

Classifying animals into ecologically meaningful groups: a case study on woodland birds

Running head: classifying animal groups

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1. Abstract

Ecologists often classify species into binary groupings such as woodland or non-woodland birds. However, each ecologist may apply a different classification, which might impede progress in ecology and conservation by precluding direct comparison between studies. This study describes and tests a method for deriving empirically-based, ecologically-relevant species groups, using Australian woodland birds as a case study. A Bayesian hierarchical model investigates how vegetation and species traits drive birds' preference for woodland vegetation, characterised by low density trees with an open canopy structure. Birds are then classified according to their affinity to areas with high tree cover and woodland vegetation. Interestingly, no traits are strongly associated with species occurrence in woodland habitats, but occurrence in open country and forests differ depending on dispersal ability and foraging habits. Our results suggest that Australian woodland birds may be united by their avoidance of both sparsely-treed and densely-treed habitat, rather than by shared traits.

Classifying species according to our groupings provides results consistent with literature on how woodland birds respond to clearing, grazing and urbanisation. Thus, our model is consistent with current ecological understanding regarding woodland birds; it also provides more nuanced inference across 'closed-woodland', 'open-woodland', 'forest' and 'open country' groups. We propose that our modelling approach could be used to classify species for other locations and taxa, providing transparent, ecologically-relevant animal groupings.

Key words: Bayesian hierarchical model, classification, occurrence, traits, woodland birds

2. Introduction

Destruction and degradation of suitable habitat is thought to threaten woodland birds worldwide (Gregory et al., 2007; Rayner et al., 2014) and, as a result, considerable resources are spent on both managing and monitoring these bird assemblages (Birdlife Australia, 2015; Douglas and Fox, 2015; EBCC, 2014; Forestry Commission England, 2009; Ingwersen and Tzaros, 2011). However, decisions about how to manage woodland birds are complicated by conflicting evidence about the relationship between woodland birds and their habitat, and the nature and magnitude of any decline in woodland birds (Rayner et al., 2014). For instance, there is disagreement about how Australian woodland birds respond to vegetation extent (Mac Nally and Horrocks, 2002; Major et al., 2001) and fragmentation (Amos et al., 2013; Radford et al., 2005). This disagreement could be attributed to regional composition differences (Polyakov et al., 2013), or differences in the temporal (Yen et al., 2011) or spatial scale (Lindenmayer et al., 2010) of sampling. However, it could also reflect underlying disagreement about exactly what constitutes a ‘woodland bird’.

Fraser et al (2017) demonstrate that inconsistency in classifying species as ‘woodland birds’ can change the direction and magnitude of trends in indices of ‘woodland bird’ prevalence, even when the data and analyses are the same. Inconsistent classification of woodland birds persists for three main reasons.

1. Classification of vegetation can be inconsistent (Bruehlheide and Chytrý, 2000; Čarni et al., 2011; de Cáceres and Wiser, 2012). In Australia, botanists typically distinguish between vegetation types according to the canopy cover of the vegetation’s tallest (dominant) strata (Specht, 1970). In this context, vegetation is classified as ‘woodland’ if it has a trees over 10m tall and a foliage projective cover less than 30%. Vegetation is classified as ‘forest’ if it has trees over 10m tall and a foliage projective

cover more than 30%. However, bird researchers don't always subscribe to these classifications, often not assessing the structure of the vegetation, and may classify habitat based on coarse scale maps or on the presence of trees (Fraser et al., 2015).

2. Habitat preference is a continuum from species that only occur in one habitat type to species that are equally prevalent in several habitats. Some species may be easy to classify but many are difficult to reliably assign to a single category (Regan et al., 2002). Classification imprecisely simplifies the habitat preference continuum that depends on a range of different factors, including where and for how long the species occurs in other habitats, whether it depends on woodlands for critical life stages, and so on.
3. There are no dedicated species lists or guidelines to assist researchers and managers when determining which species they should classify as woodland birds. In the absence of such guidance, researchers idiosyncratically classify woodland birds, and have variously considered: any species that occurs in a woodland; any species that is more common in woodlands than other habitats; or species that possess particular life history traits that mean they depend on woodlands (e.g. nesting and foraging requirements) (Fraser et al., 2015).

This spectrum of classification schemes means that researchers classify woodland birds inconsistently (Fraser et al., 2017, 2015). Inconsistent classification creates a barrier to understanding the ecology of, and managing woodland birds. There are three possible solutions to this problem: study trends in all bird species individually; study trends in all birds within woodland habitats; and classify bird species into transparent and reliable categories that make ecological sense.

Studying species individually is appealing in that it avoids deconstructing the continuum of habitat preference and therefore preserves the unique relationship of different species to their

environment. Many studies take this approach by studying individual species and providing fine-scale assessments of that species' response to certain drivers. However, this kind of analysis provides information that is too detailed to answer some broad-scale, community-level questions. For example, studying trends of multiple individual species might find that some species were increasing and others decreasing (e.g. Reid, 1999), but evaluating shared patterns between species might be difficult (e.g., landscape-wide declines in a group of species sharing the same habitat).

Studying all bird species occurring within a particular habitat type similarly avoids the ambiguity of dividing species into groups based on their habitat preferences. In the case of woodland birds, this makes intuitive sense because the overriding concern about these species relates to the destruction of woodland habitat (Hugh A Ford, 2011; Haslem and Bennett, 2008; Radford and Bennett, 2007). Some researchers conduct their studies on this basis (Fraser et al., 2015) but the approach does not account for landscape-scale changes in bird prevalence caused by habitat destruction. For example, consider a landscape with 50 patches of woodland each with an average of 10 bird species: if half of these patches are cleared but the remaining 25 have the same average bird richness, a study that is only conducted on birds in woodland habitat would not detect a decline.

Grouping species together can discern broader scale responses. If species are grouped according to their habitat preference, it is possible to investigate whether species that prefer a particular habitat (e.g. woodlands) are more likely to be in decline compared to species with different habitat preferences. This can be useful for multi-species conservation efforts because it identifies a group of vulnerable species and the habitat types that could be targeted for protection or management. Further, the process of delineating a faunal group can facilitate its protection. For example, identifying an Australian 'woodland bird' community has allowed researchers to apply for Federal protection for the whole group under the

Environment Protection and Biodiversity Conservation Act 1999 (HF pers. obs.). However, as established above, it is important that these groups are identified transparently, based on sound ecological theory.

In this study, we aim to develop a definition of woodland birds that provides a consistent basis for understanding woodland bird ecology, monitoring and conservation. We explore the definition of ‘woodland bird’ by examining the relationship between species traits and relative occurrence in woodlands and other habitat types. By considering traits and relative occurrence of birds, we hope to identify a list of bird species that prefer woodland habitats and are thus likely to be threatened by the destruction and degradation of woodlands in Australia (Bradshaw, 2012; Hugh A. Ford, 2011). We use a hierarchical model to examine which species demonstrate a preference for woodlands, which traits are associated with a preference for woodland vegetation, and how these change depending on study regions and how ‘woodland’ vegetation is defined. We aim to understand the traits associated with birds’ preference for woodland habitats and develop a justifiable and objective classification of woodland birds. We demonstrate the application of this method for an Australian case study, but this approach has broad relevance to other regions and taxa. For example, woodland, farmland and generalist bird groups are inconsistently classified across Europe (Fraser et al., 2017). This inconsistent classification can inhibit the acquisition of important ecological knowledge by introducing uncertain terminology and precluding direct comparison between studies (Herrando-Perez et al., 2014). The approach used in this article could be applied to other inconsistently classified groups to provide scientific, objective classification schemes.

3. Methods

We compiled information on the occurrence of all Australian bird species (excluding waterbirds) and their nesting, foraging and dispersal traits, as well as the distribution of

‘woodlands’ as determined using three different definitions. We used these data to fit a hierarchical model of species occurrence (see Pollock et al. 2012) in which the relationship between species occurrence and vegetation is mediated by species traits. Based on the results of this model, we developed a classification in which species are grouped according to habitat preference. Finally, we applied our classification to three existing woodland bird case studies to examine how the inference based on our classifications compared with and added to the original findings of the case studies. Each of these aspects of our methods is described below.

3.1. Hierarchical Models

We used hierarchical generalised linear models in R version 3.3.3 (R Core Development Team, 2017) to examine the variables correlated with woodland occupancy in four datasets; one for the whole of Australia and one for each of the three ecoregions in which woodland vegetation occurs - ecoregion 4, *temperate broadleaf and mixed forests*; ecoregion 7, *tropical and subtropical grasslands, savannas and shrublands*; and ecoregion 12, *Mediterranean forests, woodlands and shrublands* (Figure 1). These statistical models suit datasets with a hierarchical structure, partitioning explained and unexplained variation between different levels of a dataset (Gelman and Hill, 2007). Separate ecoregion analyses were conducted to account for regional differences in woodland bird species composition at this scale.

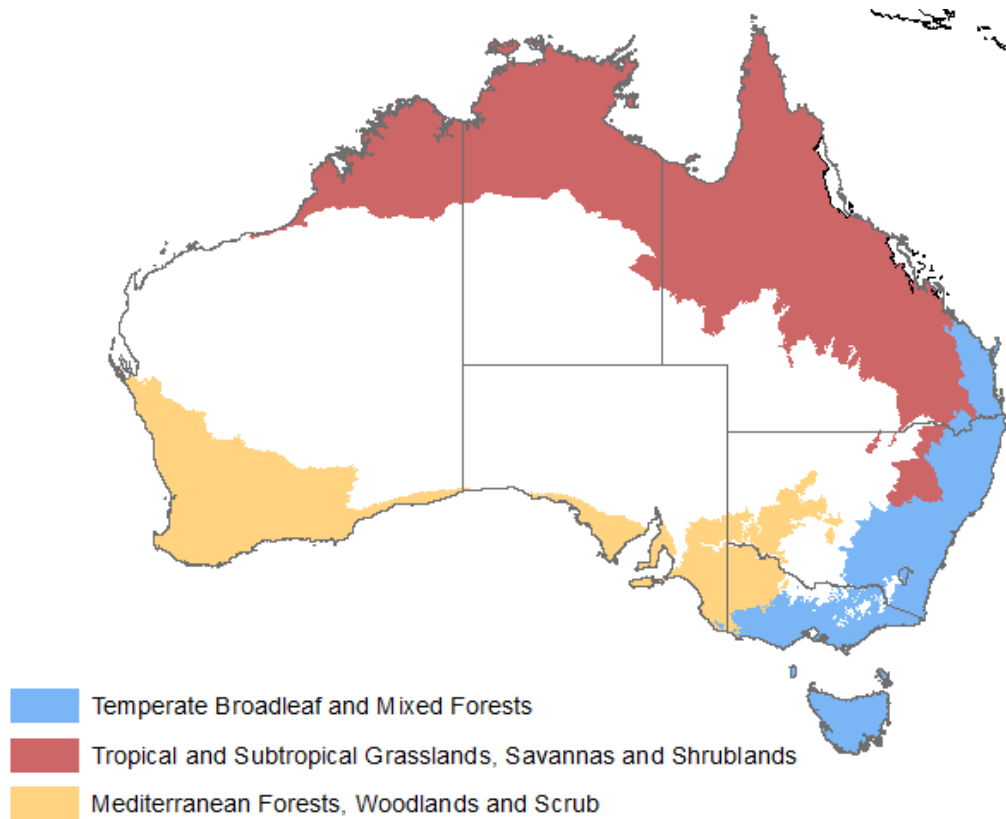


Figure 1: The distribution of the three studied Ecoregions, from the World Wildlife Fund ecoregions map (Olson et al., 2001)

