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Weather effects on birds of different size are mediated by long-term climate and vegetation type in endangered temperate woodlands

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Running Head: Interacting climate, weather and vegetation type effects on bird size

ABSTRACT

Species occurrence is influenced by a range of factors including habitat attributes, climate, weather and human landscape modification. These drivers are likely to interact, but their effects are frequently quantified independently. Here we report the results of a 13-year study of temperate woodland birds in south-eastern Australia to quantify how different sized birds respond to the interacting effects of: **(1)** short-term weather (rainfall and temperature in the 12 months preceding our surveys), **(2)** long-term climate (average rainfall and maximum and minimum temperatures over the period 1970 to 2014), and **(3)** broad structural forms of vegetation (old-growth woodland, regrowth woodland, and restoration plantings).

We uncovered significant interactions between bird body size, vegetation type, climate and weather. High short-term rainfall was associated with decreased occurrence of large birds in old-growth and regrowth woodland, but not in restoration plantings. Conversely, small bird occurrence peaked in wet years, but this effect was most pronounced in locations with a history of high rainfall, and was actually reversed (peak occurrence in dry years) in restoration plantings in dry climates. The occurrence of small birds was depressed - and large birds elevated - in hot years, except in restoration plantings which supported few large birds under these circumstances.

Our investigation suggests that different mechanisms may underpin contrasting responses of small and large birds to the interacting effects of climate, weather and vegetation type. A diversity of vegetation cover is needed across a landscape to promote the occurrence of different sized bird species in agriculture-dominated landscapes, particularly under variable weather conditions. Climate change is predicted to lead to widespread drying of our study region and restoration plantings, especially in currently climatically-wet areas may become critically important for conserving bird species, particularly small-bodied taxa.

KEYWORDS: Rainfall and temperature effects on biodiversity, climate change, weather, revegetation, birds, south-eastern Australia

INTRODUCTION

A core aim of ecology is to understand and quantify factors influencing the occurrence of organisms (Elith & Leathwick, 2009, Elton, 1927, Krebs, 1978). This is a major challenge because of the diversity of factors acting at different spatial and temporal scales that can affect when and where species occur (Fourcade *et al.*, 2017, Levin, 2009, Mackey & Lindenmayer, 2001). Yet, an understanding of these factors is essential for effective species conservation and management, particularly given the major extinction crisis currently facing the world’s biodiversity (Krebs, 2008, Worboys *et al.*, 2015).

Climate is a key large-scale factor shaping species occurrence (Elton, 1927, Krebs, 1978, Parmesan, 1996). Short-term weather is another factor that can affect species occurrence, with numerous studies documenting the effects of weather variables, including extremes of temperature and rainfall on various groups of biota (Bateman *et al.*, 2012, Gibbs *et al.*, 2011, Moran-Ordonez *et al.*, 2018, Stenseth *et al.*, 2002). Combined, climate and weather in part shape vegetation communities, which provide habitat for many vertebrate species (Levin, 2009, Morrison *et al.*, 2006).

Drivers of biodiversity decline, such as habitat loss and climate change, are often studied independently, but these drivers interact (Bowler *et al.*, 2018, Brodie, 2016, Driscoll *et al.*, 2011). For example, empirical analyses (e.g. Cox *et al.*, 2013, McAlpine *et al.*, 2007) and meta-analysis (Mantyka-Pringle *et al.*, 2012) suggest the negative effects of habitat loss may be exacerbated by climate change (Peci *et al.*, 2017, Stephens *et al.*, 2016, Urban, 2015). Similarly, the effects of climate change may be particularly pronounced during periods of extreme weather (McDonald *et al.*, 2015, Nimmo *et al.*, 2016, Sinclair *et al.*, 2016, Tayleur *et al.*, 2015). By contrast, the effects on some species of climate change or extreme weather can be buffered by habitat structure (Betts *et al.*, 2017). In addition, interactions between climate, weather and habitat are expected to influence the occurrence of species with different life-history attributes in different ways (Vollstadr *et al.*, 2017).

The preceding commentary suggests climate, weather, habitat characteristics and life-history attributes can be important determinants of species occurrence in terrestrial environments. How these four factors interact is, however, poorly known for species across the majority of ecosystems globally (Bowler *et al.*, 2018). Addressing this knowledge gap is important because it may help predict which kinds of species are likely to benefit from attempts to reverse habitat loss such as through large-scale restoration programs (see Crouzeilles *et al.*, 2016) in landscapes subject to both rapid climate change and extreme weather conditions. We used a large-scale (1.8 m ha), long-term (2002-2015) study of temperate woodland birds in south-eastern Australia to quantify the interacting effects of short-term weather, long-term climate, and vegetation on a suite of bird species of different body sizes. We focused our investigation of weather and climate to aspects of rainfall and temperature, and our investigation of vegetation to broad structural forms (i.e. old-growth woodland, regrowth woodland and restoration plantings) that are known to support different assemblages of birds (Lindenmayer *et al.*, 2012).

We examined bird body mass as it is a key ecological trait and linked to abundance, energy use, and geographic range size (Calder, 1984, Lomolino & Perault, 2007, Schmidt-Nielsen, 1984). Global analyses suggest that large-bodied vertebrates are at particular risk of decline (Tilman *et al.*, 2017). However, low body mass taxa are thought to be at risk from land clearing and other practices associated with agricultural production (Ripple *et al.*, 2017). In Europe, small-bodied birds are declining, whereas large species are increasing (Inger *et al.*, 2014). In contrast, in Australian temperate woodlands, recent temporal analyses have demonstrated that small-bodied birds, some of which are species of conservation concern, are increasing whereas large birds are declining (Lindenmayer *et al.*, 2018). As such, we focused on body size because it is correlated with bird temporal trends in our study region (Fig. 1), and is a useful general proxy for other life history attributes, such as diet, movement patterns, and nesting biology (see Fig. S1).

The overarching question which motivated our investigation was: *Is the effect of annual weather variation on bird occurrence related to bird body size, and are effects buffered by vegetation type and the long-term climatic characteristics of a location?* To answer this question, we tested three multi-facetted predictions about potential interacting drivers of occurrence of birds of different body size.

Prediction 1: Bird occurrence will increase in wet and decline in dry periods. Rainfall is a factor limiting plant growth in temperate woodlands (Lindenmayer *et al.*, 2010), and high rainfall can result in resource pulses (Illan *et al.*, 2014, Tayleur *et al.*, 2015) such as nectar, seeds and insect prey (Barea & Watson, 2007, McGoldrick & Mac Nally, 1998). Increases will occur for all birds but be greatest for small-bodied species because of their generally higher reproductive rates (Ford, 1989, Gill, 1995, Sæther, 1987), dependence on local resource availability (Schoener, 1968), and tendency to feed on insects (Figure S1), all of which allow populations to grow rapidly in response to favourable weather. For temperature effects, we predicted bird occurrence will be depressed by elevated temperature because of thermal stress (Gardner *et al.*, 2016, Sinclair *et al.*, 2016), with effects most pronounced for small birds given their higher volume to surface-area ratio.

