



Tests of predictions associated with temporal changes in Australian bird populations

David B. Lindenmayer^{a,b,c,*}, Peter Lane^a, Martin Westgate^a, Ben C. Scheele^{a,b}, Claire Foster^a, Chloe Sato^a, Karen Ikin^a, Mason Crane^{a,c}, Damian Michael^{a,b}, Dan Florance^{a,c}, Philip Barton^a, Luke S. O'Loughlin^a, Natasha Robinson^{a,b}

^a Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia

^b Threatened Species Recovery Hub, National Environmental Science Program, Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia

^c Sustainable Farms, Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia

ARTICLE INFO

Keywords:

Woodland birds
South-eastern Australia
Time-series data
Life-history traits
Species declines and increases
Conservation

ABSTRACT

Global biodiversity loss is the cumulative result of local species declines. To combat biodiversity loss, detailed information on the temporal trends of at-risk species at local scales is needed. Here we report the results of a 13-year study of temporal change in bird occupancy in one of the most heavily modified biomes worldwide; the temperate woodlands of south-eastern Australia. We sought to determine if temporal changes in bird species were different between three broad native vegetation types (old-growth woodland, regrowth woodland and restoration plantings) and between species traits (body size, migratory status, rarity, woodland dependency, or diet). We found evidence of decline for over a quarter of all bird species for which we had sufficient data for detailed analysis (30 out of 108 species). In contrast, only 14 species increased significantly. Temporal change of birds was linked to life-history attributes, with patterns often being habitat-dependent. Nectarivores and large-bodied birds declined across all vegetation types, whereas small-bodied species increased, particularly in restoration plantings. Contrasting with patterns documented elsewhere, resident but not migratory species declined, with this trend strongest in restoration plantings. Finally, our analyses showed that, as a group, common birds tended to decline whereas rare birds tended to increase, with effects for both most pronounced in restoration plantings. Our results highlight the benefit of targeted restoration planting for some species, but also demonstrate that many common species that have long-persisted in human-dominated landscapes are experiencing severe declines.

1. Introduction

The earth is facing a major global extinction crisis with significant species losses forecast for many groups of biota (Pimm et al., 2014; Ceballos et al., 2017). For example, data from the (IUCN, 2016) suggest that 13% of the world's bird species might be facing extinction in the next 50 years (Tilman et al., 2017). Global patterns of species extinction are, of course, underpinned by local and regional trends in populations (e.g. Sanderson et al., 2006; Inger et al., 2015), and detailed temporal studies of local and regional species are essential to understand broader biodiversity changes. Such information is also critical to help better determine those species in need of conservation interventions (Muir, 2010) and, in turn, guide associated investments in appropriate land use management such as landscape restoration (Crouzeilles et al., 2016)

or expanded reservation (Pringle, 2017).

Globally, landscapes converted to agricultural land uses have suffered significant losses of biodiversity (Tilman et al., 2017), including birds. The effects of agriculture on biodiversity has been particularly profound in Australia (Williams and Price, 2011) with Australian bird biota under considerable pressure (Ford, 2011). Detailed long-term studies are required to determine which species are declining and/or are under threat in agriculture-dominated environments. Yet, there are relatively few large-scale, long-term studies within the vast majority of Australian agro-ecosystems that encompass many species (Lindenmayer et al., 2014). This shortfall inhibits examination of patterns of temporal change in Australian avifauna, thus limiting our ability to identify species declines, or conversely, examples of species recovery.

Here we report the results of a 13-year time series study of temporal

* Corresponding author at: Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia.
E-mail address: david.lindenmayer@anu.edu.au (D.B. Lindenmayer).

change in bird populations within the endangered temperate box gum grassy woodlands of south-eastern Australia. This is an agriculture-dominated biome containing one of the most heavily modified natural ecosystems globally, with > 85% cleared or altered to create grazing pastures and croplands for agriculture (Benson, 2008). Yet, it maintains high biodiversity value supporting over 170 bird species including > 20 of conservation concern (Lindenmayer et al., 2016b). There are long-held concerns about the status of Australia's woodland birds (Ford, 2011) due, in part, to substantial historical and ongoing changes to their habitat. Extensive revegetation efforts through restoration plantings (Lindenmayer et al., 2016a), as well as natural regeneration (Sato et al., 2016), have been among the management responses to past losses of woodland cover. Native vegetation cover in the Australian temperate woodland belt is now comprised of three broad structural kinds of vegetation – old-growth woodlands, naturally regenerated regrowth woodland, and restoration plantings. These kinds of vegetation are spatiotemporally dynamic, exhibit marked differences in structure (Ikin et al., 2015) and represent different kinds of habitat for distinct assemblages of birds (Lindenmayer et al., 2012a). On this basis, one of the objectives of this investigation was to compare and contrast temporal changes in bird species in these three broad structural vegetation types.

There is an increasing body of work relating patterns of landscape change to the functional traits of species (Barnagaud et al., 2014). Some of this work has revealed that taxa with particular kinds of attributes will respond more or less favourably over time to landscape change in human-modified landscapes (e.g. Newbold et al., 2013; Lindenmayer et al., 2015). We therefore tested a series of predictions about what life-history traits of species were associated with temporal changes in birds. Specifically, we tested the following five predictions:

Prediction 1. *That large-bodied species are more likely to decline than small-bodied species.* Several studies elsewhere around the world have indicated that large-bodied species are more extinction prone than small-bodied species in human-modified environments (e.g. Haddad et al., 2015; Tilman et al., 2017). However, elsewhere in Australian woodlands, large-bodied birds are more strongly associated with heavily modified and degraded agricultural landscapes (Lindenmayer et al., 2012b) with several studies in Australia suggesting that many birds of conservation concern are small-bodied taxa (Reid, 1999; Montague-Drake et al., 2009). On this basis, we tested whether the temporal patterns in birds of different body size in our long-term study were consistent with global patterns.

Prediction 2. *That migratory species are more likely to decline than resident species.* Several studies have found that migratory species are at risk of decline and extinction due to a range of factors including habitat loss (including along migration routes), climate change, and hunting (Runge et al., 2015; Gilroy et al., 2016). By testing this prediction, we sought to determine if the temporal patterns we observed were broadly consistent with those documented in other parts of the world.

Prediction 3. *That rare species are more likely to decline than common species.* Many studies of extinction proneness suggest that rare species are at particular risk of decline (reviewed by (reviewed by Lindenmayer and Fischer, 2006)) in part due to small population sizes but also because they are often habitat specialists disadvantaged by human-induced landscape change (Colles et al., 2009). However, recent work in Europe found the opposite effect with more common species undergoing declines (Inger et al., 2015). Given this, we tested whether the patterns of temporal change we observed mirrored those quantified elsewhere such as in Europe.

We also tested a further two predictions that relate specifically to Australian temperate woodlands and particular kinds of bird species in those environments.

Prediction 4. *That insectivores are more likely to decline than other dietary groups.* Widespread land clearing associated with agricultural development in the temperate woodland ecosystems of south-eastern Australia has been associated with changes in insect populations and communities (Gibb and Cunningham, 2010; Barton et al., 2016). Many

of the bird species in temperate woodland ecosystems are insectivores (Higgins, 1991–2006) and on this basis, insectivorous birds as a distinct dietary group may also be subject to greater levels of change relative to birds in other broad dietary categories (see Lindenmayer et al., 2012b). We therefore sought to determine if there were relationships between diet and temporal patterns of change in birds and test the prediction that insectivores would be more susceptible to decline than species that consume other kinds of food.