We primarily aimed to investigate birds' preference for woodland vegetation, and how the strength and nature of that preference is mediated by species' traits (full model code available in Appendix 1). For each of the four datasets, we modelled the observed presence or absence Y_{ij} of each species i (number of species=458, 298, 308, and 234 respectively for Australia, Ecoregion 4, Ecoregion 7 and Ecoregion 12) at each site j (number of bird sites=5891, 2640, 632, and 1314 respectively) as a random sample from a Bernoulli distribution:

$$Y_{i,j} \sim \text{Bernoulli}(p_{i,j})$$

where $p_{i,j}$ is the predicted probability that species i is present at site j . The logit of the predicted probability $p_{i,j}$ is a species-specific function of woodland preference, which is comprised of an association with 'woodland' habitat (w , the percentage of land within a

500m radius of the survey site that supports ‘woodland’ vegetation according to the National Vegetation Information Scheme) and with tree cover (t , the percentage of land within a 500m radius that is covered by tree canopies):

$$\text{logit}(p_{i,j}) = \alpha_i + x_i \log(w_j + 1) + z_i \log(t_j + 1),$$

where α_i is the intercept term for each bird species i and x_i and z_i define the influence of w_j (percentage woodland vegetation) and t_j (percentage tree cover), respectively, on the probability of occurrence of species i . Including a term for percentage woodland cover provides information about the type of habitat in that area, while including a term for percentage tree cover provides information about how much habitat there is in an area. Prior to including them in the model the values for w_j (percentage woodland vegetation) and t_j (percentage tree cover) were centred and standardised by subtracting the mean and dividing by the standard deviation. It was necessary to add 1 to the (centred and standardised values for) w_j and t_j before taking the logarithms because both variables had instances of 0 values. The intercept term α_i was assigned an uninformative Normal(0, 100²) prior distribution. Species preference for woodland habitat, x_i , was modelled as a function of eight bird traits thought to influence woodland preference (see Table 1):

$$x_i = \alpha_x + \beta_h h_i + \beta_n n_i + \beta_g g_i + \beta_s s_i + \beta_b b_i + \beta_a a_i + \beta_c c_i + \beta_d d_i + \varepsilon_{xi}$$

where α_x is the intercept term and β_h , β_n , β_g , β_s , β_b , β_a , β_c and β_d are coefficients explaining the influence of each bird trait on x_i (see Table 1 for traits), and ε_{xi} accounts for extra variation between species. The α and β coefficients are all assigned uninformed Normal(0, 100²) prior distributions. Between-species variation ε_{xi} is drawn from a Normal(0, σ_{zi}^2) distribution with σ_{zi}^2 assigned a Uniform(0,100) prior.

Species reliance on tree cover, z_i , is also modelled as a function of eight bird trait variables

$$z_i = \alpha_z + \gamma_h h_i + \gamma_n n_i + \gamma_g g_i + \gamma_s s_i + \gamma_b b_i + \gamma_a a_i + \gamma_c c_i + \gamma_d d_i + \varepsilon_{zi}$$

where α_z is the intercept term and $\gamma_h, \gamma_n, \gamma_g, \gamma_s, \gamma_b, \gamma_a, \gamma_c, \gamma_d$ are coefficients explaining the influence of each bird trait on z_i , all assigned uninformative Normal(0, 100²) prior distributions. Between-species variation ε_{zi} is drawn from a Normal(0, σ_{zi}^2) distribution with σ_{zi}^2 assigned a Uniform(0,100) prior (Table 1).

Table 1: Definition of model terms, β coefficients relate to percentage woodland vegetation, γ coefficients relate to percentage tree cover.

Variable	Symbol	Coefficient
Hollow Nesting	h_i	β_h
		γ_h
Tree Nesting	n_i	β_n
		γ_n
Ground Foraging	g_i	β_g
		γ_g
Shrub Foraging	s_i	β_s
		γ_s
Bark Foraging	b_i	β_b
		γ_b
Aerial Foraging	a_i	β_a
		γ_a
Canopy Foraging	c_i	β_c
		γ_c
Dispersal Distance (centred and standardised)	d_i	β_d
		γ_d
Error term	ε_{X_i}	
	ε_{Z_i}	

In total, we fit six models to explore whether variation in the definition of woodland or regions would influence the traits associated with woodland preference or the birds regarded as ‘woodland birds’.

Three models use the Australia-wide dataset and investigate the impact of defining woodlands differently by considering woodlands to be: any area with a treed overstorey, areas classed as woodlands under the National Vegetation Information System (NVIS) and, areas classed as eucalypt woodland under the NVIS. Operationally, this means that the values of w_j are altered to reflect different definitions of woodland in each of the three models.

Another three models used the most commonly studied interpretation of woodland vegetation (eucalypt woodlands as defined by the NVIS) to investigate regional differences between three ecoregions: ecoregion 4, *temperate broadleaf and mixed forests*; ecoregion 7, *tropical and subtropical grasslands, savannas and shrublands*; and ecoregion 12, *Mediterranean forests, woodlands and shrublands* (Figure 1).

3.2. Data

We obtained species occurrence data for 468 Australian bird species from the BirdLife Australia Atlas (BirdLife International and NatureServe, 2014). The BirdLife Australia Atlas comprises bird survey data collected by volunteers. Unlike many bird atlases that collect data in specified grid cells (Gibbons et al., 2007), Birdlife Australia's atlas data is collected by volunteers at sites they choose, with exact coordinates recorded for each survey. This allows for fine resolution analyses and close links between the bird survey and landscape-scale data, but means that data are biased toward areas that are more attractive or close to major settlements. We use data gathered using 500 m² area searches, where the volunteer records the geographical reference at the centre of their site and all birds seen or heard in their survey area, including those flying overhead. Volunteers can choose the shape of the 500m² area they survey and how long they survey it for, provided that they survey for more than 20 minutes and less than one week. The data are validated by Birdlife, ensuring that the geographical references are sensible and that the species are within their known range. We

selected a subset of the available Birdlife data, only including data from 2011 (corresponding with the year that the tree cover layer we use was developed) and excluding 10 species that were recorded fewer than ten times each (to avoid creating uninformative models).

Species trait data were compiled using the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB) and an unpublished traits database derived from HANZAB (Luck, unpublished data). Traits extracted for each species were: wingspan, mass, diet, feeding guild, foraging location and nest location and type. Data on wingspan, mass and diet were then used to calculate the dispersal potential of birds following Garrard et al.'s (2012) model.

Vegetation data were extracted from three spatial layers using R version 3.3.3 (R Core Development Team, 2017) with packages 'dismo' (Hijmans et al., 2016) and 'raster' (Hijmans, 2015). A tree cover layer with data from 2011 was derived from the Global Land Cover Facility map, providing the percentage of each 30-m grid cell that is covered by tree canopy. We used these data to calculate the percentage of land within 500m of the bird survey site that was covered by the tree canopy (% tree cover).

Information on the type of vegetation represented by the tree cover data was derived from NVIS (National Vegetation Information System) version 4.1 (resolution 100 m). This database divides Australia's vegetation into 32 Major Vegetation Groups including several groupings specifying 'forest' vegetation and 'woodland' vegetation, where woodland vegetation has a canopy cover of 5-30% and forest vegetation has a canopy cover of >30%. This classification is slightly different from the Specht (1970) classification which specified woodlands as anything with a treed overstorey but <30% tree cover. The NVIS classification provides more clarity around the distinction between woodland and more open habitat types. We used the NVIS data to calculate the percentage of land within 500 m of bird surveys that

comprised ‘woodland’ vegetation (% woodland cover), following three different definitions of woodland used by Australian ornithologists (from Fraser et al 2015):

- i) any vegetation where the dominant stratum is trees, excluding rainforest;
- ii) any treed vegetation with an open canopy structure (5-30% canopy cover) (NVIS woodlands; Specht, 1970);
- iii) eucalypt-dominated vegetation with an open canopy structure (5-30% canopy cover; NVIS Major Vegetation Groups 5, 11, 12, 14, and 32).

To explore the relationship between bird occurrence and vegetation, we calculated the percentage of the landscape within a 500m radius of bird occurrence data points consisting of tree cover and woodland vegetation (under the three above definitions) from the vegetation layers (*sensu* Montague-Drake et al. 2011).

Our resulting dataset included species occurrence data and percentage tree and woodland cover for 458 species and 5891 sites across Australia. However, bird species’ relationships to habitat may vary across regions (Fraser et al., 2015; Polyakov et al., 2013). As such, we further divided our data into three ecoregions (Olson et al., 2001) representing the areas in which the majority of woodland bird research takes place in Australia (Rayner et al. 2014; Figure 1): ecoregion 4, *temperate broadleaf and mixed forests*, which included data for 298 species across 2640 sites; ecoregion 7, *tropical and subtropical grasslands, savannas and shrublands*, which included data for 308 species across 632 sites; and ecoregion 12, *Mediterranean forests, woodlands and shrublands*, which included data for 234 species across 1314 sites.

3.3. Examination of Model Output

3.3.1 Coefficient analysis

We studied the model coefficients (β and γ) of all six models to determine whether preference for woodland vegetation (x_i) or tree cover (z_i) were significantly related to bird trait variables. For each coefficient we examined the magnitude of the effect and its significance based on whether the 95% credible intervals crossed zero.

3.3.2 Null species analysis

We conducted a sensitivity analysis to determine how each trait impacts on bird species' probability of occurrence, p_i . To do this we calculated the mean probability of occurrence of a 'null' species. A 'null' species has a median dispersal ability and does not nest in trees or tree hollows, or forage on the ground, in shrubs, on bark, in the air, or in the canopy. We then compared this to nine 'hypothetical' species that vary from the null species in one trait. Relative to the 'null' species, each hypothetical species possesses one of the following traits: high dispersal distance; low dispersal distance; nests in trees; nests in tree hollows; forages aerially; forages on the ground; forages on bark; forages in shrubs; or forages in the canopy. We calculated the percentage change in probability of occurrence of the hypothetical species compared to the null species for three vegetation types: open country (10% eucalypt woodland vegetation cover, 15% tree cover within a 500m radius), woodland (90% eucalypt woodland vegetation cover, 80% tree cover within a 500m radius) and forest (10% eucalypt woodland vegetation cover, 80% tree cover within a 500m radius).

