



Do migratory and resident birds differ in their responses to interacting effects of climate, weather and vegetation?

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Abstract

Aim: Knowledge of the individual and collective effects of habitat, weather variability and climate on bird populations is limited, with the result that species vulnerability to the collective impacts of global change is poorly understood. We quantified the effects of interactions between these potential drivers on the occurrence of resident, migratory and nomadic birds in Australian temperate woodlands.

Location: A 1.8 million hectare temperate woodland belt in south-eastern Australia.

Time period: 2002–2015.

Major taxa studied: Temperate woodland birds.

Methods: We used logistic mixed models to quantify the factors affecting the occurrence of three groups of birds (residents, partial migrants and nomads) at 203 long-term field sites located in three vegetation types (restoration plantings, natural regrowth woodland and old growth woodland) surveyed repeatedly between 2002 and 2015. Potential explanatory variables included vegetation type, three long-term climate variables (mean annual rainfall, maximum temperature and minimum temperature), and the three corresponding weather variables for 12 months preceding each survey.

Results: We found four-way interactions between bird movement category, type of vegetation cover and rainfall (both as a long-term climate variable and as a short-term weather variable). Increased occurrence of nomads and partial migrants, but not resident species, was associated with high short-term rainfall. The effects were more marked in long-term climatically wet areas, and also differed between vegetation types. Models for maximum and minimum temperature were simpler than those for rainfall but showed evidence of partial migrants and nomadic species avoiding low minimum or high maximum temperatures in some vegetation types.

Main conclusions: Our analyses revealed that birds with different movement patterns exhibit different responses to weather and long-term climate. Nomadic species in particular respond to rainfall strongly in climatically wet locations (presumably

because of large pulses in resources). Drying conditions resulting from climate change may therefore create problems for the future persistence of nomadic bird species.

KEYWORDS

biodiversity in agricultural landscapes, bird movement, landscape restoration, rainfall temperature, temperate woodland, weather effects

1 | INTRODUCTION

Rapid climate change is expected to cause increasingly variable and extreme short-term weather conditions (Garcia, Cabeza, Rahbek, & Araujo, 2014; Greenville et al., 2018; Steffen et al., 2009). Both long-term climate and short-term weather can have a range of impacts on biodiversity (Urban, 2015). These include shaping species distribution patterns (Elith & Leathwick, 2009; Elton, 1927; Krebs, 1978; Parmesan, 1996) by affecting the availability of food, shelter and other resources for many animal groups (Bateman, VanDerWal, & Johnson, 2012; Gibbs, Chambers, & Bennett, 2011; Stenseth et al., 2002), as well as influencing key physiological processes such as the ability of animals to offload heat (Gardner et al., 2016). Further, the impacts of climate change and weather extremes on biodiversity may be magnified in landscapes already subject to extensive human modification (Brodie, 2016; Deo et al., 2009; Driscoll, Felton, Gibbons, Felton, & Munro, 2011; McAlpine et al., 2007; Sergio et al., 2014). Some functional groups of taxa are thought to be at particular risk of decline (Tilman et al., 2017; Urban, 2015). For example, migratory species are thought to be among the most severely declining taxa, not only due to climate change and extreme weather, but also due to habitat loss, hunting and poor levels of formal reservation in some or in all of their range (Barlein, 2016; Both et al., 2010; Gilroy, Gill, Butchart, Jones, & Franco, 2016; Liminana, Soutullo, Arroyo, & Urios, 2012; Moller, Rubolini, & Lehikoinen, 2008; Runge et al., 2015; Sanderson, Donald, Pain, Burfield, & Bommel, 2006).

Given that migratory species face significant physiological challenges during long-distance travel (Guillemete et al., 2016), the capacity of the environment to meet each species' requirements for food and habitat is critical to their persistence. Slight changes in the availability of critical habitats, in weather conditions during breeding or overwintering, or in the timing, quality or quantity of food resources (i.e. interactions between weather and habitat) can heavily influence survival in migratory populations and species (e.g. Both et al., 2010; Will, Kitaiskaia, & Kitaysky, 2018). Consequently, migratory species' capacity to persist in, for example, restored areas and other areas of native vegetation cover within otherwise largely cleared agricultural areas, might be undermined by variations in weather in response to climate change (Deo et al., 2009; Mantyka-Pringle, Martin, & Rhodes, 2012; McAlpine et al., 2007). However, research to understand the individual and collective effects of climate suitability, weather variability and habitat on species with different movement patterns, including migratory species, is data-intensive. This means that knowledge of species vulnerability to these drivers is poorly

understood in many instances. Yet, such improved understanding is essential for guiding informed landscape management, including vegetation restoration within agricultural areas.

In the investigation reported here, we used long-term (13 year) data on birds from a large-scale (1.8 m ha) study to quantify the influence of climatic conditions and weather variables on the occupancy of restored (replanted) woodlands, naturally regenerated (regrowth) woodlands, and old growth woodland by three functional groups of birds: residents, partial migrants, and nomadic species. The three vegetation types that we studied are characterized by major differences in vegetation structure (Ikin et al., 2015; Lindenmayer, Michael, et al., 2016b) and microclimatic conditions (Cleugh, 2003). The spatial extent of our large-scale study encompassed a gradient from climatically cool, wet sites to hotter, drier sites. Importantly, our investigation was conducted between 2002 and 2015, a period that spanned the Millennium Drought and a succeeding wetter period (Nimmo, Haslem, Radford, Hall, & Bennett, 2016; van Dijk et al., 2013). This enabled us to explore the impacts on birds with different movement patterns of weather and climate interactions, as well as their interacting effects with broad vegetation type.

In a previous investigation focusing on patterns of temporal change in bird populations in temperate woodlands, we found that mobile species (i.e. partial migrants and nomadic taxa) were increasing, whereas residents were declining (Lindenmayer et al., 2018). Here, we explore possible reasons why such temporal patterns might be occurring by testing the overarching question: *How does variation in weather influence residents versus partial migrants and nomadic species, and are the effects buffered by the long-term climatic characteristics of a location and vegetation type?* We made the following predictions:

Prediction #1: The occurrence of birds would be greater on sites characterized by wet or cool long-term climate relative to dry or hot sites, irrespective of movement pattern, due to more available resources (especially as rainfall is likely to be a key factor limiting vegetation growth, flowering, and pulses of insect prey in temperate woodland environments; Nimmo et al., 2016; Seddon, Macias-Fauria, Long, Benz, & Willis, 2016).

Prediction #2: The occurrence of birds would increase during periods of elevated short-term rainfall and decreased short-term temperatures (Marchant, Guppy, & Guppy, 2016; although see Bennett et al., 2014) because of reduced physiological stress (Gardner et al., 2016), more food resources (Barea & Watson, 2007; Marchant et al., 2016; McGoldrick & Mac Nally, 1998), and enhanced breeding success (e.g. Barea & Watson, 2007; Gibbs et al., 2011; Hennan, Goodman, & White, 2015; Marchant et al., 2016). The effects on birds (irrespective

of movement patterns) of increased high rainfall would be muted on climatically dry sites (characterized by low long-term average rainfall) as such areas may support fewer resources.

Prediction #3: The number of sites occupied by nomadic species will increase during periods of increased rainfall due to their capacity for spatio-temporal tracking of pulses of resources (Dingle, 2008).

Prediction #4: The effects of weather variables would be mediated by broad vegetation type. Restoration plantings lack large old trees and associated resources such as pollen, nectar and nest sites (Ikin et al., 2015; Vesk, Nolan, Thomson, Dorrrough, & Mac Nally, 2008). They are also characterized by specific microclimatic conditions such as greater shading by densely stocked trees (Betts, Phalan, Frey, Rousseau, & Yang, 2018; Cleugh, 2003; e.g. a paucity of large shade trees). On this basis, we postulated that drought and elevated temperature effects would be strongest in restoration plantings for migrants and nomads given their additional energy and physiological demands relative to residents (Dingle, 2008).

