



Influence of landscape composition and configuration on birds in working lands with extensive forest plantations

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Abstract

Context Working lands with forest plantations are widespread. To sustain biodiversity in these landscapes there is a need to understand how species respond to patterns such as the amount and configuration of remnant vegetation.

Objectives We examine how the occurrence and reporting rate of bird species are shaped by landscape composition and configuration in working lands with extensive forest plantations in south-eastern Australia.

Methods We used a whole-of-landscape study design, surveying birds in 36 landscapes (each a circle 1 km in diameter) with blue gum (*Eucalyptus globulus*) plantations. Landscapes varied in the proportion (0–72%) and arrangement of remnant vegetation. Birds were surveyed four times (8 sites per landscape)

at a total of 288 sites. We modelled responses of bird species as a function of remnant vegetation amount and configuration, and the diversity of landscape elements.

Results We detected 107 bird species and quantified how landscape elements influenced birds at three levels: sites within landscapes, the landscape (1 km diameter circle) and the extended landscape (3 km diameter circle). Analyses focused on 26 species observed at $\geq 10\%$ of sites. Site-level analyses revealed 12 species were more likely to occur in remnants than plantations. The amount of remnant vegetation was positively correlated with four species at the landscape-level and five species at the extended landscape. Well-connected remnant patches positively influenced five species at the landscape-level and three species at the extended landscape. The diversity of landscape elements positively influenced two species at the landscape-level and two species at the extended landscape. Some bird species were associated with landscape elements at each level, others at only one or none.

Conclusions Bird distributions are linked to the presence, amount and configuration of remnant vegetation within forestry landscapes. We recommend maintaining and increasing the extent and connectivity of remnant vegetation to support native birds.

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Introduction

Working lands, such as forest plantations, rangelands and farms, make up large areas of Earth's terrestrial surface and have a critical role to play in biodiversity conservation (Kremen and Merenlender 2018; Estrada-Carmona et al. 2022). Yet, conserving species while meeting the increasing demands of human populations requires new approaches to understanding and managing landscapes. Landscape ecology offers a valuable framework for managing working lands in ways that sustain biodiversity (Wiens 2009). By considering patterns and processes across mosaics or landscapes—not just at the level of individual sites—land managers can design production systems that also support native wildlife, including birds (Santos et al. 2021; Jones et al. 2023). To date, most empirical studies using a 'whole mosaic' as the unit for analysis (*sensu* Bennett et al. 2006) have been completed in working lands characterised by agriculture. While these studies provide valuable information about the amount (Lindenmayer et al. 2020; Šálek et al. 2022), connectivity (Siqueira et al. 2021) and diversity (Bennett et al. 2022) of landscape elements within the context of an agricultural matrix, there is a need for whole-of-landscape studies in working lands distinguished by the production of wood in forest plantations.

Forest plantations occur on all continents with permanent human settlement (FAO 2020) and now comprise 131 million ha globally, with more than 3 million hectares planted per year from 2015 to 2020 (FAO 2020). In Australia, forest plantations cover more than 1.7 million ha, 40% of which is hardwood trees such as eucalypts and 60% softwood trees such as pines (ABARES 2024). Forest plantations managed for wood and/or carbon differ from other working lands, such as farmland, because they are dominated by trees, mostly in even-aged stands of native or non-native species (FAO 2020). On one hand, this provides opportunities for species that can use planted trees for shelter and foraging. For example, some birds typically associated with native forests have been shown to nest and forage within eucalypt plantations in southeastern Australia (Law et al. 2014). On the other hand, forest plantations comprised of a single tree species may lack many structural and floristic characteristics found in remnant native vegetation that are important for birds (Castano-Villa et al. 2019).

While studying individual patches of remnant vegetation and the local context of forestry plantations is important, we contend that advancing understanding of species distributions will benefit from landscape-level approaches—where the response and predictor variable characterise the landscape as a whole and account for patterns of remnant vegetation across production landscapes.

Three main properties of working lands characterised by trees are likely to shape bird distributions: the amount, configuration and diversity of landscape elements (Villard et al. 1999; Bennett et al. 2006). The amount (sometimes referred to as extent) of a landscape element such as remnant vegetation can be an important determinant of species population size and resource availability (Nogueira et al. 2021), and thus affect where species occur. While many forest bird species prefer large amounts of native vegetation (Maseko et al. 2020), it is plausible that some species persist in plantation landscapes with small amounts of remnant vegetation—particularly if they primarily use young plantation stands and more open areas, or if planted species provide complementary habitat (Porro et al. 2020). The configuration, or spatial arrangement, of landscape elements also plays a critical role in shaping bird distributions by influencing how species move through the landscape to find food, nesting sites, mates and refuge from predators (Paxton et al. 2023). Some species only occur in plantation landscapes when remnant patches are well-connected (Lacoretz et al. 2021). A third property, landscape diversity, can help ensure that birds have access to a variety of resources across different landscape elements and uses. For example, some insectivorous birds may forage in open habitats or areas with short canopies but need areas with mature trees for breeding and nesting (Ram et al. 2020). Understanding the role of each of these landscape properties, as well as the role of broader biogeographic gradients such as climate, is necessary for developing biodiversity-friendly management practices in forested working lands.

The distribution of bird species in forested working lands is also likely to vary with their ecological traits, including those relating to food, shelter and breeding (Frishkoff and Karp 2019). For instance, recent work indicates different population trends of canopy-foraging insectivores (increasing) versus canopy-foraging nectarivores (declining) in working

lands with an agricultural matrix in southeastern Australia (Haslem et al. 2023). Based on the traits of birds in Australian working lands dominated by trees, we hypothesise that small insectivores such as thornbills and fairy-wrens will depend on the dense understorey found in remnant vegetation. By contrast, ground-foraging granivores, such as pigeons and quails, may prefer the more open ground habitat provided by plantations near tree cover. Other whole-of-landscape studies have examined trait-based associations of individual bird species with landscape properties in agricultural settings (Hall et al. 2022; Mariano-Neto and Santos 2023; Haslem et al. 2024) and managed natural forests (McGarigal and McComb 1995; Roberts and King 2017). Few have applied this approach to forest plantations (but see Cardoso et al. 2023).

Here, we use a whole-of-landscape approach to examine how the occurrence and reporting rate of bird species is shaped by landscape composition and configuration in forested working lands in south-eastern Australia (Fig. 1). Plantations of blue gum (*Eucalyptus globulus*) for wood production are an important economic land use in the region. Managers of these plantations are increasingly challenged by the need to produce wood while also maintaining or improving biodiversity in the areas under their management. We tested how the amount and configuration of remnant vegetation, and the diversity of several elements, influence the distribution of bird species at a landscape-level, where each landscape was defined as a circle with a 1 km diameter. To complement this whole-of-landscape analysis, we also examined how site location within landscapes (in remnant vegetation