3.4. Woodland bird groups and case studies

The majority of bird conservation efforts are concerned with providing additional habitat for birds (Lindenmayer et al., 2012; Thomson et al., 2007). However, each species has slightly different requirements which complicates conservation decision making. Grouping species according to their habitat association is appealing because of its potential to allow researchers and conservationists to target habitat management for multiple species. However, as species

have varying requirements, several bird groups are necessary. Using the responses to woodland vegetation and tree cover from the hierarchical models described above, we delineated species into five groups according to their habitat preference (full species lists for each group in each region are provided in the Appendix 2):

- 1) *Closed-woodland species*. The occurrence of species i is positively related to woodland vegetation cover and tree cover. These species are defined as those where the lower credible intervals of the estimated association with woodland vegetation (x_i) and with tree cover (z_i) are positive. In other words, these species occur most in areas where there is a large amount of treed vegetation with an open canopy structure (woodlands: NVIS classification, Specht, 1970);
- 2) *Open-woodland species*. The occurrence of species i is positively related to woodland vegetation cover, but is not demonstrably associated with increased tree cover. These species are defined as those where the lower credible interval of the estimated association with woodland vegetation (x_i) is positive, but the lower credible interval for association with tree cover (z_i) is negative. In other words, these species occur most in areas where there is a small amount of treed vegetation (usually due to clearing) with an open canopy structure (woodlands: NVIS classification, Specht, 1970). This group includes species with positive (but uncertain) coefficients for tree cover and species that respond negatively to tree cover;
- 3) *Forest species*: The occurrence of species i is positively related to tree cover but is not demonstrably related to increased woodland vegetation cover. These species are defined as those where the lower credible interval of the estimated association with tree cover (z_i) is positive but the lower credible interval for (x_i) woodland vegetation type is negative. In other words, these species occur most where there is a large amount of treed vegetation with a closed canopy structure (forests: Specht, 1970).

This group includes species with positive (but uncertain) coefficients for woodland vegetation and species that respond negatively to woodland vegetation;

- 4) *Open country species*: The occurrence of species i is negatively related to both woodland vegetation cover and tree cover. These species are defined as those where the upper credible intervals of the estimated association with woodland vegetation (x_i) and for association with tree cover (z_i) are negative. In other words, these species occur most in habitats which have very low tree cover, little of which is classed as woodland vegetation; and
- 5) *Uncertain species*: based on occurrence data, species i does not fit into any of the above groupings (either both credible intervals span zero, or one credible interval spans zero and it does not qualify for the other four categories listed above).

In order to determine what these five bird groups add to current understanding, we compared results gained using our bird groups with the original results of three case studies which investigate key hypotheses relating to woodland birds: 1) that birds in groups 1 and 2 (considered woodland birds) are more abundant in woodlands than other habitat types, and less abundant in more heavily grazed landscapes (Martin and McIntyre, 2007); 2) that they occur less frequently in more urbanised areas (Ikin et al., 2012); and 3) that they are declining, especially in ecoregion 4 (Barrett et al., 2004).

3.4.1. Case Study 1: Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats (Martin and McIntyre, 2007)

Martin and McIntyre (2007) investigated the impact of habitat type (pasture, riparian or woodland) and grazing level (low, moderate or high) on the abundance of birds in Queensland. They found that woodlands were more species rich and had a greater abundance of birds than cleared habitats, and that the species richness and abundance of birds in treed

habitat types decreased with increasing grazing intensity. For cleared and woodland habitat types and low, medium and high grazing levels, we used raw data provided by the authors to estimate species richness (mean and 95% CIs) for each of the four informative bird groups (*closed-woodland*, *open-woodland*, *forest* and *open country*) we derived for Ecoregion 7. We expected that species richness of woodland birds (i.e. groups *closed-woodland* and *open-woodland*) to be higher in woodland habitats than in cleared, pasture habitats, and to be lower in areas subject to higher intensity grazing.

3.4.2. Case Study 2: Pocket parks in a compact city: how do birds respond to increasing residential density? (Ikin et al., 2012)

Ikin *et al.* (2012) studied the relationship between bird richness and different elements of the urban matrix in Canberra. Using an information theoretic approach, they compared alternative hypotheses to determine which elements of the urban matrix most closely matched the data. They found that woodland bird richness was most likely to be positively associated with number of large eucalypts, percentage of the landscape used for greenspace, and percentage tree and shrub cover. They found likely negative associations with number of trees per hectare, residential block size and number of residential blocks. We used their data and models to replicate this approach for each of the four informative bird groups (*closed-woodland*, *open-woodland*, *forest* and *open country*) we derived for Ecoregion 4. We expected to find that richness of woodland birds (i.e. groups *closed-woodland* and *open-woodland*) would relate to the same habitat components as in the original study of Ikin *et al.* (2012).

3.4.3. Case Study 3: Comparison of atlas data to determine the conservation status of bird species in New South Wales, with an emphasis on woodland-dependent species (Barrett et al., 2004)

Barrett *et al.* (2004) reviewed changes to the distribution and number of bird species in New South Wales over the 20-year period between Birds Australia Atlases 1 and 2. They estimated the percentage change in reporting rate of New South Wales bird species, including a summary which reveals that 40% of woodland bird species declined between Atlases. We use these data to calculate percentage of species declining between the two Atlases for each of the four informative bird groups (*closed-woodland*, *open-woodland*, *forest* and *open country*) we derived for Ecoregion 4. Based on prevalent concern about a decline in woodland birds (Rayner *et al.*, 2014), we expected to see a greater number of declining species in *closed-woodland* and *open-woodland* bird communities than other bird communities.

4. Results

4.1. Coefficient analysis

4.1.1 Analysis of difference in woodland definition

Regardless of which definition of ‘woodland’ vegetation we used, the relationship between bird occurrence and percentage tree cover (z) is significantly more positive for tree nesting (γ_n is positive) species and more negative for ground foraging (γ_g is negative) and aerial foraging (γ_a is negative) species when considering the full Australian dataset (Figure 2). There was also some evidence that the relationship between occurrence and tree cover is more positive for bark foraging species (γ_b is positive) and more negative for species with higher dispersal ability (γ_h is negative), although the 95% credible intervals for these estimates include zero. Evidence of traits influencing the relationship between bird occurrence and woodland vegetation (x) was less definitive, as indicated by mean estimates of β falling closer to zero

(Figure 2). However the relationship between bird occurrence and woodland vegetation is more positive for tree nesting and aerial- and canopy-foraging species.

There was little difference in responses when considering ‘woodland’ to refer to all woodlands or eucalypt woodlands. However, when considering ‘woodland’ to refer to all treed habitats excluding rainforests, the mean estimates for the coefficients of ‘woodland’ preference (x) were closer to zero and had narrower confidence intervals than the estimates for the other woodland types.

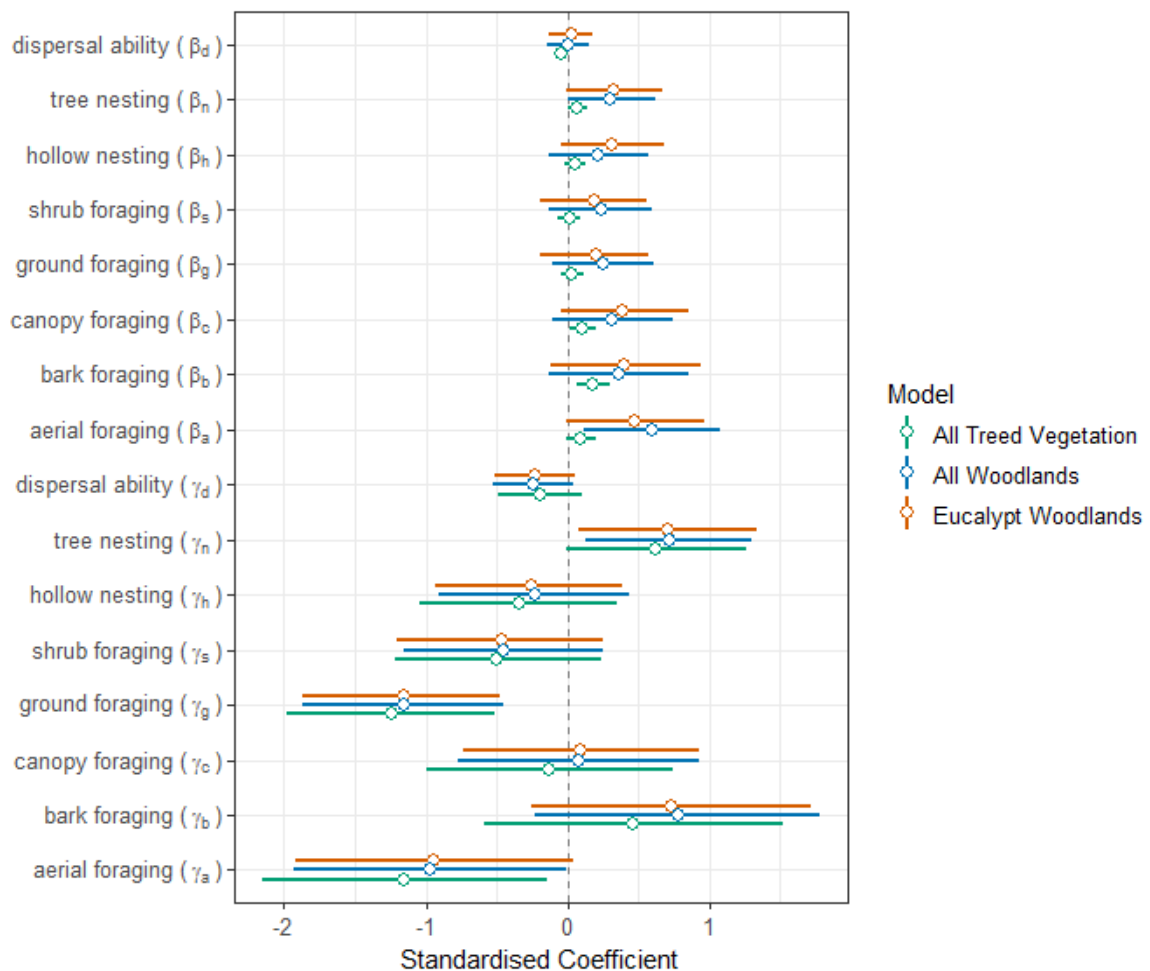


Figure 2: Standardised coefficients for Australia-wide models predicting the ‘woodland’ preference of birds when considering ‘woodlands’ as: all woodland vegetation (blue), eucalypt woodland vegetation (red), or any treed habitat type (excluding rainforest) (green).

Coefficients representing associations between woodland vegetation cover and species traits are denoted by β and those representing associations between tree cover and species traits are denoted by γ . Circles represent means, lines represent 95% credible intervals.

4.1.2. Analysis of regional differences

As there was little difference in model coefficients between ‘all woodlands’ and ‘eucalypt woodlands’ (Figure 2), and the majority of existing Australian woodland bird studies consider birds of eucalypt woodlands, we only used data from eucalypt woodlands for our regional analyses (Figure 3).