2 | METHODS

2.1 | Study area

Our study encompassed a 1.8 million ha agricultural area within the South West Slopes region of New South Wales, south-eastern

Australia (Figure 1). The region was formerly dominated by temperate native eucalypt woodland (Lindenmayer et al., 2010) but has been cleared of an estimated 85% of its original cover to facilitate livestock grazing and cereal cropping. It is one of the most heavily modified agricultural regions worldwide (Fischer et al., 2009; Lindenmayer, Michael, et al., 2016b) and characterised by a wide range of landscape degradation problems such as soil erosion, secondary salinity and tree dieback (Lindenmayer, Michael, et al., 2016b). In an effort to tackle these problems, major restoration programs have been undertaken (Lindenmayer, Lane, et al., 2016a). There has also been significant natural regeneration of temperate eucalypt woodlands, particularly over the past 15 years (Lindenmayer et al., 2012). Thus, woody vegetation in the South West Slopes region can be grouped in three broad categories: actively replanted eucalypt woodland (restoration plantings), naturally regenerated eucalypt woodland (regrowth woodland) and old growth eucalypt woodland (Lindenmayer, Michael, et al., 2016b).

2.2 | Study design

Our investigation comprised 65 restoration planting sites, 66 regrowth woodland sites and 72 old growth woodland sites. These are the three major types of vegetation on farms throughout the study region. Importantly, we selected sites so that they encompassed the

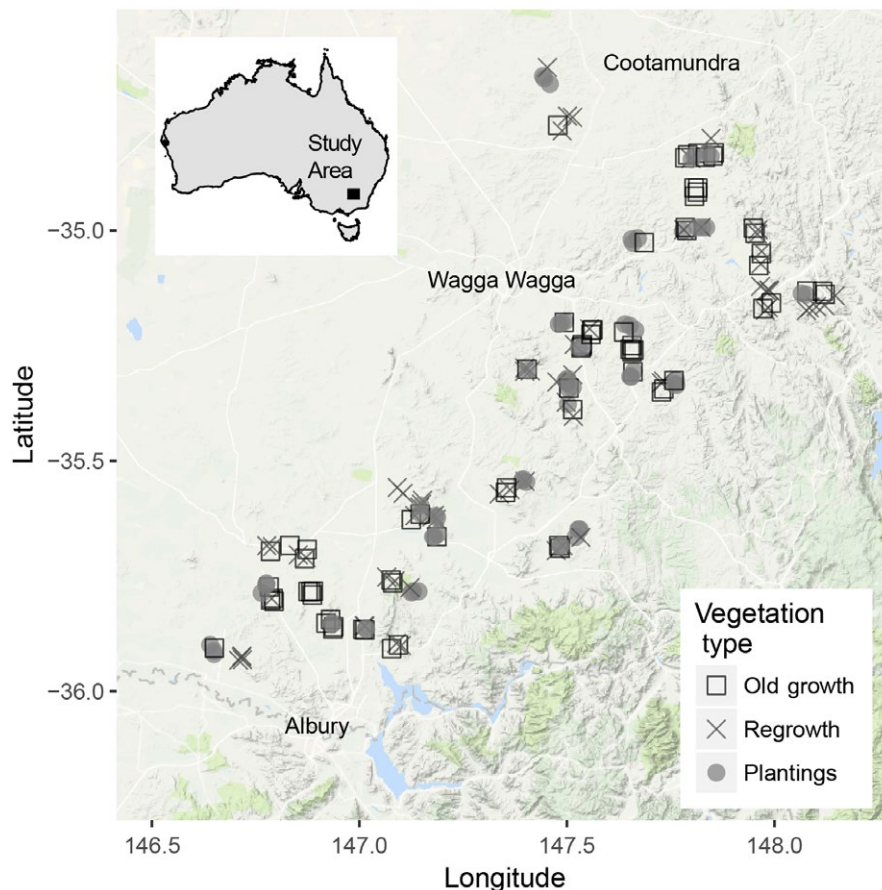


FIGURE 1 Location of the study area and long-term field sites in the South West Slopes of south-eastern Australia

TABLE 1 Number of sites surveyed in each of the eight spring surveys between 2002 and 2015 in each of three vegetation types

Vegetation type	Survey year								Total
	2002	2004	2006	2008	2009	2011	2013	2015	
Plantings	39	46	65	65	65	65	61	58	464
Old growth	68	72	72	72	72	70	69	69	564
Regrowth	61	66	66	66	66	64	61	60	510
Total	168	184	203	203	203	199	191	187	1,538

range of conditions typically found in the broader region; from large to small patches, from heavily to lightly grazed. Sites were a minimum of 500 m apart and typically more than 1–2 km (Cunningham, Lindenmayer, Crane, Michael, & MacGregor, 2007). Much of the South West Slopes bioregion is characterized by subdued topography and the sites we selected were typically 200–400 m above sea level.

Restoration plantings were areas of planted understorey and overstorey native vegetation with a mix of native and exotic ground cover. Woody plants were typically spaced 2 m apart, but there was not a standard set of spacing or plant species composition protocols applied in revegetation efforts. All restoration plantings were at least 7 years old at the start of this investigation (2002) and many were 10–20 years old. Most restoration plantings had been established to mitigate problems associated with soil erosion and/or salinity. 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 stands were typically dominated by large scattered trees that were 200 or more years old. To ensure broad inference from our analyses, our 203 sites varied in: (a) size (0.3–60.3 ha for restoration plantings, 0.5–53.8 ha for regrowth and old growth woodland patches) and (b) the amount of vegetation cover (4%–30%) in the surrounding farm and landscape (Cunningham et al., 2014).

2.3 | Bird surveys and movement data

We completed a total of 1,538 surveys (comprising 9,377 point counts) in eight spring seasons between 2002 and 2015 (Table 1). We conducted surveys in October (spring) because it is when the majority of species in our study area are present and actively calling. Surveys were conducted in accordance with The Australian National University Animal Ethics Committee Protocols A2015/38, A2012/44, C.RE.63.09 and C.RE.48.06.

We gathered bird data using repeated 5-minute point-interval counts (*sensu* Pyke & Recher, 1983) at 0, 100 and 200 m along a fixed transect at each site. These transects did not cross habitat boundaries but were contained fully within a given vegetation type. An expert observer recorded all bird species seen or heard within 50 m of the survey point. The vast majority (>95%) of all detections were made from calls. In any given year, each site was surveyed by at least two observers on different days, giving a minimum of six point-interval counts in each survey. We

did not undertake surveys during poor weather (rain, high wind, fog or heavy cloud cover). We completed surveys between dawn and 3 hr after dawn, with the order in which sites were surveyed on the second day of sampling reversed relative to the first day. The second survey was typically conducted 2–4 days after the first survey. These protocols reduce the effects of observer heterogeneity and day of survey effects (Lindenmayer, Wood, & MacGregor, 2009).

We extracted data on the movement status of the 41 species of birds from data in Garnett et al., (2015). We identified three categories of birds: those that: (a) are largely resident, with juveniles undertaking local dispersal over short distances; (b) are nomadic at an annual timescale, with irregular spatial and temporal movement depending on resource availability; or (c) are partially migratory—that is, some individuals regularly move away from breeding areas after nesting but others may remain year round.

We investigated whether our survey methodology had adequately sampled birds in each movement category and vegetation type using species accumulation curves, and compared these with expected peak richness calculated using Chao's method (Chao, 1987). Across the whole study, we detected 166 species, 96% of the 173 species predicted by the Chao method. Observed species richness was always within the 95% confidence interval of expected richness for all combinations of vegetation type and movement status, though estimates for partial migrants and nomadic species were much more variable than for other trait categories (full results are given in Supporting Information Appendix S1).