Prediction 5: *That woodland bird species are more likely to decline than open-country species.* Land-clearing removed large areas of temperate woodland vegetation leaving remnant woodland patches and “open-country” cleared paddocks and croplands which now comprise 70–85% of the land area in this region (Cunningham et al., 2014). The terrestrial bird species inhabiting our study region can be broadly classified as being woodland associated or open-country associated (i.e. not associated with woodland). Given the predominance of cleared areas in our study, we predicted a temporal decline in woodland-associated species and an increase in open-country species. Earlier work in a comparable landscape made long-term predictions of bird occurrence based on the availability of woodland versus cleared pasture environments and habitat selection for open-country and woodland habitats (Fischer et al., 2010). This study provided an opportunity to test those earlier predictions.

2. Methods

2.1. Study area

Our study region was an 18,000 km² agricultural area within the South-west Slopes region of New South Wales, south-eastern Australia (Fig. 1). The South-west Slopes region was formerly dominated by temperate native woodland, but has been cleared of an estimated 85% of its original cover to facilitate livestock grazing and cereal cropping (Benson, 2008). In response to conservation concerns, the region has been the target of major restoration planting programs (Cunningham et al., 2014). There has also been significant natural regeneration of temperate woodlands over the past 10 years in our study region (Sato et al., 2016). Thus, there are three broad structural kinds of woodland vegetation cover: actively replanted or restored woodland (termed restoration plantings), naturally regenerated woodland (termed regrowth woodland), and old-growth woodland. Our study comprised 203 sites, including 65 restoration plantings, 66 patches of regrowth woodland, and 72 patches of old-growth woodland. Importantly, different assemblages of birds are associated with these different kinds of woodland habitats (Lindenmayer et al., 2012a), and it was therefore appropriate to explore temporal trends in relation to these three broad kinds of vegetation cover.

Restoration plantings were areas of planted native vegetation characterized by a mix of local endemic and exotic ground cover, understorey and overstorey plant species. Woody plants were typically spaced 2 m apart, but there was not a standard set of spacing and plant species composition protocols applied in revegetation efforts. All restoration plantings were at least seven years old at the start of this investigation in 2002, and many were 10–20 years old. Restoration plantings were established to mitigate problems associated with soil erosion and/or salinity, and provide on-farm habitat for wildlife (Lindenmayer et al., 2016a). Regrowth woodland refers to existing living trees recovering after disturbance by fire, clearing or both; or regeneration of trees from seeds germinating after being dropped by overstorey trees. Old-growth woodland was dominated by large old scattered trees was typically 200 or more years old.

For the analyses reported here, we focused on a size range of patches of old-growth woodland, regrowth woodland, and restoration plantings that were broadly similar to avoid the potential for confounding between patch size and vegetation type. Within-group variability in patch attributes (size, shape, aspect etc.) exceeded between

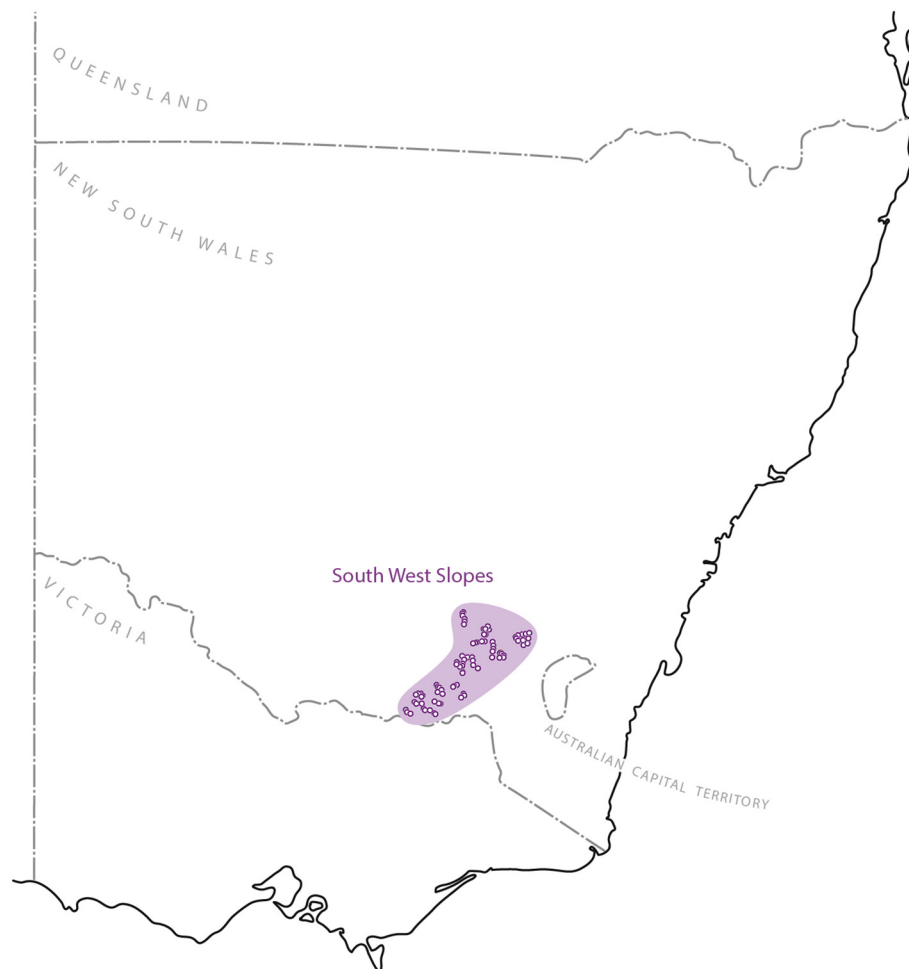


Fig. 1. Map of the study region.

group variation (Ikin et al., 2015). Notably, differences in key attributes such as stand height and stem density between the three broad vegetation types were much greater than within-group variability (Ikin et al., 2015; Lindenmayer et al., 2016a).

In addition to vegetation type, we used satellite data to calculate a measure of the extent (ha) of native vegetation (termed “vegetation extent”) in an area of 500 m radius around the centroid of the permanent transect established at each site. The mean value was 5.0 ha and the median value was 2.25 ha, with values ranging from 0 (19% of the values) to 53 ha. The amount of surrounding vegetation was slightly lower around plantings (mean = 3.6 ha) than regrowth (mean = 4.7 ha) and old growth woodland (mean 6.6 ha).

2.2. Bird surveys

We completed all bird surveys in spring; however, due to farm access and other logistical restrictions, not all sites could be surveyed in all survey years. For restoration plantings, we completed counts at 39 sites in 2002, 46 in 2004, and 65 in 2006, 2008, 2009 and 2011, 61 in 2013, and 58 in 2015. This resulted in a total of 464 site-by-year observations (hereafter termed “surveys”). For old-growth woodland, we surveyed 68 sites in 2002, 72 in 2004, 2006, 2008 and 2009, 70 in 2011, and 69 in 2013 and 2015, giving 564 site-by-year surveys. For regrowth woodland, we surveyed 61 sites in 2002, 66 in 2004, 2006, 2008 and 2009, 64 in 2011, 61 in 2013 and 60 in 2015, giving 510 site-by-year surveys.