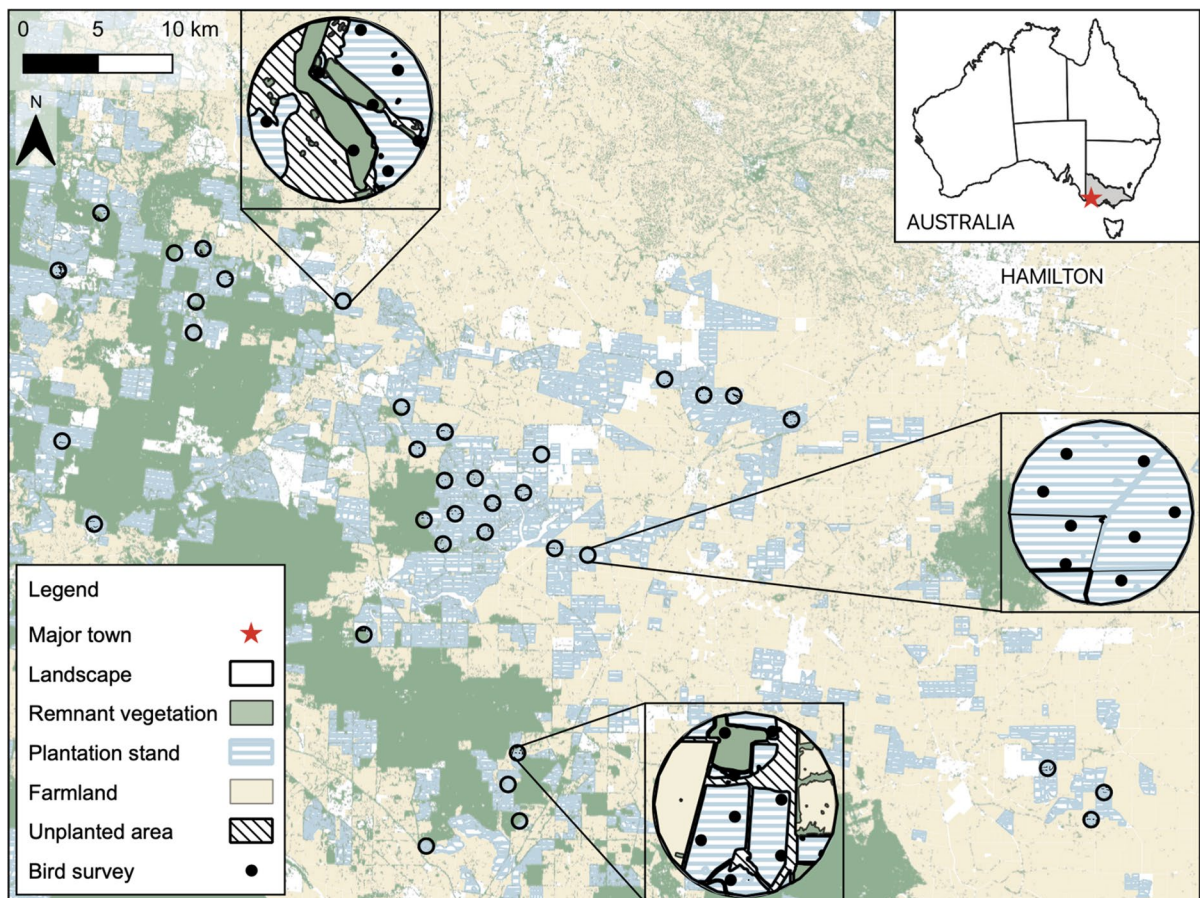


Fig. 1 Study design including 36 landscapes (78.54 ha) of southwestern Victoria, Australia. Birds were surveyed four times at eight sites per landscape. Each landscape varied in the

amount of remnant vegetation (range: 0–72%), and its arrangement, with the remaining area made up of plantation, farmland, unplanted area and water bodies

or plantations) influenced birds, and how landscape elements at an extended scale (a 3 km diameter buffer) shaped bird responses. We focus on individual species of birds to identify those that are most sensitive to changes in landscape properties, and those that are more resilient, reasoning that our site and landscape definitions align with the scales at which many birds use and move through habitat. This will help guide management of forest plantations in the context of nature positive initiatives that support the Kunming-Montreal Global Biodiversity Framework.

Materials and methods

Study area

The study was undertaken in southwestern Victoria, Australia (Fig. 1). The study area, part of what the forest industry describes as the “Green Triangle”, spans 6,000,000 ha and contains forestry plantations and native forest and woodlands, as well as areas used for grazing and cropping. Blue gum (*Eucalyptus globulus*) plantations, a tree species not native to the study area, cover approximately 120,000 ha within the study area (ABARES 2024). These plantations were mostly established between the mid-1990s and 2010 on land previously used as pasture. Plantations are managed on short rotations (harvested every 10–15 years) to produce woodchip for export. Remnant vegetation (sometimes called native vegetation) consists of grassy and open woodlands dominated by *Eucalyptus* trees, including river red gum (*E. camaldulensis*), brown stringybark (*E. baxteri*), messmate stringybark (*E. obliqua*), swamp gum (*E. ovata*) and manna gum (*E. viminalis*) and a shrub layer including species from the *Acacia*, *Melaleuca*, *Hakea*, and *Leptospermum* genera. Historical clearing for agriculture has substantially reduced and modified native vegetation in the study area.

Study design

We examined the occurrence of birds across 36 study landscapes. A gradient of remnant vegetation was sampled by selecting landscapes for study ranging from 0 to 72% of this element. Each study landscape was 1 km in diameter (78.54 ha) and was separated from the nearest landscape by a mean minimum

distance of 2 km. We define remnant vegetation as patches and linear strips of native vegetation and lone native trees, as well as some small areas of planted windbreaks (predominantly *Cupressus* and *Pinus spp.*) which provide standing vegetation not subject to harvesting.

The landscapes also comprised plantation, farmland for sheep and cattle grazing and crops, unplanted areas (including firebreaks, roads and other areas without trees) and water bodies (including artificial water sources used for agriculture and water sources that lacked natural vegetation). The proportion of blue gum plantation in study landscapes ranged from 22 to 97%. Most blue gum plantations (95%) were ≤ 6 years old and contained smaller tree girths than remnant vegetation (mean diameter at breast height measured at 114 of 288 sites was 18 cm versus 28 cm, respectively). The proportion of farmland in study landscapes ranged from 0 to 26%.

Bird surveys

Birds were surveyed at eight sites within each landscape (a total of 288 sites). Bird surveys were completed four times at each site, twice during the bird breeding season (September–November 2021–2023) and twice during the non-breeding season (March–May 2021–2022). A bird survey consisted of a 10-min point count at a site, where the same observer (EKT) recorded aural and visual cues of birds, recording both species presence and abundance at four distance categories: 0–10 m, 10–25 m, 25–50 m and > 50 m. Surveys were conducted from dawn until midday. Surveys were not conducted during periods of heavy rain, or conditions of high wind or temperature. The sequence of site visitation was rotated between survey rounds. Each bird survey site was placed at a mean minimum distance of 250 m (sd=35 m, range 187–391 m) from another site to reduce the risk of spatial autocorrelation and located at a mean minimum distance of 181 m (sd=101 m, range=5–492 m) from a study landscape boundary. Bird survey sites within each study landscape were allocated in proportion to the amount of remnant vegetation—approximately one site per 12.5% of remnant vegetation. Landscapes with less than 12.5% of remnant vegetation still included one site placed within a remnant patch when one was present. Survey sites not allocated to remnant vegetation were located

in plantations. Farmland, water bodies and unplanted areas were not directly surveyed.

Most birds were identified to the species-level, but some taxa were difficult to distinguish based on calls alone, when they were not visible. For further analyses, we grouped the long-billed corella (*Cacatua tenuirostris*) and little corella (*C. sanguinea*) as one group—corella species. Similarly, the Australian raven (*Corvus coronoides*), forest raven (*C. tasmanicus*) and little raven (*C. mellori*), were grouped as raven species.

Spatial analysis

Analyses were completed at three levels that we refer to as site, landscape and extended landscape (detailed below). Spatial layers at the site and landscape-level detailing the elements of study landscapes were sourced from DigitalGlobe satellites at a resolution < 2 m, provided by blue gum plantation managers PF Olsen. To ensure mapping accuracy, we visited remnant vegetation patches within each landscape. Spatial layers at the extended landscape were sourced from the Victorian Government's land use layer (<https://discover.data.vic.gov.au/dataset/victorian-land-use-information-system-2016-2017>). Using Quantum Geographical Information System (QGIS) software (version 3.28.9-Firenze, <http://qgis.org>), vector spatial layers were converted to raster files in which each pixel represented a 10 m² area. The land use layer was mapped at a coarser resolution (minimum parcel size of 12.5 ha) than the DigitalGlobe layers. For extended landscape mapping, we prioritised the finer-scale DigitalGlobe data for the 1 km core (the area made up of the 1 km landscape-level) and added the land use layer as an outer ring to extend it to a 3 km diameter. Both the landscape-level and extended landscape layers were then analysed in FRAGSTATS (version 4.2, <https://fragstats.org/>) to calculate three metrics:

- (1) *Amount of remnant vegetation* is the extent of remnant vegetation, calculated as the proportion of pixels within each landscape (PLAND; following FRAGSTATS terminology);
- (2) *Remnant configuration* was calculated as the percentage of pixels of remnant vegetation next to pixels of the same type (where high values of like adjacencies, closer to 100, indicate a domi-

nance of a single, large patch of remnant vegetation in a landscape, whereas low values, closer to zero, indicate fragmented patches of remnant vegetation) (PLADJ). We opted to use percentage of like adjacencies to measure configuration, rather than alternatives such as total edge or number of patches, because we anticipated the clustering of remnant vegetation would be particularly important for bird species in the study area. For two landscapes with very low amounts of remnant vegetation it was not possible to calculate the measure of configuration, so later we imputed the mean value of like adjacencies to enable their inclusion in modelling of bird distributions;

- (3) *Landscape diversity* measures the diversity and evenness in distribution of different landscape elements in each study landscape, using the Shannon diversity index, where higher values of this index indicate a greater mix of landscape elements (in which five landscape elements were mapped: plantation, farmland, remnant vegetation, unplanted areas and water bodies (SHDI) (Supplementary Fig. 1).