2.4 | Climate and weather variables

We assembled information to calculate the long-term averages (1970–2014) for three climate variables: mean annual rainfall, mean maximum annual temperature and mean minimum annual temperature for use in statistical modelling of bird occupancy. We also compiled information for three weather variables over a 12-month period preceding each survey. Our rainfall variable was estimated mean monthly rainfall. Our temperature variables were mean monthly minimum temperature (hereafter termed minimum temperature) and mean monthly maximum temperature (hereafter maximum temperature). Maps of these data plotted from 2000 to 2016 show that the field sites in our investigation encompassed a gradient from climatically wet and cool through to dry and hot locations (Supporting Information Appendix S2a–c). The gradients

for minimum and maximum temperature were marked, including in October when our field surveys for birds were conducted.

Our climate and weather variables were derived from monthly national grids (<http://dap.nci.org.au/thredds/remoteCatalogService?catalog=http://dapds00.nci.org.au/thredds/catalogs/rr9/collection/ANUClimate.xml>). We utilized thin-plate smooth splines described by Hutchinson (1995) to generate climate and weather variables for each of our 203 field sites. This method has been widely applied to estimate daily and monthly climate surfaces as well as long-term climate averages (McKenney et al., 2011).

All three climate variables were correlated as follows: the two temperature variables positively with one another, and negatively with rainfall. However, between the weather variables, only annual maximum temperature and rainfall in the preceding 12 months had a correlation coefficient > 0.3. Notably, hot, dry conditions in our study region are driven by El Niño events and combinations of cool, dry years and hot, wet years are extremely rare. We found limited correlation between climate and weather variables (Supporting Information Appendix S3 and S4). Although our large region has a strong climate gradient, the study sites were mostly spread parallel to this gradient (due to the distribution of the box-gum woodland; as shown in Supporting Information Appendix S2). This, combined with our study region being a very climatically variable, means that between-year differences in weather were far greater than among-site differences (with the wettest sites in some years being the driest in others; see Supporting Information Appendix S3).

Given correlations between rainfall and temperature variables, we fitted separate models for each of rainfall, minimum temperature and maximum temperature. We used predictions between the 10 and 90 percentiles of the values for the climate and weather variables to illustrate the fitted models of bird occurrence (see below).

2.5 | Statistical analysis

We modelled bird count data using generalized linear mixed models focusing on bird taxa with > 3% occurrence in at least one vegetation type (as a simple proportion of the surveys; $N = 41$ species; see Supporting Information Appendix S5). Specifically, we modelled the proportion of times each species was observed out of the several point-counts (usually six) in each survey using a binomial distribution with over-dispersion (Wedderburn, 1974) and the logit link function, similar to the approach used by Cunningham et al., (2014). We included the counts of all species in a single model, and allowed for their different relative occurrence by including a random effect for species, assuming a normal distribution for the variation of mean occurrence on the logit scale. We also included a random effect for site, to account for the repeated-measurements structure of the data. We added random slopes for year for each species to adjust for the (positive and negative) temporal trends already established in earlier investigations in our study region (Lindenmayer et al., 2018).

To test the set of predictions outlined in the Introduction, we fitted fixed effects for the three broad vegetation types, linear effects of each of the three climate variables in turn (mean annual rainfall,

mean maximum temperature and mean minimum temperature averaged over the period 1970–2014) together with a linear effect of the corresponding weather variables (mean monthly rainfall, mean monthly maximum and mean monthly minimum temperature), and movement status as a categorical variable with three levels (residents, partial migrants and nomadic species). We also modelled interactions between all of these variables. For example, the model we fitted for rainfall was as follows: vegetation type * movement status * long-term rainfall * rainfall in the preceding 12 months + time.

We constructed further models for maximum temperature and then minimum temperature by replacing the rainfall variables with the temperature variables. All continuous variables were scaled to a mean of zero and a standard deviation of one prior to running each model. We fitted models using GenStat (Release 19.1) and summarized the effects of interest using predictions (Lane & Nelder, 1982), which are fitted means classified by some or all of the variables in a model, adjusted for (i.e. averaged over) the effects of any remaining variables. We checked for spatial autocorrelation in the residuals of the models and found no evidence of significant effects.

3 | RESULTS

We recorded a total of 177 individual species over the 13-year duration of this study. Of these, 41 were sufficiently common to facilitate detailed additional statistical analyses; we excluded the 95 species present in <3% of the surveys (Supporting Information Appendix S5). We also excluded 22 waterbirds given major differences in their habitat requirements relative to terrestrial bird taxa. The 41 species targeted in our analyses included 23 residents, 13 partial migrants and 5 nomadic species.

3.1 | Rainfall effects

We identified a significant four-way interaction between bird movement status, long-term rainfall, rainfall in the preceding 12 months, and vegetation type (Wald Statistic = 11.0, $p = 0.026$; Figure 2, Supporting Information Table SA6.1). There were limited effects of 12-month rainfall and long-term rainfall on the occurrence of residents. The strongest responses were on regrowth woodland sites located in climatically wet areas where occurrence decreased after high levels of rainfall in the preceding 12 months. For partial migrants, occurrence in regrowth woodland more than doubled (from 3.1% to 6.7%) after high 12-month rainfall relative to low 12-month rainfall, but only on climatically wet sites. A similar pattern was uncovered for restoration plantings (4.2% to 7.8%). By contrast, for old growth woodland, partial migrants responded to high 12-month rainfall on climatically dry sites, where occurrence nearly doubled (from 3.5% to 6.5%) after high levels of rainfall in the preceding 12 months, relative to low levels of rainfall.

Nomadic species showed the strongest responses to rainfall in old growth woodland. In old growth woodland after high levels of rainfall in the preceding 12 months, occurrence of nomadic species almost doubled on climatically wet sites, but halved on climatically

