling), $\gamma_{c[i]}$, depends on whether the site is on a floodplain ($F_i = 1$) or not ($F_i = 0$), with β_1 being a measure of the effect of aridity in non-floodplain ecosystems and β_2 being the difference of that effect in floodplain ecosystems. We included F as a covariate in the model to account for species associations with floodplains, thereby allowing us to identify a moderating effect of floodplains on aridity (β_2) that is independent of species apparent preference or disfavour of floodplain habitat. Where the effect of aridity is negative ($\beta_1 < 0$), $\beta_2 > 0$ indicates a moderating influence of floodplains, resulting in a less negative or positive association with aridity in floodplains. We included specific vegetation type (V , nested within F) and the percentage cover of native vegetation (C) in the surrounding landscape (500 m radius) to account for species–habitat associations and for the effects of landscape context (Thomson and others 2009). The river corridor-specific aridity effects ($\beta_{1,c}, \beta_{2,c}$) and covariate effects ($\beta_{3,c}, \beta_{4,c}, \beta_{5,c}$) comprise overall mean (fixed) effects, B_n , and random variation with variance σ_n^2 . The spatial random error components (ϵ_i) are for sub-region (Interim Biogeographic Regionalisation for Australia, Department of the Environment 2012b) (ϵ_1) and site (ϵ_2), which were modelled as independent and identically distributed. We used linear combinations to estimate the marginal posterior distributions for the mean association between species occurrence and aridity in the floodplain ecosystem ($B_{ff} = B_1 + B_2$).

Species Traits

We grouped species into guilds within the following ecological traits: body mass, nesting substrate, foraging substrate, diet, habitat preference and movement dynamics (Table 1). We tested whether (1) the effects of aridity on species occurrence (B_1) and (2) moderating effect of floodplains on aridity effects (B_2 for species where $B_1 > 0$) were related to species ecological traits. We used a random effects model to partition the variation in B_1 and B_2 among species traits. We included as a random effect the phylogeny of our species constructed from Jetz and others (2012) to control for species relatedness. Models were weighted by the inverse variance of the species-specific posterior distributions of the response variables B_1 and B_2 . The proportion of variation explained by each trait and phylogeny was calculated from the posterior means of the random effects variance parameters (Gelman, 2005). We used uninformative (flat) inverse-Wishart priors. Posterior distributions were sampled with chains of 100,000 iterations after 15,000 iteration burn-in periods and a thinning rate of 100. Three independent chains were run for each model and convergence was checked using the Gelman–Rubin diagnostic test in the package 'coda' in R (Plummer and others 2006).

Model Fitting

Species occurrence and vegetation greenness models were fitted using integrated nested Laplace approximations (INLA) using the INLA package (Rue and others 2009). INLA uses deterministic approximations to posterior marginal distributions for Bayesian inference, which makes it an accurate

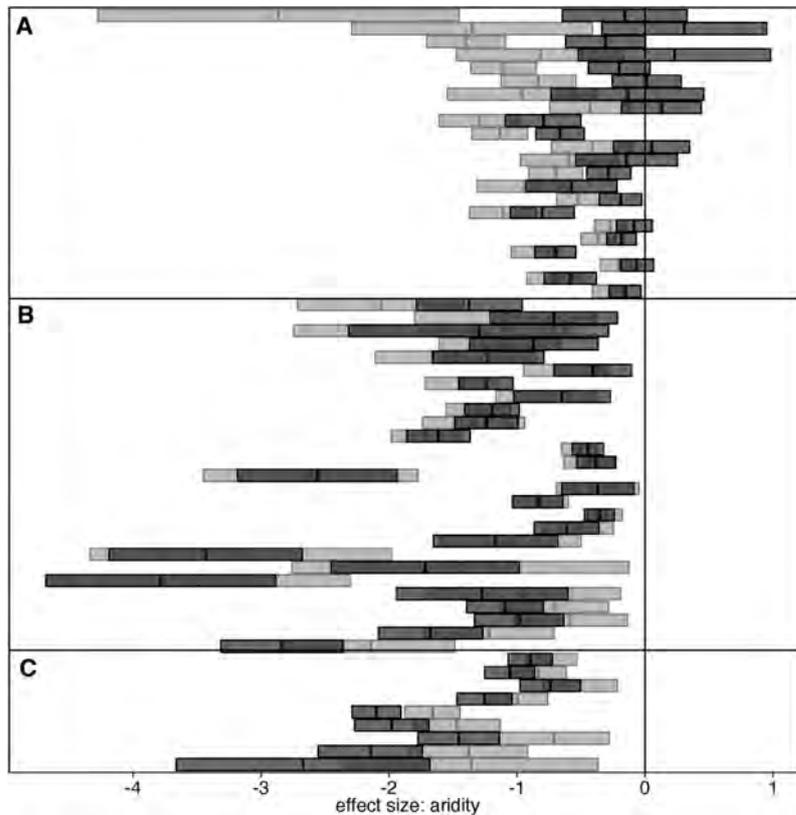


Figure 3. Species associations with aridity in non-floodplain ecosystems (*light grey*) and floodplain ecosystems (*dark grey*) for species that had a negative association with aridity in non-floodplain ecosystems ($\text{Pr}(B_1 < 0) > 0.9$). Bars represent 80% credible intervals for posterior distributions, central line indicates mean. Species are arranged according to those with (A) strong evidence for a less negative association with aridity in floodplain ecosystems ($\text{Pr}(B_2 > 0) > 0.9$), these species are listed in Table 2 (B) no evidence for a difference in the association with aridity between ecosystems and (C) strong evidence for a more negative association with aridity in floodplain ecosystems ($\text{Pr}(B_2 < 0) > 0.9$). All species and mean effect sizes are listed in Table S1.

and computationally efficient solution for large datasets (Rue and others 2009). We used the MCMCglmm package (Hadfield 2010) in R to fit the species trait models because this package allows for the incorporation of a phylogenetic tree and weighting of the response variable based on uncertainty. We considered a posterior probability of $\text{Pr}(\text{parameter} > 0) > 0.9$ as strong evidence that the parameter had a positive association to the response variable, and a posterior probability of $\text{Pr}(\text{parameter} < 0) > 0.9$ as strong evidence for a negative association (Kass and Raftery 1995).

RESULTS

Vegetation Greenness

Floodplain vegetation had greater NDVI compared to non-floodplain vegetation ($\delta_1 = 2.25$, $\text{SD} = 0.39$, $\text{Pr}(\delta_1 > 0) > 0.9$) after accounting for the effects of aridity, which had a negative association with NDVI ($\delta_2 = -10.8$, $\text{SD} = 0.27$, $\text{Pr}(\delta_2 > 0) > 0.9$).

Species Occurrence

For all but one species (yellow-throated miner *Manorina flavigula*), the associations between species occurrence and aridity were in the same direction for both river corridors, so we report on the mean trend across river corridors. Of the 130 species that we analysed, 58 (45%) showed strong evidence of lower occurrence with higher aridity in non-floodplain ecosystems ($\text{Pr}(B_1 < 0) > 0.9$, Figure 3, see Table S1 in Supporting Information), but the effect of aridity was moderated in floodplain ecosystems for 22 of these species (38%) ($\text{Pr}(B_2 > 0) > 0.9$, Figure 3A; Table 2): 12 species showed no association with aridity in floodplain ecosystems ($\text{Pr}(B_{fr} < 0)$ and $\text{Pr}(B_{fr} > 0) < 0.9$) and, while still negative, the adverse effects of aridity on species occurrence were less in floodplain ecosystems compared to non-floodplain ecosystems for ten species (Figure 3A). Only nine species showed a more negative association with aridity in floodplain ecosystems than in non-floodplain ecosystems ($\text{Pr}(B_2 < 0) > 0.9$, Fig-

Table 2. List of Species For Which the Negative Effect of Aridity on Occurrence Was Moderated in Floodplain Vegetation (that is, Effect of Aridity in Floodplain Vegetation Was Positive, Neutral or Less Negative than in Non-floodplain Vegetation)

| Common name | Scientific name |
|---------------------------|-----------------------------------|
| Scarlet robin | <i>Petroica multicolor</i> |
| Spotted bowerbird | <i>Chlamydera maculata</i> |
| Chestnut-rumped thornbill | <i>Acanthiza uropygialis</i> |
| Inland thornbill | <i>Acanthiza apicalis</i> |
| Yellow thornbill | <i>Acanthiza nana</i> |
| Red-capped robin | <i>Petroica goodenovii</i> |
| White-browed babbler | <i>Pomatostomus superciliosus</i> |
| Spiny-cheeked honeyeater | <i>Acanthagenys rufogularis</i> |
| Silvereye | <i>Zosterops lateralis</i> |
| Apostlebird | <i>Struthidea cinerea</i> |
| Little raven | <i>Corvus mellori</i> |
| Australian raven | <i>Corvus coronoides</i> |
| Dusky woodswallow | <i>Artamus cyanopterus</i> |
| Rufous whistler | <i>Pachycephala rufiventris</i> |
| Little friarbird | <i>Philemon citreogularis</i> |
| Striped honeyeater | <i>Plectorhyncha lanceolata</i> |
| Yellow-rumped thornbill | <i>Acanthiza chrysorrhoa</i> |
| Grey butcherbird | <i>Cracticus torquatus</i> |
| Black-faced cuckoo-shrike | <i>Coracina novaehollandiae</i> |
| Laughing kookaburra | <i>Dacelo novaeguineae</i> |
| Grey shrike-thrush | <i>Colluricincla harmonica</i> |
| Australian magpie | <i>Gymnorhina tibicen</i> |

Species are listed in order of effect size depicted in Figure 3A. Nomenclature follows Christidis and Boles (2008).

ure 3C), whereas the other 27 species showed no substantial difference in the negative association with aridity in floodplain ecosystems compared to non-floodplain ecosystems (Figure 3B). Twenty-nine species (22%) showed a positive association between occurrence and aridity ($\Pr(B_1 < 0) > 0.9$) in non-floodplain ecosystems; the associations differed for just seven of these species in floodplain ecosystems: two had a more positive association with aridity in floodplain ecosystems and five species had a less positive association with aridity in floodplain ecosystems (see Table S1 in Supporting information). The occurrence of 43 species in non-floodplain ecosystems was not strongly related to aridity (see Table S1 in Supporting information).

Species Traits

Habitat guild explained most of the variation in species response to aridity (53%), while other traits and phylogeny explained very little variation (<4% each; Figure 4A). Species that occupy forest and woodland habitats on average were more likely to have a negative association with aridity in non-floodplain ecosystems ($\Pr(\text{effect} > 0) > 0.9$)

(Figure 4B). Species traits explained little variation in whether floodplain ecosystems mediated the negative effect of aridity on species occurrence (Figure 4C); 6% of the variation in B_2 was attributed to nesting substrate (Figure 4C, D), whereas other traits and phylogeny each explained less than 2% of variation (Figure 4C).

DISCUSSION

The occurrence of 45% of terrestrial bird species in non-floodplain ecosystems along the Murray and Darling river corridors was negatively associated with aridity. Aridity can influence the occurrence of faunal species through two mechanisms: (1) abiotic conditions that impose direct physiological limitations on species occurrence, and (2) limitations on occurrence based on the availability of habitat resources provided by vegetation, which itself is influenced by aridity. Temperatures in arid landscapes fluctuate greatly, maximum temperatures are high, rainfall is sporadic and free water is limited (Davis and others 2013). As aridity increases, energy needs and evaporative water loss increase, which can result in selective pressure on biota related to basal metabolic rates (Tieleman and

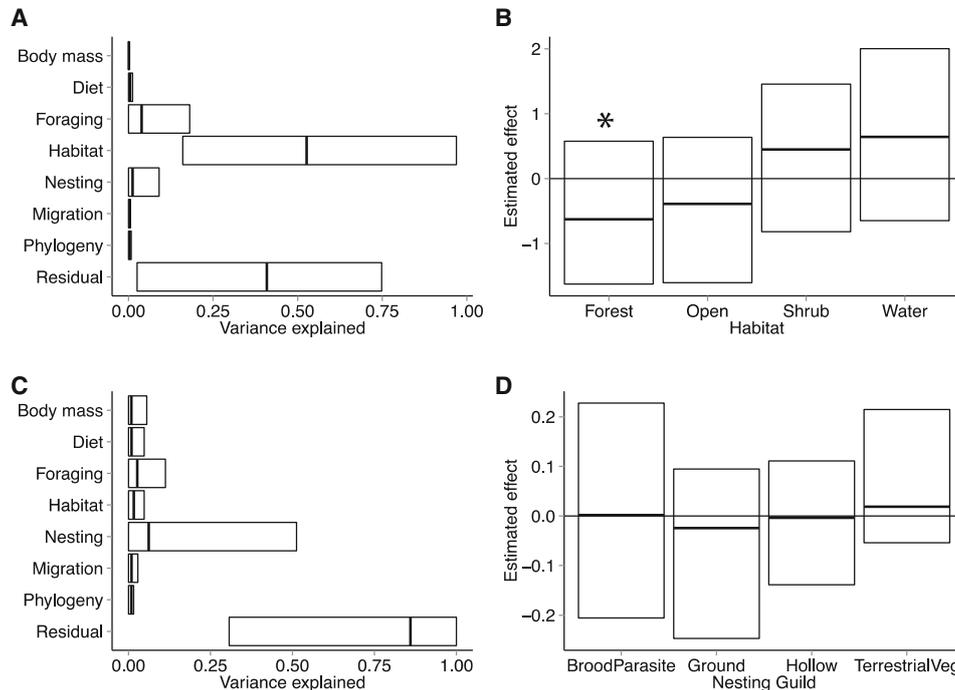


Figure 4. Mean (*central line*) and 95% credible intervals for **(A)** variance components by species trait for species response to aridity index, with habitat guild explaining the most variation in species associations with aridity; **(B)** estimated effects of aridity index on each habitat guild (effects < 0 = negative association with aridity); **(C)** variance components by species trait for the extension of species distributions by floodplain ecosystems, with nesting guild explaining the highest amount of variance among the species traits; and **(D)** estimated effects of floodplains on species aridity association by nesting guild (positive effect indicates floodplain ecosystems facilitate species occurrence in more arid regions). *Asterisks* indicate effects with $Pr > 0.9$.

others 2003). Arid ecosystems are resource limited compared to more mesic ecosystems because low water availability limits primary production (Knapp and Smith 2001). Tree cover generally decreases in more arid regions (Schulze and others 1996; Scholes and others 2002). Among habitat guilds, the occurrences of species that prefer forest and woodland habitat were most negatively affected by aridity, suggesting that declines in tree cover in arid regions may play an important role in limiting species occurrence.

Floodplains moderated the negative effects of aridity on the occurrence of species in the Murray and Darling river corridors, with 38% of species that were negatively affected by aridity in non-floodplain ecosystems showing weaker or no decrease in occurrence with higher aridity in floodplain ecosystems. Conversely, there was little difference in the association between aridity and

species occurrence in floodplain ecosystems for species whose occurrence was positively associated with aridity in non-floodplain ecosystems. Along the aridity gradient, floodplain sites had higher NDVI than other vegetation, indicating that floodplain forest and woodland is more productive than other vegetation (Wang and others 2004), probably due to higher water availability and greater soil fertility (Naumburg and others 2005; Ballinger and Lake 2006). These outcomes suggest that floodplain ecosystems act as a 'green tongue', allowing species to occupy drier regions than they would otherwise (Figure 1). Floodplain ecosystems moderated the effect of aridity across habitat, foraging, nesting and dietary guilds, which suggests that there may be greater amounts of a broad range of resources in floodplain forests and woodlands compared to other habitats in arid regions. Floodplain vegetation of the Murray–Darling Basin is dominated by

species of *Eucalyptus*, which provide a higher abundance of food (for example, nectar and carbohydrate rich exudates) and nesting resources (for example, hollows) for birds compared to tree species that dominate non-floodplain in arid zones, such as *Acacia* spp. (Pavey and Nano 2009; Tischler and others 2013). Resource availability in floodplain ecosystems is likely to be more reliable during periods of low rainfall because floodplain vegetation has access to water through streams, floods or groundwater (Selwood and others 2015b).

Cooler and wetter microclimatic conditions in floodplain ecosystems may facilitate the occurrence of species in more arid regions than they could otherwise occur based on annual rainfall or temperature. We did not collect data on site microclimate conditions, and available climate data are at a more coarse resolution than our sampling units (Bureau of Meteorology (Australia) 2015c, 2015b). However, extensive canopy cover and proximity to water may moderate microclimate in floodplain ecosystems, resulting in lower daytime temperatures and higher relative humidity than in adjacent habitats (Brosofske and others 1997; Danehy and Kirpes 2000), especially in arid zones where non-floodplain habitat has relatively low canopy cover. Arid zones experience lower night-time temperatures compared with more mesic regions with higher canopy cover, which may place relatively greater energetic demands on birds during the night (Körtner and others 2001). Higher vegetation cover in floodplain ecosystems is likely to provide greater availability of micro-refuges for animals to shelter from hot daytime conditions and also warmer nighttime conditions. Relief from the pressure of climate conditions in floodplain ecosystems may allow some species to expand farther into arid zones. Access to water in arid zones can assist birds to ameliorate the effects of evaporative water loss (Fisher and others 1972), so that proximity to water in floodplain ecosystems may facilitate species occurrence in arid regions (McCluney and Sabo 2009).

Riparian and floodplain ecosystems provide an interconnected network of vegetation throughout landscapes and over regions (Fremier and others 2015). Despite extensive clearing for agriculture, the floodplain forests and woodlands of the Murray–Darling Basin remain some of the largest and more contiguous vegetation types in south-eastern Australia (McGinness and others 2010). The higher connectivity of floodplain vegetation compared to other vegetation types, particularly in much modified landscapes, may contribute to the broader distribution of species ranges in floodplain ecosystems along these river corridors. Changes in species

composition with increasing loss of landscape cover are less apparent in riparian vegetation than in other vegetation types (Bennett and others 2014). It is possible that floodplain ecosystems facilitate the extension of species distributions into arid zones through the provision of more continuous corridors of vegetation for movement of individuals and therefore, meta-population persistence, which may otherwise be hindered in more fragmented non-floodplain vegetation. There is genetic evidence that this is the case for a woodland-dependent marsupial, the yellow-footed antechinus *Antechinus flavipes* (Lada and others 2008).

Our finding that floodplains facilitate the occurrence of species in more arid regions is consistent with greater distinctness of floodplain and riparian faunal assemblages from adjacent assemblages in arid regions than in wetter regions (Woinarski and others 2000; Sabo and others 2005). Previous work in our study region found that terrestrial bird assemblages are more differentiated between floodplain and adjacent habitats along the Murray River as mean annual rainfall decreases (Tzaros 2001). The extension of species distributions into arid regions along tongues of floodplain vegetation probably contributes to greater differences in local species composition between floodplain and other vegetation, and so, increases local and regional species richness (Sabo and others 2005).

Areas that provide relief from high temperatures, have greater water availability, and support more vegetation biomass will become increasingly important for species persistence as climate change increases drying in many parts of the world (Hartmann and others 2013; Reside and others 2014). Floodplain ecosystems provide drought refuges for fauna from which individuals can disperse when conditions moderate (Seabrook and others 2011; Selwood and others 2015b) and more stable species assemblages during drought than other vegetation types (Haslem and others 2015; Nimmo and others 2016). Here, we show that floodplain ecosystems moderate the effect of aridity on species occurrence, which further highlights the important role that these zones play in enabling species persistence in drying climates. Riparian zones enabled the persistence of mesic plant communities in past geological periods of climate drying (Meave and others 1991) and floodplain ecosystems have the potential to be important areas for species persistence and adaptation under human-induced climate change (Capon and others 2013).

The degree to which floodplain ecosystems differ from surrounding uplands depends on flood frequency and duration, flow intermittency and

groundwater depth (Brand and others 2011). Human land-use and drying climate conditions may reduce the contrast in vegetation productivity between floodplain and non-floodplain ecosystems by affecting water availability. Multiple anthropogenic pressures have affected the floodplain ecosystems of the Murray–Darling river system (Mac Nally and others 2011). Reduced flood frequency and changed flooding regimes have led to extensive dieback of floodplain forests and woodlands, and the drying climate is exacerbating these effects (Horner and others 2009). Changes to groundwater depth and salinity have contributed to forest dieback (Cunningham and others 2011). Therefore, the ameliorative effect of floodplains on aridity is likely to be less than it was prior to regulation of the Murray–Darling river system. The ongoing pressures of human land-use and a drying climate may further dampen the capacity for floodplain ecosystems to carry bird species into more arid climate zones.

Floodplains are not immune to the effects of climate drying and terrestrial fauna in these ecosystems may have limited resistance to drought and recovery in wetter periods (Selwood and others 2015a). Many floodplain ecosystems have been much disturbed by human land use, which may further limit their resistance to climate change (Whitford and others 1999). Floodplain ecosystems around the world have experienced reduced stream-flow and inundation due to water extraction for human land use, high levels of urban and agricultural development (Tockner and Stanford 2002), disruptive land uses such as grazing, timber extraction and secondary impacts such as salinity and alien plant invasions (Richardson and others 2007; Mac Nally and others 2011). The maintenance of intact floodplain vegetation and ecological restoration of modified floodplain ecosystems will maximize the value of these areas for terrestrial fauna in arid zones, particularly as climate change intensifies (Seavy and others 2009). We have shown that floodplain ecosystems are important for contributing to regional terrestrial bird assemblages. Management of floodplain ecosystems, including environmental water allocations, should include the setting and monitoring of goals for terrestrial biota alongside aquatic and water-dependent biota, which are usually the focus for management in such ecosystems.

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Chapter 6

**High-productivity vegetation is important for lessening
drought-induced declines in woodland birds**

High-productivity vegetation is important for lessening drought-induced declines in woodland birds

Katherine E. Selwood^{1,3*}

Melodie A. McGeoch¹

Rohan H. Clarke¹

Ralph Mac Nally²

*Corresponding author: Katherine.selwood@unimelb.edu.au

¹ School of Biological Sciences, Monash University, Vic. 3800, Australia

² Institute for Applied Ecology, The University of Canberra, Bruce ACT 2617, Australia

³ School of Biosciences, The University of Melbourne, Parkville Vic, 3010, Australia

Key words: NDVI, vegetation productivity, species resistance, vegetation greenness, climate refugia, climate change, drought, landscape cover, vegetation structure, topography

Abstract

1. Locations where ecological assemblages show high resistance (= the maintenance of positive or stable population trends, or less severe declines, compared to other locations) to climate pressures, such as drought, are likely to be important refuges for biota in changing climates. We asked whether characteristics of locations, including vegetation structure, vegetation productivity, landscape context and the physical environment, were associated with the capacity of bird assemblages to withstand prolonged drought.
2. We used a multi-species index to quantify trends in bird assemblages during a 13-year drought at >500 locations (>18,000 surveys) in the Murray-Darling Basin, southeastern Australia, using data from the Atlas of Australian Birds. We investigated whether the resistance of bird assemblages was associated with: (1) vegetation structure; (2) vegetation productivity (vegetation greenness); (3) landscape context (patch size, landscape vegetation cover); or (4) physical environment (elevation, terrain, topography, availability of surface water, distance to permanent water).
3. Vegetation productivity, indicated by vegetation greenness (Normalized Difference Vegetation Index) and clumping of ground cover were positively associated with the index of drought resistance, while assemblages in areas with high landscape vegetation cover were more vulnerable to drought. There was little evidence that variables characterizing the physical environment were associated with drought resistance of bird communities.
4. *Synthesis and applications* Bird assemblages in locations with high vegetation cover and low vegetation productivity (e.g. arid and semi-arid ecosystems) are more vulnerable to prolonged drought, and so may require greater

conservation attention during drought periods. Maintaining vegetation productivity and protecting high-productivity sites may be an effective strategy for increasing the resistance of bird assemblages to more frequent and severe droughts that are projected for the Murray-Darling Basin and other regions of the world. Remotely sensed vegetation greenness may be a promising source of information for identifying drought refuges for birds and possibly other biota, particularly if linked to ground measurements of vegetation.

Introduction

Climate change is a key driver of biodiversity change (Bellard *et al.* 2012). Increases in the frequency and severity of climate extremes, such as drought, heat-waves and extreme weather events, may pose a greater threat to ecosystem function than gradual increases in mean temperature or aridification (Parmesan, Root & Willig 2000; Jentsch & Beierkuhnlein 2008). Climate extremes may have severe local effects on ecosystems, and it is difficult to manage pressures of climate change at local or even regional scales. Strengthening the capacity of local ecosystems to withstand climate extremes such as drought ('resistance' = the maintenance of positive or stable population trends, or less severe declines, compared to other locations) is likely to be a key management strategy for minimizing the adverse effects of climate change on biota (Nimmo *et al.* 2015).

Drought is occurring with increased frequency, severity and extent in many parts of the world (Sheffield & Wood 2008), and poses a major threat to many ecosystems (Mitchell *et al.* 2014). Drought reduces resource availability for animals, including food, shelter and nesting resources and xeric climate conditions place physiological pressures on individuals (Albright *et al.* 2010). Locations where biota show resistance to drought, are likely to be important climate refuges, and locations where biota show low resistance may require priority conservation during drought. Identifying environmental characteristics that affect the resistance of animal assemblages contribute important information to two approaches for mitigating the effects of climate extremes: (1) predicting and protecting those locations that are likely to be resistant to climate extremes; and (2) identifying environmental variables that might be manipulated to improve resistance of the resident biota (Nimmo *et al.* 2015).

There are four types of environmental variables that may affect the resistance of animal assemblages to climate pressures by influencing abiotic and microclimatic conditions or resource availability: (1) vegetation structure; (2) vegetation productivity; (3) landscape context; and (4) the physical environment.

Locations in which vegetation is in better condition may be more likely to sustain populations through climate extremes, such as drought (Mac Nally *et al.* 2014). In-site vegetation structure affects the local availability of food and nesting resources and micro-refuges, which affect population vital rates (Selwood, Mac Nally & Thomson 2009). Vegetation productivity may affect drought resistance of animal assemblages because more-productive ecosystems have more food and habitat resources and so, support more individuals and more species (Hurlbert 2004). Vegetation productivity is linked to the reproductive success and survival of animals (Rasmussen, Wittemyer & Douglas-Hamilton 2006) so that more-productive ecosystems are likely to sustain more-viable populations. Analogues of vegetation productivity can be estimated by remotely sensed measures of vegetation greenness, such as the Normalized Difference Vegetation Index (NDVI) (Wang *et al.* 2004). 'Ecosystem greenspots', locations where vegetation productivity is relatively high, are likely to be refuges for animals during drought by providing more-stable ecological resources (Mackey *et al.* 2012).

Landscape context may affect the ability of fauna to withstand drought, especially for mobile taxa such as birds. Fragmented vegetation may be more susceptible to drought-induced degradation (Bennett *et al.* 2015), while ready access to food resources in the surrounding landscape may increase the capacity of animals to survive hot and dry periods (Bennett *et al.* 2014). Last, the physical environment consists of the abiotic elements that influence microclimatic conditions and water

availability of ecosystems, which can affect biotic resistance. For example, gullies provide more-sheltered and more-mesic microclimates than nearby ridges, which may protect individuals from climate extremes (Mac Nally, Soderquist & Tzaros 2000). Ecosystems with locally low water availability, (e.g., ridges), or regionally low water availability (e.g. arid climate zones) may be particularly vulnerable to drought because they are already water-limited, while wetter locations, such as those with high water retention or in mesic climate zones may have greater capacity to withstand drought (Weltzin *et al.* 2003).

We used a multi-species index based on trends in the occurrences of drought-declining bird species to quantify the resistance of bird assemblages to a prolonged drought, the ‘Big Dry’, at >500 locations in the Murray-Darling Basin, southeastern Australia. The Big Dry (1997 – 2010), was the most severe drought on record in southeastern Australia (Verdon-Kidd & Kiem 2009) and had profound effects on bird assemblages, with widespread declines (Bennett *et al.* 2014; Selwood *et al.* 2015a; Selwood *et al.* 2015b). Prolonged droughts are expected to become more frequent in the region (Timbal *et al.* 2015), so identifying drought refuges is vital. We focus on birds as exemplars because they are much more mobile than other faunal groups, and should be more able to respond to spatial variation in conditions. Moreover, there are much more available data for birds than for other taxa. We investigated whether site characteristics are associated with the resistance of bird assemblages to drought by relating bird-assemblage resistance to: (1) vegetation structure; (2) vegetation productivity; (3) landscape context; and (4) the physical environment. We expected that the following conditions would increase the resistance of bird assemblages to the drought:

1. Local availability of ecological resources (measured by ground, shrub and tree cover, plant species diversity and fallen timber);
2. Highly productive ecosystems (measured by using vegetation greenness);
3. Potential availability of resources in the surrounding landscape (measured by patch size, landscape vegetation cover); and
4. Sheltered landscapes with high water availability (measured by elevation, terrain, topography, surface water, distance to permanent water).