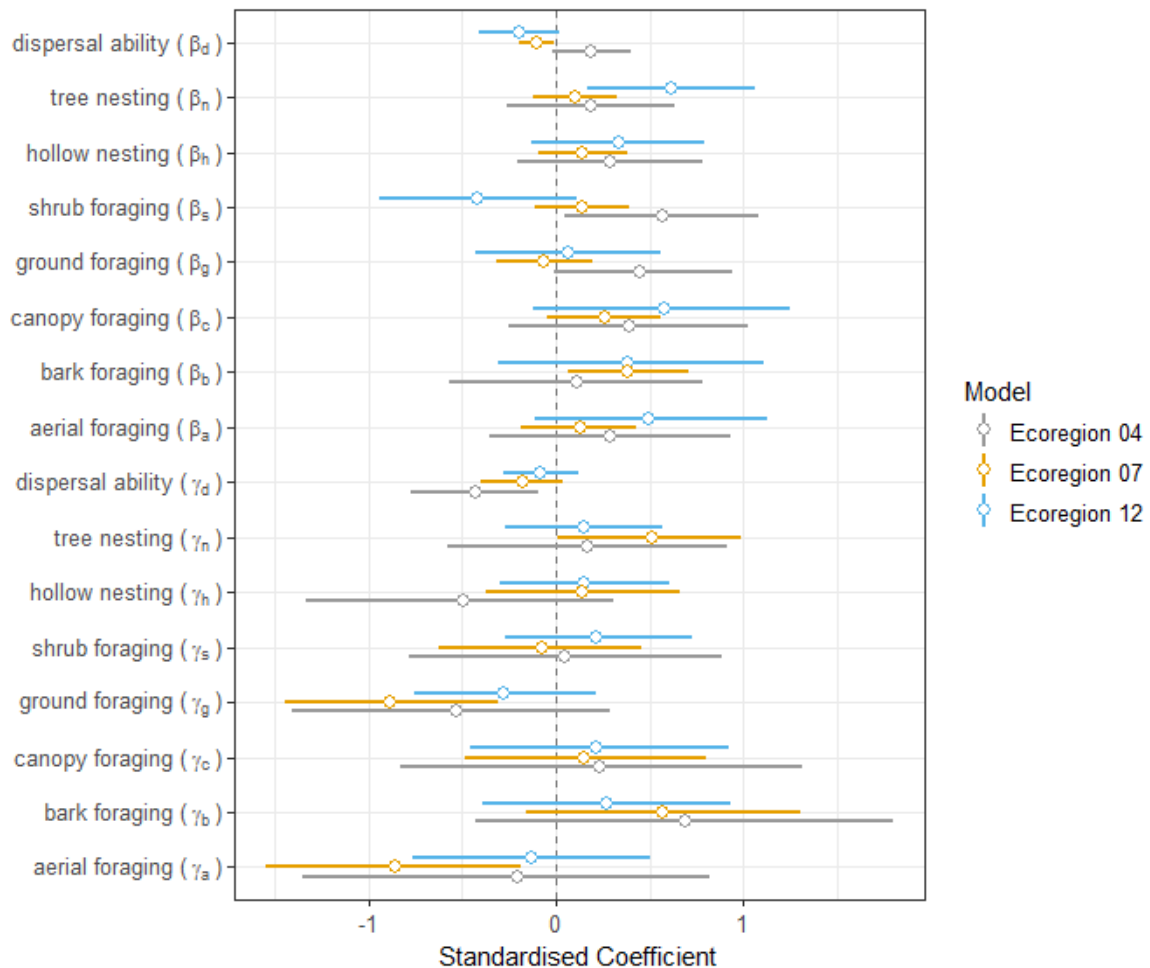


Figure 3: Standardised coefficients for models predicting eucalypt woodland preference in Ecoregions 4 (grey), 7 (orange) and 12 (blue). Coefficients representing associations between

woodland vegetation cover and species traits are denoted by β and those representing associations between tree cover and species traits are denoted by γ . Circles represent means, lines represent 95% credible intervals.

4.1.2.1. Ecoregion 4: temperate broadleaf and mixed forests

The only trait to significantly influence the relationship between occurrence and tree cover (z) in Ecoregion 4 was dispersal ability, which had a negative association (γ_d is negative; Figure 3). The lack of other significant relationships may be attributable to high variability in the data, as indicated by wide 95% credible intervals (Figure 3). The bark foraging and tree nesting traits may make the relationship between tree cover and occurrence more positive (γ_b and γ_n are positive) though the relationships are uncertain (credible intervals cross 0). The relationship between occurrence and woodland habitat (x) was more positive for shrub foragers and potentially ground foragers (β_s and β_g are positive), although the latter is less certain.

4.1.2.2. Ecoregion 7: Tropical and subtropical grasslands, savannas and shrublands

In ecoregion 7, the relationship between bird occurrence and percentage tree cover (z) is significantly more positive for tree nesting (γ_n) species and more negative for ground foraging (γ_g) and aerial foraging (γ_a) species (Figure 3). The relationship between occurrence and percentage tree cover may also be more positive for bark foraging (γ_b) species but the 95% credible intervals overlap zero (Figure 3). The relationship between the percentage of habitat within a 500 m radius that is classed as Eucalypt woodland (x) and bird occurrence was significantly more positive for bark foraging species (β_b) and negatively related to dispersal ability (β_d).

4.1.2.3. Ecoregion 12: Mediterranean forests, woodlands and shrublands

In ecoregion 12 (Figure 3), traits had no significant impact on the relationship between bird occurrence and tree cover (z) but the relationship between occurrence and percentage woodland vegetation (x) is significantly more positive for tree nesting (β_n) species and more negative for species with high dispersal ability (β_d). The canopy foraging trait (β_c) may also make the relationship more positive but is uncertain.

4.2. Null species analysis

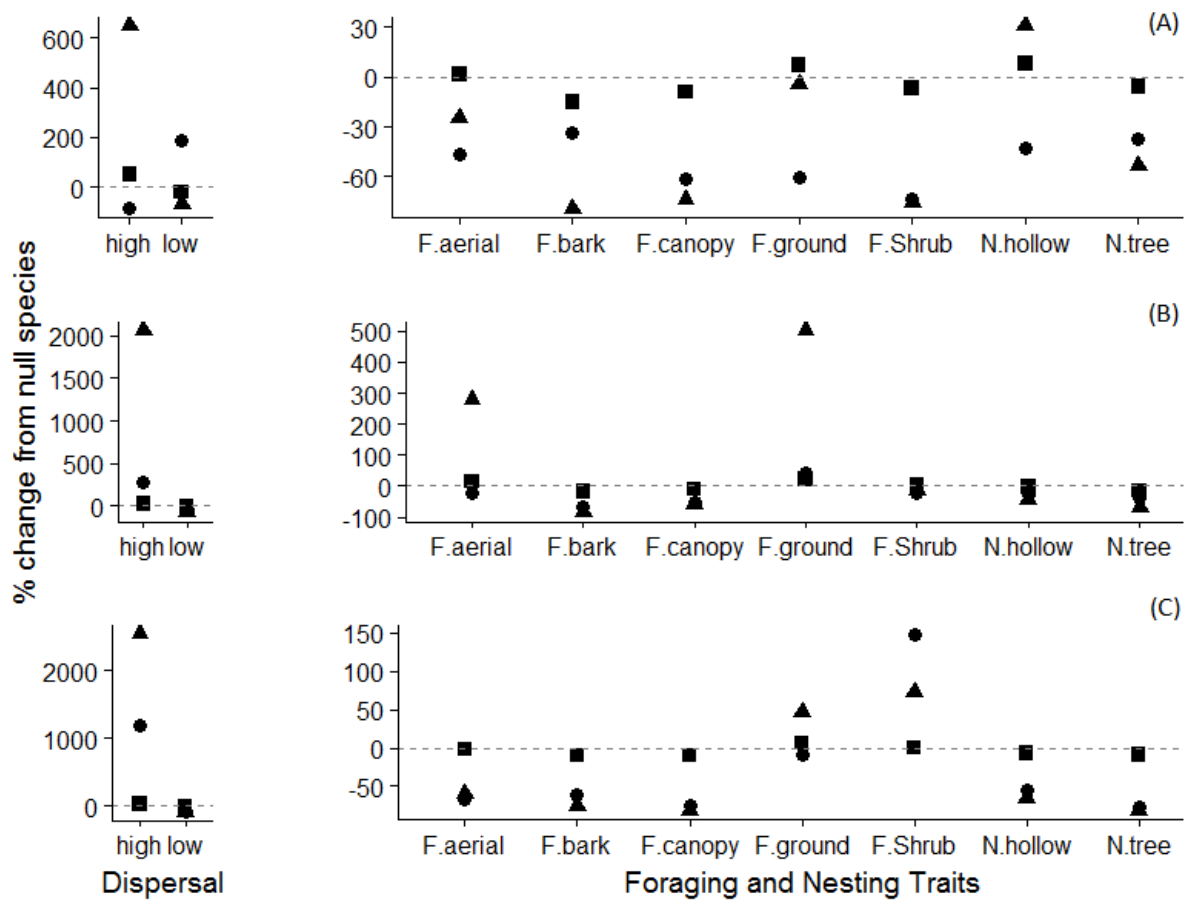


Figure 4: Percentage change in probability of occurrence associated with a bird having a particular trait relative to a 'null species' in open country (triangle), woodland (square) and forest (circle) habitats in A) ecoregion 4, B) ecoregion 7 and C) ecoregion 12. The 'null species' has a median dispersal distance and does not have any of the other traits. Graphs to the left of the panel express change associated with species having high and low dispersal

abilities. Graphs to the right of the panel express changes associated with foraging (e.g. F.bark) and nesting traits (e.g. N.hollow). The scale of the y axis is different for dispersal vs nesting and foraging trait graphs.

In each of the ecoregions and for all traits, the squares representing probability of occurrence in a woodland habitat (high percentage tree cover and high percentage woodland cover within 500m) are close to zero (Figure 4). This indicates that the probability of species occurring in woodland habitats is not strongly related to species traits. In contrast, the probability of species occurring in forest and open country habitats was quite sensitive to changes in traits. In all ecoregions, species with high dispersal ability were much more likely to occur in open country habitats than the null species (Figure 4). All other trait relationships varied regionally.

In ecoregion 4, species with low dispersal ability were more likely to occur at forest sites than the null species but in ecoregion 12 (and to a lesser extent ecoregion 7), species with high dispersal ability were more likely to occur at forest sites than the null species (Figure 4A). Similarly, in ecoregion 4, the presence of any of the foraging or nesting traits reduced a species' probability of occurring in forest habitats and bark foraging, canopy foraging, shrub foraging and tree nesting traits reduced species' probability of occurring in open country habitats, when compared to the null species. In ecoregion 7, aerial foraging and ground foraging traits dramatically increased the probability of species occurring in open country habitats compared to null species (Figure 4B). In ecoregion 12, shrub foraging species were more likely to occur in both forest and open country habitats and ground foragers were more likely to occur in open country habitats than null species (Figure 4C).

4.3. Variation in species lists

For the Australia-wide dataset, the composition of our five bird groups differed only slightly depending on the type of vegetation considered ‘woodland vegetation’. Of the 458 species included in the model, 412 were classified into the same group when considering eucalypt vs all woodland vegetation (an additional 33 species were classed as uncertain under one of these two vegetation classes). Of these species, 73 were classified differently if the model considered ‘woodlands’ to include all treed vegetation types except rainforest (see Appendix 2 for species lists).

Bird lists differed substantially between ecoregions. Of the 420 species which occurred in Ecoregions 4, 7 or 12, 155 occurred in all three ecoregions and 154 only occurred in one ecoregion. Of the 266 species which occurred in more than one region, our classification scheme classed 111 species into the same group in all regions in which they occurred. Only one species was consistently categorised as a closed-woodland bird across regions but 12 species were consistently open-woodland birds, 23 forest birds and 12 open country birds. A total of 26 species were always classed as belonging to a woodland category (i.e. closed- or open-woodland) and only 12 species were sometimes classed as open country and sometimes in one of the forest and woodland associated groups (Appendix 2).