Prediction 2: Rainfall effects will be buffered by vegetation type with positive responses to increased rainfall being greatest in old-growth woodland for all birds (irrespective of body size). This is because the large trees which characterize old-growth woodland (Ikin *et al.*, 2015) are generally absent in restoration plantings (Vesk *et al.*, 2008), with such trees producing the greatest pulses of resources in response to elevated rainfall (Lindenmayer & Laurance, 2016, Wenk & Falster, 2015). For temperature effects, the densely spaced trees in restoration plantings (Lindenmayer *et al.*, 2016a) will provide greater levels of shade relative to more open old-growth woodlands (Cleugh, 2003), and be favoured by small-bodied birds during periods of extreme heat.

Prediction 3: Increases of all birds (irrespective of size) after high rainfall will be muted on climatically-dry sites (characterized by low long-term average rainfall) as they may support fewer resources. We expected these buffering effects of long-term climate to be most marked for small birds as they have smaller territories (Schoener, 1968) and are more dependent on local resources than large birds (Ford, 1989, Gill, 1995). Given the potential for Australian environments to respond to pulse events such as high rainfall years (Greenville *et al.*, 2018, McMahon *et al.*, 1992), we also expected that short-term weather events would be proportionally more important than long-term climate in terms of their effects on all birds.

MATERIALS AND METHODS

Study area

Our study region was a 1.8 million ha agricultural area within the South-west Slopes region of New South Wales, south-eastern Australia (Fig. 2). The South-west Slopes was formerly dominated by temperate woodland (Lindenmayer *et al.*, 2010), but an estimated 85% of its original vegetation cover has been cleared to facilitate livestock grazing and cereal cropping. Subsequently, the region has been the target of major woodland restoration planting programs (Lindenmayer *et al.*, 2016a). There also has been significant natural regeneration of temperate woodlands, particularly over the past 15 years (Lindenmayer *et al.*, 2012). Thus, there are three broad structural kinds of vegetation cover: actively replanted (termed restoration plantings; Fig. 2b), regrowth woodland, that naturally regenerated after fire or following a reduction in grazing pressure (Fig. 2c) and old-growth woodland (Fig. 2d).

Study design

Our investigation was based on 203 sites covering three eucalypt-dominated vegetation growth types: restoration plantings (65 sites), old-growth woodland (72 sites), and regrowth woodland (66 sites). Restoration plantings were areas of planted native woody vegetation characterized by a mix of native 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 (2002) and many were 10-20 years old. Regrowth 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: **(1)** size (0.3-60.3 ha for restoration plantings, 0.5-53.8 ha for regrowth and old-growth woodland patches) and (2) the amount of woody vegetation cover (4% to 30%) in the surrounding landscape (Cunningham et al., 2014). Notably, we found only a weak correlation between vegetation type, patch size and measures of connectivity in the surrounding landscape (as determined using the metrics from the Circuitscape approach in McRae *et al.*, 2008).

Bird surveys and body-size data

We conducted eight spring bird surveys between 2002 and 2015 (Table 1). We completed bird surveys in spring because this is when the majority of species in our study area are present and actively calling. We gathered bird data using repeated five-minute point-interval counts (*sensu* Pyke & Recher, 1983) at 0 m, 100 m and 200 m along a fixed transect at each site. An expert observer recorded all bird species seen or heard within 50 m of the transect point. In any given year, each site was surveyed by at least two expert observers on different days, giving a minimum of six point-interval counts in each survey. We completed surveys between dawn and three hours after dawn with the order in which sites were surveyed on the second day of sampling reversed relative to the first day. We did not undertake surveys during poor weather (rain, high wind, fog or heavy cloud cover). These protocols reduced the effects of observer heterogeneity, day of survey effects, and time of day effects (Lindenmayer *et al.*, 2009).

We recorded a total of 177 species over the 13-year duration of this study. To facilitate detailed statistical analyses, we excluded species not present in at least 3% of the surveys in at least one of the vegetation types, leaving 41 species for inclusion in detailed statistical analyses (Table S1).

We extracted data on body size for the 41 species of birds from compilations of bird biology and ecology published in various ornithological monographs (e.g. Higgins, 1991-2006, Higgins, 2001, Higgins & Peter, 2002, Higgins *et al.*, 2001). Body sizes varied from 6–638 g with a median value of 50 g. Importantly, the Noisy Miner (*Manorina melanocephala*) which can structure bird communities in temperate woodlands (Mac Nally *et al.*, 2012) was rare or absent from many of our sites and has been declining in our study area over the past decade (Lindenmayer *et al.*, 2018). From a conservation perspective, eight bird species of conservation concern were recorded sufficiently often to be included among the 41 species modelled (see Fig. 1).

We explored relationships between body size and data we obtained on other life history attributes such as movement patterns, diet, foraging substrate, and nest type and found generally weak levels of correlations between them (Table S2). This confirmed out decision to focus on a single trait (*viz*: body size).

Climate and weather variables

For use in statistical modelling of bird occupancy, we compiled information for the long-term averages (1970-2014) for three climate variables: mean annual rainfall, mean maximum temperature, and mean minimum temperature. The field sites in our investigation encompassed a gradient from climatically wet and cool through to dry and hot locations (Fig. S2).

We also compiled information for three short-term weather variables over a 12-month period preceding each survey as biologically meaningful potential explanatory variables for statistical modelling. 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). Importantly, our investigation was conducted between 2002-2015 and spanned the Millennium Drought and a subsequently much wetter period (Nimmo *et al.*, 2016, van Dijk *et al.*, 2013, and see Fig. S3).

Our long-term climate and short-term weather variables were time-series data derived from monthly national grids (Hutchinson et al., 2014; http://www.emast.org.au/our-infrastructure/observations/anuclimate_data/). 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 daily climate surfaces as well as long-term climate averages (e.g. McKenney *et al.*, 2011).

We found that all three long-term climate variables were strongly correlated: the two temperature variables positively with one another, and negatively with rainfall (see Table S3). Given correlations between rainfall and temperature variables, we elected to fit a separate model for each of rainfall, minimum temperature and maximum temperature.

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 (N = 41 species; see Table S1). Specifically, we modelled the percentage 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 intercept for species, assuming a normal distribution for the variation of mean percentage occurrence on the logit scale. We also included a random effect for site, to account for the repeated-measurements structure of the data.