Methods

Bird surveys

We used bird-survey data from BirdLife Australia's New Atlas of Australian Birds program, specifically, information from the standard 2-ha/20-min surveys, from January 1998 to December 2009 (Barrett *et al.* 2003). We used sites at which vegetation structure and cover data at the survey location had been recorded by bird surveyors on a standard 'habitat form' (Table 1; BirdLife Australia 2012). We included only those sites that were surveyed for ≥ 4 years. We considered this a minimum period for detecting trends because other research in the region has detected changes in bird assemblages during the Big Dry in 4 yr (Haslem *et al.* 2015). We excluded sites that had incomplete information on site coordinates (accuracy >100 m), vegetation variables (see *Site characteristics*) or that had been surveyed <10 times. The resulting dataset was for 546 sites with 18,306 bird surveys (mean number of surveys per site = 24.6, standard deviation = 22.8) (Fig. 1).

Climate data

We obtained spatial rainfall and temperature data (modeled at 500 m resolution) for the survey years (Bureau of Meteorology (Australia) 2015b; Bureau of Meteorology (Australia) 2015a). We calculated mean annual temperature and rainfall anomalies, compared to the Australian Bureau of Meteorology's standard historic baseline of 1961–1990, at each site, in each year of the study using QGIS (QGIS Development Team 2013).

Multispecies drought-resistance index

We developed a multispecies index to measure the resistance of drought-declining bird assemblages at each site, which we call the 'Drought Resistance Index' (DRI). This index resembles the multispecies indices used by Gregory *et al.* (2009) and Stephens *et al.* (2016) to compile trends in groups of birds for which climate suitability is either increasing or decreasing. Multispecies indices aggregate information on groups of species into scalar measures. Although the absolute values of multispecies indices are difficult to interpret on their own, indices are useful for comparing composite trends in species in time or space in response to anthropogenic pressures (Stephens *et al.* 2016).

Our index was based on 'drought-declining' species. We defined these as species with a mean negative temporal trend in occurrence (t_i , Table S1) during the Big Dry that were identified in a previous study that measured trends in the occurrence of terrestrial bird species using data from > 39,000 surveys in > 28,000 sites in the Murray-Darling Basin (Selwood *et al.* 2015b). The widespread extent of the drought meant that there were no concurrent 'controls' to determine whether species declines were caused, or enhanced, by the drought. Furthermore, the spatially explicit Atlas of Australian Birds commenced in 1998, so there were not comparable pre-drought baselines. As such, it is possible that some of these 'drought-declining'

species were declining for reasons other than drought, such as lags caused by historic land-use change in the region (Ford 2011).

Each species was given a weighting such that highly drought-declining species contributed more heavily to the DRI. We calculated the weight w_i for species i as:

$$w_i = \frac{(|t_i| - \min(|t_S|))}{(\text{range}(|t_S|))},$$

where: t_i is a species' overall trend during the Big Dry [from Selwood *et al.* (2015b); Supplementary Table S1] and S is the list of drought-declining species, including all species with a mean negative trend, regardless of the statistical magnitude of t_i (i.e., the posterior probability that $t_i < 0$).

For each site j , we estimated temporal trends for each species i over the Big Dry period. The model was $\text{probit}(p_{i,j}) = \alpha_0 + X_{i,j} \times \text{year}$, where: $p_{i,j}$ is the probability of observing species i at site j in a single survey; α_0 is the intercept; and $X_{i,j}$ is the temporal trend parameter, with year ranging from 1 (1998) to 12 (2009). We assumed all trends were linear (Selwood *et al.* 2015b). Site trends were fitted using the *glm* function in R (R Core Team 2015).

The DRI was calculated by summing $w_i \times X_{i,j}$ for all drought-declining species at each site j , giving a composite indicator of species' trends at that site weighted by species' drought sensitivities. Larger values of the DRI indicated greater drought resistance of drought-declining species. To be included in the analysis, a site must have had a minimum of ten surveys in the survey period, but there was no minimum number of observations for a species trend to be included in the DRI.

To provide a measure of uncertainty in the DRI values, we generated 1000 bootstrapped samples of $\sum_{i=1}^n w_i \times X_{i,j}$ for each site with replacement from the set of species present at site j , and summed $w_i \times X_{i,j}$ for each bootstrapped sample ($n =$

number of species present at site j) using the package ‘boot’ (Canty & Ripley 2015) in R. The variances and confidence intervals for each site were calculated from the 1000 samples.

Site characteristics

1. Vegetation structure

We estimated vegetation structure from data recorded in Habitat forms of the New Atlas of Australian Birds program (Table 1; BirdLife Australia 2012). Variables included estimated cover and diversity of small shrubs, tall shrubs, trees and ground cover and the amount of fallen timber (Table 1). While other variables were included on the Habitat form, we only included variables that had near-complete data for all sites (< 10 sites [1.8%] missing information for each variable) to maximize the number of sites included in the analysis. The cover and diversity of tall and small shrubs were intercorrelated ($r > 0.70$) so we excluded all but small shrub cover, because it was most highly correlated with all three other shrub variables.

2. Vegetation productivity

To obtain an estimate of the average vegetation productivity of a site, we extracted the mean annual Normalized Difference Vegetation Index (NDVI) using site coordinates (Table 1). The NDVI is strongly related to vegetation productivity, and links between NDVI and the fraction of absorbed photosynthetic active radiation intercepted are well documented (Pettoirelli *et al.* 2005).

3. Landscape context

We measured the percentage cover of native vegetation to indicate resource availability in the surrounding landscape for each site using ‘maptools’ (Bivand & Lewin-Koh 2013) and ‘raster’ (Hijmans & van Etten 2013) in R (Table 1). We used a 500-m radius because this scale has previously been shown to be a good predictor of bird species response in the study region (Thomson *et al.* 2009). The area of vegetation patches in which sites

were located was obtained from Atlas of Australian Birds Habitat forms (Table 1).

4. Physical environment

We used spatial information on elevation, topographic wetness index, frequency of surface water presence, and distance to permanent water sources using site coordinates (Table 1) and information on site terrain from habitat forms (Table 1) to characterize the physical environment of sites. We obtained the mean annual aridity of sites, but this was highly correlated with NDVI ($r = 0.79$) so we excluded it from the analysis (Table 1). We included NDVI rather than aridity because we believed that NDVI would be more directly linked to bird responses than aridity because NDVI links vegetation productivity and hence probable resource availability to climate (Pettorelli *et al.* 2005).

Statistical analysis: predictor pre-processing

All pairwise-correlations for retained continuous predictors were ≤ 0.55 . The distributions of the retained predictors were near normally or near uniformly distributed. We standardized (mean = 0, standard deviation = 1) the predictors to make the ranges of all predictors comparable and to assist in model convergence. We assigned values of -1 and 1 to binary categorical predictors to allowed us to treat them as continuous variables with effectively standard normal distributions; missing values (NAs) then were assigned standard normal priors for the Bayesian multiple regression (see below).

Statistical analysis 1: Bayesian multiple regression

We used three approaches that have differing capabilities to interrogate the data. First, we utilized the flexibility of Bayesian multiple regression (BMR) to propagate the uncertainties in the response variable and to impute ‘automatically’ sporadic missing values in the predictors. The model was:

$$DRI_i \sim N(z_i, \sigma_{DRI_i}^2); z_i \sim N(\mu_i, \sigma^2); \mu_i = \alpha + \sum_{j=1}^P \beta_j X_{ij}.$$

$$\alpha \sim N(0, \sigma^2 = 4); \beta_j \sim N(0, \sigma_\beta^2); \sigma, \sigma_\beta \sim U(0, 0.2).$$

Here, DRI_i is the estimated value for site i , with variance $\sigma_{DRI_i}^2$. z_i is the value of DRI with uncertainty propagated, and is modeled as a function of the mean μ_i and variance σ^2 . μ_i is a function on the intercept α [prior: $N(0, \sigma^2 = 4)$] and a linear combination of regression coefficients (β_j) and P site-specific predictor values (X_{ij}). The β_j values have exchangeable priors with mean 0 and variance σ_β^2 . All missing predictor values were assigned standard normal priors [$N(0,1)$]. We used the ‘cut()’ function to prevent feedback to the model-parameter fitting.

Model fit was assessed using posterior predictive assessment (Gelman, Meng & Stern 1996), which assesses measure of fit (PPfit) between the observed and fitted values (sum of absolute deviations) with a distribution of discrepancies between ‘plausible’ values derived from the fitted model and the fitted values. If the discrepancy of observed values is similar to the mean of the discrepancy of the plausible samples, then the model ‘predicts’ the data well. PPfit is held to be good if $0.05 < \text{PPfit} < 0.95$.

We made inferences on the importance of predictors by measuring the posterior probability distributions (PPD) of the β_j . Given uninformative priors, if < 0.1 of the PPD for β_j were > 0 , then the predictor is regarded as having a negative association with the response; if > 0.9 of the PPD for β_j were > 0 , then the predictor is regarded as having a positive association with the response (Kass & Raftery 1995).

Statistical analysis 2: Bayesian model averaging

We used Bayesian model averaging (BMA) to estimate the relationships between DRI and the predictors. The software used, `bic.glm` in the BMA package (Raftery *et al.*

2015) in R, fits generalized linear models using the ‘leaps and bounds’ algorithm and the Bayesian information criterion approximation to Bayes factors (Hoeting *et al.* 1999). However, `bic.glm` cannot accommodate missing values so these analyses were conducted with only complete-data sites (414 or 76% of sites used in the Bayesian multiple regression); `bic.glm` cannot propagate uncertainties in the response. We assumed a Gaussian errors model, which was checked and supported by post-fitting assessments. We used the posterior probability that a variable had a non-zero coefficient [$\text{Pr}(\text{inc})$] as a measure of the influence of that variable on the DRI. We considered values of $\text{Pr}(\text{inc}) > 0.75$ to be strong evidence that a given predictor variable influenced the DRI (Viallefont, Raftery & Richardson 2001).

Statistical analysis 3: Hierarchical partitioning

The two approaches above are useful for identifying potentially influential predictors but do not provide a break-down of ‘explained variation’, so we used the `hier.part` package in R (Walsh & Mac Nally 2003) to estimate the individual explanatory power of the predictors identified in the BMR and the BMA. Note that `hier.part` does not cater for missing values so analyses are for the 414 full-complement sites.

Results

Climate

Annual rainfall was below average at most sites (median site anomaly < 0) for 10 of the 13 years of the Big Dry (Fig 2a). The mean cumulative rainfall anomaly of sites for the study period was -882 mm relative to the baseline average for 1961–1990. Mean annual temperature was consistently above average at most sites (median site anomaly > 0) for all of the Big Dry (Fig. 2b).

Drought resistance

Eighty-nine species were identified as drought-declining. The number of drought-declining species recorded at each site, and hence, the number of species contributing to a site's DRI, ranged from 2–50, with a mean of 17.3 and standard deviation of 8.0. The majority of species had weightings of <0.200 , with the mean weighting being 0.167 (Fig. S1, Table S1). The distribution of site values of DRI was near normal (Fig. S2), ranging from -0.367 to 0.400 , with a mean of -0.025 and standard deviation of 0.161. The bootstrapped 95% confidence intervals generally were centered around the DRI value for each site (Fig. S3).

Relationships between the DRI and predictors

The model fitted the data well for the BMR (PPfit = 0.39) for 545 sites. The regression parameters for four predictors were substantially different from 0, with DRI being associated positively with NDVI and negatively with ground cover spread (clumped vs not clumped), landscape cover, and small shrub cover (Table 2). For fewer sites (414), the results for the BMA produced three of the same important predictors [$\text{Pr}(\text{Inc}) > 0.75$], but with small shrub cover having a small $\text{Pr}(\text{Inc})$ (Table 2). The signs of the regression parameters were the same as for the BMR, although the coefficients and their standard deviations were larger. The smaller values for BMR probably are due to the 'shrinkage' associated with use of exchangeable priors for the regression parameters, but also reflects the incorporation of uncertainties in the response (DRI). The results of the hierarchical partitioning were consistent with the BMA outcomes, with small shrub cover having a small amount of independent explanatory power compared with the other three predictors (Table 2).

Discussion

Bird assemblages in sites with more productive vegetation, indicated by vegetation greenness, showed greater resistance to prolonged drought, while bird assemblages in landscapes with high vegetation cover were more vulnerable. Ground cover spread was the only vegetation structural characteristic that affected the resistance of bird assemblages, while measures of the physical environment showed no association with the index of drought resistance.

The lack of association between DRI and physical landscape characteristics that are thought to provide relief from xeric climate conditions (e.g. gullies, proximity to water) indicate that the Big Dry predominantly may have affected bird-assemblage resistance through reduced resource availability rather than through physiological pressures. This inference is supported by our finding that vegetation greenness was the most important predictor of the DRI. Vegetation greenness, measured by NDVI, has been used successfully to estimate resource quality, abundance and dynamics for many groups of animals, including birds (Pettorelli *et al.* 2005; Pettorelli *et al.* 2011). It is likely that greener sites, those with greater values of NDVI, had more resources that enabled bird populations to persist in the face of the Big Dry. Locations with high vegetation greenness, and hence vegetation productivity, probably will provide more resources for birds because plants provide food (seeds, fruit, nectar, invertebrates), nesting materials, shelter and breeding substrates (Hurlbert 2004; Berry, Mackey & Brown 2007). Although we did not find effects of gullies or water availability *per se* on the DRI, these variables might be important at local scales where relatively greater water availability and topographic sheltering may create 'ecosystem greenspots' (Mackey *et al.* 2012).

We did not examine the direct effects of aridity on the DRI because aridity was highly, negatively correlated with NDVI, so it is possible that aridity has a strong influence on bird resistance. Vegetation productivity declines with aridity (Roderick, Berry & Noble 2000), so that aridity may be an important governor of bird-assemblage resistance to drought as a driver of vegetation productivity. Arid ecosystems are more sensitive to declines in rainfall (Weltzin *et al.* 2003), so higher aridity (and thus, lower productivity) sites may have experienced greater absolute or proportional declines in productivity during the Big Dry, which could explain the reduced resistance in low-productivity landscapes. It is also possible that the aridifying conditions of drought caused local extirpations at sites located at the edge of species climatic distributions because the occurrences of many Murray-Darling Basin bird species are negatively associated with aridity (Selwood *et al.* 2016).

Bird assemblages in landscapes (c. 0.8 km²) with high vegetation cover tended to be more vulnerable to drought, with lower DRI values (Fig. 3, lower panel). We suspect that this is because assemblages in high-cover landscapes probably were in a better initial state (higher species richness, higher abundance) so the absolute change in the DRI was greater than in low-cover sites (i.e., high-cover landscapes had ‘more to lose’). It is also possible that the lower DRI values at sites with high landscape cover were associated with the response of species that are commonly found in high-cover landscapes, such as habitat or dietary specialists (Ford *et al.* 2001; Tschardtke *et al.* 2008). These species may be more vulnerable to resource declines during drought because they have less flexibility in their resource use.

Ground cover was the only aspect of vegetation structure that was associated with the DRI: bird assemblages at sites where vegetative ground cover was more clumped exhibited greater resistance. This relationship may be driven by ground

foraging birds. ‘Clumped’ ground cover is likely to indicate the presence of grass tussocks, which are important breeding and foraging substrates for many woodland birds (Ford *et al.* 2001). Clumped ground cover interspersed with bare ground is likely to be good foraging habitat for insectivorous ground foragers (Schaub *et al.* 2010). While other aspects of vegetation structure appeared unrelated to the DRI, the variables that we used from the Atlas program, were designed to be coarse, ordinal measures based on visual estimates by volunteer bird observers (Table 1). More-detailed measurements of vegetation might reveal other relationships between bird resistance and vegetation structure, which have been documented elsewhere (Bennett *et al.* 2015). Furthermore, it is possible that there are species- or guild-specific relationships between vegetation structure and drought resistance that could not be detected by using a composite species index such as the DRI.

Synthesis and applications

Bird assemblages in locations with high vegetation cover were more vulnerable to prolonged drought probably because they have not already been as much affected by land-use change and so have greater scope to decline. Bird assemblages in locations with low vegetation productivity, such as arid and semi-arid ecosystems, are also more likely to be affected by drought. This suggests that during prolonged droughts, high-cover landscapes and low-productivity ecosystems should be preferentially targeted for conservation actions compared to more modified areas in high productivity areas (e.g. mesic climate zones). If vegetation productivity promotes resistance, then ecological restoration for other purposes, such as reversing the effects of human land-use actions, may also increase the resistance of animal communities to prolonged drought.

Sites with locally high vegetation greenness are likely to be important for increasing assemblage-resistance, especially in regions where mean productivity is relatively low. Vegetation greenness is higher at sites that are topographically sheltered and that have more reliable water availability, such as run-on areas (sites of more concentrated or reliable surface or subsurface water flow), floodplains and riparian zones (Mackey *et al.* 2012; Selwood *et al.* 2016). Protecting these sites, and maintaining their vegetation productivity and condition through the provision of environmental water (Horner *et al.* 2016), and ecological restoration, is likely to enhance the resistance of bird assemblages to more-frequent and severe droughts that are projected for this and other southern Australian regions.

While high-productivity landscapes are less vulnerable to drought, and are likely to be important for promoting the resistance of bird assemblages to increased drought frequency, these same landscapes are likely to become the focus of human responses to drying climate conditions, such as large-scale water diversion and storage and the conversion of native vegetation to agricultural or forestry plantations (Capon *et al.* 2013; Chapman *et al.* 2014). As such, it is probable that new conflicts will arise between the needs of humans and the biota. Conversely, faunal assemblages in high cover landscapes that have so far largely escaped the pressures of human land-use are likely to now be affected by climate change.

Vegetation greenness has been used to identify ‘ecosystem greenspots’, locations that may function as drought refuges, by maintaining relatively high vegetation productivity (Mackey *et al.* 2012). Our findings suggest that vegetation greenness may also identify drought-resistant refuges for birds. Models that link remotely sensed vegetation data to ground measurements of vegetation, including vegetation structure, are potentially useful for explaining animal responses to climate

changes and for forecasting the effects of future climate scenarios (Lada *et al.* 2014; Mac Nally *et al.* 2014). More-detailed studies into the relationships between animal responses to drought, vegetation greenness (including its temporal variability) and vegetation structure, are likely to be useful identifying locations that are critical for supporting resistant animal assemblages. The ability to identify refuges will enable more effective conservation management and planning, under drying climate conditions, especially in high cover landscapes.

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Author contributions

KS and RM conceived the study, KS and RM analysed the data, KS wrote the manuscript with contributions from RM, RC and MM.

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Table 1. Site characteristics tested as potential predictors of drought resistance in drought-declining bird assemblages. Asterisks indicate that information was obtained from the Atlas of Living Australia (2015), ‘^’ indicates variables that were excluded from analysis due to high correlation with other variables ($r > 0.70$).

| Variable categories | Site characteristic | Description | Source |
|--------------------------------|--|--|--|
| <i>Vegetation structure</i> | Small shrub cover (shrubs 0.5–2 m) | 0 = absent, 1 = some, 2 = many | Habitat forms (BirdLife Australia 2012) |
| | Small shrub diversity [^] | 0 = absent, 1 = one species, 2 = two or three species, 3 = > three species | Habitat forms |
| | Small shrub type | Categorical: exotic or native | Habitat forms |
| | Tall shrub cover (shrubs 2–8 m) [^] | 0 = absent, 1 = some, 2 = many | Habitat forms |
| | Tall shrub diversity [^] | 0 = 0 species, 1 = 1 species, 2 = 2–3 species, 3 = >3 species | Habitat forms |
| | Tree cover (trees > 8 m) | 0 = absent, 1 = some, 2 = many | Habitat forms |
| | Tree diversity | 0 = 0 species, 1 = 1 species, 2 = 2–3 species, 3 = >3 species | Habitat forms |
| | Ground cover | 0 = mostly bare, 1 = partly covered with grass/herbs, 2 = mostly covered | Habitat forms |
| | Ground cover spread | Clumped / unclumped | Habitat forms |
| | Fallen timber (fallen trees or branches > 2 m) | 0 = 0 pieces, 1 = 1–5 pieces, 2 = 6–15 pieces, 3 = >15 pieces | Habitat forms |
| <i>Vegetation productivity</i> | Vegetation greenness (NDVI)* | Mean annual Normalized Difference Vegetation Index for 2001–2006 | Bureau of Rural Sciences (Australia) (2007); Carroll et al. (2004) |
| <i>Landscape context</i> | | | |

| | | | |
|-----------------------------|------------------------------|---|--------------------------------------|
| <i>Physical environment</i> | Landscape cover | Percentage cover of native vegetation within a 500 m radius | Department of the Environment (2014) |
| | Patch size | Size of discrete vegetation patch that site is located within: 1 = <3 ha, 2 = 3–10 ha, 3 = 11–30 ha, 4 = 31–100 ha, 5 = 101–400 ha, 6 = >400 ha | Habitat forms |
| | Elevation* | m above sea level (log transformed) | Geoscience Australia (2001) |
| | Topographic wetness index* | $\ln(a/\tan B)$ where a is the upslope per unit contour length and $\tan B$ is the local slope | Williams (2010) |
| | Surface water* | Percentage of observations 1987–2014 of water from satellite imagery | Geoscience Australia (2015) |
| | Terrain | Gully or other (flat, slope, ridge) | Habitat forms |
| | Distance to permanent water* | Euclidean distance to permanent natural water features | Williams (2010) |
| | Aridity* [∧] | Annual mean aridity index | CSIRO (2010) |

Table 2 Summary of outcomes from the three analyses of the relationship between DRI and the predictor variables. PPD = posterior probability distribution, Pr(Inc) = probability inclusion in best models, PPfit = posterior predictive assessment fit, SD = standard deviation.

| Quantity | Ground cover spread | NDVI | Landscape cover | Small shrub cover |
|---|---------------------|--------|-----------------|-------------------|
| <i>Bayesian multiple regression (545 sites; PPfit = 0.39)</i> | | | | |
| PPD | 0.006 | 0.941 | 0.030 | 0.034 |
| Estimate | -0.0032 | 0.0034 | -0.0035 | -0.0034 |
| SD | 0.0022 | 0.0023 | 0.0021 | 0.0020 |
| <i>Bayesian model averaging (414 sites)</i> | | | | |
| Pr(Inc) | 97.6 | 92.8 | 91.2 | 7.3 |
| Estimate | -0.0189 | 0.0151 | -0.0174 | - |
| SD | 0.006 | 0.0067 | 0.0078 | - |
| <i>Hierarchical partitioning (414 sites)</i> | | | | |
| Independent % | 29 | 38 | 29 | 4 |

Figure legends

- Figure 1. The study region of the Murray-Darling Basin, Australia (shaded grey, top left). Study sites are denoted by white circles on the enlarged map, with bands indicating long-term mean annual rainfall increasing from west (200–300 mm rainband) to east in 100-mm intervals.
- Figure 2. Climate anomalies for the study sites over the Big Dry, (a) deviation of mean annual temperature from long-term average (1961–1990) in °C, and (b) deviation of total annual precipitation from long-term average in mm.
- Figure 3. Plots of DRI against the two important continuous predictors, NDVI (upper) and landscape cover within 500 m (lower). Regression lines and lower and upper 95% confidence intervals are shown.

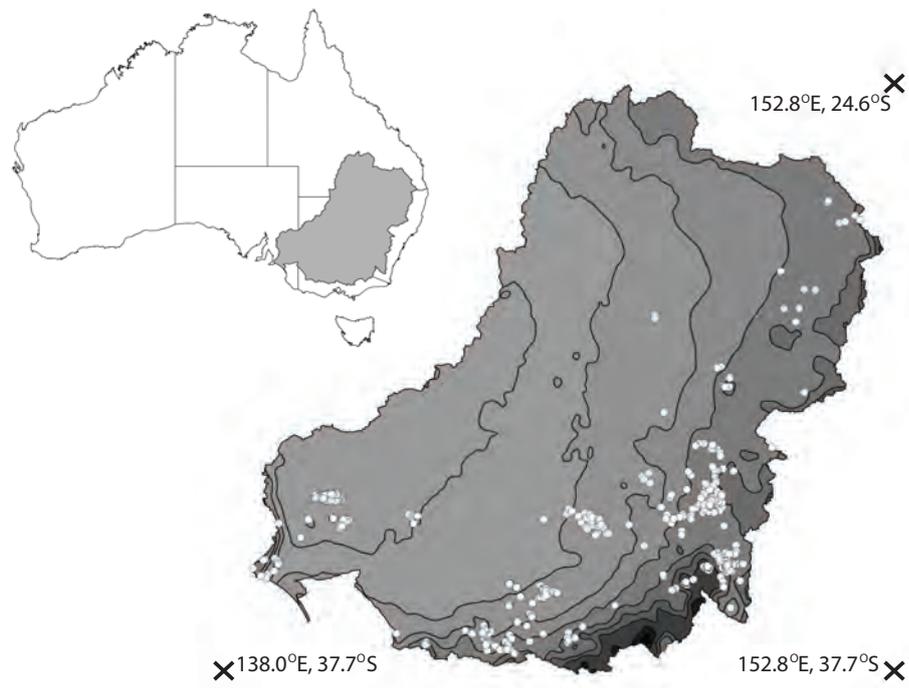


Figure 1

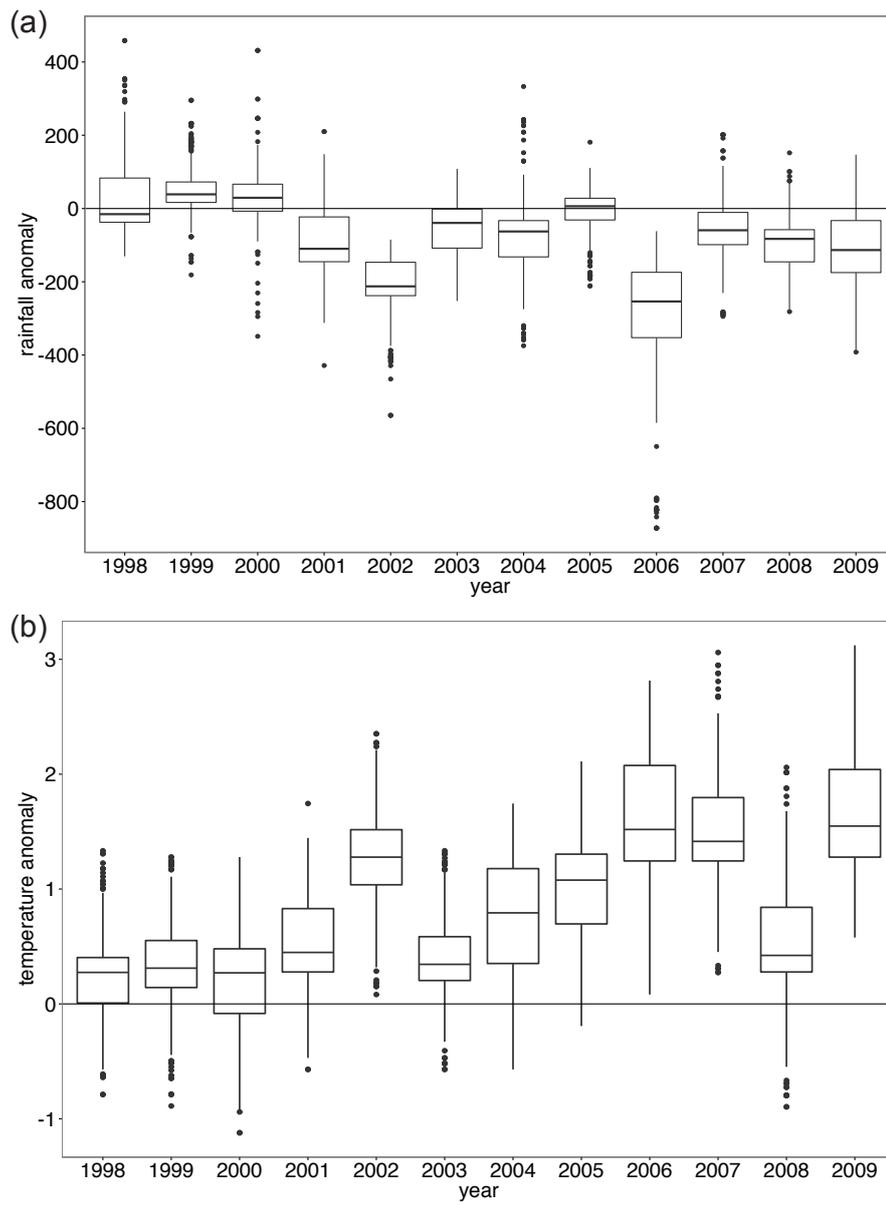


Figure 2

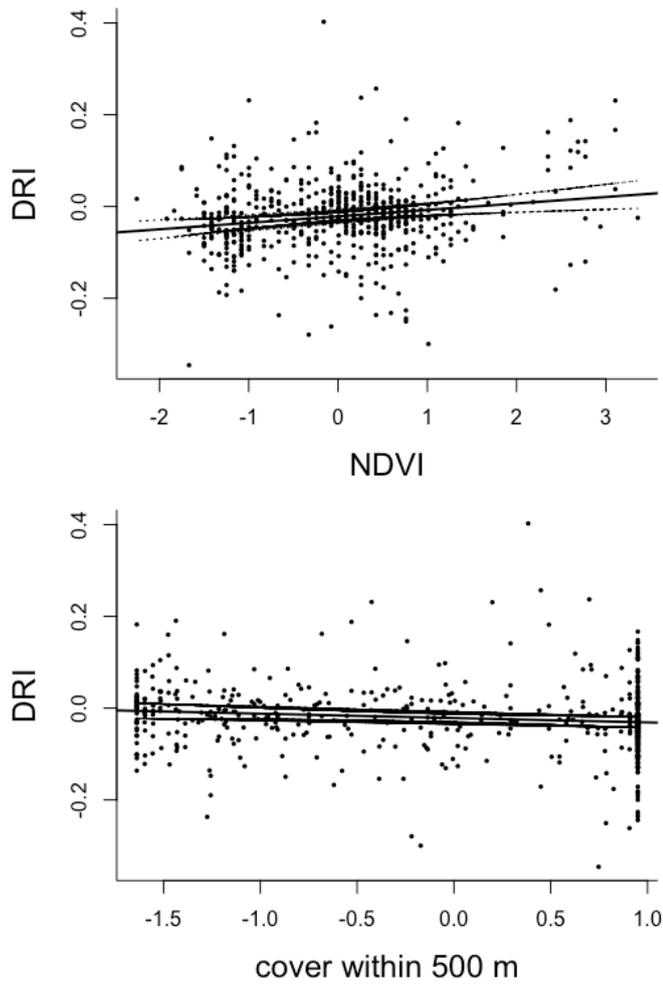


Figure 3

Chapter 7

Conclusion

Conclusion

The effects of climate on demographic rates and population viability of plants and animals are, on average, equal to or greater than the effects of human land-use (Chapter 2, Fig. 1), which highlights the importance of considering the ecological effects of climate stressors, such as drought. The objectives of this thesis were to explore (1) the resistance and resilience of floodplain bird assemblages; (2) the potential of floodplains as refugia from drought and (3) from aridity; and (4) the relative importance of landscape characteristics for promoting bird resistance to drought. The complementary studies of this thesis advance our understanding of the effects of extreme drought on bird assemblages, and the potential of floodplain ecosystems for moderating the effects of a drying climate (Fig. 1).