We gathered bird data using repeated five-minute point-interval counts (sensu Pyke and Recher, 1983) at 0 m, 100 m and 200 m along a

fixed transect at each site. Bird species seen or heard within 50 m of each point were recorded. Detections > 50 m from the count point were not included in our analyses. In any given year and season, each site was surveyed by at least two observers on different days, giving a minimum of six point-interval counts in each survey. We conducted surveys for up to four hours from dawn on a given day. We did not undertake surveys during poor weather (rain, high wind, fog, or heavy cloud cover). A site surveyed early in the morning on the first day of counts was surveyed later in the morning on second day of counts. These protocols reduced the effects of observer heterogeneity, time of day, and day of survey effects (Lindenmayer et al., 2009). The total dataset for our study comprised 9377 point counts.

2.3. Bird life history and other attributes

We constructed an extensive database of life history attributes for all birds recorded in our study region over the past 13 years. Body mass, movement, habitat (open-country versus woodland) and dietary data were derived from compilations of bird biology and ecology published in various ornithological monographs (see Luck et al., 2012). Birds identified as those of conservation concern followed (Reid, 1999; Montague-Drake et al., 2009).

We assigned each bird species to one of two categories of movement status: migrants (68 species) and residents (40 species). Resident species were those which did not undertake large-scale movement, including latitudinal migration, elevational migration or nomadic movements. We used body mass as a proxy for size, which we analyzed as a continuous variable, which we log-transformed (base e) in all

models. However, we present our results at three representative size categories: small (\bar{x} = 12 g, range 6–25 g, n = 46 species, e.g. Striated Pardalote); medium (\bar{x} = 55 g, range 26–114 g, n = 34 species, e.g. Brown Songlark); and large (\bar{x} = 245 g, range 118–790 g, n = 28 species, e.g. Australian Hobby): 28 species. We categorised species based on habitat preferences as either a “woodland” species (those birds associated only with, or mostly with woodland) or “open-country” species (remaining birds that do not have any preference for woodland habitat). Recent research has determined that this classification does represent an ecological meaningful grouping, and “woodland birds” are not simply a collection of species united by shared traits (Fraser et al., 2015). We defined rare species as those with < 1% occurrence on average in the 2002 and 2004 surveys (n = 57), moderately common species as those with 1–10% occurrence on average (n = 35), and common species as those with 10% or more occurrence on average (n = 15). Finally, we assigned birds to one of four broad diet categories: those that primarily consumed (1) invertebrates, (2) nectar, (3) seeds, and (4) vertebrates. We acknowledge that many species in categories 2, 3 and 4 supplement their diet with invertebrates.

We checked the correlation between the four trait variables we investigated, and found that no correlation was > 0.42 in magnitude (Appendix 1), with the exception of a correlation of 0.56 between the linear effect of body size and the contrast between birds that consume vertebrates.

2.4. Statistical analyses

We recorded a total of 177 individual species over the 13-year duration of this study. Of these, 22 were waterbirds and were excluded from the study. A further 47 species were excluded because there were insufficient detections to facilitate robust statistical analyses. We tested our five predictions using data from the 108 individual bird species detected in at least four of the eight survey years (Appendix 1).

We took a two-stage approach to our analysis. We began by investigating individual species trajectories over time, accounting for differences in occurrence between our three broad vegetation types. We followed this by a set of assemblage-wide analyses to investigate the association between species traits, site-level covariates (i.e. patch type) and time.

We used generalized linear mixed models (GLMMs) in GenStat (Release 18.1) for both sets of analysis. Our response variable for all analyses was the proportion of times each species was observed at a site (out of a possible 6 point counts) in each survey year. All models were fit using a binomial distribution with over-dispersion (Wedderburn, 1974) and the logit link function (Cunningham et al., 2014). For presentation purposes, we summarized the effects of interest using predictions adjusted for all the other variables in the model (Lane and Nelder, 1982): specifically, predictions were calculated at the mean values of continuous variables (such as body mass), and averages were calculated over the predictions at each level of categorical variables (such as diet), with equal weights for each level.

For our analysis of individual species trajectories, we first fitted a GLMM for each species that included a fixed effect of time (linear on the logit scale) and a random effect of site, and then added fixed effects of broad vegetation type and its interaction with time (see Appendices 1 and 3).

For our analysis of trait responses to environment, we included all species in a single model, and allowed for the different relative occurrences of species by including random effects for species and site, assuming Normal distributions for the variation of mean percentage occurrence on the logit scale. We fitted fixed effects for broad vegetation type and time (again linear on the logit scale); for four trait variables: migratory vs resident species, body size, woodland versus open-country, and invertebrate vs nectar vs seed vs vertebrate diets. We also allowed interactions between vegetation types, time and each of the trait variables (but no interactions between trait variables),

summarized as follows:

$$\text{Logit}(\% \text{presence}) = \text{time} * \text{vegetation type} * (\text{migratory status} + \text{body size} + \text{habitat})$$

We fitted a separate model to investigate the interaction of rareness of species with other variables: this included the effects listed above plus the effect of rareness, but excluding the effects of the remaining trait variables:

$$\text{Logit}(\% \text{presence}) = \text{time} * \text{vegetation type} * \text{frequency class}$$

As part of preliminary data analyses, we fitted a model that included vegetation extent corresponding to the amount of native vegetation surrounding each site. We found no significant interaction between vegetation extent and broad vegetation type, between vegetation extent and time, or vegetation extent and both time and broad vegetation type. In addition, the inclusion of vegetation extent made no significant difference to the model with life history traits. On this basis, and to facilitate presentation of the most parsimonious models, we elected to exclude vegetation extent from subsequent statistical analyses.

We did not conduct detectability/occupancy analyses for a number of reasons. Most importantly, past analyses on the topic of detection/occupancy (e.g. Welsh et al., 2013) suggest that the current statistical methods for detection/occupancy may not improve model fit and in some cases can make the outcomes worse. Moreover, it is currently not possible to determine when detection occupancy analysis improves model fit and when it does not (Welsh et al., 2015).

3. Results

3.1. Temporal trajectories

Averaged over all three vegetation types, our analyses revealed a significant decline ($P < 0.05$) in 30 species and a significant increase in 14 species between 2002 and 2015 (Fig. 2). Below we provide examples of birds that decreased and increased, first for those of conservation concern, then common species, and finally exotic taxa. We present deviance statistics that reflect measures of model fit in Appendix 4.

Of the 30 species that exhibited a statistically significant decline, four are of conservation concern (Dusky Woodswallow *Artamus cyanopterus* [Supplementary Fig. 1a], Eastern Robin *Eopsaltria australis*, Black-chinned Honeyeater *Melithreptus gularis* and Masked Woodswallow *Artamus personatus*), eight are common (> 10% occurrence on average during the first two years of surveys) (White-plumed Honeyeater *Lichenostomus penicillatus* [Supplementary Fig. 1b], Crested Pigeon *Ocyphaps lophotes*, Red-rumped Parrot *Psephotus haematonotus*, Striated Pardalote *Pardalotus striatus*, Magpie Lark *Grallina cyanoleuca*, Noisy Miner *Manorina melanocephala*, Galah *Eolophus roseicapilla*, and Grey Shrike-thrush *Colluricincla harmonica*) and three are exotic species (House Sparrow *Passer domesticus*, Common Blackbird *Turdus merula* and European Goldfinch *Carduelis carduelis*). Of the 14 species that significantly increased, three are of conservation concern (Diamond Firetail *Stagonopleura guttata*, [Supplementary Fig. 1c], Rufous Whistler *Pachycephala rufiventris* and White-winged Triller *Lalage tricolor*) and two were considered common (Superb Fairy-wren *Malurus cyaneus* and Rufous Songlark *Megalurus mathewsi*) (Fig. 2).