In each of the three models, we fitted fixed effects for the three vegetation types, linear effects of the long-term climate variables (mean annual rainfall, mean maximum temperature, or mean minimum temperature averaged over the period 1970 to 2014), a linear effect of the three short-term weather variables (mean monthly rainfall, mean monthly maximum and mean monthly minimum temperature), and a quadratic effect of body size on the log scale. We estimated both linear and quadratic effects (on the log scale of body-size) because we expected that any effects would be reasonably linear on this scale, and that an additional quadratic effect in the model would allow us to assess how well this linearity held. We also modelled interactions between all of these variables. Each model also included a random slope for time 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). For example, the fixed effects in the model we fitted for rainfall was:

vegetation type*(body size+ body size^2)*long-term rainfall*rainfall over 12 months + time.

We constructed models for maximum temperature and then minimum temperature by replacing the rainfall variables in the above with the temperature variables. We fitted models using GenStat (Release 18.1) 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.

RESULTS

We identified a significant four-way interaction between long-term climate, short-term weather, vegetation type, and bird body size in all three of the fitted models (Tables S4-S6). Weather variables had important effects on bird occurrence with greater effect sizes than those for climate (Tables S4-6). However, effects in all three analyses were dominated by an interaction between vegetation type and body size, where small birds were found almost twice as often in plantings as in old-growth or regrowth, whereas the reverse was true for large birds.

Rainfall effects

The linear and quadratic components of the four-way interaction mentioned above had Wald statistics of 9.8 and 9.1 (P=0.01 and 0.01, Table S4). In old-growth and regrowth woodland, the occurrence of large-bodied birds was highest during periods of low rainfall; but climatically-wet locations supported fewer large-bodied birds during periods of high rainfall (Fig. 3). By contrast, small birds were at highest abundance in wet years, particularly in regrowth sites. Climatically-wet regrowth habitats showed the highest variation in bird assemblages as a function of rainfall; in wet years these sites were dominated by small birds, while in dry years large birds were more common. Indeed, for small birds, occurrence was always lowest during dry years, except in climatically-dry plantings.

Temperature effects

Our results for long-term and short-term temperature were similar to those for rainfall, but in reverse – which was expected given the strong inverse correlation between rainfall and temperature (Table S4). The effects for the temperature-based climate and weather variables were weaker than those for rainfall. However, in the model for maximum temperature, the quadratic component of the four-way interaction between body size, long-term temperature, 12 month mean temperature and vegetation type was again significant, with a Wald statistic of 7.2 (P = 0.03, Table S5). In the model for minimum temperature, the linear component was statistically significant, with a Wald statistic of 8.5 (P=0.02, Table S6). We found that large birds were more common than small birds during hot years in both regrowth and old-growth habitats. However, this pattern was reversed in cold years, with small birds becoming more common at the expense of large birds (Fig. 4). In plantings, occurrence of small birds was always highest in years with low maximum temperatures.

The effects we uncovered for minimum temperature were broadly similar to those outlined for maximum temperature, with the most pronounced responses being for large birds in old-growth and regrowth woodland. In both vegetation types, large bird occurrence was elevated in hot years, but not in cool years (Table S5, Fig. S4).

DISCUSSION

Patterns of species occurrence are determined by multiple drivers (Krebs, 1978, Levin, 2009), including weather conditions, long-term climate, and vegetation cover (Brodie, 2016, Mackey & Lindenmayer, 2001). These drivers also may interact with species life history traits (Vollstadr *et al.*, 2017). Previous research has compared the effects on birds of land cover and climate attributes (e.g. Howard *et al.*, 2015, Nimmo *et al.*, 2016), but interactions with weather and their intersection with key life history characteristics (such as body size) have rarely been investigated. We therefore sought to extend previous studies by answering the question: *Is the effect of annual weather variation on bird occurrence related to bird body size, and are effects buffered by vegetation type and the long-term climatic characteristics of a location?*

We found bird responses to short-term weather varied markedly depending on bird body size, broad vegetation type, and long-term climate. Some of our key results contrasted strongly with those expected under the three multi-facetted predictions we outlined at the outset of this investigation. A simple prediction, especially for temperate woodlands (where rainfall can often be a limiting factor; Lindenmayer *et al.*, 2010), was that bird occurrence would increase during wet periods and decline during dry periods (Marchant *et al.*, 2016; although see Bennett *et al.*, 2014). Consistent with this (see Prediction #1 in the Introduction), small bird occurrence was positively associated with wet years. The effects of rainfall were buffered by vegetation type but in more complex ways than forecast in Prediction #2. The increased occurrence of small-bodied birds in wet years was not marked in old-growth woodland (in contrast with Prediction #2) but occurred primarily in restoration plantings and regrowth woodland. As predicted at the outset of this study (see Prediction #3), the increased occurrence of small-bodied birds was most pronounced in climatically-wet sites (Fig. 3). Opposite to Prediction #1, and in contrast to the pattern for small birds, we unexpectedly found that the occurrence of large-bodied birds was elevated in dry years compared with wet years. These effects were buffered by vegetation type with the greatest increase in large-bodied birds occurring in old-growth, but also in regrowth woodland.

The results of our investigation also contained evidence of interactions between body size, vegetation type, and temperature (both as a short-term weather variable and as a long-term climate variable) (Fig. 4, Tables S5-S6). Small and large birds exhibited marked differences in response to maximum temperature. Consistent with Prediction #1, the occurrence of small birds was depressed in hot years. However, unexpectedly, large-bodied species exhibited the opposite response. These differing responses were broadly consistent across long-term cool versus hot sites, but were mediated by vegetation type. Opposite to Prediction #2, we found that large birds responded positively to hot years in old-growth and regrowth woodland but not in restoration plantings. Small birds were more prevalent in cool years, but differences between hot and cool years were lower in restoration plantings than old-growth or regrowth woodland (Fig. 4). This result suggests that, consistent with Prediction #2, restoration plantings reduced the effects of temperature on small-bodied birds.

At the outset of this study we expected that short-term weather events would be more important than long-term climate in terms of their effects on all birds (see Prediction #3). Effect sizes in our statistical models (see Table S4-6) were broadly congruent with this *a priori* prediction and consistent with earlier observations of the potential for Australian environments to respond to pulse events such as high rainfall years (McMahon *et al.*, 1992, Greenville *et al.*, 2018).

Studies elsewhere in the world have revealed important relationships between climate and weather variables and vegetation structure. For example, work in the forests of the Pacific Northwest of the USA has shown that old-growth forests buffer the effects of temperature (Frey *et al.*, 2016), as well as the effects of temperature increases, on some species of birds (Betts *et al.*, 2017). Similarly, Nimmo *et al.* (2016) found that riparian vegetation was an important refuge for woodland birds during prolonged droughts, especially wetter areas on fertile soils. These findings, together with the results of the study reported here, suggest that particular structural kinds of vegetation cover may act as micro-refuges for weather and/or climate-sensitive taxa.