Landscapes were situated across a rainfall gradient that could plausibly affect bird species distributions. Long-term (30-year) average annual rainfall data from the centre of each landscape was calculated with data from the Bureau of Meteorology (https://reg.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp). Mean rainfall ranged from 629 to 760 mm with a mean landscape rainfall value of 710 ± 38 mm (sd).

Statistical analysis

We pooled records of birds across four survey periods at eight sites per landscape, i.e. landscapes ($n=36$) were the unit of inference. We calculated two response variables per landscape: (a) the occurrence of each bird species (presence or absence at a landscape) and (b) the reporting rate (proxy for abundance), the number of sites (out of 8) at which each species was recorded per landscape, across all surveys.

We analysed bird species responses using generalised linear models (GLMs) with binomial distributions for both occurrence and reporting rate data. The former modelled as presence or absence in a

landscape, the latter modelled as a binomial proportion of the number of presences out of 8 sites. Eighteen very common species (present at > 30 landscapes) were not modelled due to lack of variation in their occurrence and reporting rate. There was suitable occurrence and reporting rate data to analyse 26 individual bird species present at $\geq 10\%$ of sites. Bird data were modelled as a function of four predictor variables: amount of remnant vegetation, configuration of remnant vegetation, landscape diversity, and rainfall. As a second step, we also ran models which explored the role of remnant amount at a larger scale than the original study landscapes i.e. the extended landscape. To do this, we extended the diameter of the circle centred on each landscape to 3 km and calculated the amount and configuration of remnant vegetation, landscape diversity and rainfall in an area of ~ 707 ha.

The amount of remnant vegetation was highly correlated with the configuration of remnant vegetation at the landscape-level (Pearson correlation coefficient = 0.7) (Supplementary Fig. 2). To navigate this correlation between variables, we used a “residual regression” approach (Graham 2003; Dormann et al. 2013) where remnant amount was prioritised over configuration (like adjacencies) as our study was designed to target variation in remnant amount. This included modelling remnant configuration as a function of remnant amount and using the residuals from this model (a proxy of configuration independent of remnant amount) as a predictor of bird species occurrence and reporting rate. This proxy of configuration was termed “residual remnant configuration” and included in the models with the three other predictor variables. Other variables were not highly correlated with the amount of remnant vegetation (Pearson correlation coefficient < 0.5).

All variables were standardised before modelling by subtracting the mean from each predictor variable and dividing by two standard deviations to assist with comparison of effects sizes and uncertainty (Gelman and Hill 2007). We compared models using estimates of effect size, 95% confidence intervals around model coefficients, percentage deviance explained (% Dev), and p-values. Overdispersion was checked for each model using the Pearson chi-square statistics and deviance, with values close to 1 indicating the model was appropriate.

In addition to the landscape-level analyses, we tested if the same 26 bird species were more likely

to occur at sites in either remnant vegetation or plantation areas. A site was either located within remnant vegetation ($n=60$) or within a plantation area ($n=228$). We assessed if occurrence of each bird species, pooled across four survey periods, was influenced by the two site types using Generalised Linear Mixed Models (GLMMs) with a binomial distribution and a logit link function, where study landscape was included a random intercept and site type (plantation or remnant) was a fixed effect.

All analyses were undertaken in R (version 2023.06.2+561, <https://www.R-project.org/>). We used the ‘ggplot2’ (<https://ggplot2.tidyverse.org/>), ‘glmmTMB’ (<https://cran.r-project.org/web/packages/glmmTMB/index.html>), ‘DHARMa’ (<https://cran.r-project.org/web/packages/DHARMa/index.html>) and ‘dotwhisker’ (<https://cran.r-project.org/web/packages/dotwhisker/index.html>) packages. We interpreted levels of statistical significance along a continuum: $p\text{-value} \geq 0.1$ little or no evidential support of a relationship; < 0.1 weak evidence; < 0.05 moderate evidence; < 0.01 strong evidence and < 0.001 very strong evidence (Muff et al. 2022).

Results

A total of 25,209 observations of 107 bird species were made across the 36 study landscapes (Supplementary Table 1). Insectivores were the most frequently observed feeding group ($n=51$ species), followed by granivores ($n=20$ species), water birds ($n=16$ species), carnivores ($n=13$ species) and nectarivores ($n=7$ species). Ten species were recorded in all 36 study landscapes, while 18 species only occurred in a single landscape. Below we distinguish between three levels of analyses: the site, landscape and extended landscape.

Effect of amount of remnant vegetation on bird species

Site-level

Twelve of 26 species showed evidence of a preference for remnant vegetation sites over plantation sites (Supplementary Table 2). For example, the New Holland honeyeater (*Phylidonyris novaehollandiae*) was approximately 12 times more likely to be observed in remnant vegetation ($n=22$ of 60 sites) than blue gum

plantations (n=15 of 288 sites). The white-browed scrubwren (*Sericornis frontalis*) was 5.5 times more likely to be observed at sites comprised of remnant vegetation (n=27 of 60 sites) than sites within blue gum plantations (n=29 of 228 sites). No species preferred plantation sites over remnant vegetation.

Landscape-level

Of the 26 bird species modelled, five showed evidence of a response to the amount of remnant vegetation (Figs. 2, 3, 4; Supplementary Fig. 3; Supplementary Tables 3–4). We detected moderate evidence of a positive relationship between occurrence and reporting rate of the white-throated treecreeper (*Cormobates leucophaea*) and increasing remnant vegetation amount (occurrence model: coefficient = 31.91 ± 14.88 SE, p-value = 0.032; reporting rate model: coefficient = 3.63 ± 1.69 SE, p-value = 0.031). The probability of occurrence of the white-throated treecreeper rose sharply as amount of remnant vegetation increased: from below 0.2

in landscapes with 5% remnant vegetation, reaching 0.5 at 7% of remnant vegetation, and 0.9 at 9%. The olive-backed oriole (*Oriolus sagittatus*) showed moderate evidence of a positive relationship between occurrence and amount of remnant vegetation (coefficient = 5.64 ± 2.7 SE, p-value = 0.037) and weak evidence of this relationship when reporting rate was examined (coefficient = 1.73 ± 1.03 , p-value = 0.092). For the striated pardalote (*Pardalotus striatus*), we detected weak evidence of a positive relationship between occurrence and amount of remnant vegetation (coefficient = 3.33 ± 1.73 , p-value = 0.054). The fan-tailed cuckoo (*Cacomantis flabelliformis*) showed moderate evidence of a positive relationship between reporting rate and amount of remnant vegetation (coefficient = 2.84 ± 1.30 SE, p-value = 0.029). By contrast, the occurrence of the Eurasian skylark (*Alauda arvensis*), an introduced species, was negatively associated with the amount of remnant vegetation (coefficient = -14.47 ± 6.81 SE, p-value = 0.034).