3.2. Differences in trajectory between broad vegetation types

We found that 94 species were characterized by similar temporal trends in occurrence across all three vegetation types (Appendix 1, with graphs shown in Appendix 3). There were, however, species that exhibited different temporal responses across vegetation type; these typically related to temporal declines or increases in restoration plantings relative to regrowth or old-growth. For example, the Diamond Firetail

declined in restoration plantings but increased in old-growth and regrowth, respectively. The White-browed Babbler (*Pomatostomus superciliosus*) and White-winged Chough (*Corcorax melanorhamphos*) increased in restoration plantings but declined in old-growth and regrowth, respectively. Examples of species which declined most in restoration plantings compared to the other two vegetation types included the White-plumed Honeyeater (*Lichenostomus penicillatus*) and

Willie Wagtail (*Rhipidura leucophrys*).

3.3. Prediction 1: Did large birds decline more than small birds?

Averaged over time, we found that small-bodied birds were approximately twice as common in restoration plantings relative to regrowth and old-growth woodland, whereas the opposite was true for

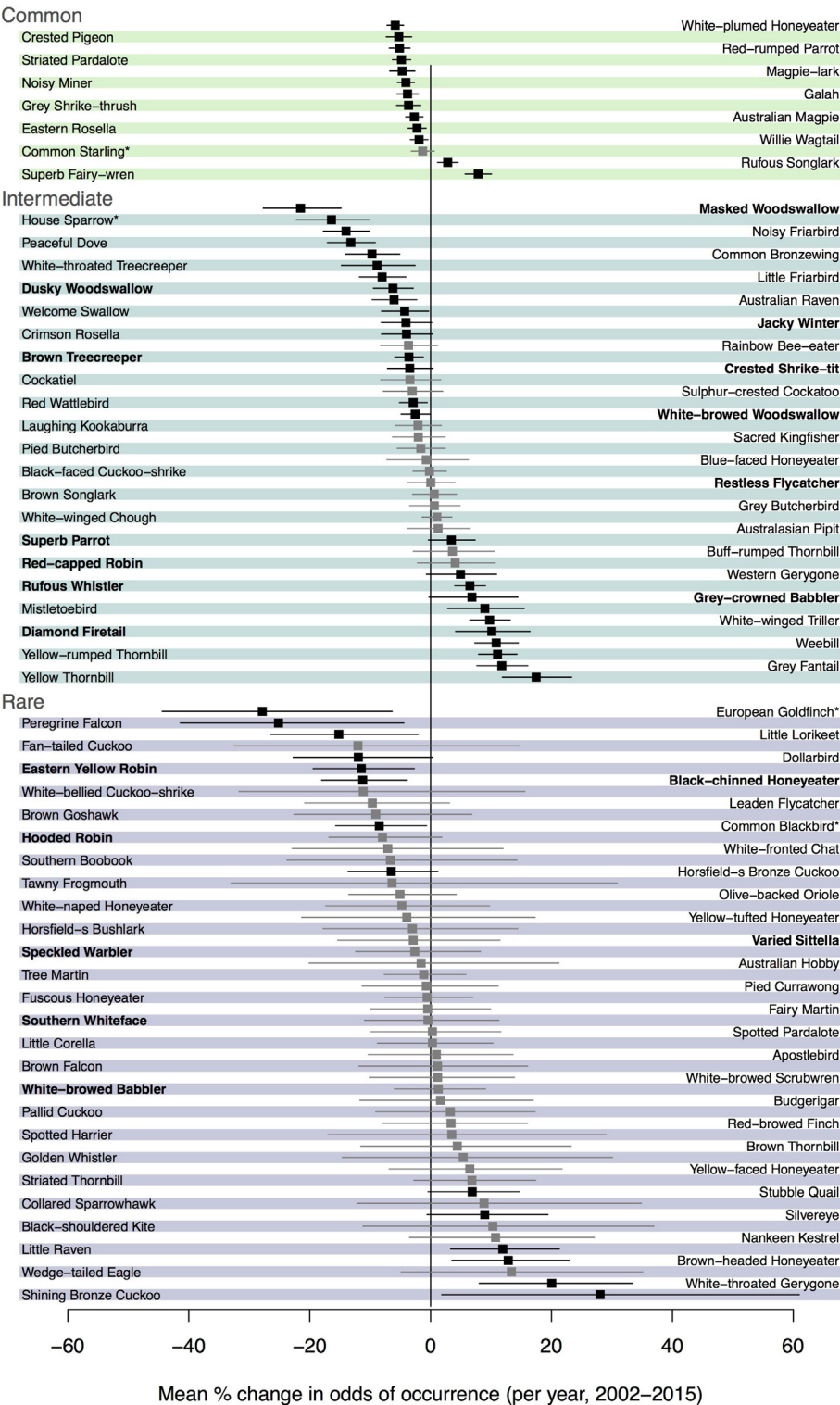


Fig. 2. Summary of individual species model results: estimated average percentage change per year in odds of occurrence and 95% confidence interval, averaged over growth types, and grouped by frequency of occurrence. Changes that are significantly different from zero are shown in black. Bold names indicate species of conservation concern, while * indicate exotic species. Birds are grouped by overall frequency of occurrence (see text).

large birds (Fig. 3). The interactions between vegetation type and the linear and quadratic effects of bird size were both statistically significant ($P < 0.001$, see Appendix 4; the fitted quadratic effects are shown in Appendix 5). The occurrence of large and medium-sized birds decreased over time in all growth types, whereas the occurrence of small birds increased in old-growth and regrowth, and to a lesser extent in plantings. The interactions between the linear effect of time and the linear and quadratic effects of bird size were significant ($P < 0.001$), and the three-way interaction involving vegetation type and the linear effect of time was also significant ($P = 0.04$; see Appendix 4).

3.4. Prediction 2: Did migratory species decline more than resident species?

Our analyses revealed that, initially, migratory species were less prevalent than residents, but resident species declined over time, especially in restoration plantings (Fig. 3b). The interactions of movement status both with time and with growth type were significant ($P < 0.001$; see Appendix 4).

3.5. Prediction 3: Did common birds decline more than rare birds?

We found that common species declined over time, especially in plantings (Fig. 3c), whereas rare species increased over time, also particularly in plantings. The interactions between occurrence categories and time and between occurrence categories and vegetation type were significant ($P < 0.001$). The interaction with time and vegetation type was also significant ($P = 0.002$).

3.6. Prediction 4: Did insectivorous birds decline more than birds with other diets?

Birds with predominantly invertebrate diets were characterized by a declining trend over time in plantings, but not in old-growth or regrowth (Fig. 3d). Nectarivores declined in all growth types, with occurrence nearly halved from 2002 to 2015 in restoration plantings. There was no evidence of change over time for granivores nor for carnivores except in plantings where occurrence halved over the 13-year period of our study. The interactions between time and diet and between growth type and diet were both significant ($P < 0.001$) (see Appendix 4), but the three-factor interaction was not significant ($P = 0.87$).

3.7. Prediction 5: Did woodland birds decline more than open-country birds?

We found that the interaction between habitat preference and time was not significant ($P = 0.25$) (see Appendix 4), although there was an indication that open-country birds declined over time (Fig. 3). Woodland birds were less prevalent on average than open-country birds throughout the 13 years of our study (Fig. 3), but they were more prevalent in regrowth sites than in old-growth or plantings. The interaction between habitat preference and growth type was significant ($P < 0.001$), but the three-variable interaction was not significant ($P = 0.66$).