Different mechanisms may underpin contrasting responses of small and large birds to the *interacting effects of climate, weather and vegetation type*

Several (and non-mutually exclusive) mechanisms may explain the differential impacts of weather, climate, and vegetation type on birds of different body sizes. It is possible that the increase in small birds in wet years could be due to high rainfall providing a pulse in resources (Illan *et al.*, 2014, Tayleur *et al.*, 2015) such as food (Barea & Watson, 2007, McGoldrick & Mac Nally, 1998), but also influencing nesting biology (Gibbs *et al.*, 2011, Heenan *et al.*, 2015, Marchant *et al.*, 2016). Most small birds are insectivorous in our study (Fig. S1), and insects can pulse rapidly in response to rainfall. A resource pulse could lead to increased survival and reproduction for small birds, particularly in denser vegetation types which provide many nesting and food resources (Barrett *et al.*, 2008, Lindenmayer *et al.*, 2018). Moreover, small birds are also (on average) able to increase in population more rapidly than large birds, due to short incubation periods, short time to maturation, and a trend for greater capacity for multiple clutches per season (Ford, 1989, Gill, 1995, Sæther, 1987). Notably, other work in Australia has shown that climate and weather can interact to influence reproductive biology in birds, such as the kinds of insulative materials used in nest construction (Heenan *et al.*, 2015).

An alternative explanation for the pattern of greater occurrence of small birds in wet years is that dry years tend to be hotter, and hot temperatures can disproportionately affect small birds due to sensitivity to temperature extremes (Gardner *et al.*, 2016). The high density of trees in restoration plantings (Cleugh, 2003) may provide critical shading effects, which may explain why differences between hot and cool years were lower in planting sites relative to generally more open vegetation environments such as in old-growth or regrowth woodlands. The lack of an increase in small birds in wet years on long-term dry sites was perplexing, however. It is possible that wetter conditions at such sites do not trigger breeding pulses in smaller-bodied bird species. If this was the case, it may be indicative of large-scale source-sink dynamics (*sensu* Pulliam *et al.*, 1992), whereby the long-term persistence of small-bodied bird species at long-term climatically-dry locations may be a product of dispersal of offspring born in long-term wet sites. Detailed, large-scale and long-term dispersal and allied site occupancy studies would be required to determine if such spatial demographic patterns were occurring.

Large birds exhibited markedly different responses to long-term climate, short-term weather, and vegetation type (and interactions between these key variables) relative to small birds. Large birds typically have a longer incubation period and time to maturation and may therefore be responsive to favourable weather conditions over longer periods than small-bodied birds (including over the 12-month temporal scale of this investigation). An additional or alternative explanation might be that in wet (and cool) years, large birds, which typically have larger territories and greater dispersal abilities than small birds (Schoener, 1968), may actively use the entire agricultural landscape (including the primarily cleared matrix surrounding remnant vegetation), and therefore may spend less time (and so are less often detected) in the wooded habitats patches where our study sites were located. In contrast, in dry and hot years, these species may focus their activities in old-growth and regrowth woodland patches. Further research focusing on long-term dynamics of birds in patches and the surrounding matrix environments is critical to understanding holistic use of landscapes, and in turn improve conservation action across the landscape (and through time).

Implications for management

The results of this study have several important implications for land management. First, given the positive effects of high rainfall were most pronounced on climatically-wet sites, there may be a need to focus management (such as active restoration efforts) in wet climates to maximize conservation return on investment, particularly for small birds. Second, given that climate change is predicted to result in drying in our study region (Steffen *et al.*, 2009), it is likely that more sites will change from experiencing climatically-wet to climatically-dry conditions. This could have important consequences, particularly for small birds in this region, if drying climactic conditions no longer allow small bird populations to increase during periods of wet weather. Third, our findings suggest that restoration plantings, regrowth woodlands and old-growth woodlands act as different habitats for birds, with the responses varying as a function of body size, long-term climate and short-term weather. This underscores the proposition that a diversity of structural vegetation types is needed to maximize the array of bird species that persist within woodland environments in landscapes dominated by agriculture (Ikin *et al.*, 2018). However, there are some important nuances beyond the collective value of these vegetation assets. For example, restoration plantings were particularly important for small birds in wet years and on long-term climatically-wet sites. In contrast, regrowth woodland appeared to be valuable for a greater range of bird species (as reflected by their body sizes) over a greater range of weather conditions and climate. Indeed, we found that regrowth woodland supported elevated levels of occurrence of large birds on climatically-wet sites in dry years and small birds on climatically-wet sites in wet years (Fig. 3). There also was evidence that in regrowth woodland, the occurrence of small birds was greater in cool years, while large birds were more common in hot years (Fig. 4). Thus, there was evidence of temporal partitioning of this vegetation resource by birds of different sizes. A fourth key finding from this study was that small birds benefit from management activities like the establishment of restoration plantings whereas large birds generally do not. There may be a significant lag period (potentially exceeding several decades) before restoration plantings become suitable for large birds. Recent changes in legislation making it easier to clear restoration plantings (http://www.environment.nsw.gov.au/vegetation/) may preclude the long-term recruitment of suitable new woodland habitat for large-bodied bird species, including those of conservation concern such as the Superb Parrot (*Polytelis swainsonii*).

Previous work has indicated that regrowth woodland and restoration plantings support some species of conservation concern (Lindenmayer *et al.*, 2016a), and hence these areas may play an important role in acting as a kind of micro-refugia from the effects of habitat loss. The role of these same areas in supporting bird species during periods of weather extremes, such as depressed rainfall, indicates they also may play a role in acting as micro-scale weather refuges. This dual refugial role work suggests that targeted local-scale actions such as the protection of existing habitat and the restoration of native vegetation cover may be particularly important for increasing the persistence of bird biota in the face of increasingly variable climates and extreme weather events (Nimmo *et al.*, 2016, Oliver *et al.*, 2016). Indeed, a key part of climate-change adaptation for bird biota will be to ensure not only a diversity of kinds of vegetation cover across agricultural landscapes, but also the establishment of more areas of restoration plantings. These may be important in currently climatically-wet areas, particularly for small-bodied taxa.

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REFERENCES

Barea LP, Watson DM (2007) Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist. Emu, **107**, 203-209.

Barrett GW, Freudenberger D, Drew A, Stol J, Nicholls AO, Cawsey EM (2008) Colonisation of native tree and shrub plantings by woodland birds in an agricultural landscape. Wildlife Research, **35**, 19-32.