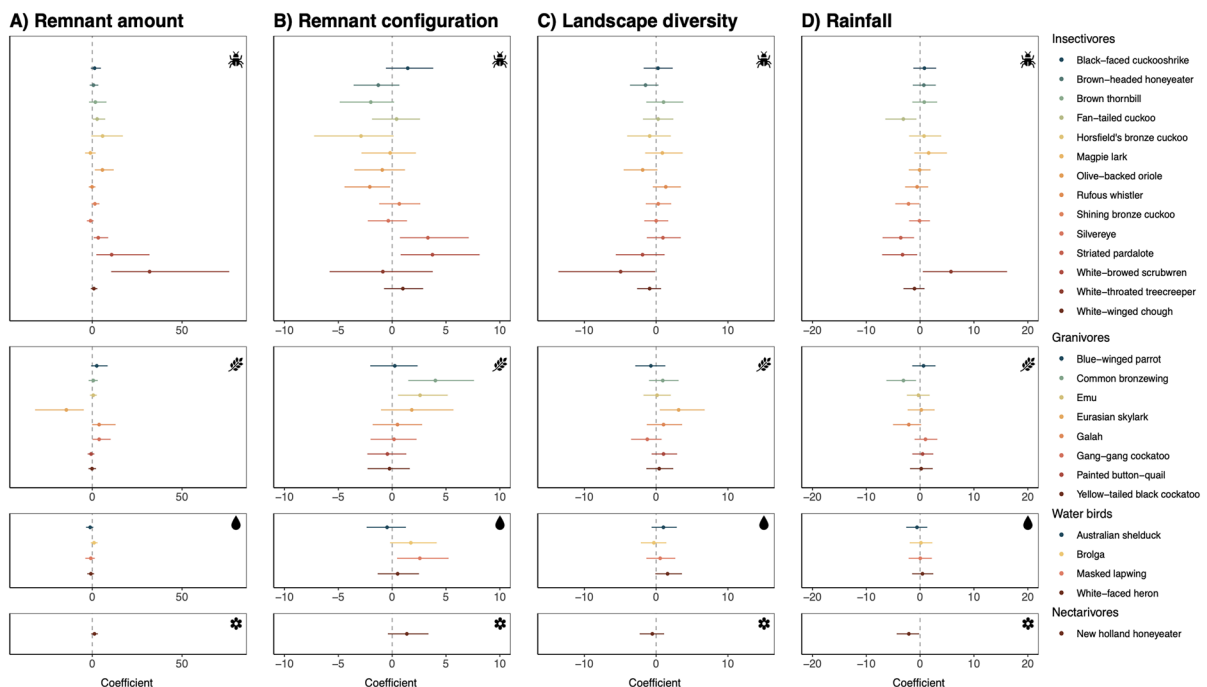


Fig. 2 Landscape-level responses of individual species occurrence to **A** remnant amount, **B** residual remnant configuration, **C** landscape diversity and **D** rainfall across forestry landscapes of southwestern Victoria, Australia, stratified by diet group where 🐛 are insectivores, 🌾 are granivores, 💧 are water

birds and 🍷 are nectarivores. Standardised model coefficients derived from generalised linear models are displayed with 95% confidence intervals. Feeding group icons derived from Microsoft PowerPoint (2024). Please note the x-axes are on different scales for visualisation purposes

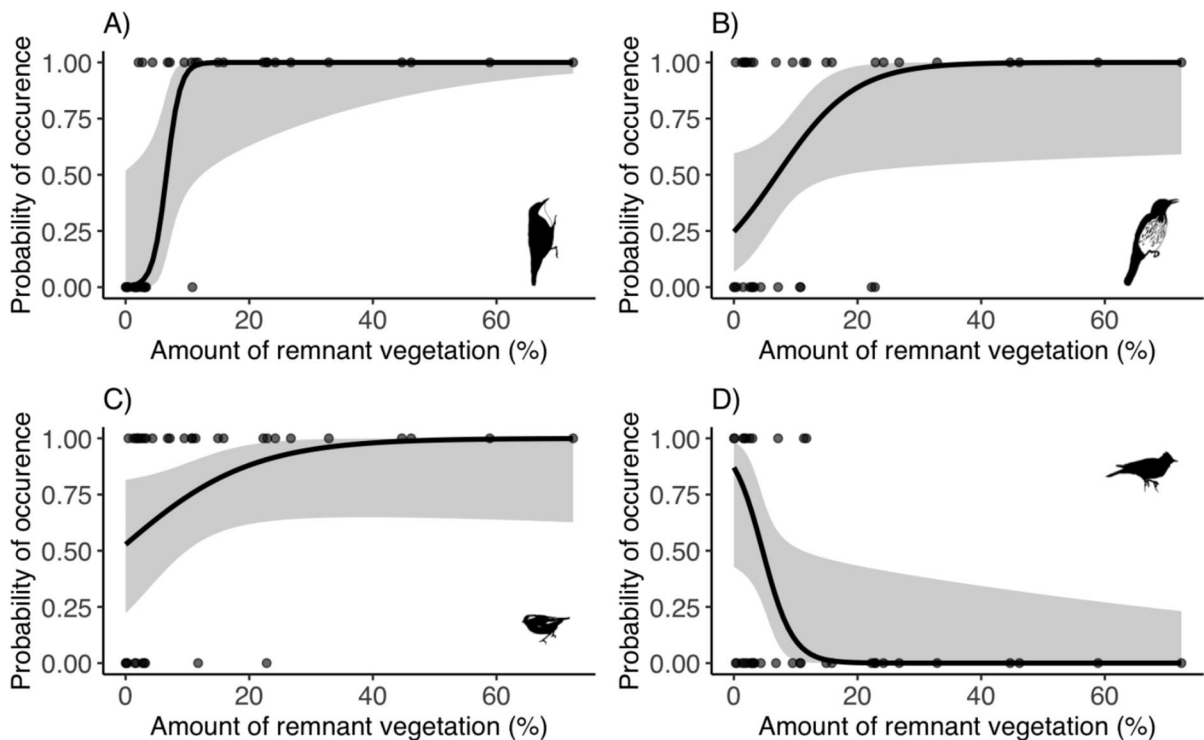


Fig. 3 Partial plots derived from generalised linear models of the probability of occurrence of three species as a function of amount of remnant vegetation (%) at the landscape-level: **A** white-throated treecreeper (*Cormobates leucophaea*); **B** olive-backed oriole; (*Oriolus sagittatus*); **C** striated pardalote (*Pardalotus striatus*); and **D** Eurasian skylark (*Alauda arven-*

sis). Other predictor variables, residual remnant configuration, landscape diversity and rainfall, have been held constant at their mean. Black lines represent modelled relationship, shaded areas represent 95% confidence intervals, black dots represent observations of birds at study landscapes, with shading of dots used to visualise overlapping values

Extended landscape-level

At the extended landscape, eight species showed evidence of responding to the amount of remnant vegetation (Supplementary Tables 5–6). Five species—the white-browed scrubwren, yellow-tailed black cockatoo (*Zanda funerea*), gang-gang cockatoo (*Callocephalon fimbriatum*), olive-backed oriole and striated pardalote—showed evidence for increasing in either occurrence or reporting rate with amount of remnant vegetation (white-browed scrubwren occurrence model: $2.20 \pm 1.33\text{SE}$, $p\text{-value}=0.097$; yellow-tailed black cockatoo occurrence model: $4.14 \pm 1.82\text{SE}$, $p\text{-value}=0.023$; gang-gang cockatoo reporting rate model: $1.87 \pm 1.07\text{SE}$, $p\text{-value}=0.081$; olive-backed oriole: $1.89 \pm 1.14\text{SE}$, $p\text{-value}=0.099$; striated pardalote model: $3.01 \pm 1.68\text{SE}$, $p\text{-value}=0.073$). We also detected moderate evidence of a negative relationship between occurrence of the Australian shelduck

(*Tadorna tadornoides*) and Eurasian skylark with remnant vegetation amount, and weak evidence of a negative relationship between occurrence of silvereye (*Zosterops lateralis*) and remnant amount (Australian shelduck model: coefficient = $-2.42 \pm 1.21\text{SE}$, $p\text{-value}=0.046$; Eurasian skylark model: $-2.86 \pm 1.40\text{SE}$, $p\text{-value}=0.041$; silvereye model: coefficient = $-2.58 \pm 1.34\text{SE}$, $p\text{-value}=0.055$).

Effect of configuration of remnant vegetation on species

Landscape-level

Of the 26 bird species modelled, six species showed evidence of responding to the arrangement of remnant vegetation (via modelling of a regressed remnant configuration variable accounting for remnant area) (Figs. 2, 5; Supplementary Fig. 3; Supplementary Tables 3–4).