4. Discussion

We sought to quantify temporal patterns of change in birds in one of the world's most heavily cleared and modified ecosystems, Australia's temperate woodlands (Fischer et al., 2009) and, in doing so, test predictions about life-history attributes associated with species trajectories in this ecosystem. Our analyses contained evidence of a significant decline in 30 species (over a quarter of those analyzed). However, temporal changes in occurrence were not consistent across bird biota as we found evidence of positive changes in a small number of species, including species of conservation concern and some rarer species. Some

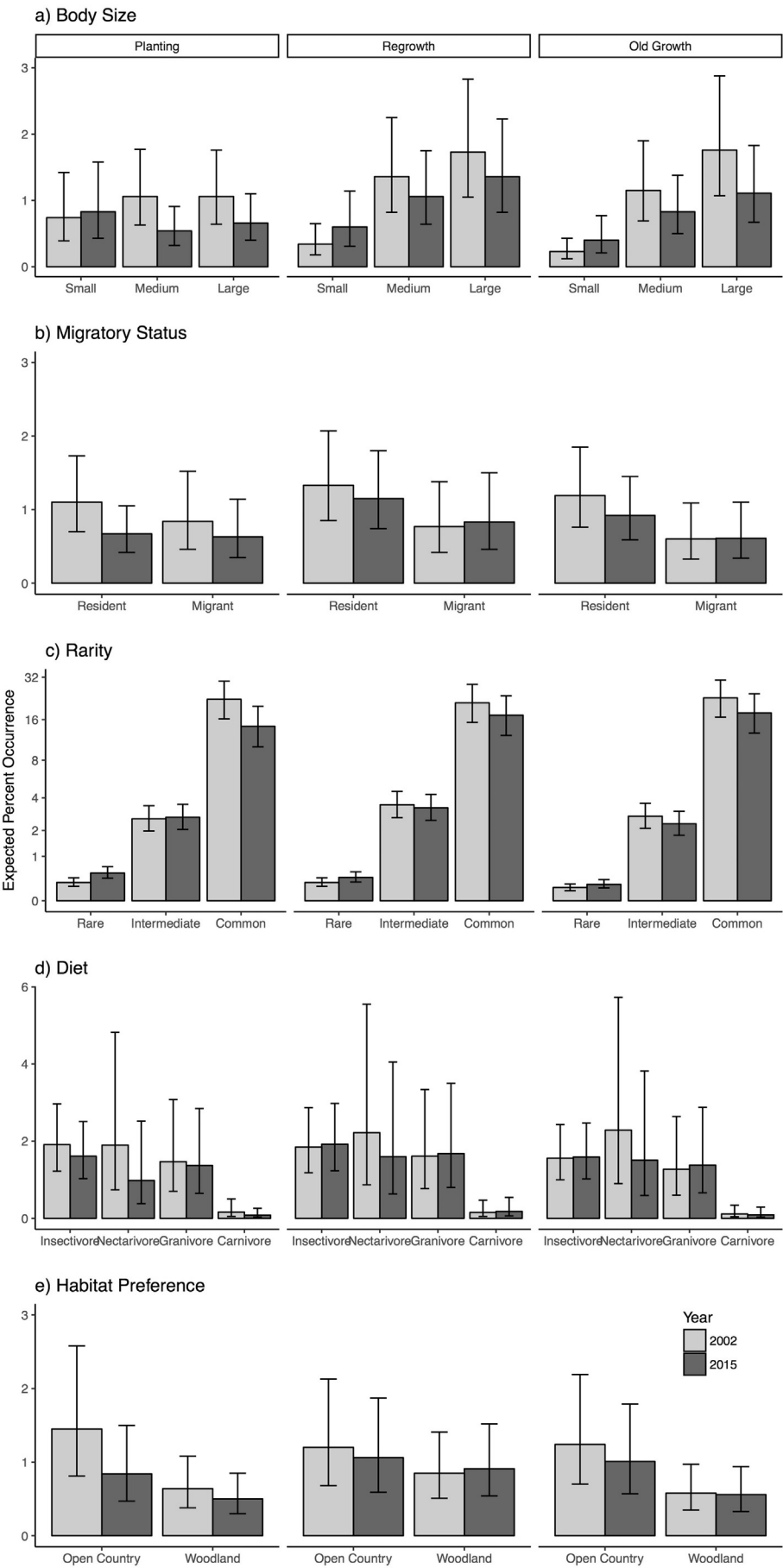
patterns we documented were not consistent with predictions derived from patterns uncovered for particular kinds of bird species (e.g. migratory versus resident taxa) elsewhere around the world (e.g. Both et al., 2010; Runge et al., 2015; Gilroy et al., 2016). In the remainder of this paper we discuss the overall temporal trends we identified and then explore associations between those trends and life history attributes that featured in the predictions we tested. We conclude with commentary on the conservation and land-management implications of our empirical study.

4.1. Overall temporal changes

Much has been written about the major losses of biodiversity at both a global and population level (e.g. Ceballos et al., 2017; Tilman et al., 2017). For the intensively monitored ecosystem in the study reported here, we found that the majority of species (64 of 108) showed no evidence of significant change over the 13 years of this investigation, illustrating the relative stability of these bird populations. However, there was also evidence of a significant decline in 30 species, more than double the number of significantly increasing bird species (14 species). Declining species included not only species of conservation concern (such as the Dusky Woodswallow, Eastern Yellow Robin, Black-chinned Honeyeater and Masked Woodswallow) but also many common species that are likely, because of their abundance, to play key role in ecosystem functions such as pollination and insect pest control. Declines in such common species may have serious consequences for the long-term integrity of temperate woodland ecosystems.

The reasons for the significant decline in many bird species remain unclear, as our study was not the kind of targeted experiment required to determine causation (Caughley and Gunn, 1996). The variety of species exhibiting declines suggest there may be multiple drivers of the observed patterns of change. A wide range of functional types of species exhibited declines including (among others) those that were large-bodied, residents, and nectar feeders. Patterns of declines often differed among vegetation types and included both birds of conservation concern as well as common species. For example, the hyper-aggressive and overabundant Noisy Miner was one common species which declined significantly over the duration of this study without any direct management (such as culling). This decline could have positive outcomes for the smaller-bodied bird species that Noisy Miners exclude from woodland they occupy (Mac Nally et al., 2012). In addition, our empirical analyses contained evidence of significant declines in three exotic species, the Common Blackbird, the House Sparrow and the Goldfinch. Species such as the House Sparrow have declined in other parts of the world (Vincent, 2005) with the use of pesticides being one explanation for population reduction (Hallmann et al., 2014). However, if the effects of pesticides were a key driver then we would anticipate a range of native species with broadly similar diets to the House Sparrow and Goldfinch (e.g. the Diamond Firetail) to have declined, which they did not. Another possible explanation for the large number of declines we quantified is the effect of the Millennium Drought which spanned the middle periods of this study (van Dijk et al., 2013). Several earlier studies have revealed that many bird species have either not recovered or continued to decline after the Millennium Drought (Bennett et al., 2014; Selwood et al., 2015). Similarly, some bird species in our study did not recover during the marked wet period following the drought, possibly as a result of extinction debts following extensive past clearing (Nimmo et al., 2016). We suggest that a longer period of monitoring than the 13 year duration of this study may be required for some bird species to recover following the Millennium Drought and, in turn, obtain a clearer picture of long-term trends in occurrence in different types of woodland. Declines in many bird species also do not appear to be associated with a loss in habitat and vegetation cover because the area of plantings and natural regeneration has increased significantly in our study region over the past decade (Cunningham et al., 2014).