Bateman BL, VanDerWal J, Johnson CN (2012) Nice weather for bettongs: using weather events, not climate means, in species distribution models. Ecography, **35**, 306-314.

Bennett JM, Nimmo DG, Clarke RH *et al.* (2014) Resistance and resillience: can the abrupt end of extreme drough reverse avifaunal collapse? Diversity and Distributions, **20**, 1321-1332.

Betts MG, Phalan B, Frey S, Rousseau J, Yang Z (2017) Old-growth forests buffer climate-sensitive bird populations from warming. Diversity and Distributions, **24**, 439-447.

Bowler DE, Heldbjerg H, Fox AD, O'Hara RB, Bohning-Gaese K (2018) Disentangling the effects of multiple environmental drivers on population changes within communities. Journal of Animal Ecology, **87**, 1034-1045.

Brodie JF (2016) Synergistic effects of climate change and agricultural land use on mammals. Frontiers in Ecology and Environment, **14**, 20-26.

Calder WA (1984) *Size, function and life history,* Cambridge, Massachusetts, Harvard University Press.

Cleugh H (2003) *Trees for Shelter - a guide to using windbreaks on Australian farms,* Canberra, Australia, Rural Industries Research and Development Corporation.

Cox WA, Thompson FR, Reidy JL, Faaborg J (2013) Temperature can interact with landscape factors to affect songbird productivity. Global Change Biology, **19**, 1064-1074.

Crouzeilles R, Curran M, Ferreira MS, Lindenmayer DB, Grelle CEV, Rey Benayas JM (2016) A global meta-analysis on the ecological drivers of forest restoration success. Nature Communications, **7**.

Cunningham RB, Lindenmayer DB, Barton P *et al.* (2014) Cross-sectional and temporal relationships between bird occupancy and vegetation cover at multiple spatial scales. Ecological Applications, **24**, 1275-1288.

Driscoll DA, Felton A, Gibbons P, Felton AM, Munro NT (2011) Priorities in policy and management when existing biodiversity stressors interact with climate-change. Climatic Change, **111**, 533-557.

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

Elton CS (1927) *Animal Ecology,* London, Sidgwick and Jackson.

Ford HA (1989) *Ecology of birds. An Australian perspective,* Chipping Norton, Surrey Beatty and Sons.

Fourcade Y, Ranius T, Ockinger E (2017) Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configfuration: Implications for climate-driven range shift in a butterfly. Journal of Animal Ecology, **86**, 1339-1351.

Frey S, Hadley A, Johnson S, Schulze M, Jones JA, Betts MG (2016) Spatial models reveal the microclimate buffering capacity of old-growth forests. Science Advances, **2**, 4, e1501392.

Gardner JL, Symonds MR, Joseph L, Ikin K, Stein J, Kruuk LE (2016) Spatial variation in avian bill size is associated with humidity in summer among Australian passerines. Climate Change Responses, **3**: 11.

Gibbs HM, Chambers LE, Bennett AF (2011) Temporal and spatial varaibaility of breeding in Australian birds and the potential implications of climate change. Emu, **111**, 283-291.

Gill FB (1995) *Ornithology,* New York, W.H. Freeman and Company.

Greenville AC, Burns E, Dickman CR *et al.* (2018) Biodiversity responds to increasing climatic extremes in a biome-specific manner. Science of the Total Environment, **634**, 382-393.

Heenan CB, Goodman BA, White CR (2015) The influence of climate on avian nest construction across large geographicla gradients. Global Ecology and Biogeography, **24**, 1203-1211.

Higgins PJ (ed) (1991-2006) *Handbook of Australian, New Zealand and Antarctic Birds. Volumes 1-6,* Melbourne, Oxford University Press.

Higgins PJ (ed) (2001) *Handbook of Australian, New Zealand and Antarctic birds. Volume 4. Parrots to Dollarbird*, Melbourne, Oxford University Press.

Higgins PJ, Peter JM (eds) (2002) *Handbook of Australian, New Zealand and Antarctic Birds. Pardalotes to Shrike-thrushes*, Melbourne, Oxford University Press.

Higgins PJ, Peter JM, Steele WK (2001) *Handbook of Australian, New Zealand and Antarctic birds. Volume 5: Tyrant-flycatchers to chats,* Melbourne, Australia, Oxford University Press.

Howard C, Stephens PA, Pearce-Higgins JW, Gregory RD, Willis SG (2015) The drivers of avian abundance: patterns in the relative abundance of climate and land use. Global Ecology and Biogeography, **24**, 1249-1260.

Hutchinson MF (1995) Stochastic space-time weather models from ground-based data. Agricultural and Forest Meteorology, **73**, 237-264.

Ikin K, Mortelliti A, Stein J *et al.* (2015) Woodland habitat structures are affected by both agricultural land management and abiotic conditions. Landscape Ecology, **30**, 1387-1403.

Ikin K, Tulloch AI, Ansell D, Lindenmayer DB (2018) Old growth, regrowth, and planted woodland provide complementary habitat for threatened woodland birds. Biological Conservation, **223**, 120-128.

Illan J, Thomas CD, Jones JA, Wong W-K, Shirley SM, Betts MG (2014) Precipitation and winter temperature predict long-term range-scale abundance changes in western North American birds. Global Change Biology, **20**, 3351-3364.

Inger R, Gregory R, Duffy JP, Stott I, Vorisek P, Gaston KJ (2014) Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology Letters, **18**, 1, 28-36.

Krebs CJ (1978) *Ecology: The experimental analysis of distribution and abundance,* New York, Harper and Row.

Krebs CJ (2008) *The Ecological World View*, Melbourne, CSIRO Publishing.

Lane PW, Nelder JA (1982) Analysis of covariance and standardization as instances of prediction. Biometrics, **38**, 613-621.

Levin SA (ed) (2009) *The Princeton Guide to Ecology*, Princeton, Princeton University Press.

Lindenmayer DB, Bennett AF, Hobbs RJ (eds) (2010) *Temperate Woodland Conservation and Management*, Melbourne, CSIRO Publishing.

Lindenmayer DB, Lane P, Westgate M *et al.* (2018) Tests of predictions associated with temporal changes in Australian bird populations. Biological Conservation, **222**, 212-221.

Lindenmayer DB, Lane PW, Barton PS, Crane M, Ikin K, Michael DR, Okada S (2016a) Long-term bird colonization and turnover in restored woodlands. Biodiversity and Conservation, **25**, 1587-1603.

Lindenmayer DB, Laurance W (2016) The ecology, distribution, conservation and management of large old trees. Biological Reviews, **92**, 1434-1458.

Lindenmayer DB, Northrop-Mackie AR, 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.

Lindenmayer DB, Wood JT, MacGregor C (2009) Do observer differences in bird detection affect inferences from large-scale ecological studies? Emu, **109**, 100-106.