4.4. Model Validation

4.4.1. Case Study 1

The majority of species included in the data from Martin and McIntyre (2007) were forest species, which may reflect that the vegetation in this study was more forest than woodland. Too few species were classed as closed-woodland or open country species to detect meaningful trends. However, there was a sufficient number of open-woodland and forest bird species to determine that they were more prevalent in woodlands than in open country habitats (Figure 5).

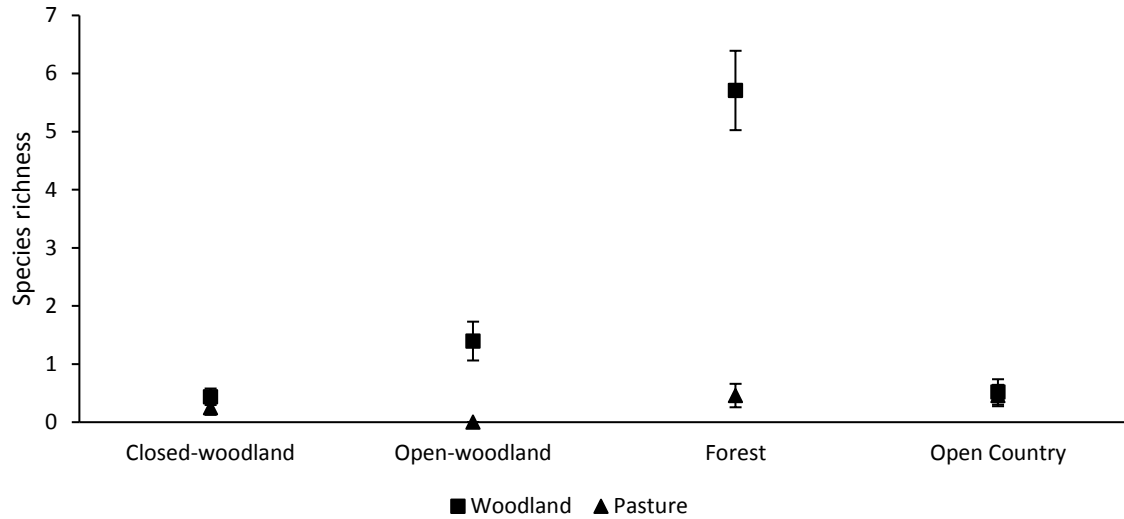


Figure 5: Mean and 95% confidence intervals of species richness by bird group in Martin and McIntyre's (2007) dataset for pasture and woodland habitat types.

The richness of open-woodland and forest birds was also higher at sites that were grazed less intensely (Figure 6). The opposite relationship was found for the richness of open country species, which increased with grazing intensity.

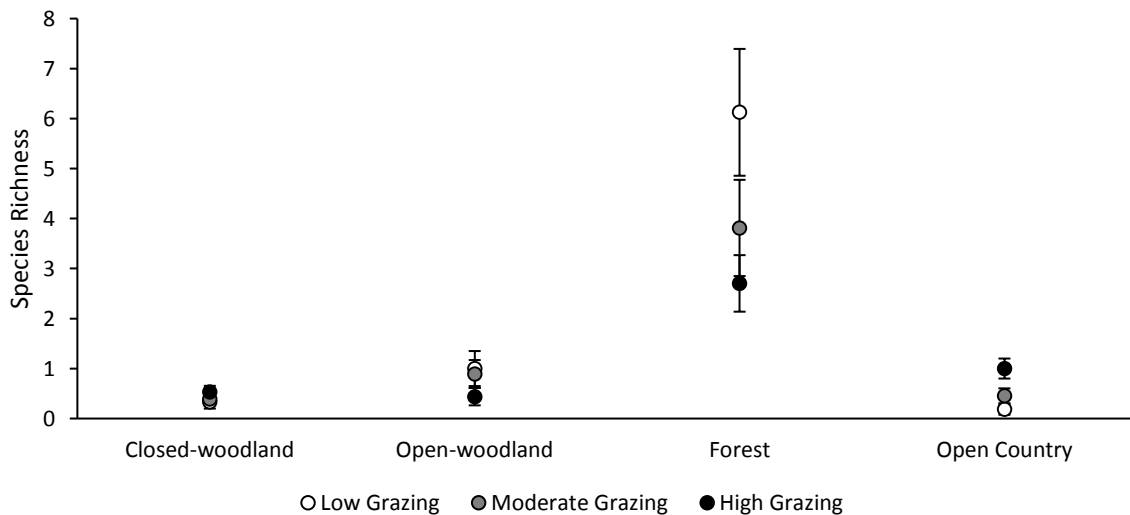


Figure 6: Mean and 95% confidence intervals of species richness by bird group in Martin and McIntyre's (2007) dataset for different levels of grazing.

4.4.2. Case Study 2

Table 2 shows model outcomes when using the methodology used in Ikin et al. (2012). In order of descending frequency, models variously included the percentage cover of trees and shrubs (n=10), percentage greenspace land use (n=8), number of trees per hectare (n=8), number of large eucalypts per hectare (n=8), residential block size (n=2), number of residential blocks (n=2), proximity to greenspace (n=2) and greenspace patch size (n=1).

All models for woodland species, three models for open-woodland species and two models for forest species showed positive relationships between richness and the percentage cover of shrubs and trees. In contrast, open country habitat species responded negatively to percentage cover of shrubs and trees in two of three models.

Tree density seemed to have a negative effect on closed-woodland, open-woodland and forest species although density of large eucalypts had a positive effect on those groups. Closed-woodland, open-woodland and open country species richness also responded positively to percentage greenspace land use.

Table 2: Best ranked models ($\Delta AICc \leq 2$) for each bird group showing number of parameters, differences in Akaike Information Criterion corrected for small sample bias (AICc) compared with the model with the lowest AICc, Akaike weights, percentage deviance explained and model coefficients

	Closed Woodland			Open Woodland						Forest Species			Open Habitat Species							
	1	2	3	1	2	3	4	5	6	7	8	9	10	1	2	3	1	2	3	
Model Summary																				
Model #	1	2	3	1	2	3	4	5	6	7	8	9	10	1	2	3	1	2	3	
Number of parameters	1	2	3	3	2	1	2	2	4	4	4	2	1	2	3	1	1	1	2	
$\Delta AICc$	0.00	0.33	1.91	0.00	0.08	0.09	0.95	1.47	1.52	1.58	1.66	1.77	1.95	0.00	0.26	1.16	0	1.47	1.85	
Akaike Weight	0.24	0.21	0.09	0.13	0.12	0.12	0.08	0.06	0.06	0.06	0.06	0.05	0.05	0.21	0.19	0.12	0.29	0.14	0.11	
% Deviance Explained	4.92	7.01	7.68	10.48	6.88	3.46	5.47	4.65	11.57	11.48	11.35	4.15	0.46	5.43	7.44	1.97	5.00	2.12	5.52	
Residual Degrees of Freedom	106	105	104	104	105	106	105	105	103	103	103	105	106	105	104	106	106	106	105	
Intercept	-0.33	-0.85	-0.86	0.89	0.90	0.90	0.90	0.90	0.89	0.89	0.89	0.90	0.90	-0.57	-0.58	-0.54	1.12	1.12	1.12	
# Trees/ha			-0.07	-0.07	-0.06				-0.06	-0.07	-0.07			-0.30	-0.31					
# Large eucalypts/ha			0.24	0.12	0.12				0.12	0.12	0.11			0.07	0.04					
% Greenspace land use		0.30		0.09		0.09	0.11		0.10		0.11							0.06	0.05	
% Tree and shrub cover	0.30	0.38	0.26				0.07				0.05		0.05			0.18	0.17	-0.09	-0.08	
Residual block size								-0.05		-0.04										
Residual blocks #								-0.12		-0.12										
Proximity of greenspace									0.02			0.02								
Greenspace patch size																				

4.4.3. Case Study 3

In the original analysis using their own classification of ‘woodland dependent’, Barrett *et al.* (2004) found that 23% of all birds and 40% of ‘woodland dependent’ birds had declined across all New South Wales habitats between Birdlife Atlas 1 (1977-1981) and 2 (1998-2001) (Figure 7). We find that 32% of closed-woodland species and 50% of open-woodland species showed evidence of decline in New South Wales between the two atlases. We found that there had also been a widespread decline in open country species (48%).

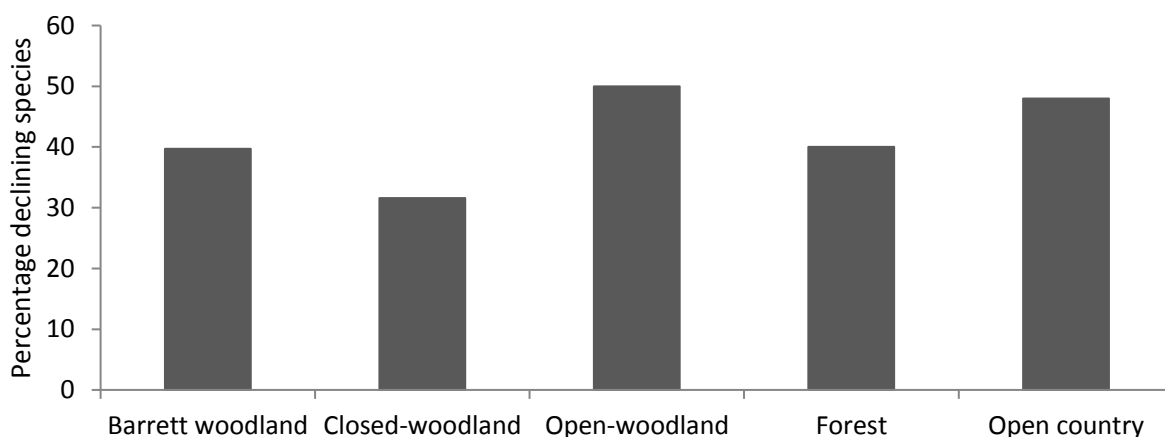


Figure 7: Percentage of species that declined between Birds Australia’s first and second atlases broken into categories based on Barrett *et al.*’s (2004) definition, and the four bird groups from our model analysis.

5. Discussion

There is a pressing need to determine exactly which bird species are ‘woodland birds’ because of widespread concern over their decline, and uncertainty about how to best manage them. This is also true for a range of other threatened faunal groups including, for example, wetland birds or coral reef fish. In this article we provide a transparent, logical and

ecologically-founded method for classifying woodland birds and describe the traits associated with birds' habitat preference. In order to provide ecologically meaningful insights, we classified birds into five groups based on their traits and relative occurrence in habitats comprising different levels of tree cover and woodland cover (typified by low density trees and open canopy structure): 'closed-woodland', 'open-woodland', 'forest', 'open country' and 'uncertain' species.

We found that the traits associated with woodland preference were very similar regardless of whether 'woodlands' included all woodland vegetation (treed vegetation with 5-30% canopy cover) or just eucalypt woodlands, but the relationships did not hold if we considered woodlands as all treed vegetation. This remains true for the species classified into our five bird groups (see Appendix 2). The classification of woodland birds is relatively robust to the difference between all woodlands and eucalypt woodlands, but researchers should consider a different list of species if defining woodlands as any vegetation community with trees. The composition of the five bird groups and the traits associated with woodland preference varied more substantially across regions, indicating that it may be meaningful to classify woodland birds differently based on broad study location. For example, the white-breasted woodswallow (*Artamus leucorhynchus*) is classed as an open country species in south eastern (ecoregion 4) and northern (ecoregion 7) Australia but is associated with open-woodlands in western and southern Australia (ecoregion 12), perhaps because other habitat types in ecoregion 12 are too arid for their persistence (Simson and Day, 1999).