We found evidence for significant increase in some species of



(caption on next page)

Fig. 3. Results from trait models: fitted mean % occurrence for 2002 and 2015 and for each vegetation type, for body size, migratory status, frequency, diet and habitat preference, with 95% confidence limits.

conservation concern: the Diamond Firetail, Rufous Whistler and White-winged Triller (Appendix 1). Other species, such as the Grey-crowned Babbler (*Pomatostomus temporalis*), showed substantial increases but high levels of year-to-year variation in detection that may have masked evidence of statistically significant temporal trends in our study (Appendix 1). Elsewhere, positive temporal responses in the Grey-crowned Babbler appear to be associated with revegetation programs (e.g. Robinson, 2006). Both the Grey-crowned Babbler and the Rufous Whistler often occupy restoration plantings and regrowth, whereas the Noisy Miner is mostly absent from these areas (Lindenmayer et al., 2012a). The area of restoration plantings and natural regrowth have increased substantially over the past decade in our study region (Cunningham et al., 2014) as well as other agricultural regions in south-eastern Australia (Geddes et al., 2011). The expansion of these vegetation types over time may explain some of the temporal changes in bird species occurrence that we have quantified.

Earlier work in agricultural landscapes relatively close to our study region (see Fischer et al., 2010) included predictions of future occurrence of 27 bird species based on models of the tree-based habitat requirements of species and projected future patterns of tree cover. Our study area supports these same bird taxa and our data provide an independent, albeit crude, “test” of the accuracy of those predictions, at least in the short term. Fischer et al. (2010) predicted that 24 of 27 species would decline and of these, 11 in this study also exhibited a significant decline. We found no significant trend for a further 10 of the species predicted by (Fischer et al., 2010) to decline, although it is possible that with a longer time series, evidence of greater congruence between the number of species predicted to decline and those actually declining might be found. Contrary to predictions by (Fischer et al., 2010), we found that three of the 24 species increased (Grey Fantail *Rhipidura albiscapa*, Mistletoebird *Dicaeum hirundinaceum* and Rufous Whistler), all of which are strongly associated with restoration plantings (see Lindenmayer et al., 2010; Appendix 1), highlighting the value of strategically revegetating areas for some elements of bird biota. (Fischer et al., 2010) also predicted a future increase in three species, for which we found evidence of an increase in one (the Rufous Songlark), no change for another, and a decline in a third (the Welcome Swallow *Hirundo neoxena*). The Welcome Swallow is strongly associated with human infrastructure such as buildings and farms dams and the reasons for its decline remain unclear.

4.2. Test of prediction 1: That large-bodied species are more likely to decline than smaller-bodied species

Consistent with our prediction at the outset of this study, large-bodied birds declined over time and across all vegetation types, but particularly in old-growth and regrowth. Large-bodied species typically have larger territories than small species (Schoener, 1968) and may require more habitat to survive thereby making them vulnerable to decline in areas extensively modified by agriculture (Haddad et al., 2015). An alternative explanation might be that large birds favour highly modified open-country environments (see Lindenmayer et al., 2012b) and they may be disadvantaged by the densely stocked vegetation characteristic of regrowth woodland and restoration plantings. However, this does not account for the temporal declines we found for typically open old-growth woodlands. Therefore, the reasons for the decline in large bodied birds remain unclear. Tilman et al. (2017) highlighted the elevated risks faced by large-bodied birds in a range of regions globally, to which the temperate woodland region of south-eastern Australia might also now be added.

In contrast to the decline in large birds, we found evidence that small-bodied bird species increased over time and in all broad

vegetation types. Small-bodied bird species were particularly prevalent in restoration plantings, consistent with the landscape texture hypothesis (Fischer et al., 2008), which predicts that small-bodied species will benefit from densely spaced trees that characterize restoration plantings and provide a greater array of nesting and foraging niches for these species whilst at the same time providing protection from predators. The general increase in the amount of plantings in the landscape (where small birds are more prevalent) may have assisted small birds in colonizing old growth and regrowth woodland. Again, this result highlights the value of targeted restoration plantings for small-bodied birds.

4.3. Test of prediction 2: That migratory species are more likely to decline than resident species

Contrary to our initial expectations, resident – but not migratory species – declined over time with the most pronounced decline being in restoration plantings. This result was particularly surprising given studies elsewhere around the world which suggest that migratory species are at increased risk of decline and extinction (Both et al., 2010; Runge et al., 2015; Gilroy et al., 2016). The reasons for our findings remain unclear, but previous work has suggested that migratory species are more likely to colonize restoration plantings over time (Lindenmayer et al., 2016a) and it is possible that this, in turn, displaces resident birds as such restored areas mature over time. The habitat suitability for resident birds may also decline as restoration plantings mature. Irrespective of the underlying reasons for our findings, they suggest a need to ensure that the conservation status (and thereby subsequent targeted management) of resident and not just migratory species is carefully examined.

4.4. Test of prediction 3: That rare species are more likely to decline than common species

We found that, as a group, common species of birds declined, whereas rare species increased; however, there were inter-specific differences in these trends. These findings are broadly consistent with those from work on birds in Europe which also reported declines in common species (Inger et al., 2015). The decline of common taxa is important given the key ecological roles abundant taxa play in ecosystems (Gaston, 2010; Winfree et al., 2015) including pollination and insect pest control. Evidence of temporal change was especially pronounced in restoration plantings (e.g. the White-plumed Honeyeater; see Supplementary Fig. 2), highlighting the high level of dynamism in bird populations in these actively revegetated environments.

4.5. Test of prediction 4: That insectivores are more likely to decline than species with other kinds of diet

We found little evidence of temporal changes in insectivores relative to birds that consume other kinds of food resources, despite vegetation type differences in the occurrence of birds with different diets. This was an encouraging result given suggestions by other researchers (e.g. Ford et al., 2001) that many at-risk species are insectivores and susceptible to decline. The reasons for the paucity of evidence for a decline in insectivores remains unclear. However, it is possible that the additional areas of regrowth and restoration plantings in our study area may provide habitat for insect biota (Gibb and Cunningham, 2010; Barton et al., 2016) that are, in turn, food for insectivorous bird species, thereby limiting population declines.

Nectar-feeding species exhibited the most pronounced declines in our study, with the strongest effects in restoration plantings. Such results are perplexing given that our 13-year study spanned both very dry

and very wet periods when temporal changes in food would be expected to occur and, more recently would be anticipated to have recovered.

4.6. Test of prediction 5: That woodland bird species are more likely to decline than open-country species

We found no evidence to support the prediction of a stronger decline in woodland birds relative to open-country birds. Indeed, there was an indication that open-country birds declined over time but the interaction between habitat preference and time was not significant. The (albeit non-significant) trend for a decline in open-country species may be associated with the increase in area over the past decade (see Cunningham et al., 2014) of vegetation that is generally not habitat for these birds such as patches of natural regeneration and restoration plantings. Notably, woodland birds were less prevalent than open-country birds despite old-growth woodland, regrowth woodland and restoration plantings (but not paddocks, croplands and other cleared areas) being targeted in our field studies. Areas of native vegetation cover varies from 3 to 30% of the landscape cover in our study region (Cunningham et al., 2014). Therefore, open areas dominate these landscapes and this may explain the greater prevalence of open-country birds in our study.