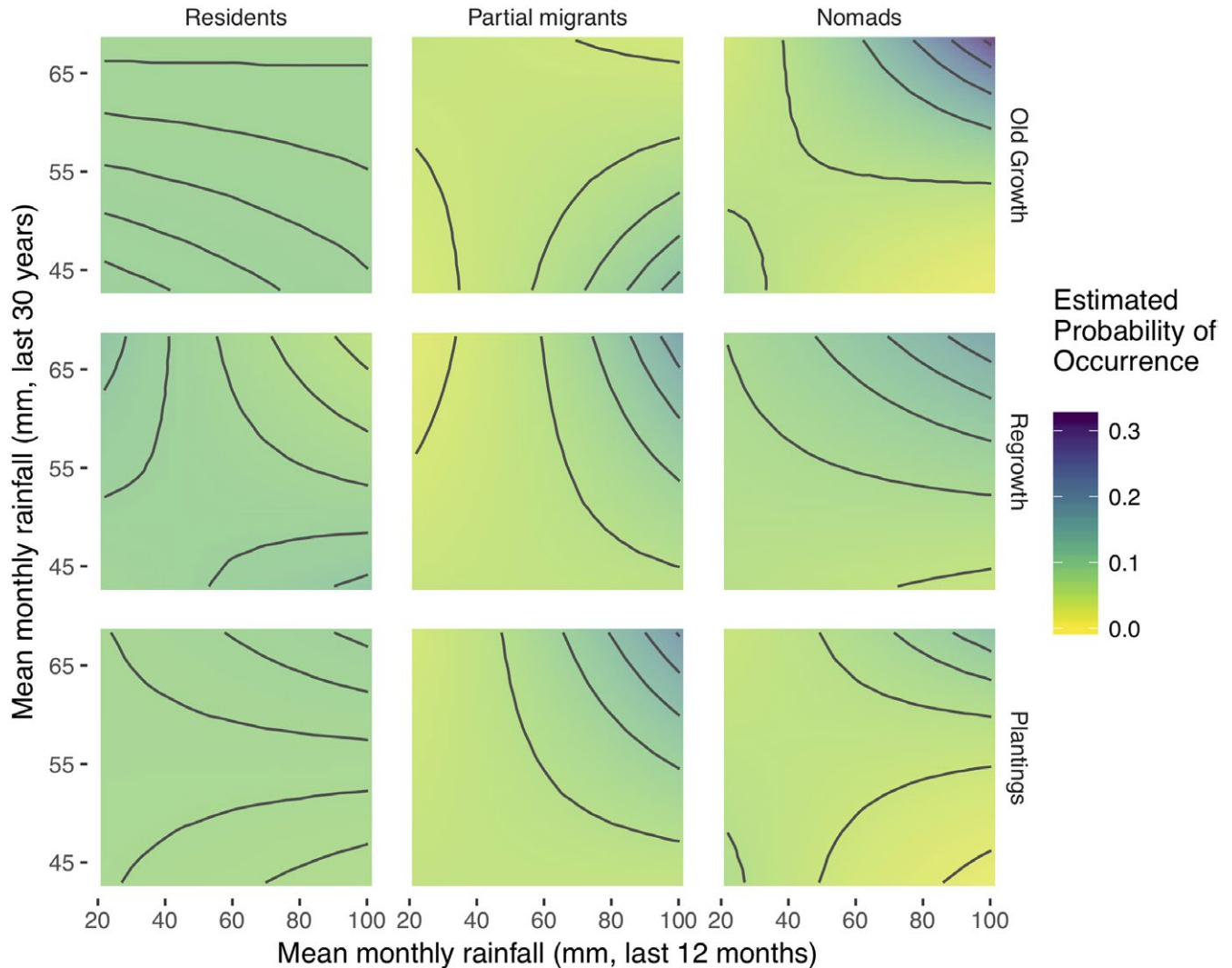


FIGURE 2 Rainfall effects for three groups of birds based on their movement status (residents, partial migrants, and nomadic species; columns) shown in relation to weather (x axis), climate (y axis), and vegetation type (old growth woodland, regrowth woodland, and restoration plantings; rows). Each panel contains five equally-spaced contours, calculated independently of the remaining panels. Predictions are shown from the full model, in which the following terms were statistically significant: 12-month rainfall; vegetation type * migratory status; long-term rainfall * migratory status; 12-month rainfall * migratory status; 12-month rainfall * long-term rainfall * migratory status and vegetation type * migratory status * 12-month rainfall * long-term rainfall

dry sites. We found a similar effect in restoration plantings and regrowth woodland, albeit weaker in climatically wet sites than recorded for old growth woodland.

3.2 | Maximum temperature effects

The model for maximum temperature contained evidence of three significant two-way interactions (Supporting Information Table SA7.1). There was a significant movement and vegetation type interaction (Wald Statistic = 61.76; $p < 0.001$), an interaction between movement and long-term maximum temperature (Wald Statistic = 7.4; $p = 0.025$), and a movement and short-term maximum temperature interaction (Wald statistic = 34.8; $p < 0.001$; Figure 3, Supporting Information Table SA7.1). Residents exhibited limited

responses to both long-term maximum temperature and short-term maximum temperature. For partial migrants, occurrence was depressed after high temperatures in the preceding 12 months, irrespective of whether sites were located on climatically cool or hot areas. In the case of nomads, occurrence in regrowth woodland peaked at 12.6% in climatically cool sites and sites experiencing low maximum temperatures in the preceding 12 months, compared to 4.3% in sites that had high 30-year average temperatures (Supporting Information Table SA7.3, Figure 3).

The interaction between movement and long-term maximum temperature showed a small increase in frequency of local and nomadic species at long-term cool sites compared to long-term warm sites, but a small decrease for partial migrants (Supporting Information Table SA7.4).

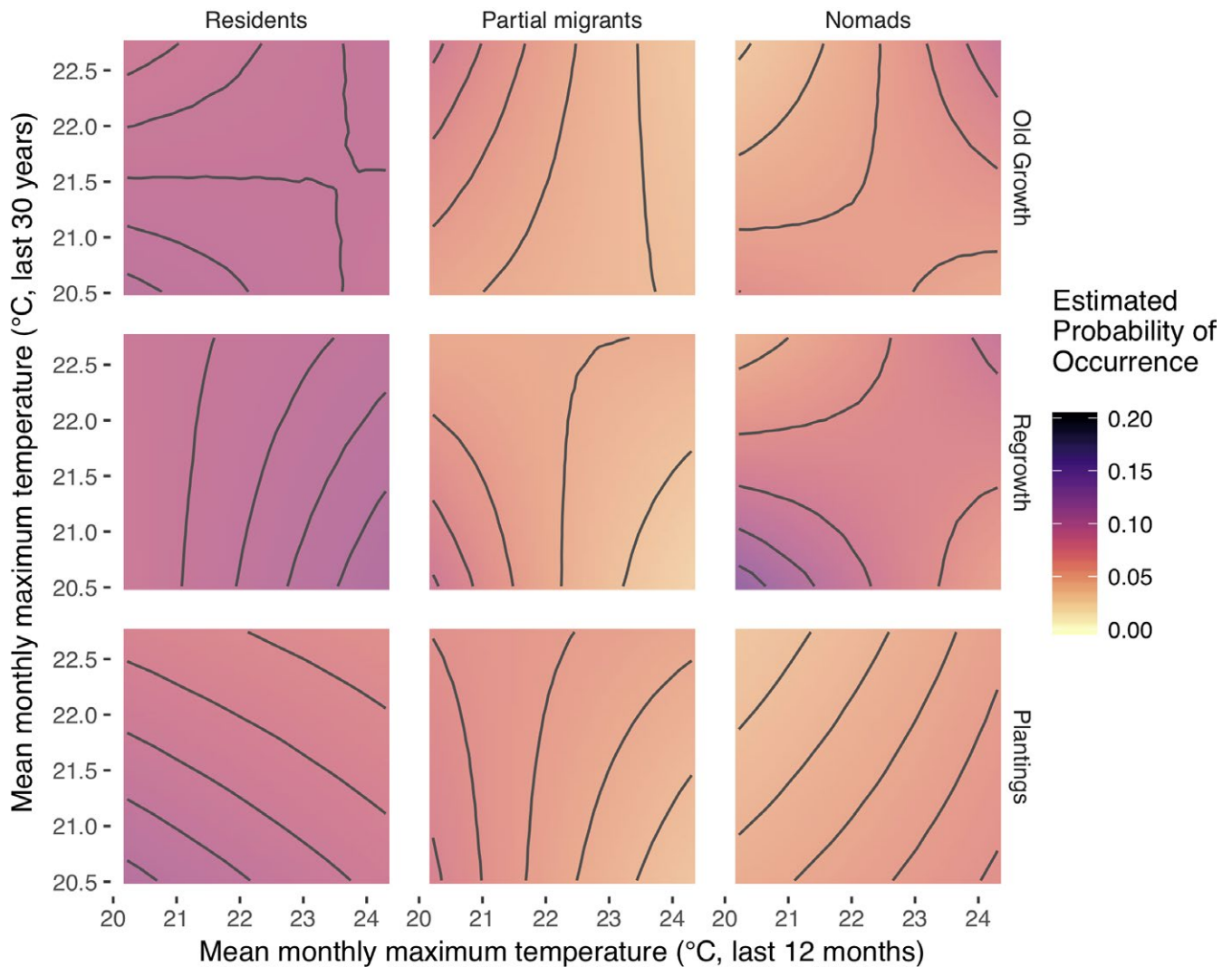


FIGURE 3 Maximum temperature effects for three groups of birds based on their movement status (residents, partial migrants, and nomadic species; columns) shown in relation to weather (x axis), climate (y axis), and vegetation type (old growth woodland, regrowth woodland, and restoration plantings; rows). Each panel contains five equally-spaced contours, calculated independently of the remaining panels. Predictions are shown from the full model, in which three terms were statistically significant, namely the interactions of migratory status with vegetation type, 12-month temperature and long-term temperature

3.3 | Minimum temperature effects

We found a significant three-way interaction (Wald Statistic = 19.3; $p < 0.001$) between bird movement, vegetation type and short-term minimum temperature (Supporting Information Table SA8.4). For resident species, we found no evidence of climate or weather effects for minimum temperature in restoration plantings (Supporting Information Table SA8.4). In regrowth woodlands, the occurrence of residents was greater on sites characterized by high values for minimum temperatures in the preceding 12 months. The same was true (but to a lesser extent) in old growth woodland (Figure 4). The pattern for partial migrants was similar, although the effect of temperature in regrowth was much smaller. (Supporting Information Table SA8.4, Figure 4). The occurrence of nomadic species was significantly greater in all vegetation types when 12-month minimum temperature was high (Supporting Information Table SA8.4, Figure 4).