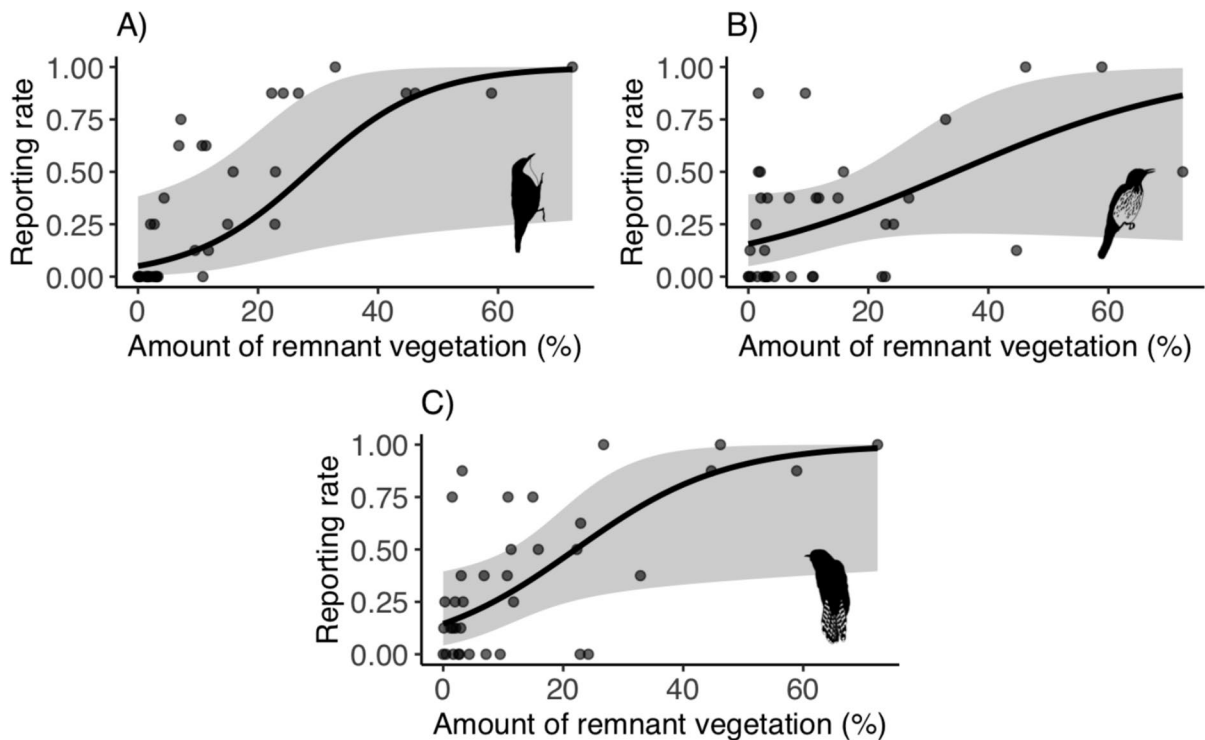


Fig. 4 Partial plots derived from generalised linear models of the reporting rate of three species as a function of amount of remnant vegetation (%) at the landscape-level: **A** white-throated treecreeper (*Cormobates leucophaea*); **B** olive-backed oriole; (*Oriolus sagittatus*); and **C** fan-tailed cuckoo (*Cacomantis flabelliformis*). Other predictor variables, residual

remnant configuration, landscape diversity and rainfall, have been held constant at their mean. Black lines represent modelled relationship, shaded areas represent 95% confidence intervals, black dots represent observations of birds at study landscapes, with shading of dots used to visualise overlapping values

Occurrence of the common bronzewing (*Phaps chalcoptera*) showed strong evidence of a positive response to increasing configuration (coefficient = 4.01 ± 1.51 SE, p -value = 0.008) i.e. this species is more likely to be present in landscapes with well-connected remnant patches. There was moderate evidence that four of these species responded to clustering of remnant vegetation: striated pardalote (coefficient = 3.32 ± 1.57 SE, p -value = 0.0347), white-browed scrubwren (coefficient = 3.74 ± 1.78 SE, p -value = 0.0358), masked lapwing (*Vanellus miles*) (coefficient = 2.57 ± 1.19 SE, p -value = 0.031), and emu (*Dromaius novaehollandiae*) (coefficient = 2.59 ± 1.15 SE, p -value = 0.0245). Modelled bird species responses to configuration were positive except for the rufous whistler (*Pachycephala rufiventris*), which was more likely to occur in landscapes with remnant vegetation that was fragmented (coefficient = -2.08 ± 1.05 SE, p -value = 0.047). We

did not detect any clear relationships between residual remnant configuration and reporting rate.

Extended landscape-level

At the extended landscape, four species showed evidence of responding to the arrangement of remnant vegetation (Supplementary Tables 5–6). Occurrence of the white-winged chough (*Corcorax melanorhamphos*), striated pardalote and emu showed evidence of a positive response to increasing configuration (white-winged chough model: coefficient = 1.91 ± 1.09 SE, p -value = 0.079, striated pardalote model: 4.86 ± 2.00 SE, p -value = 0.015; emu model: 2.30 ± 1.11 SE, p -value = 0.040). There was also weak evidence that the occurrence of the blue-winged parrot (*Neophema chrysostoma*) responded negatively to the arrangement of remnant vegetation: (coefficient = -2.68 ± 1.60 SE, p -value = 0.095).

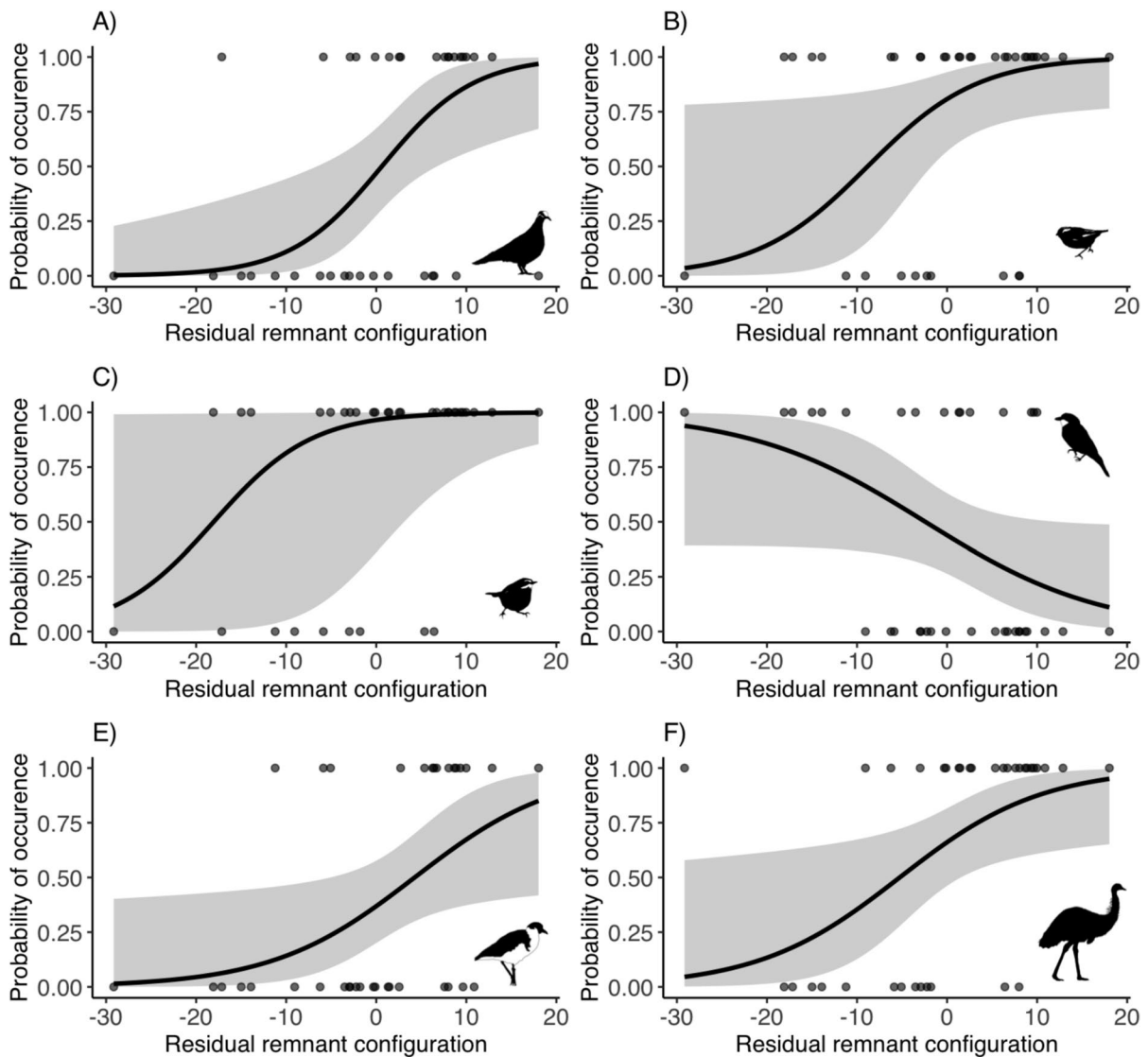


Fig. 5 Partial plots derived from generalised linear models of the probability of occurrence of six species as a function of the configuration of remnant vegetation at the landscape-level: **A** common bronzewing (*Phaps chalcoptera*); **B** striated pardalote (*Pardalotus striatus*); **C** white-browed scrubwren (*Sericornis frontalis*); **D** rufous whistler (*Pachycephala rufiventris*); **E** masked lapwing (*Vanellus miles*); and **F** emu (*Dromaius*