Lomolino MV, Perault DR (2007) Body size variation in mammals in a fragmented, temperate rainforest. Conservation Biology, **21**, 1059-1069.

Mac Nally R, Bowen M, Howes A, McAlpine CA, Maron M (2012) Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. Ecology, **93**, 668-678.

Mackey BG, Lindenmayer DB (2001) Towards a hierarchical framework for modelling the spatial distribution of animals. Journal of Biogeography, **28**, 1147-1166.

Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. Global Change Biology, **18**, 1239-1252.

Marchant R, Guppy S, Guppy M (2016) The influence of ENSO and rainfall on the numbers of breeding pauirs in a woodland bird community from south-eastern Australia. Emu, **116**, 254-261.

McAlpine CA, Syktus J, Deo RC, Lawrence PJ, McGowan HA, Watterson IG, Phinn SR (2007) Modeling the impact of historial land cover change on Australia's regional climate. Geophysical Research Letters, **34**, 22, L22711.

McDonald PJ, Luck GW, Dickman CR, Ward SJ, Crowther MS (2015) Uisng multiple-source occurrence data to identify patterns and drivers of decline in arid-dwelling Australian marsupials. Ecography, **38**, 1090-1100.

McGoldrick JM, Mac Nally R (1998) Impact of flowering on bird community dynamics in some central Victorian eucalypt forests. Ecological Research, **13**, 125-139.

McKenney DW, Pedlar JH, Rood RB, Price D (2011) Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. Global Change Biology, **17**, 2720-2730.

McMahon TA, Finlayson BL, Haines AT, Srikanthan R (1992) *Global Runoff - Continental Comparisons of Annual Flows and Peak Discharges*, Cremlingen, Germany, Catena Verlag.

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution and conservation. Ecology, **89**, 2712-2724.

Moran-Ordonez A, Briscoe N, Wintle BA (2018) Modelling species responses to extreme weather provides new insights into constraints on range and likely climate change impacts for Australian mammals. Ecography, **41**, 308-320.

Morrison ML, Marcot BG, Mannan RW (2006) *Wildlife-Habitat Relationships. Concepts and Applications*, Washington, D.C., Island Press.

Nimmo DG, Haslem A, Radford JQ, Hall M, Bennett AF (2016) Riparian tree cover enhances the resistance and stability of woodland bird communicaties during an extreme climate event. Journal of Applied Ecology, **53**, 449-458.

Oliver TH, Smither RJ, Beale CM, Watts K (2016) Are existing biodiversity conservation strategies appropriate in a changing climate? Biological Conservation, **193**, 17-26.

Parmesan C (1996) Climate and species' range. Nature, **383**, 765-766.

Peci GT, Araujo MB, Bell JD *et al.* (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, **355**, 1389.

Pulliam HR, Dunning JB, Liu J (1992) Population dynamics in complex landscapes: a case study. Ecological Applications, **2**, 165-177.

Pyke GH, Recher HF (1983) Censusing Australian birds: a summary of procedures and a scheme for standardisation of data presentation and storage. In: *Methods of censusing birds in Australia.* (ed Davies SJ) pp Page. Perth, 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.

Ripple WJ, Wolf C, Newsome TM, Hoffmann M, Wirsing AJ, McCauley DJ (2017) Extinction risk is most acute for the world's largest and smallest vertebrates. Proceedings of the National Academy of Sciences.

Sæther B-E (1987) The influence of body weight on the covariation between reproductive traits in European birds. Oikos, **48**, 79-88.

Schmidt-Nielsen K (1984) *Scaling: Why is Animal Size so Important?,* Cambridge, England, Cambridge University Press.

Schoener TW (1968) Sizes of feeding territories among birds. Ecology, **49**, 123-141.

Seddon WR, Macias-Fauria M, Long PR, Benz D, Willis KJ (2016) Sensitivity of global terrestrial ecosystems to climate variability. Nature, **531**, 229-232.

Sinclair BJ, Marshall KE, Sewell MA *et al.* (2016) Can we predict ecotherm responses to climate change using thermal performance curves and body temperatures? Ecology Letters, **19**, 1372-1385.

Steffen W, Burbidge A, Hughes L *et al.* (2009) *Australia's Biodiversity and Climate Change,* Melbourne, CSIRO Publishing.

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan J-S, Lima M (2002) Ecological effects of climate variations. Science, **297**, 1292-1296.

Stephens PA, Mason LR, Green RE *et al.* (2016) Consistent response of bird populations to climate change on two continents. Science, **352**, 84-87.

Tayleur C, Caplat P, Massimino D, Johnston A, Jonzen N, Smith HG, 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 DR, Kimmel K, Polasky S, Packer C (2017) Future threats to biodiversity and pathways to their prevention. Nature, **546**, 73-81.

Urban MC (2015) Accelerating extinction risk from climate change. Science, **348**, 571-573.

van Dijk AI, Beck HE, Crossbie RS *et al.* (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.

Vesk P, Nolan R, Thomson JW, Dorrough JW, Mac Nally R (2008) Time lags in the provision of habitat resources through revegetation. Biological Conservation, **141**, 174-186.

Vollstadr MG, Ferger SW, Hemp A, Hpowell KM, Topfer T, Bohning-Gaese K, Schleuning M (2017) Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. Global Ecology and Biogeography.

Wedderburn RWM (1974) Quasi-likelihood functions, generalized linear models and the Gauss-Newton method. Biometrika, **61**, 439-447.

Wenk EH, Falster D (2015) Quantifying and understanding reproductive allocation schedules in plants: a lifetime of decisions. Ecology and Evolution, **5**, 5521-5538.

Worboys GL, Lockwood M, Kothari A, Feary S, Pulsford I (eds) (2015) *Protected Area Governance and Management*, Canberra, Australia, ANU Press.

FIGURE CAPTIONS

Figure 1: Mean percent annual change (2002 – 2015) in occurrence of 41 bird species in Australian temperate woodlands, shown as a function of body mass. Redrawn from data in Lindenmayer et al. (2018). Labels refer to species of conservation concern.