We found evidence of significant interactions between movement and long-term minimum temperature, and between vegetation type and long-term minimum temperature (Supporting Information Table SA8.1). There was little effect of long-term temperature on residents and partial migrants, but lower occurrence of nomads at climatically hot, compared with climatically cool sites (Supporting Information Table SA8.3). The occurrence of birds of all movement types was, on average, lower at climatically hot planting and regrowth sites, but not in climatically hot old growth sites (Supporting Information Table SA8.4).

4 | DISCUSSION

The effects of key drivers of biodiversity trends such as climate, weather and vegetation cover are typically studied in isolation. In

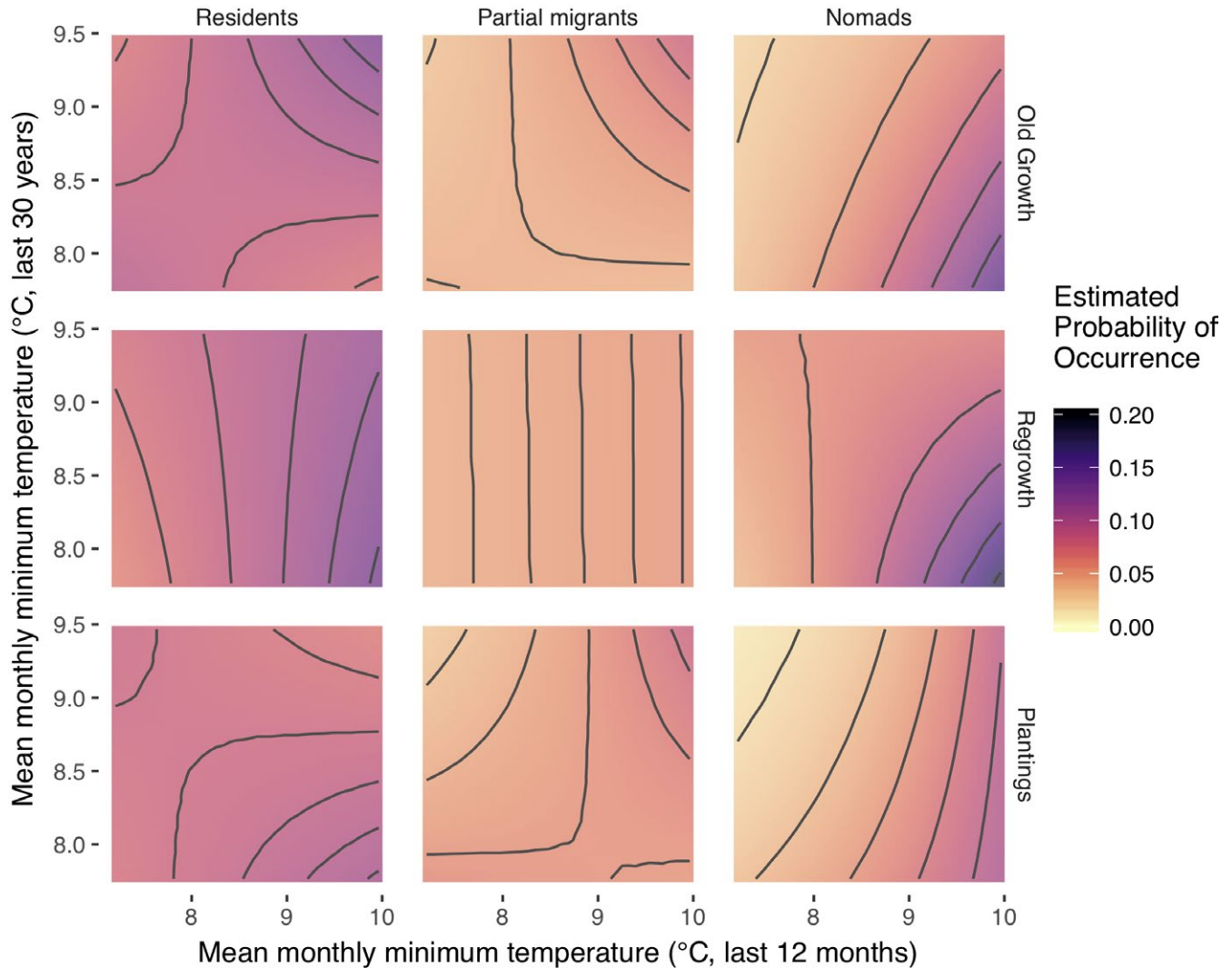


FIGURE 4 Minimum temperature effects for three groups of birds based on their movement status (residents, partial migrants, and nomadic species; columns) shown in relation to weather (x axis), climate (y axis), and vegetation type (old growth woodland, regrowth woodland, and restoration plantings; rows). Each panel contains five equally-spaced contours, calculated independently of the remaining panels. Predictions are shown from the full model, in which the following terms were statistically significant: 12-month temperature; the interaction of migratory status with both vegetation type and 12-month temperature; the interaction with long-term temperature of both vegetation type and migratory status; and vegetation type * migratory status * 12-month temperature

this study, we sought to quantify their collective effects on different functional groups of birds (corresponding to their movement status). This approach is valuable given that multiple interacting factors can underpin species declines (Caughley & Gunn, 1996; Ceballos, Ehrlich, & Dirzo, 2017; Sato et al., 2016), and understanding these interactions is important for facilitating recoveries (Crouzeilles et al., 2016; Garnett et al., 2017; Scheele, Foster, Banks, & Lindenmayer, 2017). Indeed, many Australian birds are considered to be at increased risk of extinction as a result of climate change (Nimmo et al., 2016; Urban, 2015) and habitat loss (Garnett, Szabo, & Dutson, 2011). It is important to determine whether migratory species are at particular risk, as occurs in many parts of the world (see Sanderson et al., 2006; Both et al., 2010; Barlein, 2016; Gilroy et al., 2016), especially given their role in key

ecosystem functions (Bauer & Hoyer, 2014). However, previous work focusing on patterns of temporal change in bird populations in temperate woodlands revealed that mobile species (i.e. partial migrants and nomadic taxa) are increasing, whereas residents are declining (Lindenmayer et al., 2018). This study provides further insights into such temporal patterns. Indeed, our empirical analyses of interacting effects resulted in several key findings. These included the following: (a) Four-way interactions between bird movement status, vegetation type, and long-term and short-term rainfall. (b) Simpler models for maximum and minimum temperature, respectively, although still with some interacting effects. And, (c) strong associations between different functional groups of birds and different vegetation types that were modified by weather conditions.

4.1 | Effects of weather and climate

4.1.1 | Rainfall effects

Rainfall is generally regarded as a limiting factor in Australian temperate woodlands (Lindenmayer et al., 2010; Nimmo et al., 2016), and hence, bird occurrence would be expected to increase during wet periods and decline during dry periods (Marchant et al., 2016; although see Bennett et al., 2014). Consistent with this prediction, we found generally positive impacts of increased rainfall in the preceding 12 months on the occurrence of birds. However, responses to short-term rainfall were more nuanced than a simple positive-negative pattern. This was indicated by a significant four-way interaction in our statistical model (Figure 2; see Supporting Information Appendix S6) in which bird responses to short-term rainfall varied significantly depending on: (a) whether residents, partial migrants, or nomads were being examined, (b) which broad vegetation type was being examined, and (c) the long-term climatic conditions at a site. Generally, subdued effects were identified for residents. Positive relationships between bird occurrence and short-term rainfall were most pronounced for mobile taxa (partial migrants and nomads) and at climatically wet sites, and particularly in restoration plantings and regrowth woodland. A striking effect we uncovered was for nomadic species in old growth woodland for which, after high rainfall, the presence halved in climatically dry sites but more than doubled in climatically wet sites (Figure 2).