5. Management implications and general conclusions

Documenting temporal patterns of change in biota is critical to many key aspects of conservation biology and ecology. This includes providing an overall assessment of the status of biodiversity (e.g. Ceballos et al., 2017; Tilman et al., 2017) and identifying those species (and broader functional groups of species) that require additional management interventions such as additional habitat restoration (Crouzeilles et al., 2016) or expanded habitat protection (Pringle, 2017). We found that almost twice as many species have declined as have increased over the past 13 years in the temperate woodlands of south-eastern Australia, one of the most heavily cleared and modified biomes globally. These findings suggest that the temperate woodland bird biota is at risk of becoming highly depauperate relative to what it was even just a few decades ago, despite significant restoration efforts in large parts of the biome, including the region where this study was focused. Other researchers (e.g. Garnett et al., 2011) have suggested that species of conservation concern, like those we identified as being in significant decline in this study, need targeted management. Hence, our results are important as they allow a focus of management effort on species that are truly undergoing significant decline. However, we also found compelling evidence for significant declines in some common species, some of which are likely to play critical roles in ecosystem processes. We suggest these species also need concerted conservation efforts, not only to prevent them from becoming uncommon and eventually conservation management-dependent, but also because their declines may represent future risks to key ecosystem processes mediated by formerly abundant bird taxa (see Winfree et al., 2015).

Our analyses contained evidence of significant differences in temporal trajectories of bird species between old-growth woodlands relative to restoration plantings and natural regrowth. Indeed, restoration plantings were characterized by significant declines in nectar-feeders, large birds, common birds and residents but also significant increases in small birds and rare species. Such temporal patterns results suggest that restoration plantings in particular are highly dynamic environments in which marked changes in the functional groups of birds can take place within relatively short periods of time.

This underscores the importance of a suite of land management strategies that result not only in the deliberate replanting programs to actively restore woodlands (Lindenmayer et al., 2016a) but also in the maintenance of seemingly more stable environments such as existing old-growth woodland remnants as well as regrowth woodland.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.04.007>.

doi.org/10.1016/j.biocon.2018.04.007.

Acknowledgements

The first author is the recipient of an Australian Research Council (ARC) Australian Laureate funded by the Australian Government (FL120100108). We thank the ARC, Ian Potter Foundation, The Vincent Fairfax Family Foundation, Murray Local Land Services, Riverina Local Land Services, and the New South Wales Environment Trust (2013/RD/0008) for funding that allowed this study to be completed. Key contributors to the completion of field bird surveys included Chris MacGregor, David Blair, Lachlan McBurney, Thea O'Loughlin, Sachiko Okada and members of the Canberra Ornithologists Group. Tabitha Boyer assisted in many aspects of manuscript preparation.

References

- Barnagaud, J.-V., Barbaro, L., Papaix, J., Deconchat, M., Brockerhoff, E.G., 2014. Habitat filtering by landscape and local forest composition in native and exotic New Zealand birds. *Ecology* 95, 78–87.
- Barton, P.S., Sato, C.F., Kay, G.M., Florance, D., Lindenmayer, D.B., 2016. Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodland. In: *Insect Conservation and Diversity*. 9 pp. 124–134.
- Bennett, J.M., Nimmo, D.G., Clarke, R.H., Thomson, J.R., Cheers, G., Horrocks, G., Hall, M., Radford, J.Q., Bennett, A.F., Mac Nally, R., 2014. Resistance and resilience: can the abrupt end of extreme drought reverse avifaunal collapse? *Divers. Distrib.* 20, 1321–1332.
- Benson, J.S., 2008. New South Wales vegetation classification and assessment: part 2 plant communities of the NSW south-western slopes bioregion and update of the NSW Western Plains plant communities, version 2 of the NSWVCA database. *Cunninghamia* 10, 599–673.
- Both, B., van Turnhout, C.A., Bijlsma, R.G., Siepel, H., van Strein, A.J., Foppen, R.P., 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. Ser. B* 277, 1259–1266.
- Caughley, G.C., Gunn, A., 1996. *Conservation Biology in Theory and Practice*. Blackwell Science, Cambridge, MA.
- Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological abhihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci.* 114 (30), E6089–E6096.
- Colles, A., Liouw, L.H., Prinzing, A., 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecol. Lett.* 12, 849–863.
- Crouzeilles, R., Curran, M., Ferreira, M.S., Lindenmayer, D.B., Grelle, C.E.V., Rey Benayas, J.M., 2016. A global meta-analysis on the ecological drivers of forest restoration success. *Nat. Commun.* 7.
- Cunningham, R.B., Lindenmayer, D.B., Barton, P., Ikin, K., Crane, M., Michael, D., Okada, S., Gibbons, P., Stein, J., 2014. Cross-sectional and temporal relationships between bird occupancy and vegetation cover at multiple spatial scales. *Ecol. Appl.* 24, 1275–1288.
- van Dijk, A.I., Beck, H.E., Crossbie, R.S., de Jeu, R.A., Liu, Y.Y., Podger, G.M., Timbal, B., Viney, N.R., 2013. The millennium drought in Southeast Australia (2001–2009); natural and human causes and implications for water resources, ecosystems, economy, and society. *Water Resour. Res.* 49, 1040–1057.
- Fischer, J., Lindenmayer, D.B., Montague-Drake, R., 2008. The role of landscape texture in conservation biogeography: a case study on birds in South-Eastern Australia. *Divers. Distrib.* 14, 38–46.
- Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K., Forrester, R.I., 2009. Reversing a tree regeneration crisis in an endangered ecoregion. *Proc. Natl. Acad. Sci.* 106, 10386–10391.
- Fischer, J., Zerger, A., Gibbons, P., Stott, J., Law, B.S., 2010. Tree decline and the future of Australian farmland biodiversity. *Proc. Natl. Acad. Sci.* 107, 19597–19602.
- Ford, H.A., 2011. The causes of decline of birds of eucalypt woodlands: advances in our knowledge over the last 10 years. *Emu* 111, 1–9.
- Ford, H.A., Barrett, G.W., Saunders, D.A., Recher, H.F., 2001. Why have birds in the woodlands of southern Australia declined? *Biol. Conserv.* 97, 71–88.
- Fraser, H., Garrard, G., Rumpff, L., Hauser, C., McCarthy, M., 2015. Consequences of inconsistently classifying woodland birds. *Front. Ecol. Evol.* 3, 10.
- Garnett, S., Szabo, J., Dutton, G., 2011. *The Action Plan for Australian Birds* 2010. CSIRO Publishing, Melbourne.
- Gaston, K.J., 2010. Valuing common species. *Science* 327, 154–155.
- Geddes, L.S., Lunt, I.D., Smallbone, L., Morgan, J.W., 2011. Old field colonization by native trees and shrubs following land use change: could this be Victoria's largest example of landscape recovery? *Ecol. Manag. Restor.* 12, 31–36.
- Gibb, H., Cunningham, S.A., 2010. Revegetation of farmland restores function and composition of epigeic beetle assemblages. *Biol. Conserv.* 143, 677–687.
- Gilroy, J.J., Gill, J.A., Butchart, S.H., Jones, V.R., Franco, A.M., 2016. Migratory diversity predicts population declines in birds. *Ecol. Lett.* 19, 308–317.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules,