Addressing key knowledge gaps and future directions

Resistance and resilience of floodplain bird assemblages

The Murray-Darling Basin, a region that has been much affected by human land-use (Walker et al. 1993, Mac Nally et al. 2011), is now experiencing the increasing pressures of climate change, including increased frequency and severity of drought (Timbal et al. 2015). The Big Dry had a substantial effect on bird assemblages, with many species declining during this period (Chapters 3, 4, 6) and failing to recover after the drought was broken by high rainfall (the Big Wet) (Chapters 3, 4). This signal was apparent in both floodplain and non-floodplain ecosystems (Fig. 1). In the floodplain forests, a lack of breeding activity after the Big Wet indicated that further recoveries in the short-term are unlikely unless populations are supplemented from non-floodplain areas (Chapter 3). The effects of drought appeared to be pervasive for much of the floodplain avifauna, regardless of species biological traits (species body

mass, fecundity, mobility or diet; Chapter 3) and ecological traits (habitat preference, conservation status, foraging substrate, feeding guild; Chapter 4).

The resilience of bird assemblages to drought was low in both floodplain and non-floodplain ecosystems, with a small proportion of drought-affected species subsequently recovering after two years of high rainfall (Chapters 3, 4, Fig. 1). The negative effects of prolonged drought on resource availability and bird populations did not appear to be reversed after two years of above average rainfall conditions (Fig. 1). Periods of drought followed by relatively short periods of high rainfall, which are projected for the Murray-Darling Basin (Timbal et al. 2015), may lead to stepped declines in the avifauna because decline during prolonged drought is not offset by sufficient opportunity to recover during the relatively short periods of high rainfall. High rainfall was expected to benefit bird assemblages through increased resource availability, and the relief of physiological pressures of extreme drought (Fig. 1).

An important question is whether there has been further recovery (or decline) in the Murray-Darling Basin bird assemblages since 2013. Rainfall in the Murray-Darling Basin was >10% below average in 2014 and 2015, but 26% above average in 2016 (Bureau of Meteorology 2015; 2016; 2017), so it is possible that there have been further recoveries in the avifauna. Further monitoring and analysis of trends in bird abundance, breeding and occurrences in the floodplain and non-floodplain ecosystems of the Murray-Darling Basin, including the sites surveyed in Chapter 3, will be vital for assessing the longer-term resilience of the regional avifauna.

Floodplains as refugia from drought and aridity

Birds in floodplain ecosystems were less affected by drought (Chapter 4) and aridity (Chapter 5) than other ecosystems. Floodplains are therefore likely to be important

future climate refugia probably because they provide more stable resource availability and more mesic microclimates during drought (Fig. 1). Trends in bird species occurrence in the Murray-Darling Basin during the Big Dry and after the Big Wet showed that floodplain ecosystems enhance the resistance of bird assemblages to drought (Chapter 4, Figure 1). Fewer species declined in floodplain zones and many species had less-negative trends in floodplain zones than in non-floodplain zones during the Big Dry (Chapter 4). This enhanced resistance is likely to be facilitated by more stable primary productivity in floodplain zones during drought due to shallow ground water tables, cooler and more mesic microclimates in floodplain zones or the proximity to free water for drinking (Fig. 1, Chapter 4). These conditions may have provided relief from the physiological pressures caused by hot and dry climate conditions during drought, and supported more stable resource availability (Fig. 1). Floodplains appear to moderate the effects of aridity on species occurrence, allowing species to extend into more arid regions than they are otherwise expected to occur (Chapter 5). Greater vegetation productivity on floodplains is a likely driver of this response. As such, while floodplains experience the effects of drought, they are likely to be important for enhancing the resistance of birds to drying climate conditions, including increased drought frequency and severity.

A better understanding of the mechanisms that enable floodplains to provide refuge for birds in drought and arid conditions would be useful for informing the identification of other refuge locations. Measuring microclimatic conditions (e.g. temperature, humidity) in floodplain ecosystems and adjacent non-floodplain ecosystems, would give a better understanding of the extent to which floodplain ecosystems provide relief from xeric climate conditions. Similarly, assessing differences in vegetation structure and productivity and monitoring habitat use by

birds in floodplain and adjacent ecosystems would provide an understanding of the relative resource availability in either zone. An important question is whether contrasts between floodplain and non-floodplain ecosystems are accentuated during hot periods, during drought and in more arid climate zones; and whether floodplain ecosystems experience less variability in resource availability and microclimatic conditions.

What affects bird resistance to drought?

More generally, highly productive ecosystems (indicated by vegetation greenness) are likely to support more resistant bird assemblages (Chapter 6, Fig. 1). Mean vegetation greenness was an important predictor of the resistance of bird assemblages to drought (Chapter 6). Areas with high vegetation greenness, and thus productivity, are more likely to have higher and more stable resource availability (Mackey et al. 2012), which may buffer resource declines during drought (Fig. 1). While analyses were not specific to floodplain ecosystems, the outcomes suggest that greater vegetation productivity in floodplain ecosystems may be an important factor for the greater resistance of floodplain bird assemblages to drought.

More-detailed studies into the relationships between bird responses to drought, vegetation greenness (including its temporal and spatial variability) and vegetation structure, are likely to be useful identifying locations that are critical for supporting resistant bird assemblages. Models that use remotely-sensed vegetation greenness may predict refuges for birds during drought, particularly if they are linked to on-ground vegetation measurements (Lada et al. 2014, Mac Nally et al. 2014).

Management implications: Increasing the resistance and resilience of bird communities to drought

Temporal patterns akin to the Big Dry and Big Wet are likely to become common in southeastern Australia because regional climate projections predict increased drought frequency and severity, interspersed by rainfall concentrated into intense events.

Declines in average cool season rainfall, soil moisture and run-off are expected (Timbal et al. 2015). These drying and warming climate conditions are likely to have substantial effects on the avifauna, but that these effects may be reduced in highly productive ecosystems such as floodplains.

Floodplain zones are important for reducing the effects of drought and facilitating the occurrence of birds in arid conditions. Protecting floodplain ecosystems through reservation and conservation management is likely to improve the prospects of regional bird assemblages by securing high quality refugia where bird populations can retreat to, or persist in, during drought. Historically, river red-gum floodplain forests have been much less fire-prone than upland and plains wooded ecosystems (Colloff 2014), so they may also be important as fire refugia for birds and other fauna if, as appears likely, fire frequency and severity increase in southeastern Australia (Timbal et al. 2015). Currently, only 8.6% of the total active floodplain area of the Murray-Darling Basin is protected (Fig. 2) and so, floodplains are underrepresented in the Australian reserve system, which covers 17.8% of the continent (Collaborative Australian Protected Areas Database (CAPAD) 2014). Greater protection of floodplain ecosystems is likely to afford bird assemblages more capacity to withstand the increased drought frequency and severity predicted for the region (Timbal et al. 2015).

While floodplain bird assemblages were more resistant to drought compared to

non-floodplain zones (Chapter 4), there were still substantial bird declines during the drought in floodplain zones, and floodplain bird assemblages exhibited little resilience after the Big Wet (Chapters 3, 4). An improvement in the condition of floodplain vegetation communities is likely to enhance their resistance and resilience to drought (Whitford et al. 1999), including their function as refugia. Recent increases in environmental water holdings may provide the capacity for some improvement in the condition of the Murray-Darling floodplain ecosystems (CEWO 2013, MDBA 2013), and the implications for terrestrial biota should be part of planning for the allocation of these holdings, along with water-dependent biota such as water-birds and fish. Vegetation productivity appears to be important for the resistance of birds, and floodplain forest stand condition has a positive association with bird breeding, abundance and richness (Mac Nally et al. 2014). Supporting the life-cycle requirements of floodplain vegetation communities through the restoration of near-natural flow regimes (i.e. sufficient flood duration, frequency and seasonality) (Horner et al. 2009, Horner et al. 2016) is likely to improve outcomes for bird communities and other terrestrial fauna such as mammals and herpetofauna (Lada et al. 2014).

The management of human pressures on floodplains will improve the persistence of floodplain biota. Management of grazing will assist in the recruitment of floodplain trees (Horner et al. 2016) and the maintenance of fallen timber loads by reducing wood removal, typically harvested for firewood, will increase resource availability for birds and other animals (Mac Nally et al. 2001, Mac Nally et al. 2002, Lada and Mac Nally 2008), which may enhance resistance and resilience to drought.

A drying climate may introduce new pressures that may affect the resistance and resilience of floodplain forest ecosystems along with the degradation of forest

stand condition. Two potential pressures that have much affected upland and plains woodlands and forests but have been less prevalent in floodplain forests are fire and hyperaggressive native species of birds. Fire has previously been a low risk in river red-gum forests but may become a greater pressure than before in drying and warming conditions and if flooding continues to decline (Colloff 2014, Timbal et al. 2015). The noisy miner (*Manorina melanocephala* Latham), a native despotic bird species, has increasingly invaded fragmented and open woodlands elsewhere in the region, seemingly assisted by the clearing and fragmentation of native vegetation. The expansion of colonies of this species has profound adverse effects on small-bodied birds, much reducing local richness and abundance (Thomson et al. 2015). Substantial decreases in the density of floodplain forests from a drying climate or from excessive timber harvesting may introduce the threat of noisy miners to floodplain bird assemblages (Maron 2007).

Vegetation productivity appears to have a substantial influence on the resistance of bird communities to dry climate conditions. Vegetation greenness, an indicator of productivity, is associated with resistance of drought sensitive bird assemblages (Chapter 6). Bird communities in floodplains, which are more productive than adjacent zones, are less affected by drought (Chapter 4) and aridity (Chapter 5). Alongside the restoration of natural flood regimes on floodplains, the restoration of native vegetation cover is likely to enhance the productivity of both floodplain and non-floodplain ecosystems, and may be an important strategy for augmenting the resistance of bird communities to a drying climate.

Conclusion

The effects of climate on demographic rates and population viability of plants and animals are, on average, equal to or greater than the effects of human land-use (Chapter 2, Fig. 1), which highlights the importance of considering the ecological effects of climate stressors, such as drought. The objectives of this thesis were to explore (1) the resistance and resilience of floodplain bird assemblages; (2) the potential of floodplains as refugia from drought and (3) from aridity; and (4) the relative importance of landscape characteristics for promoting bird resistance to drought. The complementary studies of this thesis advance our understanding of the effects of extreme drought on bird assemblages, and the potential of floodplain ecosystems for moderating the effects of a drying climate (Fig. 1).

Addressing key knowledge gaps and future directions

Resistance and resilience of floodplain bird assemblages

The Murray-Darling Basin, a region that has been much affected by human land-use (Walker et al. 1993, Mac Nally et al. 2011), is now experiencing the increasing pressures of climate change, including increased frequency and severity of drought (Timbal et al. 2015). The Big Dry had a substantial effect on bird assemblages, with many species declining during this period (Chapters 3, 4, 6) and failing to recover after the drought was broken by high rainfall (the Big Wet) (Chapters 3, 4). This signal was apparent in both floodplain and non-floodplain ecosystems (Fig. 1). In the floodplain forests, a lack of breeding activity after the Big Wet indicated that further recoveries in the short-term are unlikely unless populations are supplemented from non-floodplain areas (Chapter 3). The effects of drought appeared to be pervasive for much of the floodplain avifauna, regardless of species biological traits (species body

mass, fecundity, mobility or diet; Chapter 3) and ecological traits (habitat preference, conservation status, foraging substrate, feeding guild; Chapter 4).

The resilience of bird assemblages to drought was low in both floodplain and non-floodplain ecosystems, with a small proportion of drought-affected species subsequently recovering after two years of high rainfall (Chapters 3, 4, Fig. 1). The negative effects of prolonged drought on resource availability and bird populations did not appear to be reversed after two years of above average rainfall conditions (Fig. 1). Periods of drought followed by relatively short periods of high rainfall, which are projected for the Murray-Darling Basin (Timbal et al. 2015), may lead to stepped declines in the avifauna because decline during prolonged drought is not offset by sufficient opportunity to recover during the relatively short periods of high rainfall. High rainfall was expected to benefit bird assemblages through increased resource availability, and the relief of physiological pressures of extreme drought (Fig. 1).

An important question is whether there has been further recovery (or decline) in the Murray-Darling Basin bird assemblages since 2013. Rainfall in the Murray-Darling Basin was >10% below average in 2014 and 2015, but 26% above average in 2016 (Bureau of Meteorology 2015; 2016; 2017), so it is possible that there have been further recoveries in the avifauna. Further monitoring and analysis of trends in bird abundance, breeding and occurrences in the floodplain and non-floodplain ecosystems of the Murray-Darling Basin, including the sites surveyed in Chapter 3, will be vital for assessing the longer-term resilience of the regional avifauna.

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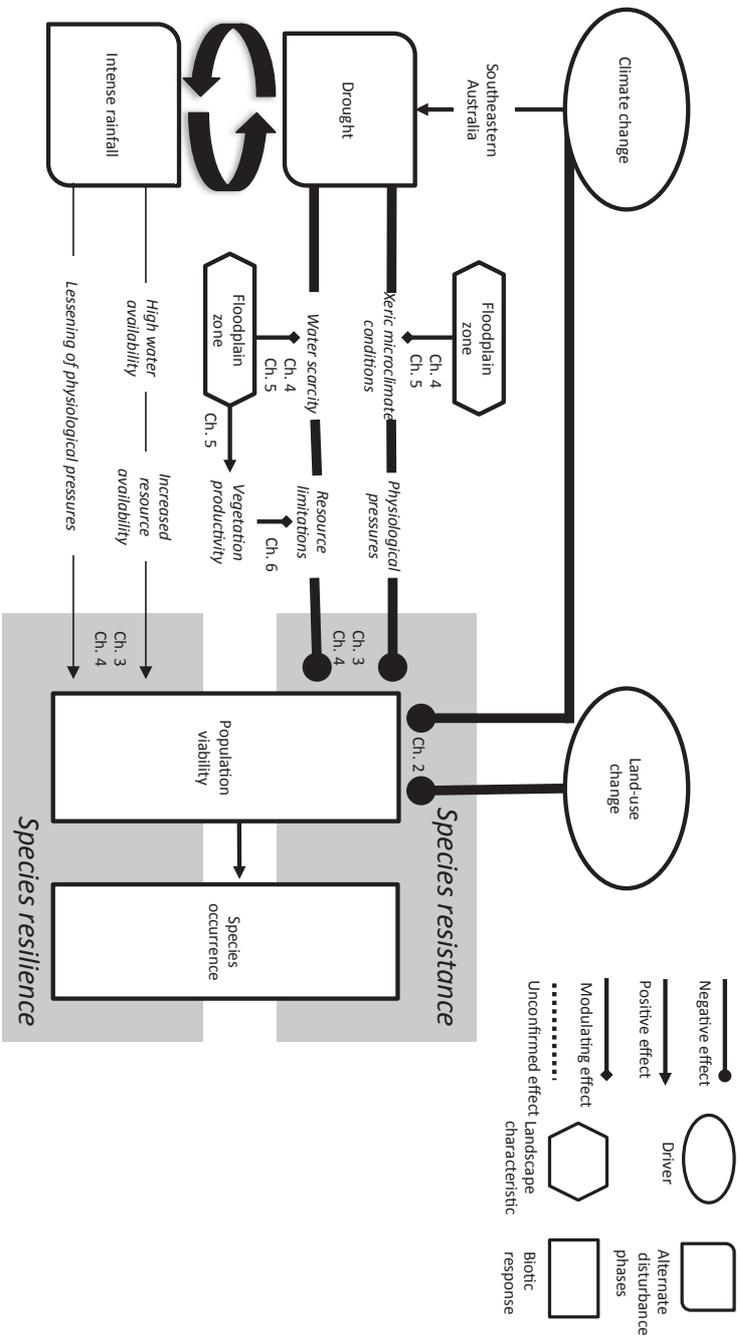


Figure 1. Conceptual diagram of the relationships documented in this thesis. Width of arrows represents the strength of the relationships (relative to parallel arrows) based on findings from this thesis. I found that climate influences population viabilities as least as much as land-use change. The negative effects of drought on birds in the Murray-Darling Basin were greater than the ameliorative effects of the Big Wet. Floodplains enhanced the resistance of many birds to the Big Dry, but did not improve resilience. Bird assemblages in locations with higher vegetation productivity had higher resistance. Floodplains had higher vegetation productivity than non-floodplain zones and moderated the effects of aridity on bird species occurrence in the Murray-Darling Basin.

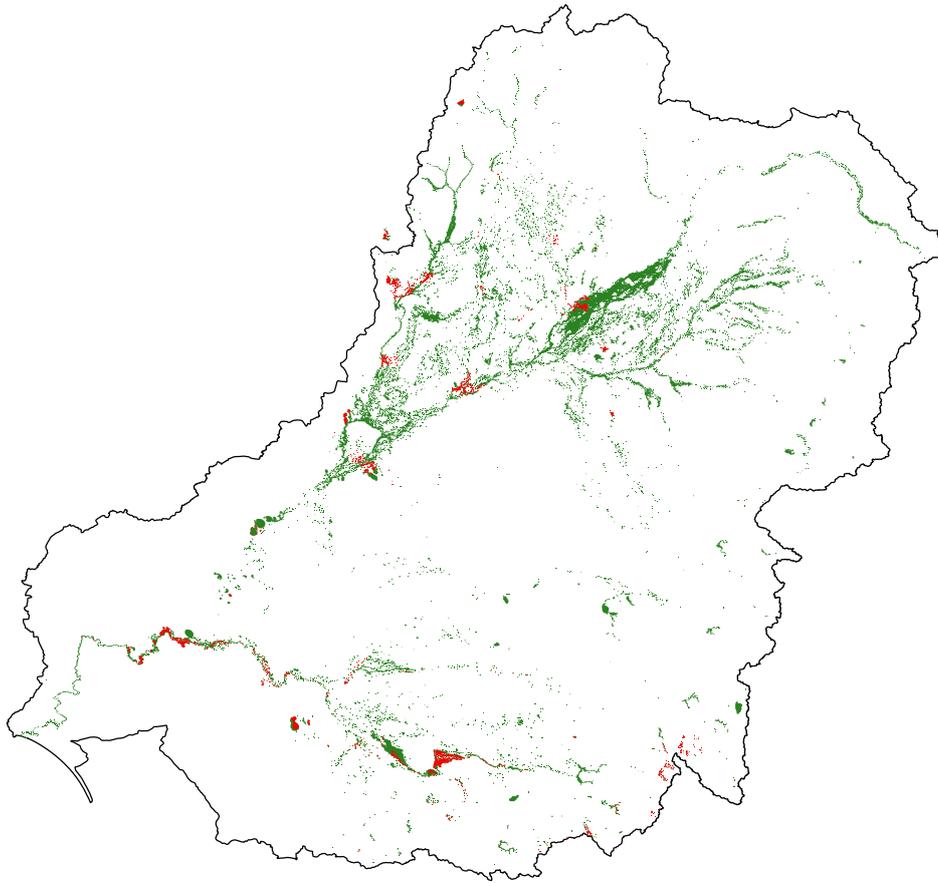


Figure 2. Protected floodplains in the Murray-Darling Basin. Active floodplain area (at least 1 in 10 year flood return period) is displayed in green from the Murray-Darling Basin Floodplain Inundation Model (Chen et al. 2012); areas in red are floodplains that are part of protected areas listed in the Collaborative Australian Protected Areas Database which includes government, indigenous and privately protected areas in Australia (Collaborative Australian Protected Areas Database (CAPAD) 2014). The extent of total floodplain area protected is 8.6%. Spatial data analysis was conducted in QGIS (QGIS Development Team 2013).

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Appendix I

Supporting material for Chapter 2

Table S1. Search terms used to locate studies that measured the effect of climate and landscape condition on demographic rates. Searches consisted of a descriptor of alternative predictor variable in combination with alternative response variables related to demography. Search terms that did not return additional studies are not listed.

| Predictors | | Response |
|---|-----|---|
| Climat* OR Fragment* OR “Habitat degradation” OR “Habitat quality” OR “Habitat loss” OR “Patch size” | AND | “Demographic rate” “Vital rate” “Birth rate” “Death rate” “Immigration rate” “Emigration rate” |

Table S2. Search terms used to locate studies that measured the effect of climate and landscape condition on variables related to demographic rates. Searches consisted of a descriptor of alternative predictor variable in combination with alternative response variables related to demography. Search terms that did not return additional studies are not listed.

| Predictors | | Response |
|---|-----|--|
| Climat* OR Fragment* OR “Habitat degradation” OR “Habitat quality” OR “Habitat loss” OR “Patch size” | AND | Reproduc* OR Breeding OR “Population dynamics” OR “Population viability” OR Demograph* OR Survival OR Recruitment OR Mortality OR Dispersal OR *migration OR “Extinction risk” |

Table S3. List of species used for the calculation of mean effect sizes for climate and landscape condition on population vital rates. For each species we show the species name, common name for animal species, geographic region, the predictor variable used in the study, the response variable measured in the study, the direction of the relationship between the predictor and response variable (direction) measured in the study, the correlation coefficient r used in calculation of mean effect size (for landscape condition, direction of the relationship with increasing landscape condition; for climate, the absolute value is reported), the source statistic from which the r value was calculated and the source publication. * indicates that the source statistic was obtained from Aguilar *et al.* (2006); DBH = diameter at breast height; ENSO = El Niño Southern Oscillation; exp. = experimental; na = not applicable; PCA = principal component from principal component analysis; NAO = North Atlantic Oscillation; SOI = Southern Oscillation Index; UVB = Ultraviolet B radiation.