We suggest that the most likely explanation for our rainfall results is that resident species have only limited abilities to move in response to weather conditions. Changes in populations and site occurrence of residents may arise because rainfall influences breeding success and post-fledging dispersal, and so increases in response to favourable conditions can be slow, and may have extended time-lags. We were unable to assess the impacts of time-lags in this study because it is likely that birds exhibit them in a species-specific way, but our analysis focused on composite movement categories. Partial migrants and nomadic species are highly mobile and may be able to track temporal and spatial variation in resources (Dingle, 2008; Keast, 1968) triggered by short-term rainfall, thereby resulting in the high levels of spatial and temporal variability in occurrence. This result is consistent with several previous studies from around the world, each showing that elevated short-term rainfall can lead to a pulse in resources (Illan et al., 2014; Tayleur et al., 2015), such as food (Barea & Watson, 2007; McGoldrick & Mac Nally, 1998), but also influence nesting biology (Gibbs et al., 2011; Hennan et al., 2015; Marchant et al., 2016).

One of the novel findings of this study was that the effects of differences in rainfall had profoundly different effects depending on whether additional precipitation occurred in old growth, restoration plantings or regrowth woodland located in climatically wet versus dry locations (Figure 2, Supporting Information Appendix S6). This effect was particularly marked for nomadic taxa in old growth woodland where after high rainfall years, a steep drop in occurrence in climatically dry sites was countered by a significant increase in the

presence in climatically wet sites (Figure 2). It is possible that part of the reason for climate and weather effects are linked with underlying differences in vegetation structure. Old growth woodland typically supports much larger and older trees than regrowth and restoration plantings (Ikin et al., 2015), especially on climatically wet sites (where rates of growth are likely to be faster and overall levels of biomass are inherently higher (Soderquist & MacNally, 2000). Positive relationships between tree size and age and the production of food resources for birds such as flowers, nectar and seeds are well established (Lindenmayer & Laurance, 2016; Wenk & Falster, 2015), and so these large trees in wet climates would supply abundant resources in response to rainfall events, attracting nomadic species. Whilst vegetation structure effects may partly explain the observed responses of nomadic species, partial migrants exhibited the opposite effect with a spike in detections on climatically dry old growth woodland after high levels of rainfall in the preceding 12 months (Figure 2). This finding warrants further investigation but could reflect a way in which partial migrants and nomads spatially partition access to resource pulses during periods of increased rainfall.

4.1.2 | Temperature effects

Our statistical models for temperature effects contained evidence of a three-way interaction (for minimum temperature) and a series of two-way interactions (for maximum temperature) (Figures 3 and 4; Supporting Information Appendices S7 and S8). Short-term changes in temperature typically do not produce pulses in resources. Rather, bird responses to temperature are likely to be largely physiological (Illan et al., 2014; Sinclair et al., 2016). We found evidence that more residents were recorded in response to higher minimum temperatures, especially in regrowth and old growth (but not in restoration plantings). It is possible that some of our findings for temperature are related to the inherent microclimatic differences within different vegetation types. The densely spaced trees in restoration plantings and associated shaded microclimatic conditions (see Cleugh, 2003) may already shelter residents from low temperatures resulting in a lack of response to increased minimum temperatures (unlike more open regrowth and old growth woodland sites).

Occurrence of nomadic species was greater after hotter short-term minimum temperatures in all vegetation types. In the case of partial migrants, occurrence was greater with higher minimum temperatures but especially in climatically hot sites in old growth and restoration plantings. Warmer minimum temperatures may reduce the amount of energy used in thermoregulation, or stimulate activity by potential prey such as invertebrates, thereby making areas more attractive for mobile bird species.

Our findings for maximum temperature were even simpler relative to those for minimum temperature, with no significant effects for residents but fewer partial migrants with greater maximum temperatures in the preceding 12 months. Temperature can affect nesting biology (Hennan et al., 2015) and elevated temperatures may stimulate mobile species to seek territories in other locations characterized by cooler short-term conditions. However, we did

not find evidence of an increase in occurrence of partial migrants in climatically cool sites in warmer years, suggesting that other, currently unknown, factors may have influenced our results, or that in these years, partial migrants favoured habitats outside of the study region. Irrespective of the ecological mechanisms underpinning the minimum and maximum temperature effects, our results highlighted markedly different responses among bird species with different movement patterns to temperature as a long-term climate variable, a weather variable, or both.

4.1.3 | Vegetation type differences in the occurrence of different functional groups of birds

Our analyses uncovered strong evidence that the probability of observing partial migrants and residents was significantly higher in restoration plantings, while nomads were more often recorded in regrowth woodland. Hence, the well-documented structural differences between the vegetation types in our study (e.g. see Ikin et al., 2015; Lindenmayer, Lane, et al., 2016a) translated into differences in the broad functional groups of species that responded to these areas.

The reasons why partial migrants and residents exhibited a strong association with restoration plantings are not clear. Previous studies have found that, consistent with the landscape texture hypothesis (Fischer, Lindenmayer, & Montague-Drake, 2008), restoration plantings support more small-bodied birds than larger species. However, there were both small- and large-bodied partial migrants and residents in this study, and hence collinearity (which is limited; correlation coefficient = -0.16) between these life history attributes cannot explain our broad vegetation type effects for species with different kinds of movement behaviour. One potential explanation for functional group relationships with broad vegetation type might be the general absence of hyper-aggressive native species like the Noisy Miner (*Manorina melanocephala*) from restoration plantings (Lindenmayer, Lane, et al., 2016a) in our study region. The negative effects of the Noisy Miner on other native bird species have been well documented (Mac Nally, Bowen, Howes, McAlpine, & Maron, 2012), and its absence from restoration plantings may make these areas more attractive for mobile species such as partial migrants, as well as sedentary taxa (i.e. residents) seeking feeding and nesting resources. Previous investigations in our study region have revealed that mobile species are increasingly likely to colonize restoration plantings over time (Lindenmayer, Lane, et al., 2016a), while, at the same time, populations of the Noisy Miner decline as restored areas age (Lindenmayer et al., 2018).

4.1.4 | Conservation and management implications

Studies in many parts of the world have found that migratory species are declining (Barlein, 2016; Both et al., 2010; Gilroy et al., 2016; Sanderson et al., 2006). However, the opposite is occurring in the highly modified temperate woodland environments within our

study region, with residents declining but mobile species increasing (Lindenmayer et al., 2018). Resident species may be at particular risk as a result of spatio-temporal variation in resources driven by fluctuations in weather and its interaction with long-term climatic conditions. Migration and other kinds of movement patterns in some Australian bird species are somewhat less predictable and more temporally and spatially variable than those exhibited by many migratory taxa in the Northern Hemisphere (Dingle, 2008; Keast, 1968). Such variability may be a response to the hyper-variable inter-annual weather conditions (especially rainfall) that characterize much of the Australian continent (McMahon, Finlayson, Haines, & Srikanthan, 1992; van Dijk et al., 2013). This may, in turn, enable mobile bird species to capitalize on spatial and temporal variation in pulses of resources associated with variable weather conditions.

Extremes of weather will be part of rapid climate change (Garcia et al., 2014), including in Australia (Steffen et al., 2009). Climate change in south-eastern Australia is forecast to result in a drying climate, with high rainfall in long-term wet sites likely to become less frequent (Steffen et al., 2009). Our analyses indicated that nomadic species respond to rainfall most strongly in climatically wet locations (presumably because of large pulses in resources) and climate change may therefore challenge the long-term viability of nomadic bird species in this region.

The results of this study have two important implications for the conservation of biodiversity. First, our study demonstrated the value for birds of restoration plantings and regrowth woodland, particularly during periods of elevated rainfall and in climatically wet locations. Second, while restoration plantings, regrowth woodland, and old growth woodland differ in their support of partial migrants, nomads and local dispersers, representatives of all three movement categories are found in the three vegetation types. This highlights the importance of farms supporting different kinds of woody vegetation to provide suitable habitat for different groups of birds.