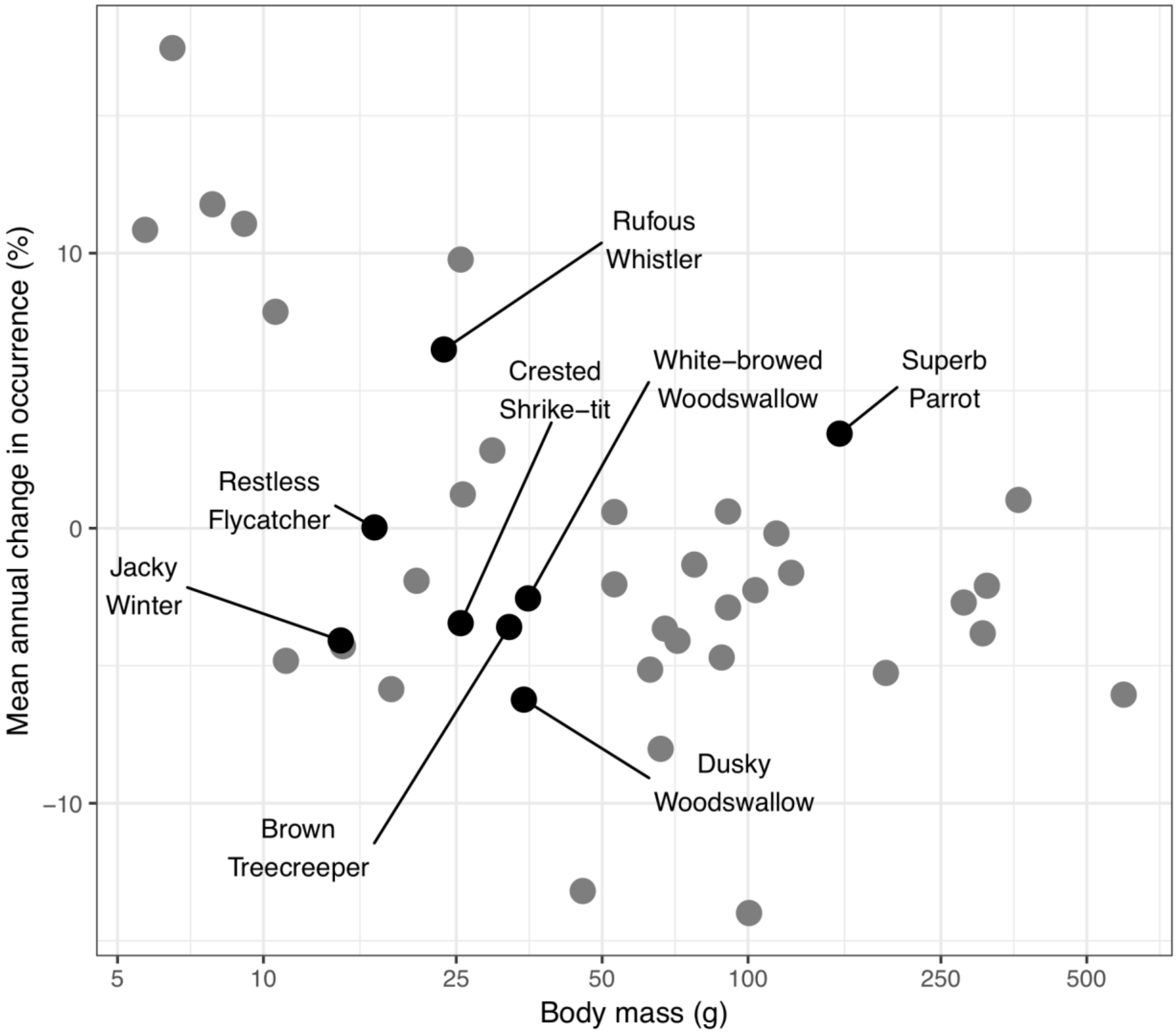
Figure 2. Location of the study area and field sites in the South-west Slopes of south-eastern Australia (a), showing the three dominant vegetation types investigated in this study: plantings (b), regrowth (c) and old-growth woodlands (d).

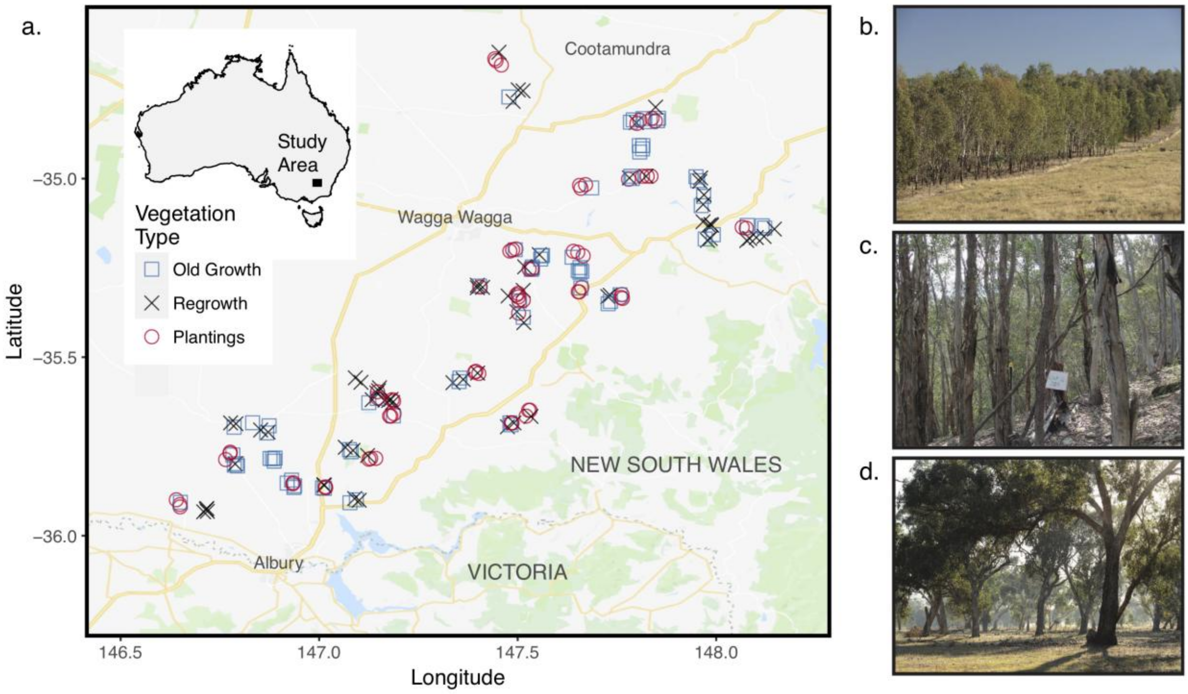
Figure 3. Predictions of bird occurrence (shown on the log scale) as a function of body mass (log scale; x axis) and mean annual rainfall (y axis), for each of three vegetation types (columns) and for sites in the 10th and 90th percentiles of long-term rainfall (top and bottom rows, respectively). Contours are calculated independently for each subpanel.