novaehollandiae). Other predictor variables, remnant amount, landscape diversity and rainfall, have been held constant at their mean. Black lines represent modelled relationship, shaded areas represent 95% confidence intervals, black dots represent observations of birds at study landscapes, with shading of dots used to visualise overlapping values

Effect of diversity on species

Landscape-level

In general, landscape diversity had a smaller effect on species distributions than other landscape variables and was influential on fewer species (2 of 26

species) (Figs. 2, 6; Supplementary Fig. 3; Supplementary Tables 3–4). We detected moderate evidence that an increase in landscape diversity increased the occurrence of the introduced Eurasian skylark (coefficient = 3.13 ± 1.54 SE, p-value = 0.042), and weak evidence for the white-faced heron (*Egretta novaehollandiae*) (coefficient = 1.59 ± 0.93 SE, p-value = 0.086).

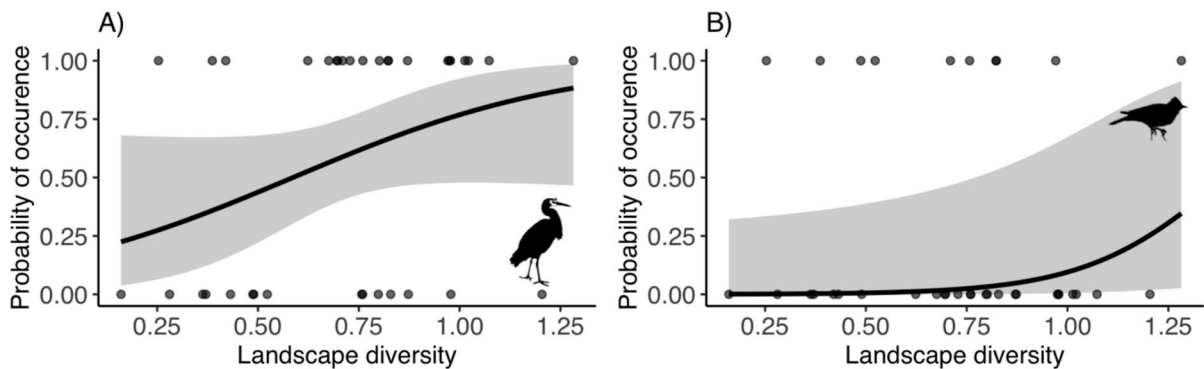


Fig. 6 Partial plots derived from generalised linear models of the probability of occurrence of two species as a function of landscape diversity at the landscape-level: **A** white-faced heron (*Egretta novaehollandiae*); and **B** Eurasian skylark (*Alauda arvensis*). Other predictor variables, remnant amount, residual

There were no relationships between reporting rate and landscape diversity for any species.

Extended landscape-level

At the extended landscape, six species showed evidence of responding to the diversity of landscape elements (Supplementary Tables 5–6). Two species—the striated pardalote and blue-winged parrot—responded positively to an increase in diversity, whereas four species: yellow-tailed black cockatoo, olive-backed oriole, brown thornbill (*Acanthiza pusilla*) and brolga (*Grus rubicunda*) decreased in occurrence as diversity of landscape elements increased.

Influences of a gradient in mean annual rainfall at the landscape-level

Mean annual rainfall had a negative effect on the occurrence of five species: fan-tailed cuckoo (coefficient = -3.11 ± 1.41 SE, p -value = 0.027), striated pardalote (coefficient = -3.60 ± 1.44 SE, p -value = 0.012), white-browed scrubwren (coefficient = -3.26 ± 1.59 SE, p -value = 0.040), common bronzewing (coefficient = -3.10 ± 1.36 SE, p -value = 0.023) and New Holland honeyeater (coefficient = -2.10 ± 1.04 SE, p -value = 0.045) (Figs. 3, 6; Supplementary Fig. 3–4; Supplementary Tables 3–4). The probability of occurrence of the striated pardalote declined sharply as rainfall increased: a mean estimate of 1.0 when mean

remnant configuration and rainfall, have been held constant at their mean. Black lines represent modelled relationship, shaded areas represent 95% confidence intervals, black dots represent observations of birds at study landscapes, with shading of dots used to visualise overlapping values

annual rainfall was 630 mm, 0.5 in landscapes with 740 mm of rainfall, and 0.3 in landscapes with 760 mm of rainfall. There was weak evidence of a negative relationship with rainfall for the occurrence of two other species, the shining bronze cuckoo (*Chrysococcyx lucidus*) and galah (*Eolophus roseicapilla*) (Supplementary Table 3).

Discussion

Whole-of-landscape approaches provide opportunities for better understanding bird distributions and developing conservation strategies across working lands. Our study shows that amount, configuration and diversity of landscape elements are important in driving bird species occurrence and abundance in working lands with forest plantations: the distributions of 22 of 26 bird species modelled were shaped by these properties at what we defined as either a landscape (circle with a 1 km diameter) or extended landscape (circle with a 3 km buffer). Interestingly, an additional 18 bird species, beyond the 26 that were modelled, were present in most landscapes (>30 of 36), including those dominated by blue gum plantations. Our study provides evidence of species that are relatively insensitive, and species that are highly responsive, to the extent of remnant vegetation in working lands, and offers ways to enhance populations of the latter.

Species associations with remnant vegetation at landscapes and sites

Ten of 26 species modelled at the landscape-level showed evidence of responding to the amount of remnant vegetation. For example, the insectivorous white-throated treecreeper was more prevalent in landscapes with higher proportions of remnant vegetation. In this case, a preference for remnant vegetation can be explained by bark type: we only observed treecreepers foraging for insects on rough-bark eucalypts, such as those found in remnant vegetation, while planted blue gums are smooth-barked and do not provide preferred insect habitat. White-throated treecreepers have also been observed to occur more abundantly in remnant vegetation in the wheat-sheep zone of New South Wales, Australia (Martin et al. 2011) indicating that white-throated treecreepers may benefit from plantings of rough-bark eucalypts in working landscapes as well as the retention of hollow-bearing trees, given their hollow dependence for breeding. The insect and fruit-feeding olive-backed oriole was also influenced by the amount of remnant vegetation in the landscape. The range of food resources preferred by this species is more likely to occur in remnant vegetation, which is characterised by greater diversity in trees and shrubs, including a mix of plants likely to contain higher insect diversity (Cunningham et al. 2005) and fruit diversity. We suggest that the habitat value of blue gum plantations for bird species with a varied diet could be improved by retaining native fruit-bearing shrubs in plantation landscapes such as kangaroo apple (*Solanum spp.*), that are often eliminated during plantings of blue gums to reduce competition.

We also explored if birds were responding to remnant vegetation at larger spatial scales. Our results indicate that some species consistently respond to remnant vegetation at both the landscape-level and extended landscape, (such as the insectivorous striated pardalote and white-throated treecreeper) but others only responded to remnant amount at the extended landscape level (such as the granivorous yellow-tailed black cockatoo and gang-gang cockatoo). This is likely because some species, such as cockatoos, perceive and use environments at larger scales. Similarly, in a landscape study in the Atlantic Forest in Brazil, the occurrence of bird species was better predicted by having bespoke models at the spatial scales most relevant to them (Bhakti et al. 2018).