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DATA AVAILABILITY

These data are available from the Dryad Data Repository at the following DOI location: <https://doi.org/10.5061/dryad.fs4k13k>.

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REFERENCES

- Barea, L. P., & Watson, D. M. (2007). Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist. *Emu - Austral Ornithology*, 107, 203–209. <https://doi.org/10.1071/MU07003>
- Barlein, F. (2016). Migratory birds under threat. *Science*, 354, 547–548. <https://doi.org/10.1126/science.aah6647>
- Bateman, B. L., VanDerWal, J., & Johnson, C. N. (2012). Nice weather for bettings: Using weather events, not climate means, in species distribution models. *Ecography*, 35, 306–314. <https://doi.org/10.1111/j.1600-0587.2011.06871.x>
- Bauer, S., & Hoyer, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, 344, 54. <https://doi.org/10.1126/science.1242552>
- Bennett, J. M., Nimmo, D. G., Clarke, R. H., Thomson, J. R., Cheers, G., Horrocks, G., ... Mac Nally, R. (2014). Resistance and resilience: Can the abrupt end of extreme drought reverse avifaunal collapse? *Diversity and Distributions*, 20, 1321–1332.
- Betts, M. G., Phalan, B., Frey, S., Rousseau, J., & Yang, Z. (2018). Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity and Distributions*, 24, 439–447. <https://doi.org/10.1111/ddi.12688>
- 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. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1259–1266. <https://doi.org/10.1098/rspb.2009.1525>
- Brodie, J. F. (2016). Synergistic effects of climate change and agricultural land use on mammals. *Frontiers in Ecology and the Environment*, 14, 20–26. <https://doi.org/10.1002/16-0110.1>
- Caughley, G. C., & Gunn, A. (1996). *Conservation Biology in Theory and Practice*. Cambridge, MA: Blackwell Science.
- Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, 114, E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>
- Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, 43, 783–791. <https://doi.org/10.2307/2531532>
- Cleugh, H. (2003). *Trees for Shelter - A Guide to Using Windbreaks on Australian Farms*. Canberra, Australia: Rural Industries Research and Development Corporation.
- 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. *Nature Communications*, 7, 11666. <https://doi.org/10.1038/ncomms11666>
- Cunningham, R. B., Lindenmayer, D. B., Crane, M., Michael, D., & MacGregor, C. (2007). Reptile and arboreal marsupial response to replanted vegetation in agricultural landscapes. *Ecological Applications*, 17, 609–619. <https://doi.org/10.1890/05-1892>
- Cunningham, R. B., Lindenmayer, D. B., Barton, P., Ikin, K., Crane, M., Michael, D., ... Stein, J. (2014). Cross-sectional and temporal relationships between bird occupancy and vegetation cover at multiple spatial scales. *Ecological Applications*, 24, 1275–1288. <https://doi.org/10.1890/13-0872.1>
- Deo, R. C., Syktus, J., McAlpine, C., Lawrence, P., McGowan, H., & Phinn, S. R. (2009). Impact of historical land cover change on daily indices of climate extremes including droughts in eastern Australia. *Geophysical Research Letters*, 38, <https://doi.org/10.1029/2009GL037666>.
- Dingle, H. (2008). Bird migration in the southern hemisphere: A review comparing continents. *Emu - Austral Ornithology*, 108, 341–359. <https://doi.org/10.1071/MU08010>
- Driscoll, D. A., Felton, A., Gibbons, P., Felton, A. M., & Munro, N. T. (2011). Priorities in policy and management when existing biodiversity stressors interact with climate-change. *Climatic Change*, 111, 533–557. <https://doi.org/10.1007/s10584-011-0170-1>
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elton, C. S. (1927). *Animal Ecology*. London, UK: Sidgwick and Jackson.
- 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. *Diversity and Distributions*, 14, 38–46. <https://doi.org/10.1111/j.1472-4642.2007.00411.x>
- Fischer, J., Stott, J., Zerger, A., Warren, G., Sherrin, K., & Forrester, R. I. (2009). Reversing a tree regeneration crisis in an endangered ecoregion. *Proceedings of the National Academy of Sciences*, 106, 10386–10391. <https://doi.org/10.1073/pnas.0900110106>
- García, R. A., Cabeza, M., Rahbek, C., & Araujo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344, 486–487. <https://doi.org/10.1126/science.1247579>
- Gardner, J. L., Symonds, M. R., Joseph, L., Ikin, K., Stein, J., & Kruuk, L. E. (2016). Spatial variation in avian bill size is associated with humidity in summer among Australian passerines. *Climate Change Responses*, 3, 11. <https://doi.org/10.1186/s40665-40016-40026-z>
- Garnett, S., Szabo, J., & Dutton, G. (2011). *The Action Plan for Australian Birds 2010*. Melbourne, VIC: CSIRO Publishing.
- Garnett, S., J. Woinarski, D. B. Lindenmayer, & P. Latch (Eds.) (2017). *Success in Conservation*. Melbourne, VIC: CSIRO Publishing.
- Garnett, S., Duursma, D. E., Ehmke, G., Guay, P.-J., Stewart, A., Szabo, J. K., ... Franklin, D. C. (2015). Biological, ecological, conservation and legal information for all species and subspecies of Australian Bird. *Scientific Data*, 2, 150061. <https://doi.org/10.1038/sdata.2015.61>
- Gibbs, H. M., Chambers, L. E., & Bennett, A. F. (2011). Temporal and spatial variability of breeding in Australian birds and the potential implications of climate change. *Emu - Austral Ornithology*, 111, 283–291.
- Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R., & Franco, A. M. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters*, 19, 308–317. <https://doi.org/10.1111/ele.12569>
- Greenville, A. C., Burns, E., Dickman, C. R., Keith, D. A., Lindenmayer, D. B., Morgan, J. W., ... Wardle, G. M. (2018). Biodiversity responds to increasing climatic extremes in a biome-specific manner. *Science of the Total Environment*, 634, 382–393. <https://doi.org/10.1016/j.scitotenv.2018.03.285>
- Guillemete, M., Woakes, A. J., Larochelle, J., Polymeropoulos, E. T., Granbois, J.-M., Butler, P. J., ... Portugal, S. J. (2016). Does hyperthermia constrain flight duration in a short-distance migrant? *Philosophical Transactions of the Royal Society Series B*, 371, 20150386.
- Hennan, C. B., Goodman, B. A., & White, C. R. (2015). The influence of climate on avian nest construction across large geographic gradients. *Global Ecology and Biogeography*, 24, 1203–1211.
- Hutchinson, M. F. (1995). Stochastic space-time weather models from ground-based data. *Agricultural and Forest Meteorology*, 73, 237–264. [https://doi.org/10.1016/0168-1923\(94\)05077-J](https://doi.org/10.1016/0168-1923(94)05077-J)
- Ikin, K., Mortelliti, A., Stein, J., Michael, D., Crane, M., Okada, S., ... Lindenmayer, D. B. (2015). Woodland habitat structures are affected by both agricultural land management and abiotic conditions. *Landscape Ecology*, 30, 1387–1403. <https://doi.org/10.1007/s10980-015-0193-5>