- C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystem. *Sci. Adv.* 1, e1500052.
- Higgins, P.J. (Ed.), 1991–2006. *Handbook of Australian, New Zealand and Antarctic Birds*. Vol. 1–6 Oxford University Press, Melbourne.
- Hallmann, C.A., Foppen, R.P., van Turnhout, C.A.M., de Kroon, H., Jongejans, E., 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* 511, 341–343.
- Ikin, K., Mortelliti, A., Stein, J., Michael, D., Crane, M., Okada, S., Wood, J., Lindenmayer, D.B., 2015. Woodland habitat structures are affected by both agricultural land management and abiotic conditions. *Landscape Ecol.* 30, 1387–1403.
- Inger, R., Gregory, R., Duffy, J.P., Stott, I., Vorisek, P., Gaston, K.J., 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecol. Lett.* 18 (1), 28–36.
- IUCN, 2016. *The IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.
- Lane, P.W., Nelder, J.A., 1982. Analysis of covariance and standardization as instances of prediction. *Biometrics* 38, 613–621.
- Lindenmayer, D.B., Fischer, J., 2006. *Habitat Fragmentation and Landscape Change*. Island Press, Washington, D.C.
- Lindenmayer, D.B., Wood, J.T., MacGregor, C., 2009. Do observer differences in bird detection affect inferences from large-scale ecological studies? *Emu* 109, 100–106.
- Lindenmayer, D.B., Knight, E.J., Crane, M.J., Montague-Drake, R., Michael, D.R., MacGregor, C.I., 2010. What makes an effective restoration planting for woodland birds? *Biol. Conserv.* 143, 289–301.
- Lindenmayer, D.B., Northrop-Mackie, A.R., Montague-Drake, R., Crane, M., Michael, D., Okada, S., Gibbons, P., 2012a. Not all kinds of revegetation are created equal: revegetation type influences bird assemblages in threatened Australian woodland ecosystems. *PLoS One* 7, e34527.
- Lindenmayer, D.B., Wood, J., Montague-Drake, R., Michael, D., Crane, M., Okada, S., MacGregor, C., Gibbons, P., 2012b. Is biodiversity management effective? Cross-sectional relationships between management, bird response and vegetation attributes in an Australian agri-environment scheme. *Biol. Conserv.* 152, 62–73.
- Lindenmayer, D.B., Burns, E., Thurgate, N., Lowe, A. (Eds.), 2014. *Biodiversity and Environmental Change: Monitoring, Challenges and Direction*. CSIRO Publishing, Melbourne.
- Lindenmayer, D.B., Blanchard, W., Tennant, P., Barton, P., Ikin, K., Mortelliti, A., Okada, S., Crane, M., Michael, D., 2015. Richness is not all: how changes in avian functional diversity reflect major landscape modification caused by pine plantations. *Divers. Distrib.* 21, 836–847.
- Lindenmayer, D.B., Lane, P.W., Barton, P.S., Crane, M., Ikin, K., Michael, D.R., Okada, S., 2016a. Long-term bird colonization and turnover in restored woodlands. *Biodivers. Conserv.* 25, 1587–1603.
- Lindenmayer, D.B., Michael, D., Crane, M., Okada, S., Florance, D., Barton, P., Ikin, K., 2016b. *Wildlife Conservation in Farm Landscapes*. CSIRO Publishing, Melbourne.
- Luck, G., Lavorel, S., McIntyre, S., Lumb, K., 2012. Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *J. Anim. Ecol.* 81, 1065–1076.
- Mac Nally, R., Bowen, M., Howes, A., McAlpine, C.A., Maron, M., 2012. Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. *Ecology* 93, 668–678.
- Montague-Drake, R.M., Lindenmayer, D.B., Cunningham, R.B., 2009. Factors affecting site occupancy by woodland bird species of conservation concern. *Biol. Conserv.* 142, 2896–2903.
- Muir, M.J., 2010. Are we measuring conservation effectiveness? In: *Report to Conservation Measures Partnership*, . http://www.conservationmeasures.org/wp-content/uploads/sites/4/2014/05/Survey-Report-Draft-2010-06-06_v3.pdf.
- Newbold, T., Scharlemann, J.P., Butchart, S.H., Sekercioglu, C.H., Alkamade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical bird species to land-use intensity. *Proc. R. Soc. B* 280, 805–810.
- Nimmo, D.G., Haslem, A., Radford, J.Q., Hall, M., Bennett, A.F., 2016. Riparian tree cover enhances the resistance and stability of woodland bird communities during an extreme climate event. *J. Appl. Ecol.* 53, 449–458.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752.
- Pringle, R.M., 2017. Upgrading protected areas to conserve wild biodiversity. *Nature* 546, 91–99.
- Pyke, G.H., Recher, H.F., 1983. Censusing Australian birds: a summary of procedures and a scheme for standardisation of data presentation and storage. In: Davies, S.J. (Ed.), *Methods of Censusing Birds in Australia*. Proceedings of a Symposium Organised by the Zoology Section of the ANZAAS and the Western Australian Group of the Royal Australasian Ornithologists Union. Department of Conservation and Environment, Perth, pp. 55–63.
- Reid, J., 1999. Threatened and declining birds in the New South Wales sheep-wheat belt. I. Diagnosis, characteristics and management. In: *Unpublished Report to NSW National Parks and Wildlife Service*. CSIRO Wildlife and Ecology, Canberra.
- Robinson, D., 2006. Is revegetation in the sheep Pen Creek area, Victoria, improving grey-crowned babbler habitat? *Ecol. Manag. Restor.* 7, 93–104.
- Runge, C., Watson, J.E., Butchart, S.H., Hanson, J.O., Possingham, H.P., Fuller, R.A., 2015. Protected areas and global conservation of migratory birds. *Science* 350, 1255–1258.
- Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J., van Bommel, F.P.J., 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biol. Conserv.* 131, 93–105.
- Sato, C., Wood, J., Stein, J.A., Crane, M., Okada, S., Michael, D., Kay, G., Florance, D., Seddon, J., Gibbons, P., Lindenmayer, D.B., 2016. Natural tree regeneration in agricultural landscapes: the implications of intensification. *Agric. Ecosyst. Environ.* 230, 98–104.
- Schoener, T.W., 1968. Sizes of feeding territories among birds. *Ecology* 49, 123–141.
- Selwood, K.E., Clarke, R.H., Cunningham, S.C., Lada, H., McGeoch, M.A., Mac Nally, R., 2015. A bust but no boom: responses of floodplain bird assemblages during and after prolonged drought. *J. Anim. Ecol.* 84, 1700–1710.
- Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. *Nature* 546, 73–81.
- Vincent, K., 2005. *Investigating the Causes of the Decline of the Urban House Sparrow *Passer domesticus* Population in Britain*. De Montfort University, Leicester, United Kingdom.
- Wedderburn, R.W.M., 1974. Quasi-likelihood functions, generalized linear models and the Gauss-Newton method. *Biometrika* 61, 439–447.
- Winfrey, R., Fox, J.W., Williams, N.M., Reilly, J.R., Cariveau, D.P., 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* 18, 626–635.
- Williams, J., Price, R.J., 2011. Impacts of red meat production on biodiversity in Australia: a review and comparison with alternative protein production industries. *Anim. Prod. Sci.* 50, 723–747.
- Welsh, A.H., Lindenmayer, D.B., Donnelly, C.F., 2013. Fitting and interpreting occupancy models. *PLoS One* 8, e52015.
- Welsh, A.H., Lindenmayer, D.B., Donnelly, C.F., 2015. Adjusting for one issue while ignoring others can make things worse. *PLoS One* 10, e0120817.