| Species | Region | Predictor variable | Response variable | Direction | r | Source statistic | Source publication |
|---|-----------|--|---------------------------------------|-----------|-------|------------------|---------------------------------|
| Landscape condition – animal emigration | | | | | | | |
| <i>Melanargia galathea</i> | Europe | Patch area (source) | Movement out of patch | + | 0.77 | R -squared | Baguette <i>et al.</i> (2000) |
| <i>Lacerta vivipara</i> | Europe | Vegetation quality (wood clearance versus grassland) | Dispersal probability | - | -0.40 | chi-squared | Boudjemadi <i>et al.</i> (1999) |
| <i>Maturus pulcherrimus</i> | Australia | Patch size | Female dispersal away from patch | - | -0.77 | chi-squared | Brooker & Brooker (2002) |
| <i>Zyganena</i> spp. | Europe | Patch size | % individuals moving to another patch | - | -0.08 | P -value | Franzén & Nilsson (2012) |
| <i>Parnassius mnemosyne</i> | Europe | Fragment size | Total emigration rate | - | -0.36 | R -squared | Valimaki & Itamies (2003) |
| Landscape condition – animal immigration | | | | | | | |

| | | | | | | | | |
|--------------------------------|----------------------------|----------------------|---|--|----|------|-------------|-------------------------------|
| <i>Melanargia galathea</i> | Butterfly | Europe | Patch area (receiving) | Movement into patch | - | 0.79 | R-squared | Baguette <i>et al.</i> (2000) |
| <i>Antechinus agilis</i> | Agile antechinus | Australia | Vegetation cover | Male to female ratio | + | 0.87 | chi-squared | Banks <i>et al.</i> (2005) |
| <i>Malurus pulcherrimus</i> | Blue-breasted fairywren | Australia | Connectivity | Post dispersal survival | + | 0.10 | chi-squared | Brooker & Brooker (2002) |
| <i>Climacteris picumnus</i> | Brown treecreeper | Australia | Fragmented <i>versus</i> unfragmented | Territories without a female | + | 0.63 | P-value | Cooper & Walters (2002) |
| <i>Emberiza hortulan</i> | Ortolan bunting | Europe | Golf course <i>versus</i> native vegetation | Pairing success | + | 0.52 | P-value | Dale (2004) |
| <i>Oporornis formosus</i> | Kentucky warbler | North America | Fragmented <i>versus</i> unfragmented | Proportion of unpaired males | na | 0 | chi-squared | Gibbs & Faaborg (1990) |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Fragmented <i>versus</i> unfragmented | Proportion of unpaired males | + | 0.93 | chi-squared | Gibbs & Faaborg (1990) |
| <i>Ochotona princeps</i> | American pika | North America | Geographic isolation | Genetic differentiation | + | 0.86 | R-squared | Henry <i>et al.</i> (2012) |
| <i>Rattus fuscipes</i> | Native bush rat | Australia | Patch size | Number of potential immigrants | + | 0.74 | chi-squared | Holland & Bennett (2010) |
| <i>Microtus pennsylvanicus</i> | Meadow vole | North America (exp.) | Vegetation cover | Settling of founding voles | + | 0.72 | P-value | Lin & Batzli (2001) |
| <i>Marmosops incanus</i> | Gray slender mouse opossum | South America | Vegetation cover | Number of immigrated individuals per capture session | + | 0.70 | P-value | Püttker <i>et al.</i> (2011) |

| | | | | | | | | |
|---|----------------------------|----------------------|---|-----------------------------------|---|-------|-------------------|------------------------------|
| <i>Dendrocopos medius</i> | Middle spotted woodpeckers | Europe | Patch size | Pairing success | + | 0.25 | <i>F</i> | Robles <i>et al.</i> (2008) |
| <i>Bufo americanus</i> | American toad | North America (exp.) | Forest <i>versus</i> agricultural landscape | Orientation of dispersal | + | 0.46 | <i>P</i> -value | Rothermel & Semlitsch (2002) |
| <i>Ambystoma texanum</i> | Small-mouthed salamanders | North America (exp.) | Forest <i>versus</i> agricultural landscape | Orientation of dispersal | + | 0.29 | <i>P</i> -value | Rothermel & Semlitsch (2002) |
| <i>Ambystoma maculatum and A. texanum</i> | Spotted salamander | North America (exp.) | Forest <i>versus</i> agricultural landscape | Orientation of dispersal | + | 0.34 | <i>P</i> -value | Rothermel & Semlitsch (2002) |
| <i>Egernia cunninghami</i> | Cunningham's skink | Australia | Deforested <i>versus</i> natural vegetation | Relatedness among potential mates | + | 0.24 | <i>P</i> -value | Stow & Sunnucks (2004) |
| <i>Parnassius mnemosyne</i> | Clouded Apollo butterfly | Europe | Fragment size | Number of immigrants | + | 0.48 | <i>R</i> -squared | Valimaki & Itamies (2003) |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Fragmented <i>versus</i> unfragmented | Pairing success | - | 0.79 | <i>F</i> | Villard <i>et al.</i> (1993) |
| <i>Sciurus vulgaris</i> | Eurasian red squirrel | Europe | Fragmented <i>versus</i> unfragmented | Immigration rate | - | 0.87 | <i>F</i> | Wauters <i>et al.</i> (1994) |
| Landscape condition – animal death rates | | | | | | | | |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Patch size | Apparent annual survival | + | -0.63 | chi-squared | Bayne & Hobson (2002) |
| 22 bird species | | North America | Distance from agricultural edge | Adult death | - | -0.05 | Kendall's tau | Gates & Gysel (1978) |
| <i>Microtus ochrogaster</i> | Prairie vole | North America (exp.) | Vegetation cover | <i>Per capita</i> mortality | - | -0.32 | <i>P</i> -value | Lin & Batzli (2001) |

| <i>Ambystoma maculatum</i> | Spotted and small-mouthed salamanders | North America (exp.) | Forest <i>versus</i> agricultural landscape | Water loss | - | -0.91 | <i>F</i> | Rothermel & Semlitsch (2002) |
|---|---------------------------------------|----------------------|---|--|---|-------|--------------------------|---------------------------------|
| Landscape condition – animal birth rates | | | | | | | | |
| <i>Bubo bubo</i> | Eagle owl | Europe | Urban area cover | Number of fledged young/pair | - | 0.25 | <i>z</i> | Bionda & Brambilla (2012) |
| <i>Lacerta vivipara</i> | Common lizard | Europe (exp.) | Vegetation connectivity | Maternity success | + | 0.22 | chi-squared | Boudjemadi <i>et al.</i> (1999) |
| <i>Microtus pennsylvanicus</i> | Meadow vole | North America (exp.) | Fragmented <i>versus</i> unfragmented landscape | Proportion of adult females pregnant | + | 0.16 | chi-squared | Bowers <i>et al.</i> (1996) |
| <i>Malurus pulcherrimus</i> | Blue-breasted fairywren | Australia | Patch size | Number of fledglings per female per year | - | -0.19 | <i>P</i> -value (<0.001) | Brooker & Brooker (2001) |
| <i>Icteria virens</i> | Yellow-breasted chat | North America | Patch size | Mean number of chats fledged per nest | + | 0.12 | <i>t</i> | Burhans & Thompson III (1999) |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Patch size | Number of fledged female young per adult female per year | + | 0.91 | <i>t</i> | Burke & Nol (2000) |
| <i>Vireo olivaceus</i> | Red-eyed vireo | North America | Fragmented <i>versus</i> unfragmented | Number of fledged female young per adult female per year | - | 0.77 | <i>t</i> | Burke & Nol (2000) |
| <i>Pheucticus ludovicianus</i> | Rose-breasted grosbeak | North America | Patch size | Number of fledged female young per adult female per year | + | 0.62 | <i>t</i> | Burke & Nol (2000) |

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|--------------------------------|-----------------|----------------------|---------------------------------------|--|---|------|---------------|------------------------------|
| <i>Catharus fuscens</i> | Veery | North America | Fragment size | Number of fledged female young per adult female per year | + | 0.65 | t | Burke & Nol (2000) |
| <i>Hylocichla mustelina</i> | Wood thrush | North America | Patch size | Number of fledged female young per adult female per year | + | 0.82 | t | Burke & Nol (2000) |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Fragmented <i>versus</i> unfragmented | Daily nest mortality | + | 0.13 | chi-squared | Donovan <i>et al.</i> (1995) |
| <i>Vireo olivaceus</i> | Red-eyed vireo | North America | Fragmented <i>versus</i> unfragmented | Daily nest mortality | + | 0.17 | chi-squared | Donovan <i>et al.</i> (1995) |
| <i>Hylocichla mustelina</i> | Wood thrush | North America | Fragmented <i>versus</i> unfragmented | Daily nest mortality | + | 0.16 | chi-squared | Donovan <i>et al.</i> (1995) |
| <i>Microtus pennsylvanicus</i> | Meadow vole | North America (exp.) | Fragmented <i>versus</i> unfragmented | Density of adult recruits | + | 0.57 | F | Dooley & Bowers (1998) |
| 21 bird species | | North America | Distance from agricultural field | Fledging success | + | 0.73 | Kendall's tau | Gates & Gysel (1978) |
| <i>Parus major</i> | Great tit | Europe | Patch size | Breeding success | + | 0.27 | P -value | Hinsley <i>et al.</i> (1999) |
| <i>Rattus fuscipes</i> | Native bush rat | Australia | Vegetation quality | Number of recruits | + | 0.90 | chi-squared | Holland & Bennett (2010) |
| <i>Hylocichla mustelina</i> | Wood thrush | North America | Forest area | Nesting success | + | 0.93 | Pearson's r | Hoover <i>et al.</i> (1995) |
| <i>Microtus pennsylvanicus</i> | Meadow vole | North America (exp.) | Vegetation cover | <i>Per capita</i> reproductive success of females | + | 0.89 | P -value | Lin & Batzli (2001) |

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|--------------------------------|------------------------|----------------------|--|-------------------------------------|---|------|--------------------|----------------------------|
| <i>Microtus ochrogaster</i> | Prairie vole | North America (exp.) | Vegetation cover | Recruitment of young from females | + | 0.47 | <i>P</i> -value | Lin & Batzli (2001) |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.76 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Hylocichla mustelina</i> | Wood thrush | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.84 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Junco hyemalis</i> | Dark-eyed Junco | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.52 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| Unspecified | | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.73 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Pheucticus ludovicianus</i> | Rose-breasted grosbeak | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.56 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Spizella passerina</i> | Chipping sparrow | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.09 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Vireo olivaceus</i> | Red-eyed vireo | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.74 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Piranga olivacea</i> | Scarlet tanager | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.44 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Setophaga citrina</i> | Hooded warbler | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.69 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |

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| Unspecified | | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.84 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Turdus migratorius</i> | American robin | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.39 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Helmitheros vermivorum</i> | Worm-eating warbler | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.65 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Empidonax virescens</i> | Acadian flycatcher | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.58 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Passerina cyanea</i> | Indigo bunting | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.47 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Emberiza variabilis</i> | Gray catbird | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.39 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Catharus fuscescens</i> | Veery | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.86 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Cardinalis cardinalis</i> | Northern cardinal | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.54 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |
| <i>Contopus virens</i> and <i>C. sordidulus</i> | Western and Eastern wood-peewee | North America | Developed land cover within 10 km radius | Number of fledged young female/year | - | 0.79 | Pearson's <i>r</i> | Lloyd <i>et al.</i> (2005) |

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|-------------------------------|---------------------|---------------|--|----------------------|---|------|---------------|-------------------------------|
| <i>Sitta europaea</i> | Nuthatch | Europe | Large forests <i>versus</i> fragment | Breeding density | + | 0.76 | F | Matthysen (1999) |
| <i>Turdus merula</i> | Blackbird | Europe | Patch size | Predation of nests | - | 0.93 | R -squared | Møller (1988) |
| <i>Oporornis formosus</i> | Kentucky warbler | North America | Distance from agricultural edge | Parasitism of nests | - | 0.31 | chi-squared | Morse & Robinson (1999) |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Fragmented <i>versus</i> unfragmented landscape | Clutch size | - | 0.39 | F | Porneluzi & Faaborg (2001) |
| <i>Strix aluco</i> | Tawny owl | Europe | Patch size | Fledging success | + | 0.03 | Pearson's r | Redpath (1995) |
| <i>Empidonax virescens</i> | Acadian flycatcher | North America | Forest cover | Daily nest mortality | - | 0.12 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Passerina cyanea</i> | Indigo bunting | North America | Forest cover | Daily nest mortality | - | 0.82 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Oporornis formosus</i> | Kentucky warbler | North America | Forest cover | Daily nest mortality | - | 0.67 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Cardinalis cardinalis</i> | Northern cardinal | North America | Forest cover | Daily nest mortality | - | 0.47 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Seiurus aurocapillus</i> | Ovenbird | North America | Forest cover | Daily nest mortality | - | 0.49 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Vireo olivaceus</i> | Red-eyed vireo | North America | Forest cover | Daily nest mortality | - | 0.55 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Helmitheros vermivorum</i> | Worm-eating warbler | North America | Forest cover | Daily nest mortality | - | 0.99 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Hylocichla ustelina</i> | Wood thrush | North America | Forest cover | Daily nest mortality | - | 0.74 | Pearson's r | Robinson <i>et al.</i> (1995) |
| <i>Piranga olivacea</i> | Scarlet tanager | North America | Forest cover | Daily nest mortality | - | 0.49 | Pearson's r | Robinson <i>et al.</i> (1995) |

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| <i>Turdus migratorius</i> | American robin | North America | Forested <i>versus</i> agricultural landscape | % successful nests | - | -0.85 | Means and standard deviations | Tewksbury <i>et al.</i> (2005) |
| <i>Bombycilla cedrorum</i> | Cedar waxwing | North America | Forested <i>versus</i> agricultural landscape | % successful nests | - | -0.98 | Means and standard deviations | Tewksbury <i>et al.</i> (2005) |
| <i>Vireo gilvus</i> | Warbling vireo | North America | Forested <i>versus</i> agricultural landscape | % successful nests | - | -0.01 | Means and standard deviations | Tewksbury <i>et al.</i> (2005) |
| <i>Setophaga petechia</i> | Yellow warbler | North America | Forested <i>versus</i> agricultural landscape | % successful nests | - | -0.40 | Means and standard deviations | Tewksbury <i>et al.</i> (2005) |
| <i>Macaca silemus</i> | Lion-tailed macaque | Asia | Tree basal area in fragment | Birth rate | + | 0.63 | Spearman's <i>r</i> | Umapathy & Kumar (2000) |
| <i>Macaca silemus</i> | Lion-tailed macaque | Asia | Patch size | Birth rate | + | 0.61 | Spearman's <i>r</i> | Umapathy <i>et al.</i> (2011) |
| <i>Sciurus vulgaris</i> | Eurasian red squirrel | Europe | Fragmented <i>versus</i> unfragmented | Juvenile survival | + | -0.69 | <i>F</i> | Hussain & Shivaji (2011) |
| <i>Eopsaltria australis</i> | Eastern yellow robin | Australia | Fragment size | Egg mass | - | 0.39 | <i>F</i> | Wauters <i>et al.</i> (1994) |
| Landscape condition – plant dispersal | | | | | | | | |

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|--|---------------|---------------------------------------|--|----|-------|---------------------|------------------------------|
| <i>Leptonychia usambarensis</i> | Africa | Fragmented <i>versus</i> unfragmented | Presence of juveniles away from parental trees | - | 0.84 | chi-squared | Cordeiro & Howe (2003) |
| 29 tree species | North America | Distance from seed source | Seedling presence | - | 0.74 | <i>P</i> -value | Hewitt & Kellman (2002) |
| <i>Heliconia acuminata</i> | South America | Continuous <i>versus</i> fragments | Seed dispersal limitation | - | 0.03 | <i>t</i> | Uriarte <i>et al.</i> (2010) |
| Landscape condition – plant death rates | | | | | | | |
| <i>Trillium ovatum</i> | North America | Patch size | Survival rate | + | -0.13 | Spearman's <i>r</i> | Jules (1998) |
| <i>Vascular epiphytes</i> | South America | Isolated <i>versus</i> forest trees | Mortality | + | -0.85 | <i>F</i> | Werner (2011) |
| Landscape condition – plant birth rates | | | | | | | |
| <i>Acacia caven</i> | South America | Fragmentation | Fruit/seed production | - | 0.31 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Aloysia gratissima</i> | South America | Fragmentation | Fruit/seed production | na | 0 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Dicliptera tweediana</i> | South America | Fragmentation | Fruit/seed production | - | 0.62 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Geoffroea decorticans</i> | South America | Fragmentation | Fruit/seed production | + | -0.15 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Heimia salicifolia</i> | South America | Fragmentation | Fruit/seed production | - | 0.57 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Ipomoea purpurea</i> | South America | Fragmentation | Fruit/seed production | + | -0.34 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Lycium cestroides</i> | South America | Fragmentation | Fruit/seed production | - | 0.61 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Mandevilla laxa</i> | South America | Fragmentation | Fruit/seed production | - | 0.60 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Mandevilla pentlandiana</i> | South America | Fragmentation | Fruit/seed production | - | 0.09 | Hedge's <i>d</i> * | Aguilar (2005) |

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| <i>Morrenia brachystephana</i> | South America | Fragmentation | Fruit/seed production | - | 0.55 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Porlieria microphylla</i> | South America | Fragmentation | Fruit/seed production | - | 0.66 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Solanum chenopodioides</i> | South America | Fragmentation | Fruit/seed production | - | 0.16 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Talinum paniculatum</i> | South America | Fragmentation | Fruit/seed production | + | -0.60 | Hedge's <i>d</i> * | Aguilar (2005) |
| <i>Cestrum oarqyu</i> | South America | Fragmentation | Fruit/seed production | - | 0.71 | Hedge's <i>d</i> * | Aguilar & Galetto (2004) |
| <i>Acacia aroma</i> | South America | Fragmentation | Fruit/seed production | + | -0.52 | Hedge's <i>d</i> * | Aizen & Feinsinger (1994) |
| <i>Acacia atramentaria</i> | South America | Fragmentation | Fruit/seed production | - | 0.03 | Hedge's <i>d</i> * | Aizen & Feinsinger (1994) |
| <i>Acacia furcatispina</i> | South America | Fragmentation | Fruit/seed production | - | 0.14 | Hedge's <i>d</i> * | Aizen & Feinsinger (1994) |
| <i>Acacia praecox</i> | South America | Fragmentation | Fruit/seed production | + | -0.27 | Hedge's <i>d</i> * | Aizen & Feinsinger (1994) |
| <i>Atamisquea emarginata</i> | South America | Fragmentation | Fruit/seed production | - | 0.46 | Hedge's <i>d</i> * | Aizen & Feinsinger (1994) |
| <i>Caesalpinia gilliesi</i> | South America | Fragmentation | Fruit/seed production | - | 0.17 | Hedge's <i>d</i> * | Aizen & Feinsinger (1994) |
| <i>Cassia aphylla</i> | South America | Fragmentation | Fruit/seed production | - | 0.21 | Hedge's <i>d</i> * | Aizen & Feinsinger (1994) |

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|--------------------------------|---------------|---------------|-----------------------|---|-------|---------------|----------------------------|
| <i>Cercidium australe</i> | South America | Fragmentation | Fruit/seed production | - | 0 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Justicia squarrosa</i> | South America | Fragmentation | Fruit/seed production | - | 0.10 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Ligaria cuneifolia</i> | South America | Fragmentation | Fruit/seed production | - | 0.25 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Mimosa detinens</i> | South America | Fragmentation | Fruit/seed production | - | 0.36 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Opuntia quimilo</i> | South America | Fragmentation | Fruit/seed production | + | -0.09 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Portulaca umbraticola</i> | South America | Fragmentation | Fruit/seed production | - | 0.20 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Prosopis nigra</i> | South America | Fragmentation | Fruit/seed production | - | 0.25 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Rhipsalis lumbricoides</i> | South America | Fragmentation | Fruit/seed production | - | 0.52 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Tillandsia lumbricoides</i> | South America | Fragmentation | Fruit/seed production | - | 0.19 | Hedge's d^* | Aizen & Feinsinger (1994) |
| <i>Aster curtus</i> | Europe | Fragmentation | Fruit/seed production | + | -0.05 | Hedge's d^* | Bigger (1999) |
| <i>Petrocoptis monticiana</i> | Europe | Fragmentation | Fruit/seed production | - | 0.05 | Hedge's d^* | Bosch <i>et al.</i> (2002) |

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| <i>Heliconia acuminata</i> | South America | Fragmentation | Fruit/seed production | - | 0.18 | Hedge's <i>d</i> * | Bruna & Kress (2002) |
| <i>Primula vulgaris</i> | Europe | Fragmentation | Fruit/seed production | - | 0.17 | Hedge's <i>d</i> * | Brys <i>et al.</i> (2004) |
| <i>Samanea saman</i> | Central America | Fragmentation | Fruit/seed production | + | -0.27 | Hedge's <i>d</i> * | Cascante <i>et al.</i> (2002) |
| <i>Leucochrysum albicans</i> | Australia | Fragmentation | Fruit/seed production | - | 0.47 | Hedge's <i>d</i> * | Costin <i>et al.</i> (2001) |
| <i>Acacia brachybotrya</i> | Australia | Fragmentation | Fruit/seed production | - | 0.50 | Hedge's <i>d</i> * | Cunningham (2000) |
| <i>Dianella revoluta</i> | Australia | Fragmentation | Fruit/seed production | - | 0.19 | Hedge's <i>d</i> * | Cunningham (2000) |
| <i>Eremophila glabra</i> | Australia | Fragmentation | Fruit/seed production | - | 0.51 | Hedge's <i>d</i> * | Cunningham (2000) |
| <i>Senna artemisoides</i> | Australia | Fragmentation | Fruit/seed production | + | -0.44 | Hedge's <i>d</i> * | Cunningham (2000) |
| <i>Dinizia excelsa</i> | South America | Fragmentation | Fruit/seed production | + | -0.41 | Hedge's <i>d</i> * | Dick (2001) |
| <i>Babiana ambigua</i> | Africa | Fragmentation | Fruit/seed production | - | -0.67 | Hedge's <i>d</i> * | Donaldson <i>et al.</i> (2002) |
| <i>Berkheya armata</i> | Africa | Fragmentation | Fruit/seed production | - | -0.05 | Hedge's <i>d</i> * | Donaldson <i>et al.</i> (2002) |
| <i>Cyanella lutea</i> | Africa | Fragmentation | Fruit/seed production | - | 0.06 | Hedge's <i>d</i> * | Donaldson <i>et al.</i> (2002) |
| <i>Gladiolus liliaceus</i> | Africa | Fragmentation | Fruit/seed production | - | 0.13 | Hedge's <i>d</i> * | Donaldson <i>et al.</i> (2002) |
| <i>Ornithogalum thyrsoides</i> | Africa | Fragmentation | Fruit/seed production | - | 0.03 | Hedge's <i>d</i> * | Donaldson <i>et al.</i> (2002) |
| <i>Pterygodium catholicum</i> | Africa | Fragmentation | Fruit/seed production | - | 0.08 | Hedge's <i>d</i> * | Donaldson <i>et al.</i> (2002) |
| <i>Trachyandra birsuta</i> | Africa | Fragmentation | Fruit/seed production | - | 0.10 | Hedge's <i>d</i> * | Donaldson <i>et al.</i> (2002) |

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| <i>Pachira quinata</i> | Central America | Fragmentation | Fruit/seed production | - | 0.30 | Hedge's d^* | Fuchs <i>et al.</i> (2003) |
| <i>Anacardium excelsum</i> | Central America | Fragmentation | Fruit/seed production | - | 0.36 | Hedge's d^* | Ghazoul & McLeish (2001) |
| <i>Dombeya acutangula</i> | Asia | Fragmentation | Fruit/seed production | - | 0.85 | Hedge's d^* | Gigord <i>et al.</i> (1999) |
| <i>Clarkia concinna</i> | North America | Fragmentation | Fruit/seed production | - | 0.43 | Hedge's d^* | Groom (2001) |
| <i>Primula elatior</i> | Europe | Fragmentation | Fruit/seed production | - | 0.51 | Hedge's d^* | Jacquemyn <i>et al.</i> (2002) |
| <i>Dianthus deltoides</i> | Europe | Fragmentation | Fruit/seed production | - | 0.74 | Hedge's d^* | Jennersten (1988) |
| <i>Oxyanthus pyriformis</i> | Africa | Fragmentation | Fruit/seed production | + | -0.19 | Hedge's d^* | Johnson <i>et al.</i> (2004) |
| <i>Gerbera aurantiaca</i> | Africa | Fragmentation | Fruit/seed production | - | 0.56 | Hedge's d^* | Johnson <i>et al.</i> (2004) |
| <i>Trillium ovatum</i> | North America | Fragmentation | Fruit/seed production | - | 0.18 | Hedge's d^* | Jules & Rathke (1999) |
| <i>Pedicularis palustris</i> | Europe | Fragmentation | Fruit/seed production | + | -0.18 | Hedge's d^* | Karrenberg & Jensen (2000) |
| <i>Peraxilla tetrapetala</i> | New Zealand | Fragmentation | Fruit/seed production | + | -0.83 | Hedge's d^* | Kelly <i>et al.</i> (2000) |
| <i>Phyteuma spicatum</i> | Europe | Fragmentation | Fruit/seed production | - | 0.58 | Hedge's d^* | Kolb (2005) |
| <i>Banksia goodii</i> | Australia | Fragmentation | Fruit/seed production | - | 0.59 | Hedge's d^* | Lamont <i>et al.</i> (1993) |
| Trees from nine families | South America | Fragmented <i>versus</i> unfragmented | Recruitment rate | + | -0.26 | Hedge's d^* | Laurance <i>et al.</i> (1998) |

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|------------------------------------|-----------------|---------------------------------|-----------------------|---|-------|--------------------|--|
| <i>Vincetoxicum hirculinum</i> | Europe | Fragmentation | Fruit/seed production | - | 0.33 | Hedge's <i>d</i> * | Leimu & Syrjänen (2002) |
| <i>Gentianella campestris</i> | Europe | Fragmentation | Fruit/seed production | - | 0.42 | Hedge's <i>d</i> * | Lennartsson (2002) |
| Sand dune grasslands | Asia | Vegetation loss and erodibility | Seedling recruitment | - | 0.74 | Hedge's <i>d</i> * | Li <i>et al.</i> (2009) |
| <i>Primula farinosa</i> | Europe | Fragmentation | Fruit/seed production | - | 0.20 | Hedge's <i>d</i> * | Lienert & Fischer (2003) |
| <i>Arnica montana</i> | Europe | Fragmentation | Fruit/seed production | - | 0.72 | Hedge's <i>d</i> * | Luijten <i>et al.</i> (2000) |
| <i>Aquilegia canadensis</i> | North America | Fragmentation | Fruit/seed production | + | -0.24 | Hedge's <i>d</i> * | Mavraganis & Eckert (2001) |
| <i>Oenothera macrocarpa</i> | North America | Fragmentation | Fruit/seed production | - | 0.01 | Hedge's <i>d</i> * | Moody-Weis & Heywood (2001) |
| <i>Rutidosia leptorrhynchoides</i> | Australia | Fragmentation | Fruit/seed production | - | 0.66 | Hedge's <i>d</i> * | Morgan (1999) |
| <i>Lychmis viscaria</i> | Europe | Fragmentation | Fruit/seed production | - | 0.05 | Hedge's <i>d</i> * | Mustajarvi <i>et al.</i> (2001) |
| <i>Lychmis viscaria</i> | Europe | Fragmentation | Fruit/seed production | - | 0.75 | Hedge's <i>d</i> * | Mustajarvi <i>et al.</i> (2001) |
| <i>Gentiana pneumonanthe</i> | Europe | Fragmentation | Fruit/seed production | - | 0.27 | Hedge's <i>d</i> * | Oostermeijer <i>et al.</i> (1998) |
| <i>Oncidium ascendens</i> | Central America | Fragmentation | Fruit/seed production | - | 0.30 | Hedge's <i>d</i> * | Parra-Tabla <i>et al.</i> (2000) |
| <i>Cochlearia bavarica</i> | Europe | Fragmentation | Fruit/seed production | - | 0.81 | Hedge's <i>d</i> * | Paschke <i>et al.</i> (2002) Paschke, Abs & Schmid (2002) |

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|----------------------------------|-----------------|---------------|-----------------------|---|-------|---------------|-------------------------------------|
| <i>Ceiba grandiflora</i> | Central America | Fragmentation | Fruit/seed production | - | 0.94 | Hedge's d^* | Quesada <i>et al.</i> (2003) |
| <i>Ceiba aesculifolia</i> | Central America | Fragmentation | Fruit/seed production | - | 0.17 | Hedge's d^* | Quesada <i>et al.</i> (2004) |
| <i>Ceiba grandiflora</i> | Central America | Fragmentation | Fruit/seed production | - | 0.31 | Hedge's d^* | Quesada <i>et al.</i> (2004) |
| <i>Enterolobium cyclocarpum</i> | Central America | Fragmentation | Fruit/seed production | - | 0.63 | Hedge's d^* | Rocha & Aguilar (2001) |
| <i>Elaeocarpus williamsianus</i> | Australia | Fragmentation | Fruit/seed production | - | 0.27 | Hedge's d^* | Rossetto <i>et al.</i> (2004) |
| <i>Pedicularis palustris</i> | Europe | Fragmentation | Fruit/seed production | + | -0.05 | Hedge's d^* | Schmidt & Jensen (2000) |
| <i>Lupinus sulphureus</i> | Europe | Fragmentation | Fruit/seed production | - | 0.65 | Hedge's d^* | Severns (2003) |
| <i>Embothrium coccineum</i> | South America | Fragmentation | Fruit/seed production | - | 0.75 | Hedge's d^* | Smith-Ramirez & Armesto (2003) |
| <i>Dyospiros montana</i> | Asia | Fragmentation | Fruit/seed production | - | 0.77 | Hedge's d^* | Somanathan & Borges (2000) |
| <i>Raphanus sativus</i> | Europe | Fragmentation | Fruit/seed production | - | 0.66 | Hedge's d^* | Steffan-Dewenter & Tschamtké (1999) |
| <i>Sinapis arvensis</i> | Europe | Fragmentation | Fruit/seed production | - | 0.27 | Hedge's d^* | Steffan-Dewenter & Tschamtké (1999) |
| <i>Illex verticillata</i> | North America | Fragmentation | Fruit/seed production | - | 0.39 | Hedge's d^* | Tewksbury <i>et al.</i> (2002) |
| <i>Trillium camschatcense</i> | Asia | Fragmentation | Fruit/seed production | - | 0.53 | Hedge's d^* | Tomimatsu & Ohara (2002) |