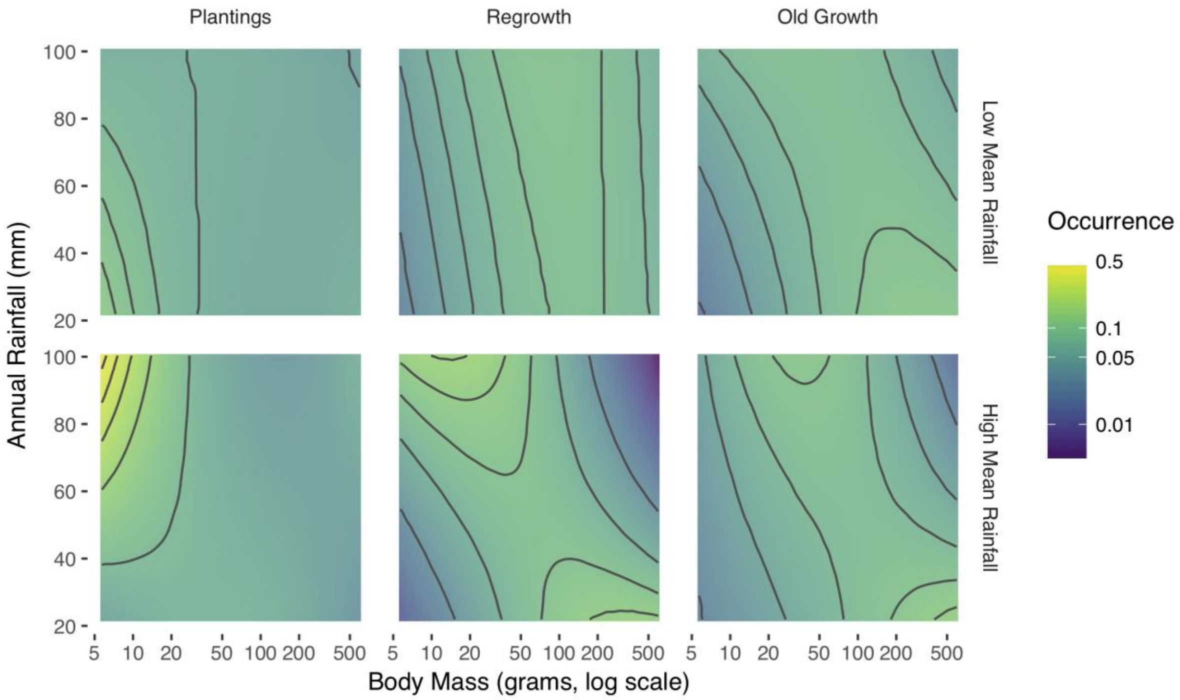
Figure 4. Predictions of bird occurrence (shown on the log scale) as a function of body mass (log scale; x axis) and mean maximum temperature (y axis), for each of three vegetation types (columns) and for sites in the 10th and 90th percentiles of long-term maximum temperatures (top and bottom rows, respectively). Contours are calculated independently for each subpanel.

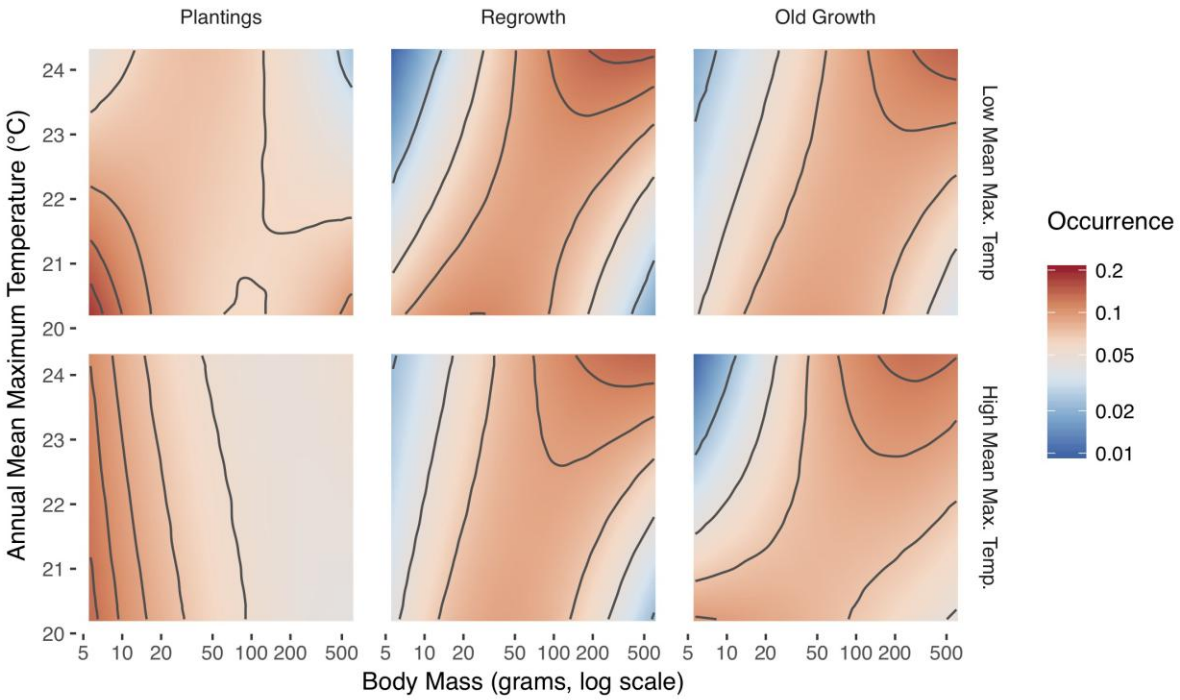
Table 1. Number of sites surveyed in each vegetation type in each of the eight spring surveys conducted between 2002 and 2015.

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**	**1538**


Rufous Whistler
Crested Shrike−tit
White−browed Woodswallow
Superb Parrot
Restless Flycatcher
Jacky Winter
Brown Treecreeper
Dusky Woodswallow
Mean annual change in occurrence (%)
10
0
−10
5
10
25
50
100
250
500
Body mass (g)


a.
Study Area
Vegetation Type
Old Growth
Regrowth
Plantings
Cootamundra
Wagga Wagga
NEW SOUTH WALES
VICTORIA
Albury
Latitude
−35.0
−35.5
−36.0
146.5
147.0
147.5
148.0
Longitude
b.
c.
d.


Plantings
Regrowth
Old Growth
Low Mean Rainfall
High Mean Rainfall
Annual Rainfall (mm)
100
80
60
40
20
Body Mass (grams, log scale)
5
10
20
50
100
200
500
Occurrence
0.5
0.1
0.05
0.01


Plantings
Regrowth
Old Growth
Low Mean Max. Temp
High Mean Max. Temp.
Annual Mean Maximum Temperature (°C)
24
23
22
21
20
5
10
20
50
100
200
500
Body Mass (grams, log scale)
Occurrence
0.2
0.1
0.05
0.02
0.01