Interestingly, our 'null species' analysis, which examined the importance of different traits on species occurrence, showed that all species (species with any traits) were equally likely to occur in woodland vegetation. However, dispersal distance and a number of foraging and nesting traits influenced the probability of birds occurring in (denser) forest and (sparser) open country habitats. This could be related to the open structure of woodlands, perhaps they

provide sufficiently open habitat to accommodate open habitat birds as well as sufficient trees to satisfy species that require trees for nesting and foraging. The result suggests that ‘woodland birds’ may be a collection of species that are relegated to woodlands because they struggle to occur in open country habitats or forest habitats rather than due to any specific combination of traits that determines a preference for woodlands. There are three potential reasons for this result: 1) as discussed above, the open structure of the woodland is suited to a wide range of species, 2) there is a high degree of interspecific competition in forest and/or open country habitats forcing less competitive species into woodlands, and 3) preference for woodlands is associated with traits that were not included in our analyses. Regardless of the reason for this result, this highlights the importance of retaining or woodland habitat for protecting a wide range of bird species.

Many researchers determine which ‘woodland bird’ species they study based on the species’ traits (Fraser et al., 2015). This seems eminently sensible when trying to determine which species depend on woodland habitats. However, if no traits (or a restricted set of traits) dictate preference for woodland habitats, these studies may include species that prefer forest or open country habitats. These studies may find weaker impacts of threats such as habitat fragmentation than would be expected for woodland birds (Fraser et al., 2015).

If woodland birds are distinguished by an inability to persist in open country or forest habitats, conservation efforts need to account for this. Typical conservation actions include planting trees; however, these revegetation attempts can often involve planting trees at a higher density than is typical in a woodland habitat (HF pers. obs). Our analyses suggest that, unless these plantings thin over time, they may be unsuitable for woodland birds when mature. Until the factors underlying birds’ preference on woodlands are well understood we recommend that conservation efforts focus on preserving existing woodlands and revegetating habitat according to Specht’s (1970) definition of woodland vegetation.

Dispersal ability and (aerial and ground) foraging traits had the strongest influence on the probability of bird occurrence when accounting for habitat. For example, according to our null species analysis, in ecoregion 7 (tropical and subtropical grasslands, savannas and shrublands), ground foraging and aerial foraging birds were more likely to occur in pasture habitats than species without those traits but this effect was not strongly evident in ecoregions 4 (temperate broadleaf and mixed forests) or 12 (Mediterranean forests, woodlands and shrublands). This may be due to differences in the habitat availability and climate between the relatively intact, sub-tropical ecoregion 7 and the degraded, drier ecoregions 4 and 12.

The effect of dispersal ability was consistently important between regions. According to our null species analysis, in ecoregions 7 (tropical and subtropical grasslands, savannas and shrublands) and 12 (Mediterranean forests, woodlands and shrublands), species were more likely to occur in open country and forest sites if they had a higher dispersal ability. In ecoregion 4, although species with high dispersal distances were still more likely to occur in open country habitats, species with low dispersal abilities were more likely to be found in forest habitats. It is intuitive that species with high dispersal ability are more likely to occur in open country habitats because, if they require trees for roosting or nesting, they are able to access them easily while also utilising open areas. The reason that species with high dispersal capabilities might be more likely to occur in forest habitats (with high tree cover and low woodland cover), as they do in ecoregions 7 and 12 is less intuitive. We attribute this to two issues. Firstly, what little forest habitat remains in ecoregions 7 and 12 is highly fragmented, so species requiring forests will need to disperse long distances to move between patches of suitable habitat (Bradshaw, 2012). Secondly, very few bird records from these regions come from within forest habitats, meaning that the model is predicting outside of the majority of the training data, where it is more uncertain. Despite this confusing artefact, our model allowed us to group species as ‘closed-woodland’, ‘open-woodland’, ‘forest’ and ‘open

country' species and we found that, using these groups, our results emulated the current understanding of woodland birds and provided further insights into some key questions about woodland, and other, bird groups. The birds in the 'uncertain' group had no strong positive or negative relationship with woodland vegetation or tree cover but are otherwise not grouped by any specific characteristics. Therefore, we do not expect them to behave in a consistent way and have excluded them from our case study analyses. To appropriately understand trends in this group it may be necessary to conduct species specific studies.

The results of our first case study are consistent with the current understanding of how woodland birds respond to clearing and grazing (Maron and Lill, 2005) and provide additional insights to the work by Martin and McIntyre (2007). Had they used our four bird groups (not including 'uncertain' species), they would have concluded that the main difference in bird assemblage between woodland and cleared sites is that cleared sites comprised fewer open-woodland and forest associated bird species. Our analyses suggest that this is because woodlands provide habitat for a wide range of species but that species must have particular adaptive traits to persist in open or forest habitats.

Our second case study also found similar results to those in the original study by Ikin et al. (2012). We showed that richness of our closed-woodland and open-woodland bird groups had very similar responses to urbanisation compared to the woodland birds investigated by Ikin et al. (2012). We were also able to extend Ikin et al.'s (2012) findings. For example, they found a possible negative relationship between woodland species richness and the number and size of residential blocks but, using the bird groups identified in this study, it is clear that this relationship is relevant to open-woodland birds only. Our results suggest that closed-woodland birds are more sensitive to the composition of the habitat, primarily requiring high cover of trees and shrubs to persist.

In our third case study, we estimated that 32% of closed-woodland species and 50% of open-woodland species had declined between 1981 and 2001, neatly surrounding Barrett et al.'s (2004) estimate of 40%. However, we did not find convincing evidence that woodland birds are more likely to have declined than other bird groups. By analysing the four bird groups separately, we showed that a greater percentage of open-woodland and open country birds had declined than any of the other bird groups. Both of these groups are associated with areas with lower levels of tree cover which may suggest that degradation of these areas through agricultural intensification is driving the majority of bird declines in the region (Attwood et al., 2009). These results need careful consideration because the data used in Barrett et al.'s (2004) study was recorded 10 years before the data we used to categorise bird groups for this study. It is possible that species' habitat preferences might change over time, particularly if there is a substantial change in habitat availability. However, the majority of habitat alteration in New South Wales occurred prior to 1980 (Bradshaw, 2012), suggesting that any shifts in habitat preference would have already occurred and would be reflected in the Barrett et al. (2004) data.

Our study provides new insights into the drivers of woodland preference in birds as well as proposing an empirically-based and tested classification of woodland birds. Our models produce lists of closed-woodland, open-woodland, forest and open country species that respond to drivers in a way that is consistent with current ecological understanding. This approach also allows a more nuanced interpretation of data than would be achieved by grouping species as 'woodland' and 'non-woodland' birds, as is common practice. Grouping 468 of Australia's bird species into 5 groups is nevertheless a coarse scaling, and alternatives may be needed for finer scale analyses.

There are other ways of classifying species that could provide similar benefits to understanding the ecology of woodland birds but many require either access to highly

detailed data and/or use of expert opinion. The EBCC Wild Bird Indicator, used across Europe, groups species as forest specialists, farmland specialists and generalists based on expert opinion (EBCC, 2014). In contrast, habitat specialisation indices are often seen as objective means of grouping species based on habitat association. There are a range of habitat specialisation indices available, some of which could have been implemented using the same type of data analysed in this paper (Chazdon et al., 2011; Gregory et al., 2005; Julliard et al., 2006). However, estimates of habitat specialisation are often sensitive to how habitat types are grouped and how many habitat types are considered, which are often determined subjectively. It is also possible to derive animal groups based on their projected dependence on different habitat types in cases where there is detailed information available regarding species' resource requirements and their availability in different habitat types (Wade et al., 2014). These methods are transparent and replicable but rely on the availability of detailed data about all species and habitat types which may not be feasible on a continental scale. All methods of grouping species are subject to certain limitations but may be useful in different contexts. We contend that our method is transparent, provides high-level understanding of habitat dependence and allows the bird species to be divided into 5 broad categories that could assist in long term monitoring of population trends, and conservation research and planning.

An important finding was that the species classified as 'closed-woodland' or 'open-woodland' birds depended on the region and whether foliage projective cover was taken into account when determining what counts as a 'woodland' (i.e. 'woodland' NVIS categories were used rather than all those with trees). We propose that Australian woodland bird researchers and managers may only wish to consider birds which are associated with woody vegetation with up to 30% canopy cover (Specht, 1970) (or 5-30% following the NVIS data) in order to ensure that their conclusions are representative of woodland birds. Further, we

suggest that it is important to account for regional differences when studying woodland birds rather than using one classification of woodland birds for all regions.

Globally, researchers face similar problems regarding inconsistent classification (Fraser et al., 2017) and our model could be easily adapted to provide similar groupings for different taxonomic groups provided that there is sufficient occurrence and trait data available.

However, in cases where finer scale conclusions are required and higher resolution data are available it may be preferable to classify species into more specific groups or study them individually. The method illustrated in this article would allow managers and researchers to understand the reasons that species belong to different groups as well as highlighting groups of species that are likely to respond similarly to habitat alteration or destruction. These groups may also provide a transparent, ecologically-sound basis for delineating animal communities that may then obtain a national (e.g. Australian Government EPBC Act Threatened Ecological Communities) or global (e.g. IUCN threatened ecosystems) threatened assessment.