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|------------------------------------|---------------|---|-----------------------------------|---|-------|--------------------|--|
| <i>Heliconia acuminata</i> | South America | Continuous <i>versus</i> fragments | Seedling establishment limitation | + | 0.86 | <i>t</i> | Uriarte <i>et al.</i> (2010) |
| <i>Lapageria rosea</i> | South America | Fragmentation | Fruit/seed production | - | 0.26 | Hedge's <i>d</i> * | Valdivia <i>et al.</i> (2006) Valdivia, Simonetti & Henriquez (2006) |
| <i>Primula elatior</i> | Europe | Fragmentation | Fruit/seed production | - | 0.92 | Hedge's <i>d</i> * | Van Rossum <i>et al.</i> (2002) |
| <i>Pinus taiblaeformis</i> | Asia | Patch size | Incidence of selfing | - | 0.62 | <i>R</i> -squared | Wang <i>et al.</i> (2010) |
| <i>Santalum lanceolatum</i> | Asia | Fragmentation | Fruit/seed production | - | 0.65 | Hedge's <i>d</i> * | Warburton <i>et al.</i> (2000) |
| <i>Brunsvigia radulosa</i> | Africa | Fragmentation | Fruit/seed production | - | 0.56 | Hedge's <i>d</i> * | Ward & Johnson (2005) |
| <i>Primula seiboldii</i> | Asia | Fragmentation | Fruit/seed production | - | 0.68 | Hedge's <i>d</i> * | Watanabe <i>et al.</i> (2003) Watanabe, Goka & Washitani (2003) |
| Epiphytes (several) | South America | Non-isolated <i>versus</i> isolated trees | Seedling density | - | 0.39 | <i>P</i> -value | Werner & Gradstein (2008) |
| <i>Calystegia collina</i> | North America | Fragmentation | Fruit/seed production | - | 0.37 | Hedge's <i>d</i> * | Wolf & Harrison (2001) |
| <i>Verticordia fimbriensis</i> | Australia | Fragmentation | Fruit/seed production | + | -0.23 | Hedge's <i>d</i> * | Yates & Ladd (2005) |
| Climate – animal emigration | | | | | | | |

| | | | | | | | | |
|---|----------------------------|---------------|--|--|--------|------|-------------------------|--------------------------------|
| <i>Zyganena</i> spp. | Burnet moth | Europe | Warm year versus cool year | % individuals moving to another patch | + | 0.29 | chi-squared | Franzén & Nilsson (2012) |
| <i>Pararge aegeria</i> | Butterfly | Europe (exp.) | Ambient temperature | Flight distance | + | 0.12 | <i>P</i> -value | Merckx <i>et al.</i> (2006) |
| <i>Passer domesticus</i> | House sparrow | Europe | Mean spring temperature | Dispersal rate | + | 0.22 | <i>z</i> | Pärm <i>et al.</i> (2011) |
| Climate – animals - immigration | | | | | | | | |
| <i>Ochotona princeps</i> | American pika | North America | Heat to moisture ratio/precipitation as snow | Genetic differentiation | na | 0.59 | <i>R</i> -squared | Henry <i>et al.</i> (2012) |
| Climate – animal death rate | | | | | | | | |
| <i>Rana sylvatica</i> | Wood frog | North America | Mean monthly rainfall | Mean adult survival | + | 0.54 | Spearman's <i>r</i> | Berven (1990) |
| <i>Malurus pulcherrimus</i> | Blue-breasted fairywren | Australia | Autumn–winter rainfall | Female survival rate | – | 0.15 | <i>P</i> -value (<0.01) | Brooker & Brooker (2001) |
| <i>Triturus cristatus</i> | Great crested newt | Europe | Winter temperature and non-aquatic-period rainfall | Between-year survival (mark–recapture) | both – | 0.75 | <i>R</i> -squared | Griffiths <i>et al.</i> (2010) |
| <i>Cyanistes caeruleus</i> (syn. <i>Parus caeruleus</i>) | Blue tit | Europe | Tropical climate influence (Standardised Sahel rainfall) | Survival rate from mark–recapture | + | 0.33 | <i>P</i> -value | Grosbois <i>et al.</i> (2006) |
| <i>Anser brachyrhynchus</i> | Svalbard pink-footed goose | Arctic | Climate PCA: Warm, wet winters and early spring | Survival rate | + | 0.49 | <i>F</i> | Kéry <i>et al.</i> (2006) |
| <i>Parus montanus</i> | Willow tit | Europe | Deviation from 30yr mean monthly temp | Monthly survival probability | – | 0.80 | Pearson's <i>r</i> | Lahti <i>et al.</i> (1998) |

| | | | | | | | | |
|---------------------------------------|-------------------|---------------|---|---------------------------|----|------|--------------------|-------------------------------|
| <i>Trichechus manatus latirostris</i> | Florida manatee | North America | Yearly storm occurrence | Survival rate | - | 0.74 | <i>P</i> -value | Langtimm & Beck (2003) |
| <i>Ochotona princeps</i> | American pika | North America | Mean winter Pacific decadal index lag 1 year | Adult female survival | + | 0.77 | Pearson's <i>r</i> | Morrison & Hik (2007) |
| <i>Microtus ochrogaster</i> | Prairie vole | North America | Precipitation | Summer stage survival | - | 0.54 | <i>R</i> -squared | Reed & Slade (2009) |
| <i>Sigmodon hispidus</i> | Hispid cotton rat | North America | Mean climate effect (temperature and rainfall measures) | Survival (various stages) | na | 0.61 | <i>R</i> -squared | Reed & Slade (2009) |
| <i>Turdus merula</i> | Blackbird | Europe | Seven climate variables (in wintering and breeding grounds) | Apparent survival | na | 0.75 | <i>R</i> -squared | Salewski <i>et al.</i> (2013) |
| <i>Sylvia atricapilla</i> | Blackcap | Europe | Seven climate variables (in wintering and breeding grounds) | Apparent survival | na | 0.56 | <i>R</i> -squared | Salewski <i>et al.</i> (2013) |
| <i>Phylloscopus collybita</i> | Chiffchaff | Europe | Seven climate variables (in wintering and breeding grounds) | Apparent survival | na | 0.62 | <i>R</i> -squared | Salewski <i>et al.</i> (2013) |
| <i>Prunella modularis</i> | Dunnock | Europe | Seven climate variables (in wintering and breeding grounds) | Apparent survival | na | 0.53 | <i>R</i> -squared | Salewski <i>et al.</i> (2013) |
| <i>Emberiza schoeniclus</i> | Reed bunting | Europe | Seven climate variables (in wintering and breeding grounds) | Apparent survival | na | 0.56 | <i>R</i> -squared | Salewski <i>et al.</i> (2013) |

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|--------------------------------|------------------------|--------------------------|---|-----------------------|-----|------|---------------------|-------------------------------|
| <i>Acrocephalus scirpaceus</i> | Reed warbler | Europe | Seven climate variables (in wintering and breeding grounds) | Apparent survival | na | 0.53 | <i>R</i> -squared | Salewski <i>et al.</i> (2013) |
| <i>Phylloscopus trochilus</i> | Willow warbler | Europe | Seven climate variables (in wintering and breeding grounds) | Apparent survival | na | 0.61 | <i>R</i> -squared | Salewski <i>et al.</i> (2013) |
| <i>Pogonomymex barbatus</i> | Red harvester ant | North America | Summer precipitation | Colony mortality | - | 0.56 | Spearman's <i>r</i> | Sanders & Gordon (2004) |
| <i>Uria lomvia</i> | Brunnich's guillemot | North America and Europe | NAO | Annual adult survival | + | 0.56 | <i>R</i> -squared | Sandvik <i>et al.</i> (2005) |
| <i>Uria aalge</i> | Common guillemot | North America and Europe | Sea surface temperature/NAO | Annual adult survival | -/+ | 0.79 | <i>R</i> -squared | Sandvik <i>et al.</i> (2005) |
| <i>Rissa tridactyla</i> | Black-legged kittiwake | North America and Europe | NAO | Annual adult survival | na | 0.73 | <i>R</i> -squared | Sandvik <i>et al.</i> (2005) |
| <i>Fratercula arctica</i> | Atlantic puffin | North America and Europe | Sea surface temperature | Annual adult survival | - | 0.41 | <i>R</i> -squared | Sandvik <i>et al.</i> (2005) |
| <i>Alca torda</i> | Razorbill | North America and Europe | Sea surface temperature | Annual adult survival | - | 0.54 | <i>R</i> -squared | Sandvik <i>et al.</i> (2005) |

| <i>Uta stansburiana</i> | Side-blotched lizard | North America (exp.) | Cold treatment | Survival time | + | 0.43 | <i>F</i> | Zani (2008) |
|--|-------------------------|----------------------|--|---|----|------|---------------------------|-------------------------------|
| Climate – animal birth rate | | | | | | | | |
| 6 spp. Vesperilinoid bat | | North America | Summer precipitation | Capture frequency of non-reproductive females | - | 0.85 | Pearson's <i>r</i> | Adams (2010) |
| <i>Bubo bubo</i> | Eagle owl | Europe | Rainfall during chick rearing | Number of fledged young/pair | - | 0.35 | <i>z</i> | Bionda & Brambilla (2012) |
| <i>Malurus pulcherrimus</i> | Blue-breasted fairywren | Australia | Annual rainfall | Number of fledglings per female per year | + | 0.14 | <i>P</i> -value (<0.01) | Brooker & Brooker (2001) |
| <i>Calyptorhynchus lathamii</i> | Glossy black cockatoo | Australia | Total annual rainfall in preceding year | Proportion of juveniles in the population | + | 0.95 | <i>F</i> | Cameron (2009) |
| <i>Lichenostomus melanops cassidix</i> | Helmeted honeyeater | Australia | Six rainfall and temperature parameters | Fledglings per egg | na | 0.96 | <i>R</i> -squared (model) | Chambers <i>et al.</i> (2008) |
| <i>Acanthochromis polyacanthus</i> | Damselfish | Australia (exp.) | Temperature | Reproductive output (egg size and number of eggs) | - | 0.33 | <i>R</i> -squared | Donelson <i>et al.</i> (2010) |
| <i>Propithecus edwardsi</i> | Milne-Edward's sifaka | Africa | ENSO phase, wet-season rainfall and months of extreme rain | Birth rate | na | 0.89 | <i>R</i> -squared | Dunham <i>et al.</i> (2010) |
| <i>Phoca hispida</i> | Ringed seal | North America | Mean Apr–May snow depth | Number of seals born/year surviving to harvest | + | 0.68 | <i>R</i> -squared | Ferguson <i>et al.</i> (2005) |

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|--------------------------------|--------------------------|----------------------|--|--|---------|-------|---------------------------|---------------------------------|
| <i>Fratrercula cirrhata</i> | Tufted puffin | North America | Sea surface temperature | Fledglings per hatchling | - | 0.71 | <i>R</i> -squared | Gjerdrum <i>et al.</i> (2003) |
| <i>Cervus canadensis</i> | Elk | North America | Previous summer temperature | Neonatal survival | - | 0.08 | <i>P</i> -value | Griffin <i>et al.</i> (2011) |
| <i>Fulmarus glacialisoides</i> | Southern fulmar | Antarctica | Sea ice concentration during summer | Proportion of birds attempting to breed | + | 0.4 | Pearson's <i>r</i> | Jenouvrier <i>et al.</i> (2003) |
| <i>Bufo boreas</i> | Western toad | North America (exp.) | Water depth and UVB level | Embryo survival | + and - | 0.72 | <i>F</i> | Kiesecker <i>et al.</i> (2001) |
| <i>Buteo buteo</i> | Common buzzard | Europe | Mean temperature in June | Brood size | - | 0.16 | Spearman's <i>r</i> | Lehikoinen <i>et al.</i> (2009) |
| <i>Ochotona princeps</i> | American pika | North America | Mean winter Pacific decadal index lag 1 year | Juvenile survival southern population | + | 0.77 | Pearson's <i>r</i> | Morrison & Hik (2007) |
| <i>Tetrao urogallus</i> | Capercaillie grouse | Europe | April temperature index (timing of warming) | Proportion of hens with broods | + | 0.41 | <i>P</i> -value (<0.0001) | Moss <i>et al.</i> (2001) |
| <i>Accipiter nisus</i> | Sparrowhawk | Europe | Mean monthly temperature in Spring | Hatchlings per egg | + | 0.53 | <i>F</i> | Nielsen & Møller (2006) |
| <i>Lacerta agilis</i> | Sand lizard | Europe | Mean daily temperature | Incidence of multiple paternity clutches | + | 0.78 | Spearman's <i>r</i> | Olsson <i>et al.</i> (2011) |
| <i>Hieraetus fasciatus</i> | Bonelli's eagle | Europe | Average annual temperature | Average fledglings/pair/year | + | 0.96 | Pearson's <i>r</i> | Ontiveros & Pleguezuelos (2003) |
| <i>Ambystoma tigrinum</i> | Eastern tiger salamander | North America | Breeding season rainfall | Number of breeding females | + | 0.47 | Kendall's tau | Pechmann <i>et al.</i> (1991) |
| <i>Ambystoma opacum</i> | Marbled salamander | North America | Breeding season rainfall | Number of breeding females | + | -0.16 | Kendall's tau | Pechmann <i>et al.</i> (1991) |

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|-----------------------------|--------------------|---------------|--|----------------------------------|---------|------|---------------------|--------------------------------|
| <i>Ambystoma talpoideum</i> | Mole salamander | North America | Breeding season rainfall | Number of breeding females | + | 0.52 | Kendall's tau | Pechmann <i>et al.</i> (1991) |
| <i>Pseudacris ornata</i> | Ornate chorus frog | North America | Breeding season rainfall | Number of breeding females | + | 0.27 | Kendall's tau | Pechmann <i>et al.</i> (1991) |
| <i>Rangifer tarandus</i> | Caribou | North America | Degree of climate-caused trophic mismatch | Calf production | - | 0.87 | Pearson's <i>r</i> | Post & Forchhammer (2008) |
| <i>Cervus elaphus</i> | Red deer | Europe | NAO during pregnancy | Cohort fecundity (two-year-olds) | + | 0.64 | Pearson's <i>r</i> | Post & Stenseth (1999) |
| <i>Rangifer tarandus</i> | Reindeer | Europe | NAO during pregnancy | Female fecundity | - | 0.38 | Pearson's <i>r</i> | Post & Stenseth (1999) |
| <i>Microtus ochrogaster</i> | Prairie vole | North America | Mean minimum temperature and total three-month precipitation | Summer stage 2 reproduction | - and + | 0.6 | <i>R</i> -squared | Reed & Slade (2009) |
| <i>Sigmodon hispidus</i> | Hispid cotton rat | North America | Mean climate effect (various) | Reproduction (various stages) | na | 0.72 | <i>R</i> -squared | Reed & Slade (2009) |
| <i>Falco naumanni</i> | Lesser kestrel | Europe | Winter rainfall at breeding grounds | Nest success rate | + | 0.42 | <i>F</i> | Rodriguez & Bustamante (2003) |
| <i>Pogonomymex barbatus</i> | Red harvester ant | North America | Summer precipitation | Colony establishment | + | 0.23 | Spearman's <i>r</i> | Sanders & Gordon (2004) |
| <i>Ficedula hypoleuca</i> | Pied flycatcher | Europe | Mean May temperature | Fledglings per egg | - | 0.14 | <i>F</i> | Sanz <i>et al.</i> (2003) |
| <i>Falco punctatus</i> | Mauritius kestrel | Africa | Delayed egg-laying due to rainfall | Number of fledglings produced | - | 0.33 | <i>F</i> | Senapathi <i>et al.</i> (2011) |

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|---|-----------------------------|-----------------|---|------------------------------------|---------|------|---------------------------|--|
| <i>Dendroica caerulescens</i> | Black-throated blue warbler | North America | SOI | Mean number of young per pair | + | 0.39 | Pearson's <i>r</i> | Sillett <i>et al.</i> (2000) |
| <i>Aquila chrysaetos</i> | Golden eagle | North America | Number of days >32°C | % pairs successfully raising young | - | 0.39 | <i>P</i> -value | Steenhof <i>et al.</i> (1997) |
| <i>Dermodohelys coriacea</i> | Leatherback turtle | Central America | Mean ambient temperature | Emergence rate | - | 0.11 | <i>P</i> -value | Tomillo <i>et al.</i> (2012) |
| <i>Haematopus ostralegus</i> | Eurasian oystercatcher | Europe | Sea level (nest flooding) | Annual fledgling production | - | 0.53 | <i>t</i> | van de Pol <i>et al.</i> (2010) |
| <i>Perisoreus canadensis</i> | Grey jay | North America | Mean monthly temperature Oct/Nov, Feb/Mar | Mean number of nestlings | - and + | 0.33 | <i>R</i> -squared | Waite & Strickland (2006) |
| <i>Saccostomus campestris</i> | Pouched mouse | Africa | Rainfall in previous two months | Litter size | - | 0.19 | Pearson's <i>r</i> | Westlin (2000) |
| Climate – plant death rate | | | | | | | | |
| Six Bornean tree species (>100 mm DBH) | | Asia | Drought occurrence | Yearly mortality of plants | + | 0.14 | Means and standard errors | Condit <i>et al.</i> (1995) |
| Eight Bornean tree species (10–99 mm DBH) | | Asia | Drought occurrence | Yearly mortality of plants | + | 0.12 | Means and standard errors | Condit <i>et al.</i> (1995) |
| <i>Arnica angustifolia</i> | | Europe | Hot days | Mean survival rate of rametes | - | 0.95 | <i>t</i> | Jakalanieni (2011) |
| <i>Abies</i> sp. and <i>Pinus</i> sp. | | North America | Average water deficit | Mortality rate | + | 0.84 | <i>P</i> -value | Van Mantgem & Stephenson (2007) |
| Climate – plant birth rates | | | | | | | | |
| <i>Vincetoxicum hirundinaria</i> | | Europe | Water addition | Number of full-size fruit/plant | + | 0.25 | <i>F</i> | Ågren <i>et al.</i> (2008) Ågren, Ehrlén & Solbreck (2008) |

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|---|---------------|--|---|---------|------|---------------------------------------|--------------------------------|
| <i>Pinus uncinata</i> | Europe | Maximum temperature April | April recruitment | - | 0.7 | Spearman's r (estimated from graph) | Camarero & Gutiérrez (2007) |
| <i>Acacia polycantha</i> | Africa (exp.) | Average temperature wk 2; minimum temperature wk 3 | Seedling mortality | + and - | 0.83 | R -squared | Chidumayo (2008) |
| <i>Acacia sieberana</i> | Africa (exp.) | Temperature average wk 4 | Seedling mortality | + | 0.57 | R -squared | Chidumayo (2008) |
| <i>Bauhinia thoningii</i> | Africa (exp.) | Temperature minimum wk 3 | Seedling mortality | - | 0.74 | R -squared | Chidumayo (2008) |
| <i>Dichrostachys cinerea</i> | Africa (exp.) | Temperature average wk 2; temperature maximum wk 2 | Seedling mortality | + | 0.87 | R -squared | Chidumayo (2008) |
| <i>Ziziphus abyssima</i> | Africa (exp.) | Temperature minimum wk 3; temperature average wk 4 | Seedling mortality | - and + | 0.54 | R -squared | Chidumayo (2008) |
| <i>Helianthella quinquenervis</i> , <i>Delphinium barbeyi</i> , <i>Erigeron speciosus</i> | North America | Timing of snowmelt | Peak number of flowers | + | 0.43 | R -squared | Inouye (2008) |
| 13 Arctic plant species | Arctic (exp.) | Heating treatment | Number of survived seedlings/number of sown seeds | - | 0.97 | F | Shevtsova <i>et al.</i> (2009) |

Table S4. Breakdown of individual studies (December 2012 and earlier) that measured demographic responses to landscape condition and climate by region and taxonomic group. ‘exp.’= experimental studies.

| | Landscape condition | Climate |
|------------------------------|------------------------|---------------|
| <i>Region</i> | | |
| Africa | 4 | 4 (1 exp.) |
| Polar | 0 | 3 (1 exp.) |
| Asia | 9 | 1 |
| Australia/New Zealand | 14 | 5 (1 exp.) |
| Europe | 29 (1 exp.) | 20 (1 exp.) |
| North America | 27 (4 exp.) | 18 (1 exp.) |
| South and Central America | 16 | 1 |
| <i>Taxonomic group</i> | | |
| Amphibians | 1 | 4 |
| Birds | 22 | 23 (3 marine) |
| Fish | 0 | 1 |
| Insects | 3 | 3 |
| Mammals | 9 | 11 (2 marine) |
| Reptiles | 2 | 3 (1 marine) |
| Plants | 62 | 8 |
| Total number of studies | 94 | 51 |

Table S5. Subset of studies (from Table S3) that showed effects of temperature and rainfall variables on birth or death rates. The direction (positive or negative) of an effect of temperature and precipitation on demographic rates is shown. Temporal scale indicates the time period for which the temperature or precipitation measure was measured. DBH, diameter at breast height.

| Reference | Species group | Effect of temperature on: | | Effect of precipitation on: | | Temporal scale |
|--|---------------|---------------------------|-------------|-----------------------------|-------------|---------------------------------------|
| | | birth rates | death rates | birth rates | death rates | |
| Berven (1990) | Amphibian | | | | – | Mean monthly |
| Griffiths <i>et al.</i> (2010) | Amphibian | | + | | + | Winter (non-aquatic period) |
| Pechmann <i>et al.</i> (1991) (<i>A. tigrinum</i>) | Amphibian | | | + | | Breeding season rainfall |
| Pechmann <i>et al.</i> (1991) (<i>A. opacum</i>) | Amphibian | | | + | | Breeding season rainfall |
| Pechmann <i>et al.</i> (1991) (<i>A. talpoideum</i>) | Amphibian | | | + | | Breeding season rainfall |
| Pechmann <i>et al.</i> (1991) (<i>P. ornata</i>) | Amphibian | | | + | | Breeding season rainfall |
| Brooker & Brooker (2001) | Bird | | | + | + | (a) Annual (b) Total autumn/winter |
| Sandvik <i>et al.</i> (2005) (Common guillemot) | Bird | | + | | | Autumn (sea surface) |
| Sandvik <i>et al.</i> (2005) (Atlantic puffin) | Bird | | + | | | Autumn (sea surface) |
| Sandvik <i>et al.</i> (2005) (Razorbill) | Bird | | + | | | Autumn (sea surface) |
| Bionda & Brambilla (2012) | Bird | | | – | | Rainfall during chick rearing |
| Cameron (2009) | Bird | | | + | | Annual total (preceding year) |
| Gjerdrum <i>et al.</i> (2003) | Bird | – | | | | Breeding season (sea surface) |
| Jenouvrier <i>et al.</i> (2003) | Bird | – | | | | Summer (sea ice concentration) |
| Lehikoinen <i>et al.</i> | Bird | – | | | | June mean |

| | | | | | | |
|---|---------|----------------|---|---|---|--|
| (2009) | | | | | | |
| Nielsen & Møller (2006) | Bird | + | | | | Spring mean monthly |
| Ontiveros & Pleguezuelos (2003) | Bird | + | | | | Annual mean |
| Rodríguez & Bustamante (2003) | Bird | | | + | | Winter rainfall at breeding grounds |
| Sanz <i>et al.</i> (2003) | Bird | - | | | | Mean May |
| Steenhof <i>et al.</i> (1997) | Bird | - | | | | Number of days >32 °C |
| Waite & Strickland (2006) | Bird | (a) - (b) + | | | | Mean monthly temperature: (a) Oct/Nov; (b) Feb/Mar |
| Donelson <i>et al.</i> (2010) | Fish | - | | | | Constant experimental temperature (breeding season) |
| Sanders & Gordon (2004) | Insect | | | + | - | Summer |
| Adams (2010) | Mammal | | | + | | Summer (breeding) |
| Griffin <i>et al.</i> (2011) | Mammal | - | | | | Previous summer |
| Reed & Slade (2009) (<i>M. ochrogaster</i>) | Mammal | - | | + | + | (a) Three-month mean minimum; (b) three-month total; (c) monthly total |
| Westlin (2000) | Mammal | | | - | | Total in previous two months |
| Olsson <i>et al.</i> (2011) | Reptile | + | | | | Mean daily |
| Tomillo <i>et al.</i> (2012) | Reptile | - | | | | Mean nest temperature |
| Condit <i>et al.</i> (1995) (Six species, >100 mm DBH) | Plant | | | | - | Annual (drought occurrence) |
| Condit <i>et al.</i> (1995) (Eight species <100 mm DBH) | Plant | | | | - | Annual (drought occurrence) |
| Jakalaniemi (2011) | Plant | | + | | | No. days/ year >25 °C |
| Van Mantgem & | Plant | | | | - | Mean water |

| | | | | | | |
|---|-----------------|----------------|----------|-----------|----------|--|
| Stephenson (2007) | | | | | | deficit of previous two years |
| Ågren <i>et al.</i> (2008) | Plant | | | + | | Water addition over two months (experimental) |
| Camarero & Gutiérrez (2007) | Plant | – | | | | Maximum temperature April |
| Chidumayo (2008) (<i>A. polycantha</i>) | Plant | (a) – (b) + | | | | One-week mean minimum |
| Chidumayo (2008) (<i>A. sieberana</i>) | Plant | – | | | | One-week mean |
| Chidumayo (2008) (<i>B. thoningii</i>) | Plant | + | | | | One-week minimum |
| Chidumayo (2008) (<i>D. cinerea</i>) | Plant | – | | | | One-week mean and maximum |
| Chidumayo (2008) (<i>Z. abyssima</i>) | Plant | (a) + (b) – | | | | One-week (a) minimum, (b) mean |
| Shevtsova <i>et al.</i> (2009) | Plant | – | | | | Whole growing season experimental heat treatment |
| Total | Positive | 4 | 4 | 11 | 3 | |
| | Negative | 13 | 0 | 2 | 5 | |
| | Both* | 3 | 0 | 0 | 0 | |

*, a species in a study exhibited both a positive and negative response to temperature or rainfall (for different temporal/parameter measures).