It is therefore important that conservation research and forest management in working lands does not solely rely on a single spatial scale (also see Wiens 1989; Monroe et al. 2022).

More broadly, whole-of-landscape studies show that the amount of remnant vegetation is an important landscape property for bird species in agricultural working lands in Mediterranean Europe (Chiatante et al. 2019), temperate southeastern Australia (Radford and Bennett 2007) and tropical areas of South America (Semper-Pascual et al. 2021). Some individual bird species' habitat requirements are likely not fulfilled in highly modified working lands, and the present study highlights the importance of retaining and managing remnant vegetation to support bird populations in treed production landscapes. In several working lands, bird species have been shown to respond to a wide range of habitat amounts; for example, woodland-dependent species in agricultural landscapes were more abundant when remnant vegetation covered at least 10% of the landscape (Radford et al. 2005), while in tropical rainforests in Africa frugivorous bird species reach their maximum richness when forest cover was 74% (Kupsch et al. 2019). In our study, a variety of relationships were observed; the white-throated treecreeper peaked in occurrence when remnant vegetation comprised approximately 10% of the landscapes at a 1 km buffer and the olive-backed oriole peaked when remnant vegetation amounted to 35%. This underscores the importance of considering the needs of individual species in working lands.

Although we identified species positively associated with the amount of remnant vegetation, we also recorded species that a) were very common in most landscapes, including those dominated by plantations, and were not modelled in the present study, b) were moderately common and modelled in the present study, but for which we did not detect a clear relationship with amount of remnant vegetation, and c) were uncommon and not modelled in the present study because even substantial field surveys generated few occurrences across the study landscapes.

Empirical data indicate that some species are resilient to varying landscape modifications sampled in the present study, including 18 species that occurred in at least 32 of 36 landscapes. This included species more common of open country, such as the insectivorous Australian magpie (*Gymnorhina tibicen*)

and granivorous sulphur-crested cockatoo (*Cacatua galerita*), and species associated with treed areas such as the insectivorous yellow-faced honeyeater (*Lichenostomus chrysops*) and carnivorous laughing kookaburra (*Dacelo novaeguineae*). We reason that the habitat requirements of these very common bird species can generally be met in forestry landscapes. In part, because of habitat resources within plantations, such as tree cover, and associated feeding resources provided by blue gums that are not found in other working lands. For example, in a study comparing whole landscapes, Haslem and Bennett (2008) observed gang-gang cockatoos in 44% of farmland matrices compared to this study which observed gang-gang cockatoos in 69% of plantation matrices. Forest plantations may therefore provide greater conservation value with lower levels of remnant vegetation than other types of land cover such as pasture or cropland.

Our modelling focused on a set of moderately common bird species. An ongoing challenge is identifying landscape determinants for rare or threatened species for which, despite relatively intensive and repeated surveys, we were unable to generate sufficient observations to detect smaller changes in species distribution associated with variation in landscape properties. For example, the black-eared cuckoo (*Chrysococcyx osculans*) was observed in only two landscapes: where remnant vegetation was more than 40% of the landscape extent. (Hope et al. 2020) This highlights the need for targeted surveying of rare or threatened species in plantation landscapes and other working lands.

Analysis of site data complemented landscape analyses, helping to understand the role of remnant vegetation on bird species occurrence at another level. Eleven species were found more frequently in sites within remnant vegetation compared to blue gum plantation. This highlights birds rely directly on the resources contained within remnant vegetation, and that simply having remnant vegetation in the landscape is not always sufficient, especially if birds are unable to access suitable patches.

Effects of remnant configuration and landscape diversity on bird species

Six bird species in our study responded positively to landscape configuration, occurring more often in

areas (1 km or 3 km buffers) where remnant vegetation was connected rather than fragmented. For example, the insectivorous white-browed scrubwren was detected more frequently in aggregated remnants, consistent with its reliance on dense, vegetation, and limited ability to cross gaps of open vegetation. Well-connected patches enable this and other low-mobility species to minimise exposure to unfavourable habitat (Lindenmayer et al. 2020). Although we used a residual regression approach to address the high correlation between amount and configuration, these variables cannot be completely disentangled by statistical modelling (Dormann et al. 2013)—a common challenge in landscape ecology (Smith et al. 2011; Lindenmayer et al. 2020), especially within working lands.

In addition to remnant vegetation amount and configuration, four species responded positively to landscape diversity at 1 km or 3 km buffers. While we only surveyed plantations and remnant vegetation, we hypothesise that some species responded to spatial variation in other elements not directly sampled; for example, water bodies for the white-faced heron and the distribution of farmland for the Eurasian skylark. White-faced herons feed in shallow water and can also forage in pastures when wetlands are unavailable (Newman and Lindsey 2011). More broadly, while our study indicates that native vegetation provides higher quality habitat for more species than highly modified working lands, it is plausible that some bird species may need supplementary resources provided by modified areas. This may include several of the very common species we observed in the study landscapes, such as the insectivorous white-eared honeyeater (*Lichenostomus leucotis*) and nectarivorous red wattlebird (*Anthochaera carunculata*).

An important consideration for future research, is that young plantations, as investigated here, differ structurally from older blue gum plantations (e.g. > 10 years) or freshly harvested plantations. Changes in shrubby cover and canopy closure are likely to alter bird species occurrence and their responses to amount of remnant vegetation, which, in turn, influences how birds respond to the arrangement and diversity of landscape elements. For example, in a study of plantations in the United States, several bird species peaked in the abundance in early stages of plantation growth and then declined at later stages (Harris and Betts 2021). Such age-related preferences

can shift how birds use landscape elements, with different elements becoming more or less important across the plantation cycle.

Environmental gradients

The landscapes we studied receive less annual rainfall in the north and more in the south. The distributions of nine species were associated with this gradient—highlighting the need to consider the climatic variation of landscapes as well as their vegetation types and configurations. For example, the common bronzewing, a ground forager, is likely decreasing in occurrence as rainfall levels rise, given rain reduces foraging opportunities by displacing food and increasing predation. In the context of applying ecological knowledge, including broad-scale gradients, such as rainfall, helps to better predict species distributions. Retaining suitable amounts of remnant vegetation across biogeographic gradients is an important consideration for land managers.

Managing species that are sensitive and resilient to landscape modification

While the primary purpose of plantations is not nature conservation, improving conservation outcomes in treed working lands may benefit production and improve social licence. A focus on the requirements of individual bird species is a useful lens for improving bird conservation with forest plantations, that can be complemented by analyses of other measures of bird communities, such as functional groups and patterns of species richness. To continue to improve bird conservation in forested working lands we recommend several management actions. First, increase the retention of remnant vegetation for species where their distribution is driven by larger areas of remnant vegetation. Second, link small patches of remnant vegetation to large patches to improve habitat connectivity. Although in some landscapes it is unrealistic to expect large sections of plantation to be converted to native vegetation, retaining small areas of remnant vegetation, or establishing patches of native vegetation, to act as ‘stepping stones’ throughout the landscape will likely enable birds to access a range of resources, and to move across landscapes. Areas that promote connectivity may include roadsides and riparian strips which are already unviable

for plantations and thereby enhancing them will not limit economic outcomes desired by plantation managers. Finally, we recommend increasing remnant vegetation extent and configuration across environmental gradients such as those spanning changes in mean annual rainfall, to ensure the habitat of species restricted to or preferring some biogeographic areas is maintained. Taken together, these actions can guide plantation management towards nature-positive outcomes to increase the contribution of working lands to conservation targets of the Kunming-Montreal Global Biodiversity Framework.