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Figures:

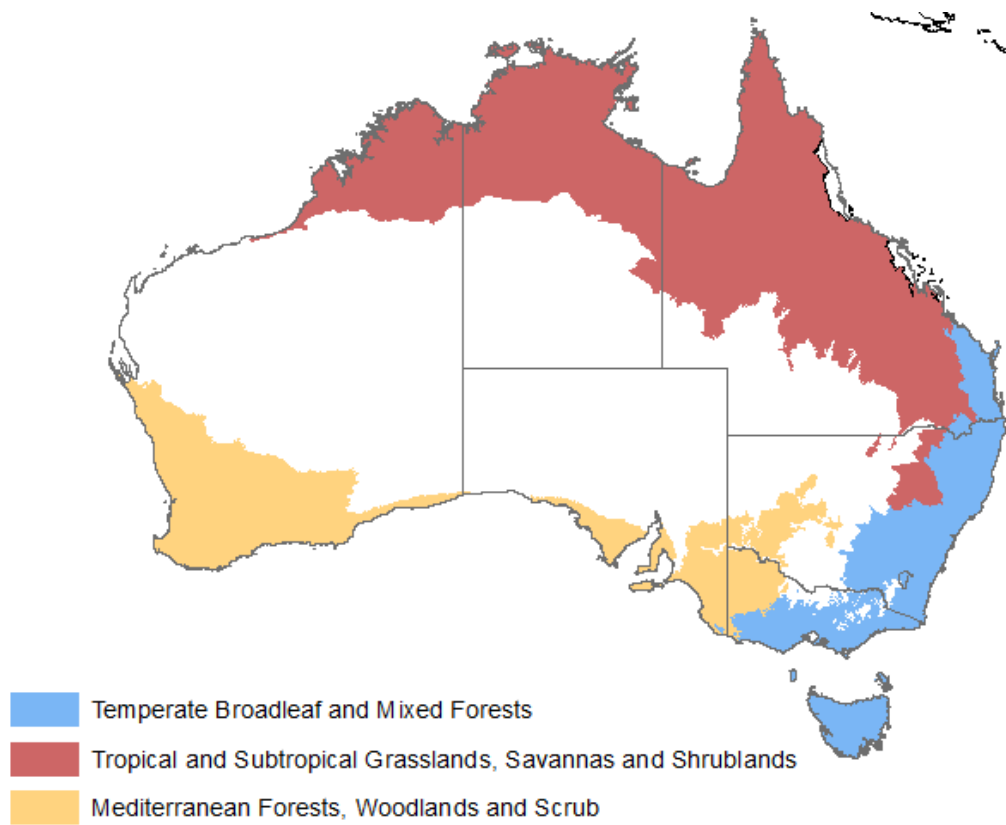


Figure 1: The distribution of the three studied Ecoregions, from the World Wildlife Fund ecoregions map (Olson et al., 2001)

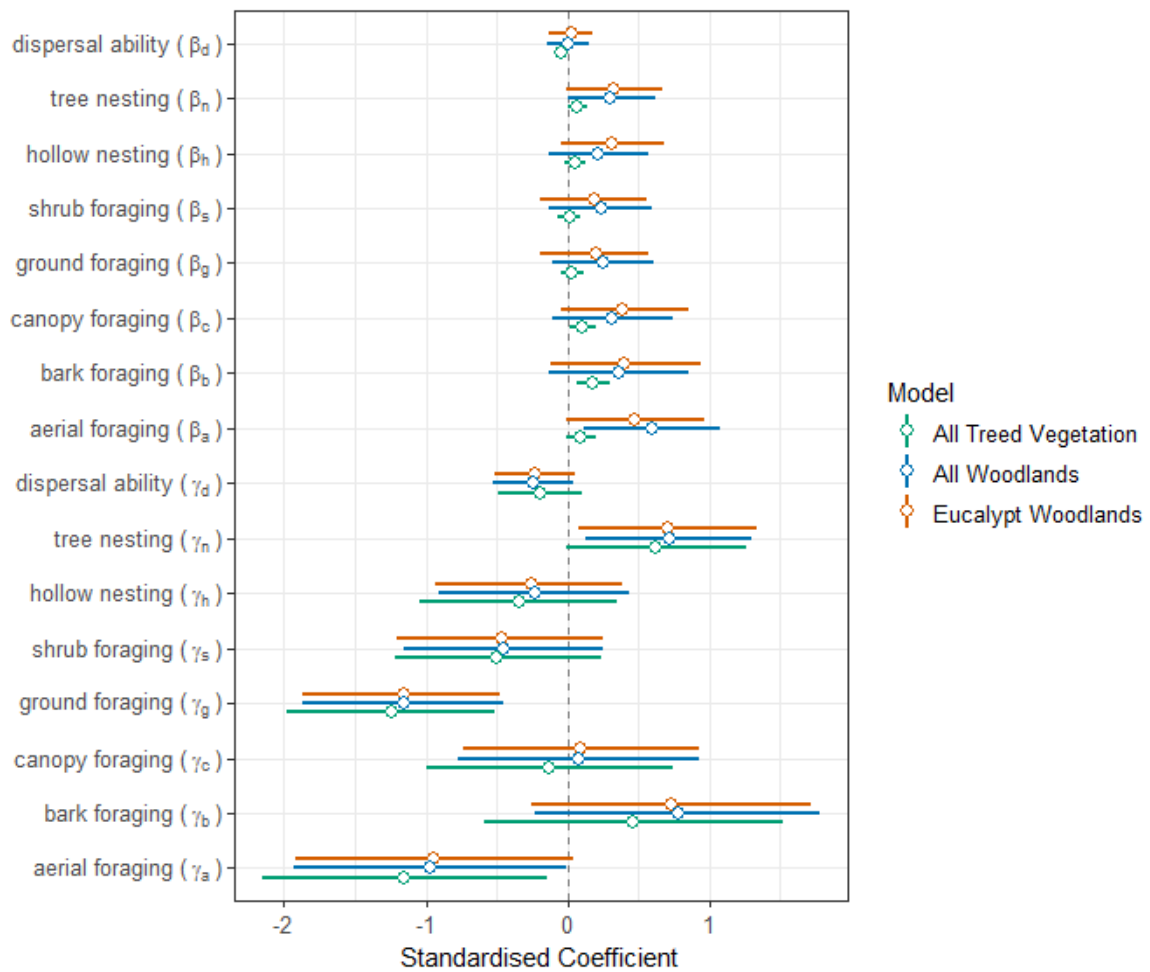


Figure 2: Standardised coefficients for Australia-wide models predicting the ‘woodland’ preference of birds when considering ‘woodlands’ as: all woodland vegetation (blue), eucalypt woodland vegetation (red), or any treed habitat type (excluding rainforest) (green). Coefficients representing associations between woodland vegetation cover and species traits are denoted by β and those representing associations between tree cover and species traits are denoted by γ . Circles represent means, lines represent 95% credible intervals.

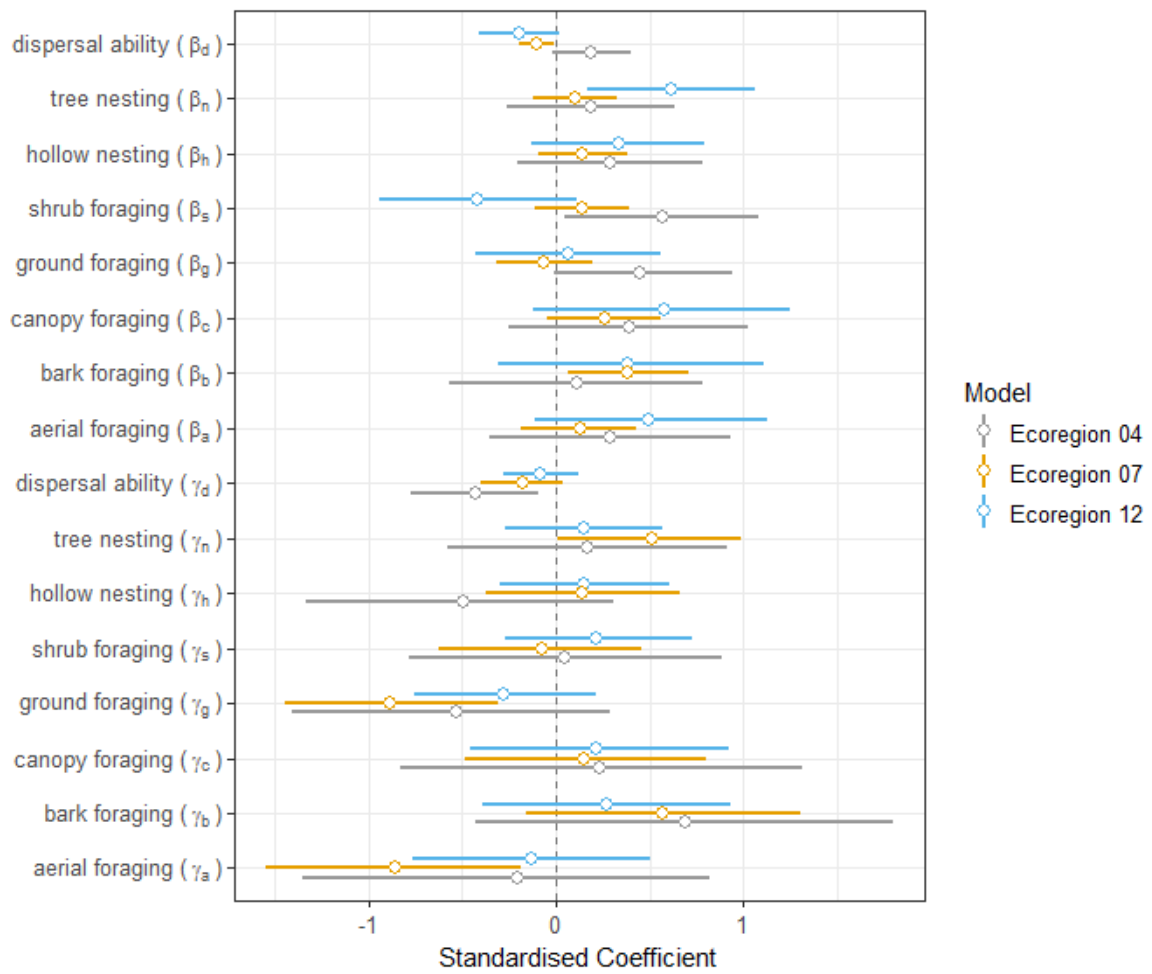


Figure 3: Standardised coefficients for models predicting eucalypt woodland preference in Ecoregions 4 (grey), 7 (orange) and 12 (blue). Coefficients representing associations between woodland vegetation cover and species traits are denoted by β and those representing associations between tree cover and species traits are denoted by γ . Circles represent means, lines represent 95% credible intervals.