Appendix II

Supporting material for Chapter 3

Supplementary material

Table S1 Lists of bird species that were: (1) common to 1998, 2009 and 2013 programs; (2) common to 1998 and 2009; (3) 1998 and 2013; (4) 2009 & 2013; (5) recorded only in 1998; (6) 2009 only; (7) 2013 only. Differences in occurrence between Gunbower Island (GB) and Barmah (B) are indicated in superscript. Scientific names are given in Table S2.

| | |
|--|--|
| (1) Common to all periods | Australian magpie, Australian raven, brown treecreeper, buff-rumped thornbill, common bronzewing ^{*not at B in 2009} , crested shrike-tit ^{*not at B in 2009} , dusky woodswallow, eastern rosella, galah, golden whistler, grey fantail, grey shrike-thrush, jacky winter, laughing kookaburra, noisy friarbird, red-capped robin, red-rumped parrot, rufous whistler, sacred kingfisher, scarlet robin, striated pardalote, striated thornbill, sulphur-crested cockatoo, superb fairy-wren, varied sitella, white-plumed honeyeater, white-throated treecreeper, white-winged chough, willie wagtail, yellow rosella, yellow-rumped thornbill ^{*not at GB in 2009} |
| (2) Common to drought only (1998 & 2009) | Black-faced cuckoo-shrike, little raven ^{*1998: GB only, 2009: B only} , long-billed corella ^{*B only} , pied currawong ^{*GB only} , superb parrot ^{*B only} , white-breasted woodswallow |
| (3) Common to | Brown-headed honeyeater, little friarbird, restless |

| | |
|-------------------|---|
| early drought and | flycatcher ^{*GB only} , spotted pardalote, white-browed |
| Big Wet (1998 & | babbler ^{*1998: B only} |
| 2013) | |
| (4) Common to | Emu ^{*GB only} , leaden flycatcher ^{*2009: B only, 2013: GB only} , masked |
| late drought and | woodswallow ^{*GB only} , rose robin |
| Big Wet (2009 & | |
| 2013) | |
| (5) Early drought | Black-chinned honeyeater, chestnut-rumped thornbill ^{*GB only} , |
| (1998) only | fan-tailed cuckoo, flame robin ^{*B only} , magpie lark ^{*B only} , |
| | mistletoebird, painted button-quail, peaceful dove, rainbow |
| | bee-eater ^{*B only} , rufous songlark ^{*B only} tree martin ^{*GB only} , |
| | weebill, welcome swallow, western gerygone, yellow |
| | thornbill |
| (6) Late drought | Black-faced woodswallow ^{*GB only} , pallid cuckoo, white- |
| only (2009) | browed scrubwren ^{*GB only} |
| (7) Big Wet only | Silvereye, diamond firetail |
| (2013) | |

Table S2 Changes in reporting rates (log-odds transformed) for all species observed in the 1998, 2009 or 2013 survey programs for the period 1998-2009 (Big Dry), 2009-2013 (post-Big Wet) and 1998-2009 (overall), and with forest stand condition. Mean and standard deviation (SD) of posterior distribution of parameter estimates are presented; coefficients in bold have a posterior probability of >90%, considered as strong evidence for an effect. Species are arranged by order (bold, all caps) and family (bold). Taxonomy follows Christidis and Boles (2008).

| Species | 1998-2009 trend | | 2009-2013 trend | | 1998-2013 trend | | Stand-condition effect | |
|------------------------|-----------------|-------|-----------------|-------|-----------------|-------|------------------------|------|
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| CASUARIFORMES | | | | | | | | |
| Casuariidae | | | | | | | | |
| Emu | 5.94 | 12.20 | 0.23 | 1.23 | 6.17 | 12.23 | 0.45 | 0.50 |
| CHARADRIIFORMES | | | | | | | | |
| Turnicidae | | | | | | | | |
| Painted button-quail | -24.94 | 14.86 | -4.62 | 27.31 | -29.56 | 32.59 | 1.14 | 0.54 |
| COLUMBIFORMES | | | | | | | | |
| Columbidae | | | | | | | | |
| Common bronzewing | -2.75 | 1.25 | 0.90 | 1.42 | -1.85 | 1.24 | -0.20 | 0.29 |
| Peaceful dove | -24.28 | 14.29 | -5.78 | 27.51 | -30.07 | 33.46 | -0.32 | 0.47 |
| CORACIIFORMES | | | | | | | | |
| Halcyonidae | | | | | | | | |
| Laughing kookaburra | -0.28 | 0.65 | 0.50 | 0.66 | 0.21 | 0.73 | 0.32 | 0.23 |
| Sacred kingfisher | -1.38 | 0.53 | -0.40 | 0.81 | -1.78 | 0.81 | 0.19 | 0.19 |
| Meropidae | | | | | | | | |

| | | | | | | | | | |
|--------------------------|-----------------------------------|--------|-------|--------|-------|--------|-------|-------|------|
| Golden whistler | <i>Pachycephala pectoralis</i> | -1.15 | 0.79 | -0.53 | 1.12 | -1.68 | 1.17 | -0.14 | 0.22 |
| Grey shrike-thrush | <i>Colluricincla harmonica</i> | -2.03 | 0.36 | -1.98 | 1.04 | -4.01 | 1.04 | 0.16 | 0.13 |
| Rufous whistler | <i>Pachycephala rufiventris</i> | -0.72 | 0.46 | 0.75 | 0.43 | 0.03 | 0.48 | -0.04 | 0.12 |
| Pardalotidae | | | | | | | | | |
| Spotted pardalote | <i>Pardalotus punctatus</i> | -8.05 | 8.17 | 5.20 | 8.21 | -2.85 | 1.15 | -0.08 | 0.28 |
| Striated pardalote | <i>Pardalotus striatus</i> | -3.69 | 0.38 | 1.00 | 0.36 | -2.69 | 0.38 | -0.20 | 0.09 |
| Petroicidae | | | | | | | | | |
| Flame robin | <i>Petroica phoenicea</i> | -33.87 | 19.14 | -19.32 | 34.04 | -53.18 | 45.33 | 0.96 | 0.84 |
| Jacky winter | <i>Microeca fascians</i> | -1.86 | 0.35 | -0.10 | 0.40 | -1.96 | 0.44 | -0.35 | 0.09 |
| Red-capped robin | <i>Petroica goodenovii</i> | 0.19 | 0.45 | -1.36 | 0.62 | -1.17 | 0.71 | -0.11 | 0.11 |
| Rose robin | <i>Petroica rosea</i> | 6.14 | 12.02 | 0.21 | 1.24 | 6.35 | 12.05 | 0.66 | 0.54 |
| Scarlet robin | <i>Petroica multicolor</i> | -0.16 | 0.69 | -0.23 | 0.83 | -0.39 | 0.91 | 0.26 | 0.24 |
| Pomatostomidae | | | | | | | | | |
| White-browed babbler | <i>Pomatostomus superciliosus</i> | -4.58 | 8.96 | 6.19 | 8.92 | 1.61 | 1.38 | 0.68 | 0.54 |
| Rhipiduridae | | | | | | | | | |
| Grey fantail | <i>Rhipidura fuliginosa</i> | -0.78 | 0.43 | 0.98 | 0.43 | 0.20 | 0.45 | 0.34 | 0.15 |
| Willie wagtail | <i>Rhipidura leucophrys</i> | -1.45 | 0.40 | -0.71 | 0.65 | -2.16 | 0.65 | 0.15 | 0.14 |
| Timiliidae | | | | | | | | | |
| Silvereye | <i>Zosterops lateralis</i> | 6.95 | 29.04 | 24.31 | 15.06 | 31.26 | 35.72 | -0.43 | 0.26 |
| PSITTACIFORMES | | | | | | | | | |
| Cacatuidae | | | | | | | | | |
| Galah | <i>Cacatua roseicapilla</i> | -0.79 | 0.36 | -1.06 | 0.55 | -1.85 | 0.59 | -0.08 | 0.10 |
| Long-billed corella | <i>Cacatua tenuirostris</i> | 0.43 | 1.37 | -5.10 | 12.80 | -4.67 | 12.85 | 0.22 | 0.48 |
| Sulphur-crested cockatoo | <i>Cacatua galerita</i> | -1.05 | 0.35 | 0.40 | 0.39 | -0.65 | 0.41 | 0.23 | 0.12 |
| Psittacidae | | | | | | | | | |
| Eastern rosella | <i>Platyercus eximius</i> | 0.01 | 0.57 | -0.34 | 0.59 | -0.33 | 0.70 | -0.06 | 0.14 |
| Red-rumped parrot | <i>Psephotus haematonotus</i> | -1.26 | 0.44 | -0.12 | 0.50 | -1.39 | 0.55 | -0.27 | 0.10 |
| Superb parrot | <i>Polytelis swainsonii</i> | 0.94 | 1.38 | -5.09 | 12.84 | -4.15 | 12.88 | 0.70 | 0.60 |
| Yellow rosella | <i>Platyercus elegans</i> | -1.10 | 0.31 | -0.56 | 0.42 | -1.67 | 0.44 | 0.04 | 0.10 |

Table S3 Parameter estimates for the effects of (a) species traits on species trends during (1) the Big Dry, (2) post-Big Wet and (3) entire period and the (b) phylogenetic heritability of trends. Posterior distributions for fixed effects were approximately Gaussian, so mean parameter estimate is presented, with 95% credible interval (95% CI) and posterior probability (P. Pr.). The posterior distribution of phylogenetic heritability was non-Gaussian, so the posterior mode and 95% credible interval is presented.

| | (1) 1998-2009 | | | (2) 2009-2013 | | | (3) 1998-2013 | | |
|---------------------------|----------------|-------------|--------|----------------|--------------|--------|----------------|--------------|--------|
| | Mean | 95% CI | P. Pr. | Mean | 95% CI | P. Pr. | Mean | 95% CI | P. Pr. |
| (a) Fixed effects | | | | | | | | | |
| Intercept | -0.29 | -2.73 2.04 | 0.85 | -0.17 | -4.89 4.48 | 0.92 | -0.41 | -5.57 3.81 | 0.88 |
| Mobility (scaled) | 0.07 | -0.36 0.49 | 0.75 | -0.68 | -1.42 0.13 | 0.08 | -0.73 | -1.41 0.06 | 0.07 |
| Fecundity (scaled) | 0.13 | -0.51 0.85 | 0.69 | 0.65 | -0.46 1.77 | 0.22 | 0.83 | -0.29 2.2 | 0.19 |
| Body mass (scaled) | 0.39 | -0.82 1.49 | 0.5 | -0.32 | -2.51 1.36 | 0.76 | 0.03 | -2.06 2.26 | 0.98 |
| Diet: | | | | | | | | | |
| Frugivorous | -0.46 | -3.77 2.65 | 0.78 | -2.21 | -7.86 4.14 | 0.47 | -3.43 | -9.56 2.2 | 0.25 |
| Granivorous | -0.92 | -3.77 1.73 | 0.51 | -0.31 | -5.32 5.35 | 0.93 | -1.78 | -7.35 3.24 | 0.49 |
| Herbivorous | 2.57 | -22.3 27.35 | 0.82 | -2.64 | -37.77 25.68 | 0.85 | 0.29 | -30.93 33.27 | 0.98 |
| Insectivorous | -0.81 | -3.06 1.85 | 0.54 | -0.77 | -5.55 3.3 | 0.75 | -1.9 | -6.47 3.22 | 0.43 |
| Nectarivorous | -2.41 | -5.38 0.83 | 0.12 | 1.01 | -4.25 6.61 | 0.71 | -1.57 | -6.68 5.12 | 0.57 |
| (b) Random effects | | | | | | | | | |
| Phylogeny | Posterior mode | 95% CI | 0.0031 | Posterior mode | 95% CI | 0.0039 | Posterior mode | 95% CI | 0.0005 |
| | 0.0031 | 0.00023 | 0.52 | 0.0039 | 0.00013 | 0.89 | 0.00089 | 0.00005 | 0.65 |

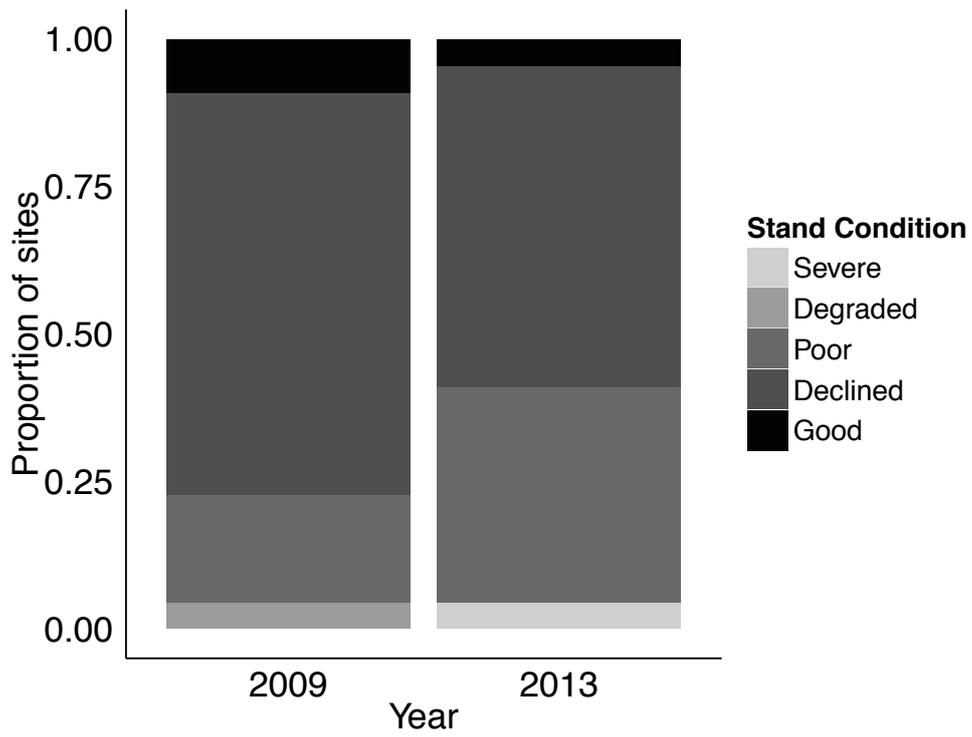


Figure S1 Proportion of sites at Gunbower Island with forest stands in severe, degraded, poor, declined or good condition in 2009 and 2013.

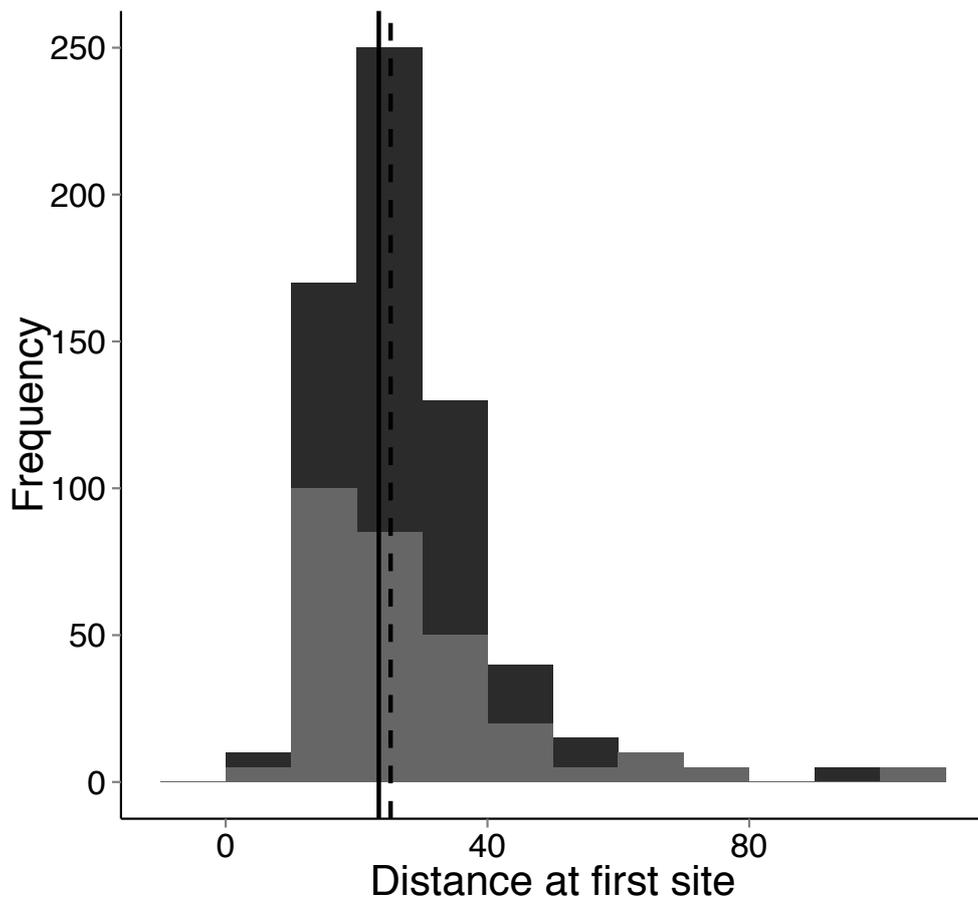


Figure S2. Histogram of detection distances at first site for individual bird observations in 2009 (dark grey, solid line is mean) and 2013 (light grey, dashed line is mean). The mean detection distance in both periods was 23.9 m. First-detection distances were not recorded in the 1998 survey program.

Appendix III

Supporting material for Chapter 4

| | | | | | |
|---------------------------|----------------------------------|---------------|---------------|-----------------|-----------------|
| Black kite | <i>Milvus migrans</i> | -0.026 | -0.020 | 0.370 + | 0.101 |
| Black-shouldered kite | <i>Elanus axillaris</i> | -0.049 | -0.033 | 0.523 + | 0.444 + |
| Blue bonnet | <i>Northiella haematogaster</i> | 0.026 | 0.107 | 0.067 | -0.244 |
| Blue-faced honeyeater | <i>Entomyzon cyanotis</i> | 0.043 | 0.020 | 0.093 | -0.014 |
| Brown quail | <i>Coturnix ypsilophora</i> | 0.071 | -0.004 | 0.243 + | 0.309 |
| Brown falcon | <i>Falco berigora</i> | -0.017 | -0.034 | 0.014 | 0.362 + |
| Brown goshawk | <i>Accipiter fasciatus</i> | -0.012 | -0.025 | 0.082 | 0.055 |
| Brown-headed honeyeater | <i>Melithreptus brevirostris</i> | -0.016 | -0.021 | 0.139 + | 0.040 |
| Brown honeyeater | <i>Lichmera indistincta</i> | 0.004 | -0.094 | 0.001 | -0.050 |
| Brown songlark | <i>Cinchoramphus cruralis</i> | <u>0.036</u> | -0.159 | -0.315 - | -0.021 |
| Brown thornbill | <i>Acanthiza pusilla</i> | -0.030 | 0.095 | -0.047 | -0.380 - |
| Brown treecreeper | <i>Climacteris picumnus</i> | -0.011 | 0.000 | -0.014 | -0.226 - |
| Budgerigar | <i>Melopsittacus undulatus</i> | -0.100 | 0.031 | 0.288 + | 0.149 |
| Buff-rumped thornbill | <i>Acanthiza reguloides</i> | -0.035 | <u>0.054</u> | 0.053 + | 0.110 |
| Chestnut-crowned babbler | <i>Pomatostomus ruficeps</i> | -0.009 | -0.032 | 0.022 | 0.305 + |
| Chestnut-rumped thornbill | <i>Acanthiza uropygialis</i> | <u>0.024</u> | -0.025 | -0.088 | <u>0.145</u> |
| Cockatiel | <i>Nymphicus hollandicus</i> | -0.075 | <u>0.016</u> | 0.031 | -0.124 |
| Collared sparrowhawk | <i>Accipiter cirrhocephalus</i> | -0.022 | 0.001 | 0.232 + | 0.133 |
| Common bronzewing | <i>Phaps chalcoptera</i> | -0.013 | -0.053 | 0.069 | -0.021 |
| Crested bellbird | <i>Oreoica gutturalis</i> | 0.033 | 0.070 | 0.158 | -0.008 |
| Crested pigeon | <i>Ocyphaps lophotes</i> | -0.057 | 0.053 | 0.047 | 0.141 |
| Crested shrike-tit | <i>Falcunculus frontatus</i> | -0.027 | -0.094 | -0.126 - | -0.198 |
| Crimson chat | <i>Epthianura tricolor</i> | 0.019 | <u>0.159</u> | -0.417 - | -0.995 |
| Crimson rosella | <i>Platyercus elegans</i> | -0.033 | <u>0.003</u> | 0.347 + | 0.062 |
| Diamond dove | <i>Geopelia cuneata</i> | -0.006 | -0.074 | -0.083 | 0.118 |
| Diamond firetail | <i>Stagonopleura guttata</i> | <u>-0.006</u> | -0.177 | 0.020 | -0.059 |
| Dollarbird | <i>Eurystomus orientalis</i> | -0.041 | -0.164 | 0.015 | -0.995 |

| | | | | | |
|---------------------------|----------------------------------|---------------|---------------|-----------------|-----------------|
| Double-barred finch | <i>Taeniopygia bichenovii</i> | -0.043 | -0.237 | 0.223 + | 1.484 + |
| Dusky woodswallow | <i>Artamus cyanopterus</i> | <u>-0.017</u> | -0.091 | -0.054 | <u>0.103</u> |
| Eastern rosella | <i>Platycercus eximius</i> | 0.002 | 0.031 | 0.148 | -0.114 |
| Eastern yellow robin | <i>Eopsaltria australis</i> | -0.031 | 0.050 | 0.023 | -0.495 |
| Emu | <i>Dromaius novaehollandiae</i> | <u>-0.038</u> | -0.093 | 0.203 + | 0.274 + |
| Fairy martin | <i>Hirundo ariel</i> | 0.011 | -0.019 | 0.041 | 0.204 + |
| Fan-tailed cuckoo | <i>Cacomantis flabelliformis</i> | <u>-0.019</u> | -0.134 | 0.018 | -0.996 |
| Flame robin | <i>Petroica phoenicea</i> | -0.006 | -0.101 | 0.114 | -0.128 |
| Galah | <i>Cacatua roseicapilla</i> | 0.000 | 0.022 | 0.058 | -0.090 |
| Gilbert's whistler | <i>Pachycephala inornata</i> | -0.053 | -0.036 | -0.127 | -0.385 |
| Golden-headed cisticola | <i>Cisticola exilis</i> | -0.142 | <u>0.036</u> | 0.225 + | -0.160 |
| Golden whistler | <i>Pachycephala pectoralis</i> | -0.059 | 0.090 | 0.170 + | -0.220 - |
| Grey butcherbird | <i>Cracticus torquatus</i> | -0.003 | <u>0.053</u> | 0.140 + | 0.298 + |
| Grey-crowned babbler | <i>Pomatostomus temporalis</i> | 0.027 | 0.064 | 0.004 | 0.051 |
| Grey currawong | <i>Strepera versicolor</i> | -0.056 | 0.222 | 0.017 | -0.563 - |
| Grey fantail | <i>Rhipidura fuliginosa</i> | -0.039 | -0.025 | 0.202 + | 0.121 |
| Grey shrike-thrush | <i>Colluricincla harmonica</i> | -0.040 | <u>0.010</u> | 0.135 + | -0.030 |
| Hooded robin | <i>Melanodryas cucullata</i> | -0.023 | -0.002 | -0.068 | 0.131 |
| Horsfield's bronze-cuckoo | <i>Chrysococcyx basalis</i> | -0.011 | -0.058 | -0.062 | -0.064 |
| Jacky winter | <i>Microeca fascians</i> | -0.019 | 0.129 | 0.031 | -0.028 |
| Laughing kookaburra | <i>Dacelo novaeguineae</i> | -0.021 | -0.044 | 0.088 + | 0.089 + |
| Little corella | <i>Cacatua sanguinea</i> | 0.088 | 0.073 | 0.108 | -0.043 |
| Little crow | <i>Corvus bennetti</i> | 0.009 | 0.090 | -0.227 - | -0.236 |
| Little eagle | <i>Hieraaetus morphnoides</i> | -0.070 | -0.094 | 0.147 + | 0.132 |
| Little friarbird | <i>Philemon citreogularis</i> | -0.017 | -0.074 | 0.065 | 0.034 |
| Little grassbird | <i>Megalurus gramineus</i> | -0.070 | -0.026 | 0.356 - | 0.123 |
| Little raven | <i>Corvus mellori</i> | 0.034 | 0.034 | 0.236 - | 0.018 |

| | | | | | |
|---------------------------|---------------------------------|---------------|---------------|-----------------|-----------------|
| Long-billed corella | <i>Cacatua tenuirostris</i> | 0.075 | 0.026 | 0.192 - | 0.297 |
| Magpie-lark | <i>Grallina cyanoleuca</i> | -0.009 | <u>0.030</u> | 0.229 | 0.075 |
| Major Mitchell's cockatoo | <i>Cacatua leadbeateri</i> | -0.027 | -0.019 | 0.087 | -0.279 |
| Masked woodswallow | <i>Artamus personatus</i> | 0.032 | <u>0.123</u> | 0.047 | -0.102 |
| Mistletoebird | <i>Dicaeum hirundinaceum</i> | <u>-0.033</u> | <u>-0.117</u> | -0.085 | 0.016 |
| Mulga parrot | <i>Psephotus varius</i> | -0.080 | 0.030 | 0.116 + | -0.333 |
| Musk lorikeet | <i>Glossopsitta concinna</i> | 0.011 | 0.040 | 0.093 | 0.049 |
| Nankeen kestrel | <i>Falco cenchroides</i> | -0.032 | -0.057 | 0.157 + | 0.297 + |
| | <i>Phylidonyris</i> | | | | |
| New holland honeyeater | <i>novaeollandiae</i> | 0.037 | 0.245 | 0.343 + | -0.183 - |
| Noisy friarbird | <i>Philemon corniculatus</i> | -0.017 | -0.027 | 0.099 | -0.173 |
| Olive-backed oriole | <i>Oriolus sagittatus</i> | -0.012 | -0.057 | -0.017 | -0.168 |
| Pale headed rosella | <i>Platyercus adscitus</i> | 0.034 | 0.202 | 0.177 | -0.334 |
| Pallid cuckoo | <i>Cuculus pallidus</i> | -0.003 | -0.067 | -0.305 - | 0.122 |
| Peaceful dove | <i>Geopelia placida</i> | 0.013 | -0.011 | 0.090 | 0.038 |
| Peregrine falcon | <i>Falco peregrinus</i> | -0.042 | -0.001 | 0.033 | -0.154 |
| Pied butcherbird | <i>Cracticus nigrogularis</i> | 0.019 | 0.071 | 0.079 | -0.057 |
| Pied currawong | <i>Strepera graculina</i> | 0.020 | <u>0.252</u> | 0.046 | -0.271 - |
| | <i>Glossopsitta</i> | | | | |
| Purple-crowned lorikeet | <i>porphyrocephala</i> | -0.003 | <u>0.087</u> | 0.023 | -0.189 |
| Rainbow bee-eater | <i>Merops ornatus</i> | -0.053 | -0.098 | 0.008 | -0.061 |
| Rainbow lorikeet | <i>Trichoglossus haematodus</i> | 0.047 | 0.048 | 0.819 + | 1.403 + |
| Red-browed finch | <i>Neochmia temporalis</i> | -0.058 | <u>0.074</u> | 0.268 + | -0.290 - |
| Red-capped robin | <i>Petroica goodenovii</i> | 0.044 | -0.061 | -0.057 | 0.098 |
| Red-rumped parrot | <i>Psephotus haematonotus</i> | 0.012 | 0.017 | 0.028 | -0.098 |
| Red-tailed black-cockatoo | <i>Calyptorhynchus banksii</i> | 0.163 | 0.147 | -0.047 | 0.265 |
| Red wattlebird | <i>Anthochaera carunculata</i> | -0.016 | <u>0.127</u> | 0.279 + | 0.013 |

| | | | | | |
|--------------------------|----------------------------------|---------------|---------------|-----------------|-----------------|
| Red-winged parrot | <i>Aprosmictus erythropterus</i> | -0.009 | -0.051 | 0.145 + | 0.617 + |
| Regent parrot | <i>Polytelis anthopeplus</i> | -0.073 | <u>0.082</u> | 0.109 | -0.260 |
| Restless flycatcher | <i>Myiagra inquieta</i> | -0.038 | <u>0.021</u> | 0.079 + | 0.025 |
| Rufous songlark | <i>Cinchoramphus mathewsi</i> | <u>0.038</u> | -0.035 | 0.070 | 0.074 |
| Rufous whistler | <i>Pachycephala rufiventris</i> | <u>-0.031</u> | -0.097 | 0.022 | 0.137 + |
| Sacred kingfisher | <i>Todiramphus sanctus</i> | -0.041 | -0.081 | 0.091 | -0.070 |
| Scarlet robin | <i>Petroica multicolor</i> | -0.043 | -0.177 | 0.167 + | 0.389 + |
| Silvereye | <i>Zosterops lateralis</i> | -0.037 | -0.013 | 0.242 + | 0.050 |
| Singing honeyeater | <i>Lichenostomus virescens</i> | 0.016 | 0.019 | 0.102 | -0.181 |
| Southern whiteface | <i>Aphelocephala leucopsis</i> | 0.025 | 0.011 | -0.153 - | -0.126 |
| Spiny-cheeked honeyeater | <i>Acanthagenys rufogularis</i> | -0.025 | 0.038 | 0.045 | 0.063 |
| Splendid fairy-wren | <i>Malurus splendens</i> | -0.016 | -0.041 | 0.175 + | -0.555 |
| Spotted bowerbird | <i>Ptilonorhynchus maculatus</i> | -0.014 | -0.035 | 0.181 + | -0.013 |
| Spotted pardalote | <i>Pardalotus punctatus</i> | -0.045 | -0.010 | 0.096 | 0.303 + |
| Striated pardalote | <i>Pardalotus striatus</i> | -0.034 | -0.045 | 0.225 + | 0.138 |
| Striated thornbill | <i>Acanthiza lineata</i> | -0.059 | -0.032 | -0.004 | 0.136 |
| Striped honeyeater | <i>Plectorhyncha lanceolata</i> | -0.042 | 0.047 | 0.249 + | 0.532 + |
| Stubble quail | <i>Coturnix pectoralis</i> | -0.034 | -0.170 | 0.167 | -0.994 |
| Sulphur-crested cockatoo | <i>Cacatua galerita</i> | 0.039 | 0.022 | 0.045 | -0.203 - |
| Superb fairy-wren | <i>Malurus cyaneus</i> | -0.013 | -0.033 | 0.211 + | 0.153 + |
| Superb parrot | <i>Polytelis swainsonii</i> | -0.037 | -0.163 | -0.025 | -0.989 |
| Swamp harrier | <i>Circus approximans</i> | -0.013 | -0.082 | 0.201 + | 0.328 + |
| Torresian crow | <i>Corvus orru</i> | 0.008 | 0.300 | -0.080 | -0.340 - |
| Tree martin | <i>Hirundo nigricans</i> | -0.017 | -0.015 | 0.066 + | 0.173 + |
| Varied sittella | <i>Daphoenositta chrysoptera</i> | -0.015 | 0.006 | -0.066 | -0.064 |
| Variiegated fairy-wren | <i>Malurus lamberti</i> | -0.042 | -0.004 | 0.117 + | -0.113 |
| Wedge-tailed eagle | <i>Aquila audax</i> | 0.010 | -0.040 | -0.111 - | -0.082 |