- Illan, J., Thomas, C. D., Jones, J. A., Wong, W.-K., Shirley, S. M., & Betts, M. G. (2014). Precipitation and winter temperature predict long-term range-scale abundance changes in western North American birds. *Global Change Biology*, 20, 3351–3364. <https://doi.org/10.1111/gcb.12642>
- Keast, A. (1968). Seasonal movements in the Australian honeyeaters (Meliphagidae) and their ecological significance. *Emu - Austral Ornithology*, 67, 159–210. <https://doi.org/10.1071/MU967159>
- Krebs, C. J. (1978). *The Experimental Analysis of Distribution and Abundance*. New York, NY: Harper and Row.
- Lane, P. W., & Nelder, J. A. (1982). Analysis of covariance and standardization as instances of prediction. *Biometrics*, 38, 613–621. <https://doi.org/10.2307/2530043>
- Liminana, R., Soutullo, A., Arroyo, B., & Urios, V. (2012). Protected areas do not fulfil the wintering needs of the trans-Saharan migratory Montagu's harrier. *Biological Conservation*, 145, 62–69.
- Lindenmayer, D. B., A. F. Bennett, & R. J. Hobbs (Eds.) (2010). *Temperate Woodland Conservation and Management*. Melbourne, VIC: CSIRO Publishing.
- 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. *Biodiversity and Conservation*, 25, 1587–1603.
- Lindenmayer, D. B., & Laurance, W. F. (2016). The ecology, distribution, conservation and management of large old trees. *Biological Reviews*, 92, 1434–1458. <https://doi.org/10.1111/brv.12290>
- Lindenmayer, D. B., Michael, D., Crane, M., Okada, S., Florance, D., Barton, P., & K., I. (2016b). *Wildlife Conservation in Farm Landscapes*. Melbourne, VIC: CSIRO Publishing.
- Lindenmayer, D. B., Northrop-Mackie, A. R., Montague-Drake, R., Crane, M., Michael, D., Okada, S., & Gibbons, P. (2012). Not all kinds of revegetation are created equal: Revegetation type influences bird assemblages in threatened Australian woodland ecosystems. *PLoS ONE*, 7, e34527. <https://doi.org/10.1371/journal.pone.0034527>
- Lindenmayer, D. B., Wood, J. T., & MacGregor, C. (2009). Do observer differences in bird detection affect inferences from large-scale ecological studies? *Emu - Austral Ornithology*, 109, 100–106. <https://doi.org/10.1071/MU08029>
- Lindenmayer, D. B., Lane, P., Westgate, M., Scheele, B., Foster, C., Sato, C., ... Robinson, N. (2018). Tests of predictions associated with temporal changes in Australian bird populations. *Biological Conservation*, 222, 212–221. <https://doi.org/10.1016/j.biocon.2018.04.007>
- 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. <https://doi.org/10.1890/10-2340.1>
- Mantyka-Pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, 18, 1239–1252. <https://doi.org/10.1111/j.1365-2486.2011.02593.x>
- Marchant, R., Guppy, S., & Guppy, M. (2016). The influence of ENSO and rainfall on the numbers of breeding pairs in a woodland bird community from south-eastern Australia. *Emu - Austral Ornithology*, 116, 254–261.
- McAlpine, C. A., Syktus, J., Deo, R. C., Lawrence, P. J., McGowan, H. A., Watterson, I. G., & Phinn, S. R. (2007). Modeling the impact of historical land cover change on Australia's regional climate. *Geophysical Research Letters*, 34, L22711. <https://doi.org/10.1029/2006GL022711>
- McGoldrick, J. M., & Mac Nally, R. (1998). Impact of flowering on bird community dynamics in some central Victorian eucalypt forests. *Ecological Research*, 13, 125–139. <https://doi.org/10.1046/j.1440-1703.1998.00252.x>
- McKenney, D. W., Hutchinson, M. F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., ... Owen, T. (2011). Customized spatial climate models for North America. *Bulletin of the American Meteorological Society*, 92, 1611–1622. <https://doi.org/10.1175/2011BAMS3132.1>
- McMahon, T. A., Finlayson, B. L., Haines, A. T., & Srikanthan, R. (1992). *Global Runoff - Continental Comparisons of Annual Flows and Peak Discharges*. Cremlingen, Germany: Catena Verlag.
- Moller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences*, 105, 16195–16200. <https://doi.org/10.1073/pnas.0803825105>
- 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. *Journal of Applied Ecology*, 53, 449–458.
- Parmesan, C. (1996). Climate and species' range. *Nature*, 383, 765–766. <https://doi.org/10.1038/382765a0>
- 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 S. J. Davies (Ed.), *Methods of Censusing Birds in Australia*, (pp. 55–63). 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.
- 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. <https://doi.org/10.1126/science.aac9180>
- Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Long-term population declines in Afro-Palaearctic migrant birds. *Biological Conservation*, 131, 93–105.
- Sato, C., Wood, J., Stein, J. A., Crane, M., Okada, S., Michael, D., ... Lindenmayer, D. B. (2016). Natural tree regeneration in agricultural landscapes: The implications of intensification. *Agriculture, Ecosystems & Environment*, 230, 98–104. <https://doi.org/10.1016/j.agee.2016.05.036>
- Scheele, B. C., Foster, C. N., Banks, S. C., & Lindenmayer, D. B. (2017). Niche contractions in declining species: Mechanisms and consequences. *Trends in Ecology and Evolution*, 32, 346–355. <https://doi.org/10.1016/j.tree.2017.02.013>
- Seddon, W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, 531, 229–232. <https://doi.org/10.1038/nature16986>
- Sergio, F., Tanferna, A., DeStephanis, R., Jimenez, L. L., Blas, J., Tavecchia, G., ... Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, 515, 410–413. <https://doi.org/10.1038/nature13696>
- Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., ... Huey, R. B. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters*, 19, 1372–1385.
- Soderquist, T. R., & MacNally, R. (2000). The conservation value of mesic gullies in dry forest landscapes: Mammal populations in the box-ironbark ecosystem of southern Australia. *Biological Conservation*, 93, 281–291. [https://doi.org/10.1016/S0006-3207\(99\)00153-6](https://doi.org/10.1016/S0006-3207(99)00153-6)
- Steffen, W., Burbidge, A., Hughes, L., Kitching, R., Lindenmayer, D. B., Musgrave, W., ... Werner, P. (2009). *Australia's Biodiversity and Climate Change*. Melbourne, VIC: CSIRO Publishing.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, J.-S., & Lima, M. (2002). Ecological effects of climate variations. *Science*, 297, 1292–1296.
- Taylor, C., Caplat, P., Massimino, D., Johnston, A., Jonzen, N., Smith, H. G., & Lindstrom, A. (2015). Swedish birds are tracking temperature but not rainfall: Evidence from a decade of abundance changes. *Global Ecology and Biogeography*, 24, 859–872.
- 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. <https://doi.org/10.1038/nature22900>

- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348, 571–573. <https://doi.org/10.1126/science.aaa4984>
- van Dijk, A. I., Beck, H. E., Crossbie, R. S., de Jeu, R. A., Liu, Y. Y., Podger, G. M., ... 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 Resources Research*, 49, 1040–1057. <https://doi.org/10.1002/wrcr.20123>
- Vesk, P., Nolan, R., Thomson, J. W., Dorrrough, J. W., & Mac Nally, R. (2008). Time lags in the provision of habitat resources through re-vegetation. *Biological Conservation*, 141, 174–186.
- Wedderburn, R. W. M. (1974). Quasi-likelihood functions, generalized linear models and the Gauss-Newton method. *Biometrika*, 61, 439–447.
- Wenk, E. H., & Falster, D. (2015). Quantifying and understanding reproductive allocation schedules in plants. *Ecology and Evolution*, 5, 5521–5538.
- Will, A. P., Kitaiskaia, E. V., & Kitaysky, A. S. (2018). Red-legged kittiwake feathers link food availability to environmental changes in the Bering Sea. *Marine Ecology Progress Series*, 593, 261–274. <https://doi.org/10.3354/meps12509>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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BIOSKETCH

Professor **David Lindenmayer** leads a group of mid- and early-career researchers at The Australian National University with a focus on long-term ecological research and monitoring across a wide range of biomes including agri-ecological areas, forests, woodlands and heathlands. The work in these projects integrates high-quality long-term biodiversity data and long-term climate and vegetation cover data with subsequent analyses based on cutting edge statistical methods. A key part of the long-term work has been a focus on the ecological and environmental benefits of large-scale landscape restoration in the endangered woodlands of south-eastern Australia.

Author contribution: DL designed the study, assisted in data collection and led the writing of the manuscript. PL led the data analysis. MC coordinated the field surveys. All authors contributed to writing and editing the paper.