Conclusions

The distribution of bird species is linked to the occurrence, amount and configuration of remnant vegetation within working lands composed of tree plantations used to produce wood and related products. While the distribution of remnant vegetation in the landscape had strong effects on selected bird species, we also recorded several species and groups of birds that are common even in landscapes with a large proportion of plantations. This information can be used to identify priority species for habitat protection and ways to improve working lands for bird conservation, including through enhancing and connecting areas of remnant vegetation at appropriate spatial scales.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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References

- ABARES 2024. Australian plantation statistics 2022–23 update. Canberra.
- Bennett AF, Radford JQ, Haslem A (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biol Conserv* 133:250–264
- Bennett AF, Holland GJ, Haslem A, Stewart A, Radford JQ, Clarke RH (2022) Restoration promotes recovery of woodland birds in agricultural environments: A comparison of 'revegetation' and 'remnant' landscapes. *J Appl Ecol* 59:1334–1346
- Bhakti T, Goulart F, de Azevedo CS, Antonini Y (2018) Does scale matter? The influence of three-level spatial scales on forest bird occurrence in a tropical landscape. *PLoS ONE* 13:e0198732
- Cardoso I, Bueno AS, Morante-Filho JC (2023) Number of forest fragments and understory plants exert opposite effects on multiple facets of bird diversity in eucalypt plantations. *Landscape Ecol* 38:1069–1083
- Castano-Villa GJ, Estevez JV, Guevara G, Bohada-Murillo M, Fonturbel FE (2019) Differential effects of forestry plantations on bird diversity: a global assessment. *For Ecol Manage* 440:202–207
- Chiatante G, Porro Z, Musacchio A, Bazzocchi A, Meriggi A (2019) Multi-scale habitat requirements of forest bird species in a highly fragmented landscape. *J Ornithol* 160:773–788
- Cunningham SA, Floyd RB, Weir TA (2005) Do Eucalyptus plantations host an insect community similar to remnant Eucalyptus forest? *Austral Ecol* 30:103–117
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46
- Estrada-Carmona N, Sánchez AC, Remans R, Jones SK (2022) Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. *Proc Natl Acad Sci* 119:e2203385119
- FAO 2020. Global Forest Resources Assessment 2020: Main Report. Rome.
- Frishkoff LO, Karp DS (2019) Species-specific responses to habitat conversion across scales synergistically restructure neotropical bird communities. *Ecol Appl* 29:e01910
- Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge
- Graham MH (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815
- Hall MA, Nimmo DG, Bennett AF (2022) Birds and insects respond differently to combinations of semi-natural features in farm landscapes. *J Appl Ecol* 59:2654–2665
- Harris SH, Betts MG (2021) Bird abundance is highly dynamic across succession in early seral tree plantations. *For Ecol Manage* 483:118902
- Haslem A, Bennett AF (2008) Birds in agricultural mosaics: the influence of landscape pattern and countryside heterogeneity. *Ecol Appl* 18:185–196
- Haslem A, Maisey AC, Clarke RH, Stewart A, Radford JQ, Bennett AF (2023) Quantifying the landscape-scale recovery of bird communities over time in response to on-farm restoration plantings. *Biol Conserv* 280:109987
- Haslem A, Clarke RH, Maisey AC, Stewart A, Radford JQ, Bennett AF (2024) Temporal dynamics in the composition of bird communities along a gradient of farmland restoration. *Ecol Appl*. <https://doi.org/10.1002/eap.2947>
- Hope, B., Kerle, A. & Doer, V. 2020. Conservation Advice: Black-eared Cuckoo *Chalcites osculans* Gould 1847 Cuculidae.
- Jones SK, Sánchez AC, Beillouin D, Juventia SD, Mosnier A, Remans R, Carmona NE (2023) Achieving win-win outcomes for biodiversity and yield through diversified farming. *Basic Appl Ecol* 67:14–31
- Kremen C, Merenlender A (2018) Landscapes that work for biodiversity and people. *Science*. <https://doi.org/10.1126/science.aau6020>
- Kupsch D, Vendras E, Ocampo-Ariza C, Batáry P, Motombi FN, Bobo KS, Waltert M (2019) High critical forest habitat thresholds of native bird communities in Afrotropical agroforestry landscapes. *Biol Conserv* 230:20–28
- Lacoretz MV, Depalma DM, Torrella SA, Zilli C, Ferretti V, Fernández GJ (2021) Can exotic tree plantations preserve the bird community of an endangered native forest in the Argentine Pampas? *Can J Forest Res* 51:1271–1280
- Law BS, Chidel M, Brassil T, Turner G, Kathuria A (2014) Trends in bird diversity over 12 years in response to large-scale eucalypt plantation establishment:

- implications for extensive carbon plantings. *For Ecol Manage* 322:58–68
- Lindenmayer D, Blanchard W, Foster CN, Scheele BC, Westgate MJ, Stein J, Crane M, Florance D (2020) Habitat amount versus connectivity: an empirical study of bird responses. *Biol Conserv* 241:108377
- Mariano-Neto E, Santos RA (2023) Changes in the functional diversity of birds due to habitat loss in the Brazil Atlantic Forest. *Front Forests Glob Change* 6:1041268
- Martin WK, Eldridge D, Murray PA (2011) Bird assemblages in remnant and revegetated habitats in an extensively cleared landscape, Wagga Wagga, New South Wales. *Pac Conserv Biol* 17:110–120
- Maseko MS, Zungu MM, Ehlers Smith DA, Ehlers Smith YC, Downs CT (2020) Effects of habitat-patch size and patch isolation on the diversity of forest birds in the urban-forest mosaic of Durban, South Africa. *Urban Ecosyst* 23:533–542
- McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol Monogr* 65:235–260
- Monroe AP, Heinrichs JA, Whipple AL, O'Donnell MS, Edmunds DR, Aldridge CL (2022) Spatial scale selection for informing species conservation in a changing landscape. *Ecosphere* 13:e4320
- Muff S, Nilsen EB, O'Hara RB, Nater CR (2022) Rewriting results sections in the language of evidence. *Trends Ecol Evol* 37:203–210
- Newman M, Lindsey A (2011) A ten-year study of herons, spoonbills and ibis at the Morpeth Wastewater Treatment Works near Maitland in NSW. *The Whistler* 5:10–18
- Nogueira OMA, Palmeirim AF, Peres CA, dos Santos-Filho M (2021) Synergistic effects of habitat configuration and land-use intensity shape the structure of bird assemblages in human-modified landscapes across three major neotropical biomes. *Biodivers Conserv* 30:3793–3811
- Paxton KL, Smetzer JR, Hart PJ, Anderson MJ, Paxton EH (2023) Landscape configuration alters movement behavior and space-use of a Hawaiian forest bird community. *J Avian Biol.* <https://doi.org/10.1111/jav.03117>
- Porro Z, Chiatante G, Bogliani G (2020) Associations between forest specialist birds and composition of woodland habitats in a highly modified landscape. *For Ecol Manage* 458:117732
- Radford JQ, Bennett AF (2007) The relative importance of landscape properties for woodland birds in agricultural environments. *J Appl Ecol* 44:737–747
- Radford JQ, Bennett AF, Cheers GJ (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biol Conserv* 124:317–337
- Ram D, Lindström Å, Pettersson LB, Caplat P (2020) Forest clear-cuts as habitat for farmland birds and butterflies. *For Ecol Manage* 473:118239
- Roberts HP, King DI (2017) Area requirements and landscape-level factors influencing shrubland birds. *J Wildlife Manage* 81:1298–1307
- Šálek M, Kalinová K, Reif J (2022) Conservation potential of semi-natural habitats for birds in intensively-used agricultural landscapes. *J Nat Conserv* 66:126124
- Santos JL, Moreira F, Ribeiro PF, Canadas MJ, Novais A, Lomba A (2021) A farming systems approach to linking agricultural policies with biodiversity and ecosystem services. *Front Ecol Environ* 19:168–175
- Semper-Pascual A, Burton C, Baumann M, Decarre J, Gavier-Pizarro G, Gómez-Valencia B, Macchi L, Mastrangelo ME, Pötzschner F, Zelaya PV (2021) How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change? *Proc R Soc Lond B Biol Sci* 288:20202466
- Siqueira, F. F., De Carvalho, D., Rhodes, J., Archibald, C. L., Rezende, V. L. & Van den Berg, E. 2021. Small landscape elements double connectivity in highly fragmented areas of the Brazilian Atlantic Forest. *Front Ecol Evolution*, 304.
- Smith AC, Fahrig L, Francis CM (2011) Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography* 34:103–113
- Villard MA, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv Biol* 13:774–783
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Wiens JA (2009) Landscape ecology as a foundation for sustainable conservation. *Landscape Ecol* 24:1053–1065

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