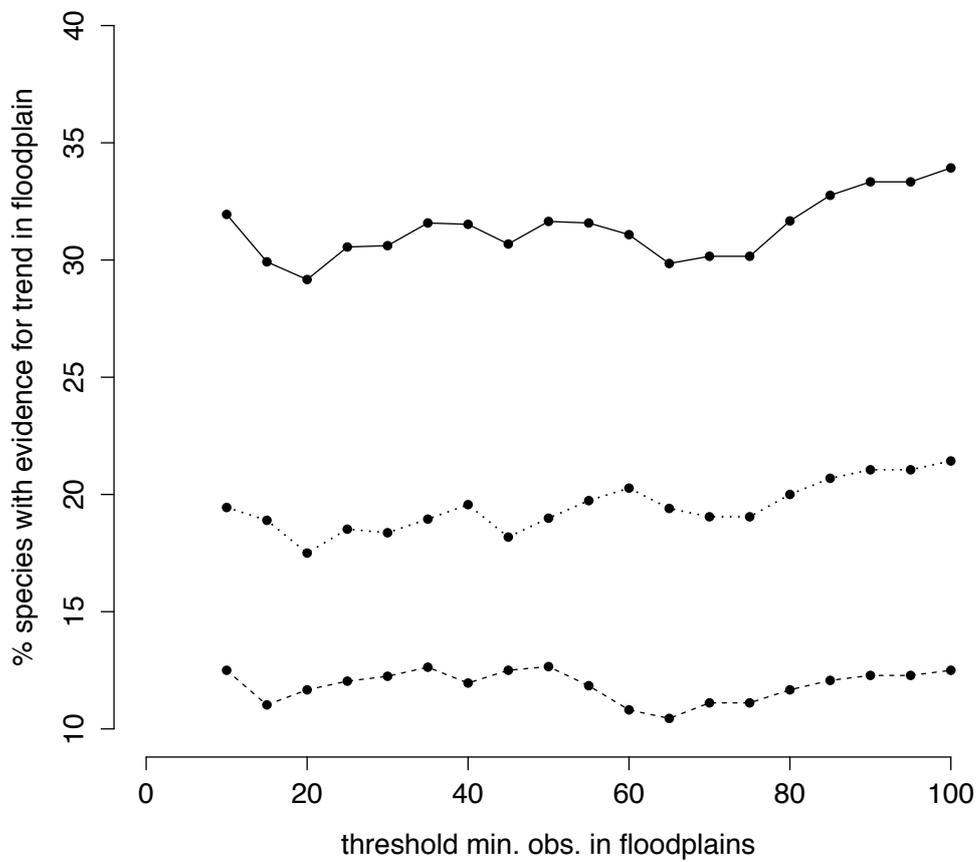
| | | | | | |
|-----------------------------|-----------------------------------|---------------|---------------|-----------------|-----------------|
| Weebill | <i>Smicrornis brevirostris</i> | 0.030 | 0.021 | 0.054 | 0.083 |
| Welcome swallow | <i>Hirundo neoxena</i> | -0.010 | -0.006 | 0.167 + | 0.055 |
| Western gerygone | <i>Gerygone fusca</i> | -0.004 | -0.118 | 0.002 | 0.060 |
| Whistling kite | <i>Haliastur sphenurus</i> | 0.036 | 0.019 | 0.333 + | 0.303 + |
| White-backed swallow | <i>Cheramoeca leucosternus</i> | <u>0.000</u> | -0.165 | -0.053 | 0.398 |
| White-bellied cuckoo-shrike | <i>Coracina papuensis</i> | -0.021 | 0.077 | 0.127 + | 0.018 |
| White-bellied sea eagle | <i>Haliaeetus leucogaster</i> | 0.096 | -0.119 | 0.069 | 0.953 + |
| White-breasted woodswallow | <i>Artamus leucorhynchus</i> | -0.008 | 0.034 | 0.089 | 0.140 |
| White-browed babbler | <i>Pomatostomus superciliosus</i> | -0.034 | -0.069 | 0.001 | 0.383 + |
| White-browed scrubwren | <i>Sericornis frontalis</i> | -0.022 | 0.148 | 0.232 | -0.249 - |
| White-browed woodswallow | <i>Artamus superciliosus</i> | <u>-0.011</u> | -0.082 | 0.118 | 0.213 |
| White-fronted chat | <i>Epthianura albifrons</i> | <u>0.029</u> | -0.036 | -0.189 - | <u>0.264</u> |
| White-fronted honeyeater | <i>Phylidonyris albifrons</i> | -0.010 | 0.360 | -0.116 | -0.687 - |
| White-naped honeyeater | <i>Melithreptus lunatus</i> | -0.051 | 0.144 | -0.005 | -0.365 |
| White-plumed honeyeater | <i>Lichenostomus penicillatus</i> | -0.025 | -0.064 | 0.226 + | 0.143 + |
| White-throated gerygone | <i>Gerygone olivacea</i> | 0.010 | 0.097 | -0.225 - | -0.997 |
| White-throated treecreeper | <i>Cormobates leucophaeus</i> | -0.018 | -0.012 | 0.008 | -0.090 |
| White-winged chough | <i>Corcorax melanorhamphos</i> | 0.010 | -0.002 | -0.013 | -0.196 - |
| White-winged fairy wren | <i>Malarus leucopterus</i> | -0.013 | 0.018 | 0.189 | 0.033 |
| White-winged triller | <i>Lalage tricolor</i> | 0.002 | -0.052 | -0.037 | -0.220 |
| Willie wagtail | <i>Rhipidura leucophrys</i> | -0.017 | -0.034 | 0.179 + | 0.088 |
| Yellow-faced honeyeater | <i>Lichenostomus chrysops</i> | -0.010 | 0.084 | 0.069 | -0.570 - |
| Yellow-plumed honeyeater | <i>Lichenostomus ornatus</i> | -0.179 | -0.111 | -0.055 | 0.190 |
| Yellow-rumped thornbill | <i>Acanthiza chrysorrhoa</i> | <u>-0.012</u> | -0.051 | 0.109 + | 0.173 + |
| Yellow thornbill | <i>Acanthiza nana</i> | -0.049 | -0.104 | 0.096 + | 0.165 + |

| | | | | | | | |
|-----------------------|----------------------------|--------|---------------|---------------|---|--------------|---|
| Yellow-throated miner | <i>Manorina flavigula</i> | -0.030 | -0.070 | 0.153 | + | 0.312 | + |
| Zebra finch | <i>Taeniopygia guttata</i> | -0.009 | 0.013 | -0.187 | | -0.016 | |

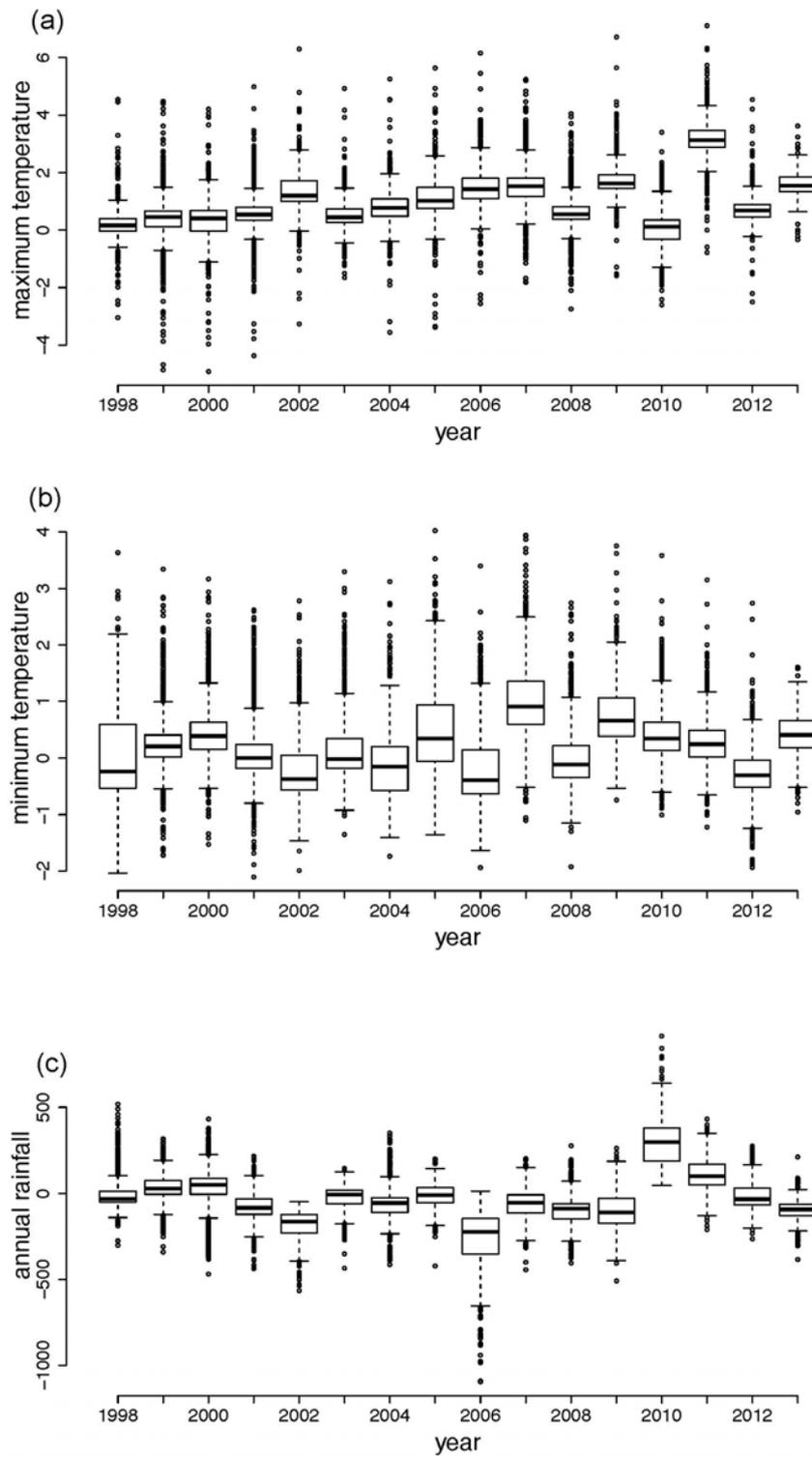
* Christidis, L. & Boles, W. (2008). Systematics and taxonomy of Australian birds. CSIRO Publishing, Collingwood, Victoria.

Appendix S2. Percentages of variation explained by species ecological traits during the Big Dry and after the Big Dry broke for non-floodplain (NFP) and floodplain (FP) zones, and difference in species trends in non-floodplain vs floodplain zones during the Big Dry and after the Big Dry broke.

| | Big Dry | | Post-Big Dry | | Trend differences | |
|----------------------|---------|-------|--------------|-------|-------------------|--------|
| | NFP | FP | NFP | FP | Big | Post- |
| | | | | | Dry | Big |
| | | | | | Dry | |
| Habitat | 2.76% | 2.64% | 0.49% | 0.01% | <0.01% | <0.01% |
| Woodland category | 2.58% | 2.56% | 0.82% | 0.01% | 0.01% | <0.01% |
| Nesting | 3.44% | 3.54% | 0.50% | 0.01% | 0.01% | <0.01% |
| Foraging substrate | 4.25% | 4.29% | 0.48% | 0.01% | 0.02% | <0.01% |
| Food | 2.38% | 2.39% | 1.51% | 0.01% | <0.01% | <0.01% |
| Conservation concern | 3.25% | 3.06% | 0.49% | 0.01% | <0.02% | <0.01% |



Appendix S3. Proportion of species showing strong evidence of a temporal trend in floodplains during Big Dry compared to the threshold for minimum number of observations. Solid line is proportion showing either positive or negative trend ($\Pr(B > 0)$ or $\Pr(B < 0) > 0.9$), dashed line is proportion showing positive trends ($\Pr(B > 0) > 0.9$), and dotted line is proportion showing negative trends ($\Pr(B < 0) > 0.9$).



Appendix S4. Boxplots of site-specific deviations in mean maximum temperature, mean minimum temperature and total annual rainfall per year of study

Appendix IV

Supporting material for Chapter 5

Appendix S1

Selwood, K.E., Clarke, R.H., McGeoch, M.A., & R. Mac Nally.

Green tongues into the arid zone: River floodplains extend the distribution of terrestrial bird species

Table S1 Effect of aridity on the probability of species occurrence in non-floodplain zones (coefficient B_1 from species occurrence model outlined in main text), difference in effect of aridity on species occurrence in floodplain zones (coefficient B_2) and effect of aridity on species occurrence in floodplain zones (coefficient B_{fr}). Mean and standard deviation (SD) of posterior distribution of parameter estimates are presented (log odds); coefficients in bold have a posterior probability of >90%, considered as strong evidence for an effect. Species are arranged by the effect of aridity on their occurrence in non-floodplain zones: (A) negative effect of aridity ($\Pr(B_1 < 0) > 0.9$), (B) positive effect of aridity ($\Pr(B_1 > 0) > 0.9$), and (C) no strong evidence for an effect of aridity on species occurrence ($\Pr(B_1 > 0) \& \Pr(B_1 < 0) < 0.9$).

| Common name | Scientific name | Aridity (Non-floodplain zone, B_1) | | Difference (B_2) | | Aridity (Floodplain B_{fr}) | |
|--|----------------------------|---------------------------------------|------|----------------------|------|--------------------------------|------|
| | | Mean | SD | Mean | SD | Mean | SD |
| (A) Negative effect of aridity | | | | | | | |
| <i>Effect of aridity moderated in floodplain vegetation</i> | | | | | | | |
| Scarlet robin | <i>Petroica multicolor</i> | -2.86 | 1.10 | 2.70 | 1.16 | -0.16 | 0.38 |

| | | | | | | | |
|--|---------------------------------|-------|------|------|------|-------|------|
| Spotted bowerbird | <i>Chlamydera maculata</i> | -1.35 | 0.73 | 1.66 | 0.86 | 0.31 | 0.50 |
| Chestnut-rumped thornbill | <i>Acanthiza uropygialis</i> | -1.40 | 0.24 | 1.09 | 0.18 | -0.31 | 0.24 |
| Inland thornbill | <i>Acanthiza apicalis</i> | -0.82 | 0.51 | 1.05 | 0.70 | 0.23 | 0.59 |
| Yellow thornbill | <i>Acanthiza nana</i> | -1.10 | 0.20 | 0.90 | 0.18 | -0.20 | 0.19 |
| Red-capped robin | <i>Petroica goodenovii</i> | -0.83 | 0.23 | 0.85 | 0.17 | 0.01 | 0.21 |
| | <i>Pomatostomus</i> | | | | | | |
| White-browed babbler | <i>superciliosus</i> | -0.96 | 0.45 | 0.83 | 0.26 | -0.14 | 0.47 |
| Spiny-cheeked honeyeater | <i>Acanthagenys rufogularis</i> | -0.43 | 0.24 | 0.56 | 0.19 | 0.13 | 0.24 |
| Silvereye | <i>Zosterops lateralis</i> | -0.41 | 0.25 | 0.46 | 0.23 | 0.05 | 0.23 |
| Apostlebird | <i>Struthidea cinerea</i> | -0.59 | 0.30 | 0.45 | 0.21 | -0.14 | 0.31 |
| Little raven | <i>Corvus mellori</i> | -0.27 | 0.10 | 0.19 | 0.14 | -0.08 | 0.11 |
| Australian raven | <i>Corvus coronoides</i> | -0.21 | 0.11 | 0.15 | 0.08 | -0.06 | 0.10 |
| Dusky woodswallow | <i>Artamus cyanopterus</i> | -1.29 | 0.25 | 0.50 | 0.18 | -0.80 | 0.23 |
| Rufous whistler | <i>Pachycephala rufiventris</i> | -1.14 | 0.17 | 0.47 | 0.13 | -0.66 | 0.15 |
| Little friarbird | <i>Philemon citreogularis</i> | -0.70 | 0.16 | 0.41 | 0.15 | -0.28 | 0.13 |
| Striped honeyeater | <i>Plectorhyncha lanceolata</i> | -0.94 | 0.29 | 0.37 | 0.21 | -0.58 | 0.28 |
| Yellow-rumped thornbill | <i>Acanthiza chrysorrhoa</i> | -0.52 | 0.13 | 0.33 | 0.13 | -0.19 | 0.13 |
| Grey butcherbird | <i>Cracticus torquatus</i> | -1.11 | 0.20 | 0.31 | 0.15 | -0.80 | 0.19 |
| Black-faced cuckoo-shrike | <i>Coracina novaehollandiae</i> | -0.37 | 0.11 | 0.18 | 0.11 | -0.18 | 0.09 |
| Laughing kookaburra | <i>Dacelo novaeguineae</i> | -0.86 | 0.14 | 0.16 | 0.10 | -0.70 | 0.12 |
| Grey shrike-thrush | <i>Colluricincla harmonica</i> | -0.70 | 0.17 | 0.12 | 0.09 | -0.58 | 0.16 |
| Australian magpie | <i>Gymnorhina tibicen</i> | -0.28 | 0.11 | 0.12 | 0.08 | -0.16 | 0.10 |
| No difference in effect of aridity in floodplain zone | | | | | | | |
| Dollarbird | <i>Eurystomus orientalis</i> | -2.06 | 0.51 | 0.69 | 0.56 | -1.37 | 0.32 |
| Flame robin | <i>Petroica phoenicea</i> | -1.09 | 0.56 | 0.38 | 0.65 | -0.71 | 0.39 |
| Double-barred finch | <i>Taeniopygia bichenovii</i> | -1.65 | 0.85 | 0.35 | 0.95 | -1.30 | 0.79 |
| Musk lorikeet | <i>Glossopsitta concinna</i> | -1.13 | 0.37 | 0.26 | 0.45 | -0.87 | 0.39 |

| | | | | | | | |
|--|----------------------------------|-------|------|-------|------|-------|------|
| Red-browed finch | <i>Neochmia temporalis</i> | -1.48 | 0.49 | 0.26 | 0.54 | -1.23 | 0.34 |
| Restless flycatcher | <i>Myiagra inquieta</i> | -0.61 | 0.26 | 0.21 | 0.18 | -0.41 | 0.24 |
| Western gerygone | <i>Gerygone fusca</i> | -1.44 | 0.22 | 0.20 | 0.26 | -1.24 | 0.17 |
| Common bronzewing | <i>Phaps chalcoptera</i> | -0.77 | 0.31 | 0.12 | 0.17 | -0.65 | 0.30 |
| Grey fantail | <i>Rhipidura fuliginosa</i> | -1.30 | 0.19 | 0.11 | 0.15 | -1.20 | 0.17 |
| Golden whistler | <i>Pachycephala pectoralis</i> | -1.34 | 0.31 | 0.10 | 0.35 | -1.24 | 0.19 |
| Red wattlebird | <i>Anthochaera carunculata</i> | -1.71 | 0.21 | 0.10 | 0.14 | -1.61 | 0.19 |
| Galah | <i>Cacatua roseicapilla</i> | -0.52 | 0.11 | 0.07 | 0.09 | -0.45 | 0.10 |
| Sacred kingfisher | <i>Todiramphus sanctus</i> | -0.44 | 0.15 | 0.06 | 0.14 | -0.38 | 0.12 |
| Eastern yellow robin | <i>Eopsaltria australis</i> | -2.61 | 0.66 | 0.06 | 0.64 | -2.56 | 0.49 |
| Rainbow bee-eater | <i>Merops ornatus</i> | -0.37 | 0.25 | 0.00 | 0.17 | -0.37 | 0.22 |
| White-winged chough | <i>Corcorax melanorhamphos</i> | -0.82 | 0.17 | -0.02 | 0.12 | -0.84 | 0.15 |
| Striated pardalote | <i>Pardalotus striatus</i> | -0.31 | 0.10 | -0.04 | 0.09 | -0.36 | 0.09 |
| Rufous songlark | <i>Cincloramphus mathewsi</i> | -0.53 | 0.22 | -0.09 | 0.19 | -0.61 | 0.20 |
| Brown-headed honeyeater | <i>Melithreptus brevirostris</i> | -1.05 | 0.43 | -0.11 | 0.28 | -1.17 | 0.38 |
| Little lorikeet | <i>Glossopsitta pusilla</i> | -3.16 | 0.92 | -0.27 | 1.03 | -3.43 | 0.59 |
| Pale headed rosella | <i>Platycercus adscitus</i> | -1.44 | 1.03 | -0.27 | 1.16 | -1.72 | 0.57 |
| Yellow-faced honeyeater | <i>Lichenostomus chrysops</i> | -3.49 | 0.93 | -0.29 | 1.15 | -3.78 | 0.70 |
| Diamond firetail | <i>Stagonopleura guttata</i> | -0.96 | 0.60 | -0.32 | 0.59 | -1.27 | 0.52 |
| White-throated treecreeper | <i>Cormobates leucophaeus</i> | -0.70 | 0.32 | -0.39 | 0.31 | -1.09 | 0.23 |
| Crested shrike-tit | <i>Falcunculus frontatus</i> | -0.58 | 0.35 | -0.40 | 0.32 | -0.98 | 0.27 |
| Pied currawong | <i>Strepera graculina</i> | -1.22 | 0.40 | -0.46 | 0.40 | -1.68 | 0.32 |
| Brown thornbill | <i>Acanthiza pusilla</i> | -2.14 | 0.51 | -0.69 | 0.58 | -2.84 | 0.37 |
| Effect of aridity is more negative in floodplain vegetation | | | | | | | |
| Crimson rosella | <i>Platycercus elegans</i> | -0.73 | 0.15 | -0.16 | 0.11 | -0.90 | 0.14 |
| Weebill | <i>Smicrorornis brevirostris</i> | -0.84 | 0.17 | -0.22 | 0.11 | -1.06 | 0.15 |
| Mistletoebird | <i>Dicaeum hirundinaceum</i> | -0.50 | 0.22 | -0.24 | 0.17 | -0.74 | 0.18 |

| | | | | | | | |
|---|--------------------------------|-------|------|-------|------|-------|------|
| Eastern rosella | <i>Platyercus eximius</i> | -0.99 | 0.18 | -0.26 | 0.19 | -1.25 | 0.17 |
| Sulphur-crested cockatoo | <i>Cacatua galerita</i> | -1.66 | 0.17 | -0.44 | 0.14 | -2.10 | |
| Spotted pardalote | <i>Pardalotus punctatus</i> | -1.47 | 0.26 | -0.51 | 0.18 | -1.98 | |
| Noisy friarbird | <i>Philemon corniculatus</i> | -0.71 | 0.34 | -0.74 | 0.32 | -1.45 | |
| Olive-backed oriole | <i>Oriolus sagittatus</i> | -1.38 | 0.36 | -0.77 | 0.46 | -2.15 | |
| Superb parrot | <i>Polytelis swainsonii</i> | -1.36 | 0.77 | -1.31 | 0.83 | -2.67 | |
| (B) Positive effect of aridity | | | | | | | |
| <i>Effect of aridity is more positive in floodplain zone</i> | | | | | | | |
| Chestnut-crowned babbler | <i>Pomatostomus ruficeps</i> | 1.76 | 0.26 | 1.38 | 0.55 | 3.14 | 0.49 |
| Southern whiteface | <i>Aphelocephala leucopsis</i> | 0.54 | 0.23 | 0.33 | 0.24 | 0.87 | 0.25 |
| <i>Effect of aridity is weaker in floodplain zone</i> | | | | | | | |
| Gilbert's whistler | <i>Pachycephala inornata</i> | 3.10 | 1.22 | -2.52 | 1.28 | 0.57 | 0.40 |
| Black-chinned honeyeater | <i>Melithreptus gularis</i> | 1.82 | 1.12 | -2.83 | 1.15 | -1.00 | 0.40 |
| Australian reed warbler | <i>Acrocephalus australis</i> | 1.33 | 0.25 | -0.58 | 0.17 | 0.75 | 0.22 |
| Pallid cuckoo | <i>Cuculus pallidus</i> | 1.01 | 0.29 | -0.74 | 0.36 | 0.27 | 0.22 |
| Tree martin | <i>Hirundo nigricans</i> | 0.61 | 0.14 | -0.17 | 0.12 | 0.43 | 0.13 |
| <i>No strong evidence for difference in effect of aridity in floodplain zone</i> | | | | | | | |
| Splendid fairy-wren | <i>Malurus splendens</i> | 1.88 | 0.90 | 0.72 | 0.85 | 2.60 | 0.94 |
| Red-tailed black-cockatoo | <i>Calyptorhynchus banksii</i> | 1.63 | 0.52 | -0.03 | 0.49 | 1.59 | 0.45 |
| White-fronted chat | <i>Ephianura albifrons</i> | 1.55 | 0.39 | -0.34 | 0.35 | 1.21 | 0.43 |
| Regent parrot | <i>Polytelis anthopeplus</i> | 1.54 | 0.69 | 0.14 | 1.04 | 1.68 | 1.11 |
| Grey currawong | <i>Strepera versicolor</i> | 1.25 | 0.44 | 0.04 | 0.69 | 1.29 | 0.53 |
| Azure kingfisher | <i>Alcedo azurea</i> | 1.23 | 0.46 | -0.07 | 0.61 | 1.16 | 0.44 |
| Little crow | <i>Corvus bennetti</i> | 1.13 | 0.34 | 0.48 | 0.46 | 1.61 | 0.45 |
| Major Mitchell's cockatoo | <i>Cacatua leadbeateri</i> | 1.09 | 0.49 | -0.46 | 0.60 | 0.63 | 0.35 |
| Little grassbird | <i>Megalurus gramineus</i> | 1.08 | 0.23 | -0.18 | 0.25 | 0.89 | 0.24 |
| White-backed swallow | <i>Cheramoeca leucosternus</i> | 0.92 | 0.36 | 0.08 | 0.53 | 1.00 | 0.40 |

| | | | | | | | |
|---|----------------------------------|-------------|------|--------------|------|--------------|------|
| Diamond dove | <i>Geopelia cuneata</i> | 0.85 | 0.39 | 0.33 | 0.48 | 1.18 | 0.33 |
| White-winged fairy-wren | <i>Malurus leucopterus</i> | 0.82 | 0.25 | -0.18 | 0.24 | 0.64 | 0.27 |
| Singing honeyeater | <i>Lichenostomus virescens</i> | 0.79 | 0.30 | 0.03 | 0.27 | 0.83 | 0.32 |
| Zebra finch | <i>Taeniopygia guttata</i> | 0.79 | 0.30 | 0.24 | 0.24 | 1.03 | 0.30 |
| Emu | <i>Dromaius novaehollandiae</i> | 0.78 | 0.25 | -0.04 | 0.24 | 0.75 | 0.24 |
| Long-billed corella | <i>Cacatua tenuirostris</i> | 0.59 | 0.32 | 0.05 | 0.36 | 0.65 | 0.29 |
| Brown songlark | <i>Cinctoramphus cruralis</i> | 0.54 | 0.31 | -0.02 | 0.48 | 0.53 | 0.47 |
| Hooded robin | <i>Melanodryas cucullata</i> | 0.54 | 0.28 | -0.20 | 0.38 | 0.34 | 0.29 |
| Welcome swallow | <i>Hirundo neoxena</i> | 0.51 | 0.12 | -0.07 | 0.09 | 0.45 | 0.11 |
| Horsfield's bronze-cuckoo | <i>Chrysococcyx basalis</i> | 0.46 | 0.18 | 0.04 | 0.24 | 0.50 | 0.15 |
| Brown treecreeper | <i>Climacteris picumnus</i> | 0.39 | 0.13 | -0.03 | 0.09 | 0.36 | 0.11 |
| Blue bonnet | <i>Northiella haematogaster</i> | 0.34 | 0.20 | -0.21 | 0.17 | 0.14 | 0.20 |
| (C) No strong association with aridity | | | | | | | |
| Shining bronze-cuckoo | <i>Chrysococcyx lucidus</i> | -0.87 | 1.03 | 0.13 | 1.16 | -0.75 | 0.57 |
| Torresian crow | <i>Corvus orru</i> | -0.87 | 1.07 | -0.25 | 1.39 | -1.12 | 0.92 |
| Bar-shouldered dove | <i>Geopelia humeralis</i> | -0.83 | 0.94 | -0.88 | 0.86 | -1.71 | 0.96 |
| Buff-rumped thornbill | <i>Acanthiza reguloides</i> | -0.77 | 0.74 | 0.51 | 0.75 | -0.26 | 0.37 |
| White-browed scrubwren | <i>Sericornis frontalis</i> | -0.65 | 0.54 | -0.89 | 0.56 | -1.54 | 0.39 |
| Red-winged parrot | <i>Aprosmictus erythropterus</i> | -0.56 | 0.50 | 0.95 | 0.56 | 0.39 | 0.33 |
| Painted button-quail | <i>Turnix varia</i> | -0.53 | 0.75 | -0.08 | 1.02 | -0.61 | 0.74 |
| Striated thornbill | <i>Acanthiza lineata</i> | -0.52 | 0.61 | 0.33 | 0.66 | -0.19 | 0.29 |
| Cockatiel | <i>Nymphicus hollandicus</i> | -0.31 | 0.31 | -0.40 | 0.22 | -0.72 | 0.31 |
| White-bellied cuckoo-shrike | <i>Coracina paptensis</i> | -0.31 | 0.70 | -0.90 | 0.76 | -1.20 | 0.54 |
| White-throated gerygone | <i>Gerygone olivacea</i> | -0.31 | 1.06 | -1.34 | 1.15 | -1.65 | 0.55 |
| White-browed woodswallow | <i>Artamus superciliosus</i> | -0.17 | 0.22 | 0.31 | 0.24 | 0.13 | 0.20 |
| Little corella | <i>Cacatua sanguinea</i> | -0.17 | 0.29 | 0.07 | 0.20 | -0.10 | 0.29 |