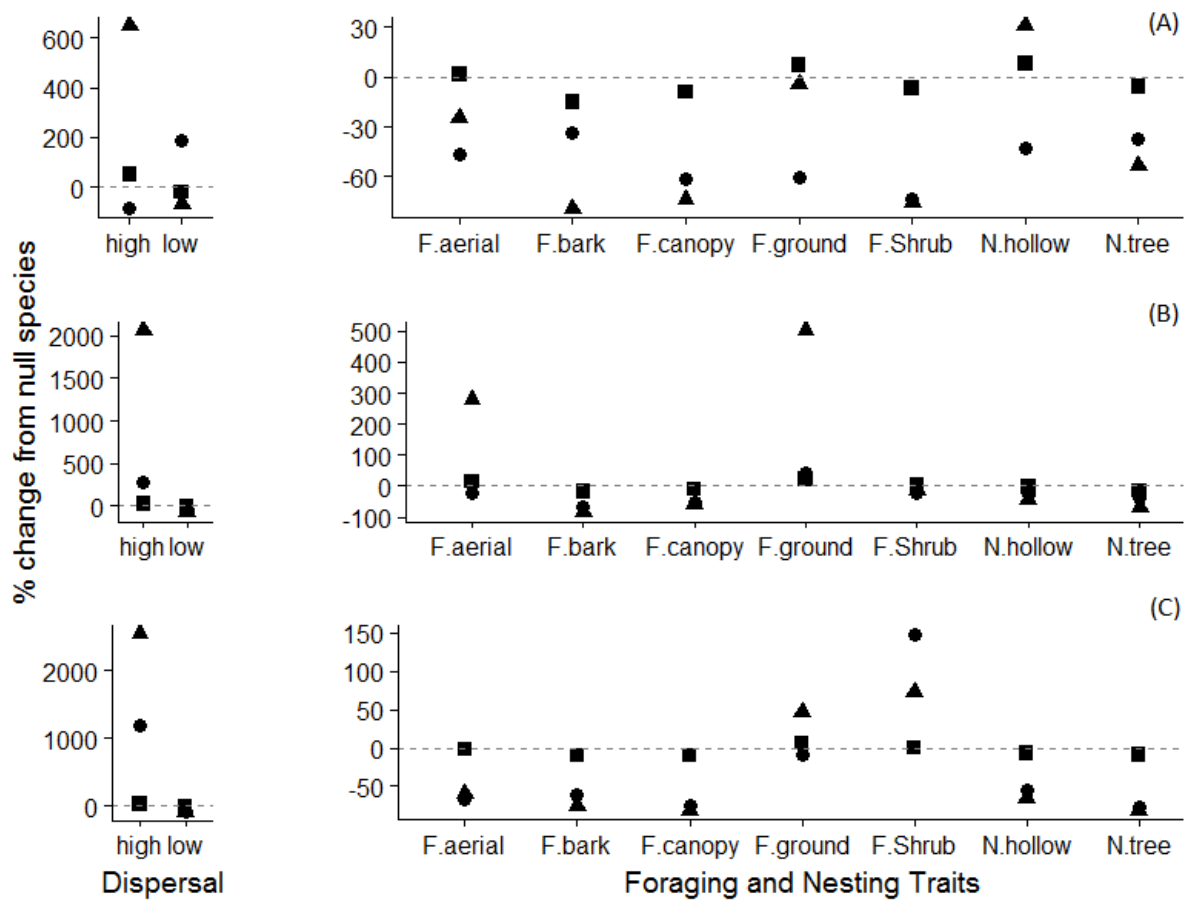


Figure 4: percentage change in probability of occurrence associated with a bird having a particular trait relative to a 'null species' in open country (triangle), woodland (square) and forest (circle) habitats in A) ecoregion 4, B) ecoregion 7 and C) ecoregion 12. The 'null species' has a median dispersal distance and does not have any of the other traits. Graphs to the left of the panel express change associated with species having high and low dispersal

abilities. Graphs to the right of the panel express changes associated with foraging (e.g. F. bark) and nesting traits (e.g. N.hollow). The scale of the y axis is different for dispersal vs nesting and foraging trait graphs.

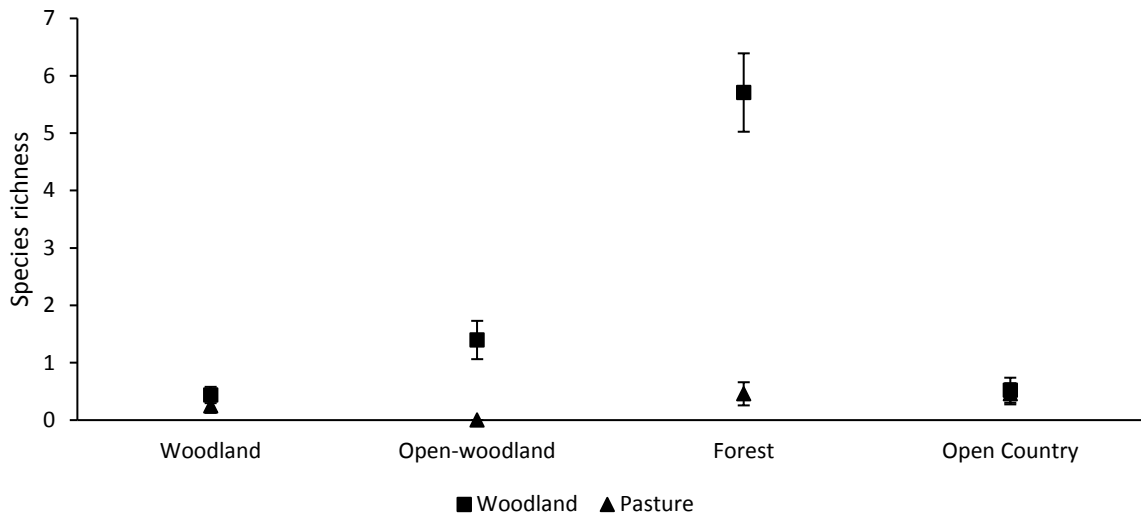


Figure 5: Mean and 95% confidence intervals of species richness by bird group in Martin and McIntyre's (2007) dataset for pasture and woodland habitat types.

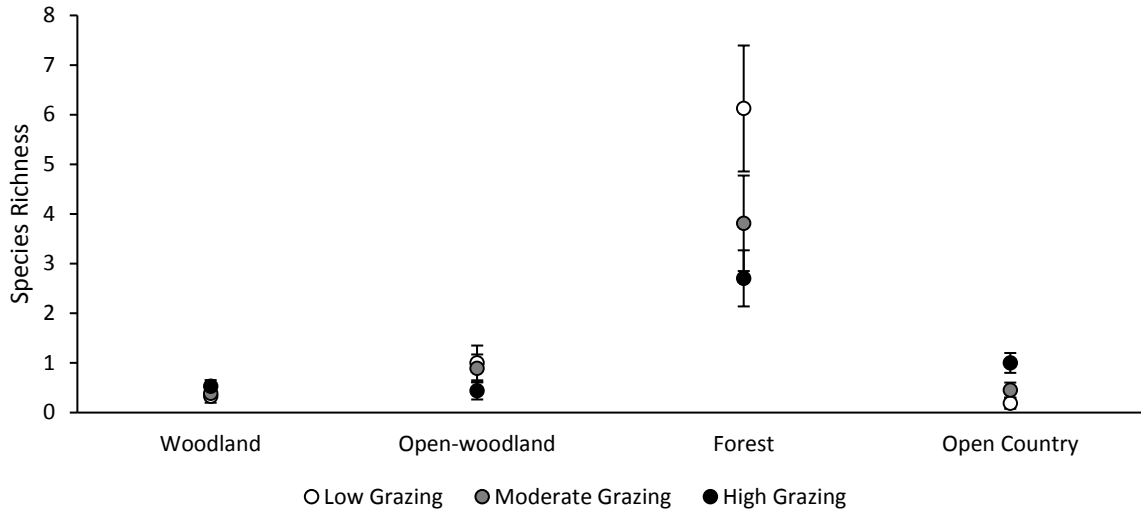


Figure 6: Mean and 95% confidence intervals of species richness by bird group in Martin and McIntyre's (2007) dataset for different levels of grazing

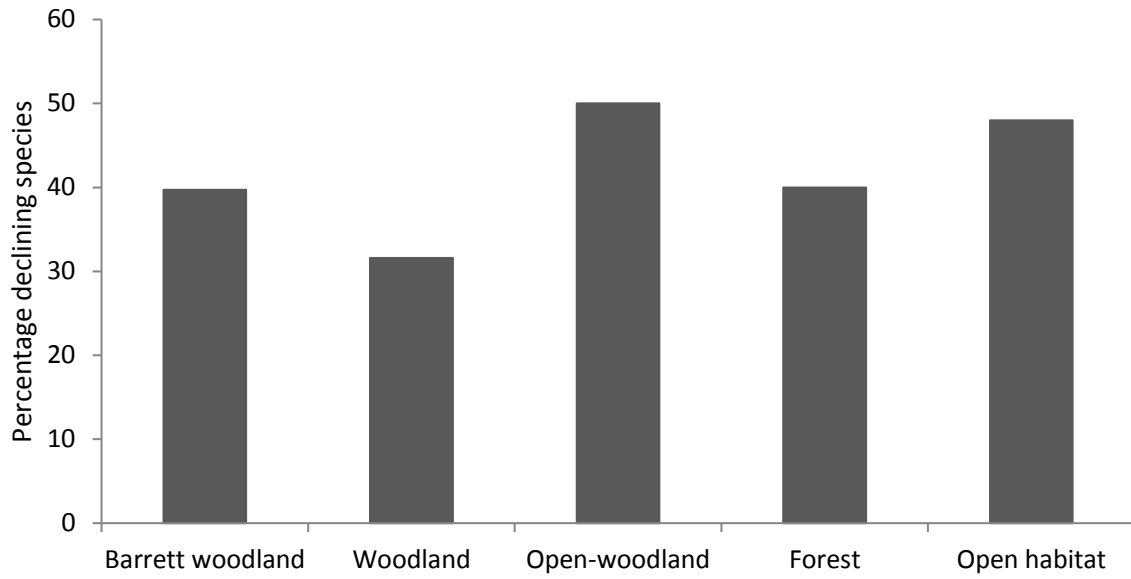


Figure 7: Percentage of species that declined between Birds Australia's first and second atlases broken into categories based on Barrett et al.'s (2004) definition, and the four bird groups from our model analysis.

Tables:

Table 1: Definition of model terms, β coefficients relate to percentage woodland vegetation, γ coefficients relate to percentage tree cover.

Variable	Symbol	Coefficient
Hollow Nesting	h_i	β_h
		γ_h
Tree Nesting	n_i	β_n
		γ_n
Ground Foraging	g_i	β_g
		γ_g
Shrub Foraging	s_i	β_s
		γ_s
Bark Foraging	b_i	β_b
		γ_b
Aerial Foraging	a_i	β_a
		γ_a
Canopy Foraging	c_i	β_c
		γ_c
Dispersal Distance (centred and standardised)	d_i	β_d
		γ_d
Error term	εX_i	
	εZ_i	

Table 2: Best ranked models ($\Delta AICc \leq 2$) for each bird group showing number of parameters, differences in Akaike Information Criterion corrected for small sample bias (AICc) compared with the model with the lowest AICc, Akaike weights, percentage deviance explained and model coefficients

	Closed-woodland Species			Open-woodland Species										Forest Species			Open Country Species			
Model Summary	Model #	1	2	3	1	2	3	4	5	6	7	8	9	10	1	2	3	1	2	3
	Number of parameters	1	2	3	3	2	1	2	2	4	4	4	2	1	2	3	1	1	1	2
	$\Delta AICc$	0.00	0.33	1.91	0.00	0.08	0.09	0.95	1.47	1.52	1.58	1.66	1.77	1.95	0.00	0.26	1.16	0	1.47	1.85
	Akaike Weight	0.24	0.21	0.09	0.13	0.12	0.12	0.08	0.06	0.06	0.06	0.06	0.05	0.05	0.21	0.19	0.12	0.29	0.14	0.11
	% Deviance Explained	4.92	7.01	7.68	10.48	6.88	3.46	5.47	4.65	11.57	11.48	11.35	4.15	0.46	5.43	7.44	1.97	5.00	2.12	5.52
	Residual Degrees of Freedom	106	105	104	104	105	106	105	105	103	103	103	105	106	105	104	106	106	106	105
Model Terms	Intercept	-0.83	-0.85	-0.86	0.89	0.90	0.90	0.90	0.89	0.89	0.89	0.90	0.90	-0.57	-0.58	-0.54	1.12	1.12	1.12	
	# Trees/ha			-0.07	-0.07	-0.06			-0.06	-0.07	-0.07			-0.30	-0.31					
	# Large eucalypts/ha			0.24	0.12	0.12			0.12	0.12	0.11			0.07	0.04					
	% Greenspace land use		0.20		0.09		0.09	0.11	0.10		0.11						0.06	0.03		
	% Tree and shrub cover	0.30	0.38	0.26				0.07			0.05		0.03	0.18	0.17		-0.09		-0.08	
	Residential block size								-0.05		-0.04									
	Residential blocks #								-0.12		-0.12									
	Proximity of greenspace								0.02				0.02							
	Greenspace patch size												0.09							



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