| | | | | | | | |
|----------------------------|-----------------------------------|-------|------|--------------|------|--------------|------|
| White-plumed honeyeater | <i>Lichenostomus penicillatus</i> | -0.13 | 0.13 | 0.17 | 0.08 | 0.04 | 0.13 |
| Brown quail | <i>Coturnix ypsilophora</i> | -0.13 | 0.40 | -0.25 | 0.49 | -0.38 | 0.42 |
| Grey-crowned babbler | <i>Pomatostomus temporalis</i> | -0.12 | 0.28 | 0.26 | 0.34 | 0.14 | 0.28 |
| White-winged triller | <i>Lalage tricolor</i> | -0.11 | 0.28 | 0.23 | 0.29 | 0.12 | 0.23 |
| Magpie-lark | <i>Grallina cyanoleuca</i> | -0.10 | 0.10 | 0.18 | 0.10 | 0.09 | 0.11 |
| Varied sittella | <i>Daphoenositta chrysoptera</i> | -0.03 | 0.46 | -1.06 | 0.76 | -1.09 | 0.69 |
| Willie wagtail | <i>Rhipidura leucophrys</i> | 0.02 | 0.16 | 0.26 | 0.08 | 0.27 | 0.16 |
| Pied butcherbird | <i>Cracticus nigrogularis</i> | 0.03 | 0.14 | 0.32 | 0.11 | 0.35 | 0.14 |
| Masked woodswallow | <i>Artamus personatus</i> | 0.04 | 0.31 | 0.19 | 0.35 | 0.24 | 0.27 |
| Jacky winter | <i>Microeca fascians</i> | 0.05 | 0.23 | 0.06 | 0.22 | 0.10 | 0.19 |
| Red-rumped parrot | <i>Psephotus haematonotus</i> | 0.05 | 0.11 | 0.31 | 0.09 | 0.36 | 0.10 |
| Crested pigeon | <i>Ocyphaps lophotes</i> | 0.08 | 0.10 | 0.33 | 0.08 | 0.41 | 0.10 |
| Fan-tailed cuckoo | <i>Cacomantis flabelliformis</i> | 0.08 | 0.91 | -0.34 | 0.97 | -0.25 | 0.41 |
| Yellow-throated miner | <i>Manorina flavigula</i> | 0.09 | 0.28 | -0.24 | 0.14 | -0.15 | 0.28 |
| Superb fairy-wren | <i>Malurus cyaneus</i> | 0.10 | 0.13 | -0.27 | 0.16 | -0.17 | 0.17 |
| Mulga parrot | <i>Psephotus varius</i> | 0.14 | 0.29 | 0.32 | 0.43 | 0.46 | 0.32 |
| | <i>Glossopsitta</i> | | | | | | |
| Purple-crowned lorikeet | <i>porphyrocephala</i> | 0.17 | 0.63 | 0.00 | 0.38 | 0.16 | 0.55 |
| Variegated fairy-wren | <i>Malurus lamberti</i> | 0.18 | 0.26 | -0.02 | 0.19 | 0.15 | 0.23 |
| Plum-headed finch | <i>Neochmia modesta</i> | 0.20 | 1.74 | -1.75 | 1.92 | -1.55 | 0.87 |
| Peaceful dove | <i>Geopelia placida</i> | 0.22 | 0.18 | -0.04 | 0.12 | 0.18 | 0.16 |
| White-breasted woodswallow | <i>Artamus leucorhynchus</i> | 0.23 | 0.22 | -0.54 | 0.24 | -0.32 | 0.21 |
| Australasian pipit | <i>Anthus novaeseelandiae</i> | 0.24 | 0.26 | 0.78 | 0.36 | 1.02 | 0.37 |
| Blue-faced honeyeater | <i>Entomyzon cyanotis</i> | 0.26 | 0.33 | -0.26 | 0.23 | 0.00 | 0.31 |
| Black-faced woodswallow | <i>Artamus cinereus</i> | 0.27 | 0.31 | -0.27 | 0.40 | 0.00 | 0.38 |
| Fairy martin | <i>Hirundo ariel</i> | 0.35 | 0.28 | -0.23 | 0.17 | 0.12 | 0.27 |

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|--------------------------|--------------------------------|------|------|--------------|------|--------------|------|
| Crested bellbird | <i>Oreoica gutturalis</i> | 0.39 | 0.38 | -0.54 | 0.52 | -0.15 | 0.46 |
| Budgerigar | <i>Melopsittacus undulatus</i> | 0.40 | 0.33 | 0.33 | 0.43 | 0.72 | 0.28 |
| White-fronted honeyeater | <i>Phylidonyris albifrons</i> | 0.41 | 0.45 | 1.50 | 0.64 | 1.91 | 0.45 |
| Leaden flycatcher | <i>Myiagra rubecula</i> | 0.91 | 1.94 | -3.45 | 2.01 | -2.54 | 0.69 |

Appendix V

Supporting material for Chapter 6

Supplementary information

Table S1: Drought-sensitive species trends in the Murray-Darling during the Big Dry

Figure S1: Histogram of species weights (w_i) for all species used to calculate the drought resistance index. The weight w_i for species i as: $w_i = \frac{(|t_i| - \min(|t_S|))}{(\text{range}(|t_S|))}$, where: t_i is a species' overall trend during the Big Dry and S is the list of drought-declining species from Table S1.

Figure S2 Histogram of drought resistance index values for the set of study sites.

Figure S3 Plot of mean DRI values (black) and 95% bootstrapped confidence intervals (grey) for sites with: (a) mean positive values of DRI; and with (b) mean negative values of DRI.

Table S1 Regional temporal trends in occurrence (t_s) for terrestrial bird species Murray-Darling Basin over the Big Dry for species with negative trends from Selwood *et al.* (2015b). Trends in bold are those with $\Pr(t_s < 0) > 0.9$. Regional trends (t_s) were used for species' weightings to calculate the Drought Resistance Index ('Weight'). Mean, minimum, maximum and standard deviations of site-specific species trends from the current study are presented, based on the subset of sites at which each species was present.

| Common name | Scientific name | Regional | | Weight | Mean | | Min. | | Max. | | St. dev. | | No. sites present |
|---------------------------|---------------------------------|-----------------|-------|--------|--------|-------|-------|------|------|------|----------|--|-------------------|
| | | trend (t_s) | site | | site | site | site | site | site | site | | | |
| Australasian pipit | <i>Anthus novaeseelandiae</i> | -0.044 | 0.233 | -0.011 | -0.285 | 0.095 | 0.062 | 43 | | | | | |
| Australian raven | <i>Corvus coronoides</i> | -0.012 | 0.051 | -0.008 | -0.252 | 0.226 | 0.068 | 382 | | | | | |
| Australian reed warbler | <i>Acrocephalus australis</i> | -0.013 | 0.057 | -0.016 | -0.244 | 0.153 | 0.093 | 39 | | | | | |
| Australian ringneck | <i>Barnardius zonarius</i> | -0.025 | 0.125 | -0.004 | -0.222 | 0.189 | 0.052 | 135 | | | | | |
| Black-chinned honeyeater | <i>Melthreptus gularis</i> | -0.070 | 0.381 | 0.021 | -0.154 | 0.342 | 0.078 | 78 | | | | | |
| Black-faced cuckoo-shrike | <i>Coracina novaehollandiae</i> | -0.041 | 0.216 | -0.013 | -0.415 | 0.231 | 0.067 | 413 | | | | | |
| Brown thornbill | <i>Acanthiza pusilla</i> | -0.030 | 0.153 | 0.004 | -0.429 | 0.333 | 0.088 | 164 | | | | | |
| Brown treecreeper | <i>Climacteris picumnus</i> | -0.011 | 0.045 | -0.010 | -0.316 | 0.194 | 0.071 | 204 | | | | | |
| Brown-headed honeyeater | <i>Melthreptus brevirostris</i> | -0.016 | 0.074 | 0.003 | -0.404 | 0.269 | 0.066 | 244 | | | | | |
| Budgerigar | <i>Melopsittacus undulatus</i> | -0.100 | 0.551 | 0.008 | -0.028 | 0.244 | 0.052 | 30 | | | | | |
| Buff-rumped thornbill | <i>Acanthiza reguloides</i> | -0.035 | 0.182 | -0.010 | -0.250 | 0.264 | 0.061 | 165 | | | | | |
| Chestnut-crowned babbler | <i>Pomatostomus ruficeps</i> | -0.009 | 0.034 | 0.010 | -0.179 | 0.219 | 0.057 | 79 | | | | | |
| Cockatiel | <i>Nymphicus hollandicus</i> | -0.075 | 0.409 | -0.003 | -0.171 | 0.195 | 0.064 | 84 | | | | | |
| Common bronzewing | <i>Phaps chalcoptera</i> | -0.013 | 0.057 | 0.007 | -0.392 | 0.248 | 0.068 | 264 | | | | | |
| Crested pigeon | <i>Ocyphaps lophotes</i> | -0.057 | 0.307 | 0.010 | -0.333 | 0.268 | 0.084 | 270 | | | | | |
| Crested shrike-tit | <i>Falcunculus frontatus</i> | -0.027 | 0.136 | 0.001 | -0.269 | 0.281 | 0.065 | 114 | | | | | |

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|---------------------------|----------------------------------|---------------|-------|--------|--------|-------|-------|-----|
| Crimson rosella | <i>Platycercus elegans</i> | -0.033 | 0.170 | -0.002 | -0.310 | 0.333 | 0.085 | 236 |
| Diamond dove | <i>Geopelia cuneata</i> | -0.006 | 0.017 | 0.013 | -0.043 | 0.098 | 0.042 | 12 |
| Diamond firetail | <i>Stagonopleura guttata</i> | -0.006 | 0.017 | 0.001 | -0.135 | 0.241 | 0.051 | 78 |
| Dollarbird | <i>Eurystomus orientalis</i> | -0.041 | 0.216 | -0.003 | -0.140 | 0.125 | 0.049 | 72 |
| Double-barred finch | <i>Taeniopygia bichenovii</i> | -0.043 | 0.227 | 0.000 | -0.242 | 0.182 | 0.063 | 47 |
| Dusky woodswallow | <i>Artamus cyanopterus</i> | -0.017 | 0.080 | -0.008 | -0.308 | 0.338 | 0.064 | 207 |
| Eastern yellow robin | <i>Eopsaltria australis</i> | -0.031 | 0.159 | -0.011 | -0.237 | 0.351 | 0.087 | 132 |
| Emu | <i>Dromaius novaehollandiae</i> | -0.038 | 0.199 | -0.005 | -0.132 | 0.123 | 0.033 | 50 |
| Fan-tailed cuckoo | <i>Cacomantis flabelliformis</i> | -0.019 | 0.091 | -0.001 | -0.167 | 0.190 | 0.052 | 82 |
| Flame robin | <i>Petroica phoenicea</i> | -0.006 | 0.017 | 0.017 | -0.154 | 0.262 | 0.066 | 65 |
| Gilbert's whistler | <i>Pachycephala inornata</i> | -0.053 | 0.284 | -0.005 | -0.162 | 0.114 | 0.045 | 83 |
| Golden whistler | <i>Pachycephala pectoralis</i> | -0.059 | 0.318 | 0.008 | -0.212 | 0.262 | 0.061 | 229 |
| Golden-headed cisticola | <i>Cisticola exilis</i> | -0.142 | 0.790 | -0.008 | -0.150 | 0.116 | 0.070 | 12 |
| Grey butcherbird | <i>Cracticus torquatus</i> | -0.003 | 0.000 | 0.000 | -0.235 | 0.262 | 0.060 | 254 |
| Grey currawong | <i>Strepera versicolor</i> | -0.056 | 0.301 | -0.001 | -0.187 | 0.225 | 0.053 | 177 |
| Grey fantail | <i>Rhipidura fuliginosa</i> | -0.039 | 0.205 | -0.010 | -0.310 | 0.231 | 0.070 | 314 |
| Grey shrike-thrush | <i>Colluricincla harmonica</i> | -0.040 | 0.210 | -0.020 | -0.405 | 0.262 | 0.077 | 409 |
| Hooded robin | <i>Melanodryas cucullata</i> | -0.023 | 0.114 | -0.002 | -0.263 | 0.146 | 0.048 | 109 |
| Horsfield's bronze-cuckoo | <i>Chrysococcyx basalis</i> | -0.011 | 0.045 | -0.012 | -0.337 | 0.181 | 0.059 | 139 |
| Jacky winter | <i>Microeca fascians</i> | -0.019 | 0.091 | -0.005 | -0.280 | 0.225 | 0.062 | 210 |
| Laughing kookaburra | <i>Dacelo novaeguineae</i> | -0.021 | 0.102 | -0.008 | -0.386 | 0.214 | 0.066 | 302 |
| Little friarbird | <i>Philemon citreogularis</i> | -0.017 | 0.080 | -0.019 | -0.266 | 0.159 | 0.060 | 121 |
| Little grassbird | <i>Megalurus gramineus</i> | -0.070 | 0.381 | 0.011 | -0.151 | 0.272 | 0.087 | 18 |
| Magpie-lark | <i>Grallina cyanoleuca</i> | -0.009 | 0.034 | -0.004 | -0.278 | 0.268 | 0.082 | 279 |
| Major Mitchell's cockatoo | <i>Cacatua leadbeateri</i> | -0.027 | 0.136 | 0.005 | -0.037 | 0.123 | 0.046 | 10 |
| Mistletoebird | <i>Dicaeum hirundinaceum</i> | -0.033 | 0.170 | -0.018 | -0.374 | 0.177 | 0.066 | 181 |
| Mulga parrot | <i>Psephotus varius</i> | -0.080 | 0.438 | -0.004 | -0.073 | 0.114 | 0.029 | 85 |

| | | | | | | | | |
|--------------------------|-------------------------------------|---------------|-------|--------|--------|-------|-------|-----|
| Noisy friarbird | <i>Philemon corniculatus</i> | -0.017 | 0.080 | -0.015 | -0.292 | 0.262 | 0.065 | 174 |
| Olive-backed oriole | <i>Oriolus sagittatus</i> | -0.012 | 0.051 | -0.011 | -0.311 | 0.085 | 0.066 | 104 |
| Pallid cuckoo | <i>Cuculus pallidus</i> | -0.003 | 0.000 | -0.018 | -0.162 | 0.185 | 0.052 | 91 |
| Purple-crowned lorikeet | <i>Glossopsitta porphyrocephala</i> | -0.003 | 0.000 | -0.008 | -0.289 | 0.152 | 0.057 | 119 |
| Rainbow bee-eater | <i>Merops ornatus</i> | -0.053 | 0.284 | -0.002 | -0.274 | 0.148 | 0.045 | 213 |
| Red wattletbird | <i>Anthochaera carunculata</i> | -0.016 | 0.074 | 0.003 | -0.230 | 0.333 | 0.082 | 357 |
| Red-browed finch | <i>Neochmia temporalis</i> | -0.058 | 0.313 | 0.005 | -0.144 | 0.340 | 0.076 | 88 |
| Red-winged parrot | <i>Aprosmictus erythropterus</i> | -0.009 | 0.034 | -0.009 | -0.131 | 0.037 | 0.045 | 14 |
| Regent parrot | <i>Polytelis anthopeplus</i> | -0.073 | 0.398 | -0.003 | -0.081 | 0.078 | 0.038 | 29 |
| Restless flycatcher | <i>Myiagra inquieta</i> | -0.038 | 0.199 | -0.008 | -0.211 | 0.251 | 0.056 | 196 |
| Rufous whistler | <i>Pachycephala rufiventris</i> | -0.031 | 0.159 | -0.024 | -0.337 | 0.214 | 0.079 | 329 |
| Sacred kingfisher | <i>Todiramphus sanctus</i> | -0.041 | 0.216 | -0.028 | -0.274 | 0.333 | 0.067 | 167 |
| Scarlet robin | <i>Petroica multicolor</i> | -0.043 | 0.227 | 0.002 | -0.167 | 0.280 | 0.071 | 92 |
| Silvereye | <i>Zosterops lateralis</i> | -0.037 | 0.193 | -0.003 | -0.277 | 0.333 | 0.067 | 162 |
| Spiny-cheeked honeyeater | <i>Acanthagenys rufogularis</i> | -0.025 | 0.125 | -0.013 | -0.268 | 0.250 | 0.057 | 178 |
| Splendid fairy-wren | <i>Malurus splendens</i> | -0.016 | 0.074 | -0.005 | -0.074 | 0.053 | 0.023 | 34 |
| Spotted bowerbird | <i>Ptilonorhynchus maculatus</i> | -0.014 | 0.063 | 0.015 | 0.003 | 0.035 | 0.014 | 4 |
| Spotted pardalote | <i>Pardalotus punctatus</i> | -0.045 | 0.239 | -0.009 | -0.381 | 0.333 | 0.080 | 353 |
| Striated pardalote | <i>Pardalotus striatus</i> | -0.034 | 0.176 | 0.006 | -0.361 | 0.311 | 0.076 | 470 |
| Striated thornbill | <i>Acanthiza lineata</i> | -0.059 | 0.318 | -0.006 | -0.429 | 0.268 | 0.083 | 147 |
| Striped honeyeater | <i>Plectorhyncha lanceolata</i> | -0.042 | 0.222 | 0.004 | -0.263 | 0.250 | 0.062 | 123 |
| Stubble quail | <i>Coturnix pectoralis</i> | -0.034 | 0.176 | -0.019 | -0.106 | 0.037 | 0.038 | 15 |
| Superb fairy-wren | <i>Malurus cyaneus</i> | -0.013 | 0.057 | -0.014 | -0.275 | 0.289 | 0.079 | 278 |
| Superb parrot | <i>Polytelis swainsonii</i> | -0.037 | 0.193 | -0.003 | -0.390 | 0.125 | 0.067 | 101 |
| Tree martin | <i>Hirundo nigricans</i> | -0.017 | 0.080 | -0.003 | -0.317 | 0.152 | 0.061 | 159 |
| Varied sittella | <i>Daphoenositta chrysoptera</i> | -0.015 | 0.068 | -0.008 | -0.157 | 0.296 | 0.050 | 141 |
| Variegated fairy-wren | <i>Malurus lamberti</i> | -0.042 | 0.222 | 0.000 | -0.260 | 0.268 | 0.066 | 83 |

| | | | | | | | | |
|-----------------------------|------------------------------------|---------------|-------|--------|--------|-------|-------|-----|
| Welcome swallow | <i>Hirundo neoxena</i> | -0.010 | 0.040 | -0.007 | -0.234 | 0.372 | 0.066 | 263 |
| Western gerygone | <i>Gerygone fusca</i> | -0.004 | 0.006 | -0.019 | -0.171 | 0.145 | 0.053 | 67 |
| White-bellied cuckoo-shrike | <i>Coracina papuensis</i> | -0.021 | 0.102 | 0.014 | -0.214 | 0.192 | 0.062 | 42 |
| White-breasted woodswallow | <i>Artamus leucorhynchus</i> | -0.008 | 0.028 | 0.014 | -0.073 | 0.344 | 0.076 | 27 |
| White-browed babbler | <i>Pomastostomus superciliosus</i> | -0.034 | 0.176 | -0.005 | -0.167 | 0.368 | 0.068 | 170 |
| White-browed scrubwren | <i>Sericornis frontalis</i> | -0.022 | 0.108 | 0.008 | -0.405 | 0.385 | 0.110 | 104 |
| White-browed woodswallow | <i>Artamus superciliosus</i> | -0.011 | 0.045 | -0.013 | -0.276 | 0.150 | 0.056 | 209 |
| White-fronted honeyeater | <i>Phylidonyris albifrons</i> | -0.010 | 0.040 | -0.006 | -0.079 | 0.373 | 0.057 | 112 |
| White-naped honeyeater | <i>Melithreptus lunatus</i> | -0.051 | 0.273 | 0.014 | -0.262 | 0.302 | 0.088 | 132 |
| White-plumed honeyeater | <i>Lichenostomus penicillatus</i> | -0.025 | 0.125 | -0.019 | -0.341 | 0.192 | 0.070 | 272 |
| White-throated treecreeper | <i>Cornobates leucophaeus</i> | -0.018 | 0.085 | 0.019 | -0.190 | 0.429 | 0.092 | 206 |
| White-winged fairy wren | <i>Malarus leucopterus</i> | -0.013 | 0.057 | 0.006 | -0.005 | 0.028 | 0.015 | 4 |
| Willie wagtail | <i>Rhipidura leucophrys</i> | -0.017 | 0.080 | -0.023 | -0.463 | 0.190 | 0.080 | 394 |
| Yellow thornbill | <i>Acanthiza nana</i> | -0.049 | 0.261 | -0.015 | -0.341 | 0.364 | 0.085 | 190 |
| Yellow-faced honeyeater | <i>Lichenostomus chrysops</i> | -0.010 | 0.040 | -0.003 | -0.352 | 0.286 | 0.078 | 204 |
| Yellow-plumed honeyeater | <i>Lichenostomus ornatus</i> | -0.179 | 1.000 | -0.032 | -0.261 | 0.053 | 0.043 | 118 |
| Yellow-rumped thornbill | <i>Acanthiza chrysorrhoa</i> | -0.012 | 0.051 | -0.005 | -0.327 | 0.387 | 0.079 | 247 |
| Yellow-throated miner | <i>Manorina flavigula</i> | -0.030 | 0.153 | -0.004 | -0.171 | 0.220 | 0.084 | 53 |
| Zebra finch | <i>Taeniopygia guttata</i> | -0.009 | 0.034 | 0.008 | -0.149 | 0.171 | 0.076 | 29 |

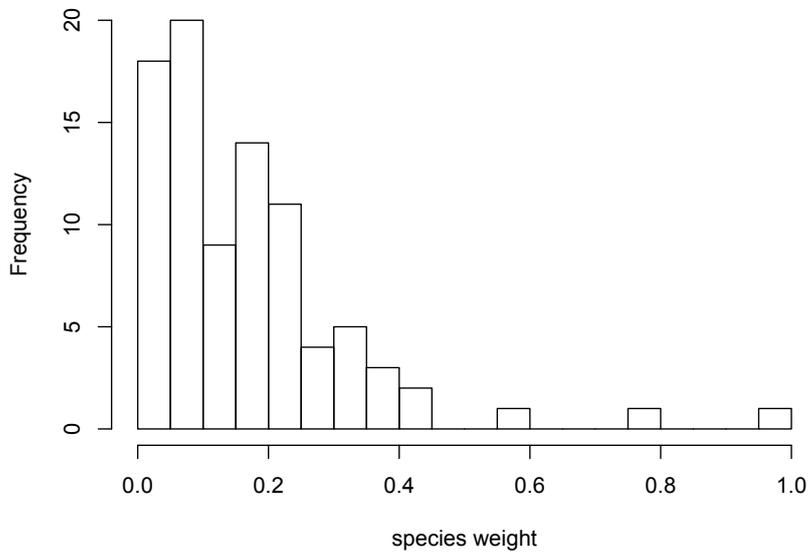


Figure S1.

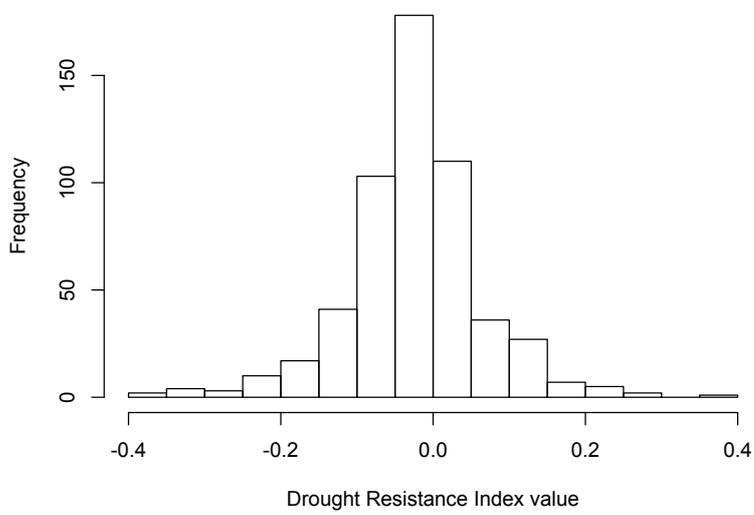


Fig. S2

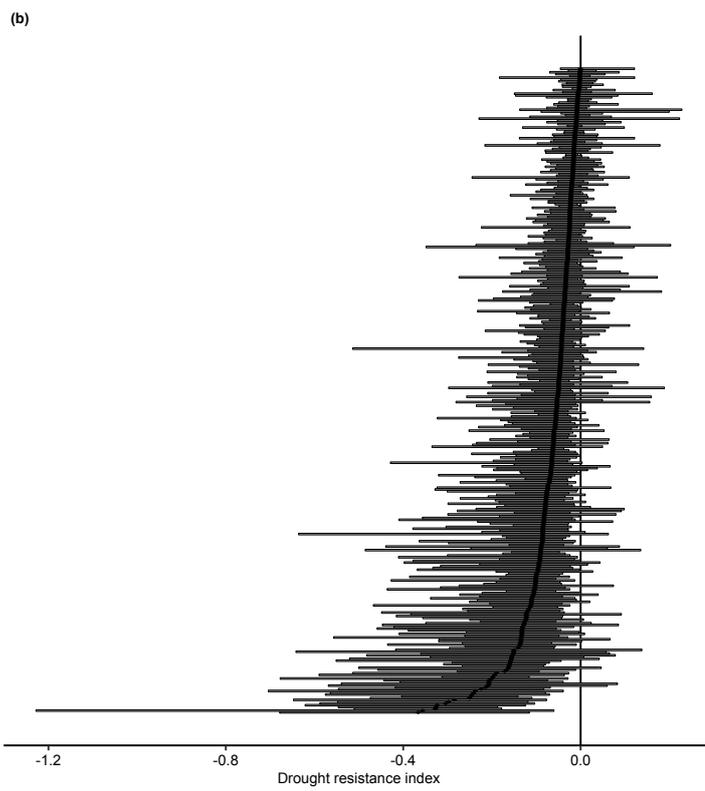
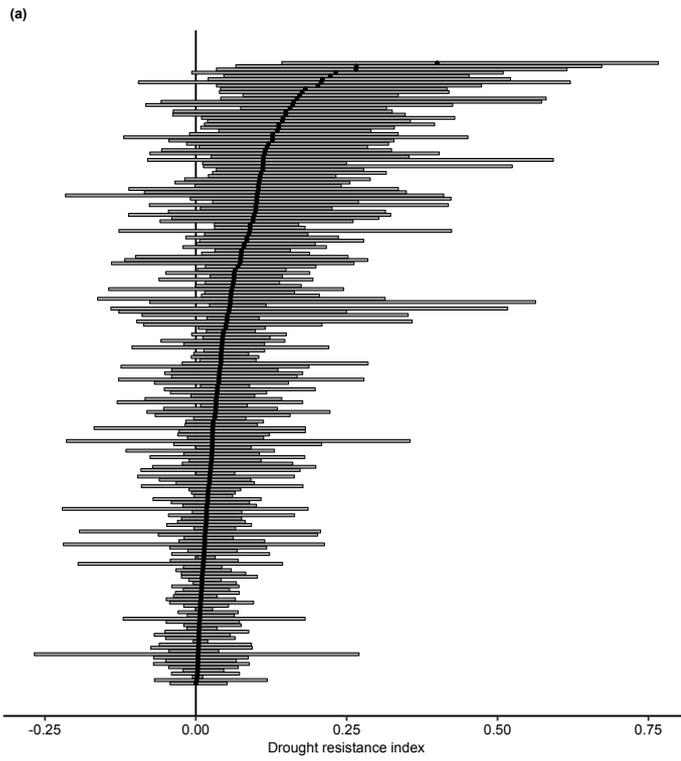


Fig. S3

References

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