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## Biological characteristics of Australian threatened birds

George Olah <sup>a,b</sup>, Robert Heinsohn <sup>a</sup>, Alex J. Berryman <sup>c</sup>, Sarah M. Legge <sup>d</sup>, James Q. Radford <sup>e</sup>  
and Stephen T. Garnett <sup>d</sup>

<sup>a</sup>Fenner School of Environment and Society, The Australian National University, Canberra, Australia; <sup>b</sup>King's Forensics, Department of Analytical, Environmental and Forensic Sciences, Faculty of Life Sciences and Medicine, King's College London, London, UK; <sup>c</sup>BirdLife International, David Attenborough Building, Cambridge, UK; <sup>d</sup>Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Australia; <sup>e</sup>Research Centre for Future Landscapes and Department of Environment and Genetics, La Trobe University, Bundoora, Australia

### ABSTRACT

Over 750 native bird species reside in or regularly migrate to Australia, many of which have experienced rapid changes in habitat extent over the past two centuries. By 2020, eight taxa were considered Extinct and 10% threatened with extinction. Understanding the underlying extrinsic and intrinsic factors that increase extinction risk can allow prioritisation of conservation management and research. Here, we use state-of-the-art phylogenetic comparative models to reveal the most important biological traits that predispose Australian bird species to elevated extinction risk. We use an extensive database of their biological traits and relate these to each species' national and global IUCN extinction risk status as assessed over the past three decades (in 1990, 2000, 2010, and 2020). We show that high evolutionary distinctiveness (uniqueness), island endemism, and an inability to take advantage of agricultural habitats were the most important traits explaining elevated extinction risk in species when phylogeny is controlled for, suggesting that extinction risk is disproportionately high in species with high evolutionary distinctiveness. Extinct taxa were characterised by large body mass and island endemism compared to taxa extant in 2020. Our study provides the largest and most up-to-date analysis of the intrinsic traits of Australian birds in relation to their extinction risk, and can be used as a baseline in future studies, for prioritisation of conservation actions, and for policy advice on a broad scale.

### Key policy highlights

- Phylogenetic analyses are a useful tool for anticipating extinction risk.
- Extinction risk over the past three decades is highest among species with a high level of evolutionary distinctiveness.
- Species-level assessments can mask higher extinction risk at the subspecies-level.
- Conservation actions that reduce extinction risk can influence the variables deemed important in predictive models.

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IUCN Red List; extinction risk; Australia; comparative models; evolutionary distinctiveness; uniqueness

## Introduction

One in eight bird species globally are threatened with extinction, and nearly half of them have a declining population trend (BirdLife International 2022). Understanding the factors that might elevate extinction risk can help ensure that species least likely to cope with environmental change may be provided with pro-active protection (Cardillo *et al.* 2008). Extinction risk is most widely evaluated using the IUCN Red List, where species are categorised from Least Concern (lowest extinction risk) to Critically Endangered (highest) according to a set of criteria (IUCN 2012). Globally, the main extrinsic factors that have led to the extinction of bird species since 1600 CE

have been habitat loss, human persecution, and introduced predators (Maxwell *et al.* 2016). However, extinction risk in birds is not randomly distributed across the phylogenetic tree, with some groups of birds more likely than others to become threatened or extinct. Among bird species globally, larger body size and lower fecundity are associated with higher extinction risk (Bennett and Owens 1997) with certain groups, such as parrots (Psittaciformes, e.g. Olah *et al.* 2016) and albatrosses (Diomedidae, e.g. Petrossian *et al.* 2022), containing more threatened species (defined as Vulnerable, Endangered, and Critically Endangered based on the IUCN Red List) than expected (Bennett and Owens 1997).

**CONTACT** George Olah  [george.olah@anu.edu.au](mailto:george.olah@anu.edu.au)

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Patterns in both threat and extinction risk vary spatially. There is therefore merit in conducting comparative meta-analyses at continental scales, to examine if global patterns hold true in regions with idiosyncratic ecological contexts to help understand the traits that cause birds to be intrinsically sensitive to change (Cardillo *et al.* 2008). While the extrinsic factors that increase extinction risk of Australian birds are relatively well understood (Maxwell *et al.* 2016; Garnett *et al.* 2019), there is less certainty surrounding the intrinsic characteristics that may make some species, or groups of species, more extinction prone. A fuller understanding of such intrinsic traits could assist in assigning conservation priority to species or groups of species that are inherently more prone to extinction.

Over 750 native bird species reside in or regularly migrate to Australia, many of which have experienced rapid changes, particularly contractions, in habitat availability since the arrival of Europeans 250 years ago, and by 2020, eight species were considered Extinct and 74 threatened (Garnett and Baker 2021). For Australian birds, there is a wide range of information available on their biological characteristics (Wilman *et al.* 2014; Garnett *et al.* 2015), distribution and abundance (BirdLife Australia 2020; Cornell Lab 2020), and genetics (Hackett *et al.* 2008), as well as numerous species-specific studies, which can all help inform the evaluation of global and regional extinction risk. This information is taken into consideration during regular revisions of the IUCN conservation status of species.

The biological characteristics of threatened Australian birds were first analysed over three decades ago at the subspecies-level (Garnett 1992). Threatened taxa were defined by IUCN categories of that time (Extinct, Critical, Endangered, Vulnerable, Rare, and Insufficiently Known), and their traits were compared statistically to those of non-threatened ('secure') species. This early study, however, lacked a well-resolved phylogeny (Freckleton *et al.* 2002) required to control for evolutionary relatedness among the species included in the analysis, which is useful for filtering out the effects of closely related taxa sharing similar traits (Fisher and Owens 2004). In recent decades, advances in genetics have largely resolved the phylogenetic relationships among birds (Jetz *et al.* 2012; McCormack *et al.* 2013; Prum *et al.* 2015). As a result, comparative phylogenetic methods have been used routinely when comparing traits of such large sets of diverse species (Franklin *et al.* 2014; Olah *et al.* 2016, 2018).

In this study, we investigate which biological traits are related to elevated extinction risk in Australian birds (at the species- and subspecies-level) assessed using the

most recent IUCN Red List categories and criteria (IUCN 2012) and applied them retrospectively to earlier assessments so that valid comparisons can be ascertained. Specifically, we ask if there is a relationship between biological traits and the retrospective extinction risk assessments made for each decade since 1990, building on a similar study for birds in northern Australia (Garnett and Brook 2007). First, we focussed on a species-level analysis of the factors influencing extinction risk, using global IUCN Red List categories in state-of-the-art phylogenetic comparative models. Second, we used the same explanatory factors in a subspecies-level analysis, based on the local application of the same categories and criteria for extinction risk (Garnett and Baker 2021). We also compare the traits of birds that are already extinct with those that are extant. Our study, which provides the largest and most up-to-date analysis on the intrinsic traits of Australian birds in relation to their extinction risk, can be used to benchmark future studies on threat in birds, set conservation priorities (Gallagher *et al.* 2021), and give policy advice on a broad scale.

## Methods

### Database construction

#### Taxonomy

We analysed two taxonomic datasets: (1) species and (2) 'ultrataxa' (monotypic species and subspecies of polytypic species, representing the terminal point in the taxonomic tree). For species, we followed the taxonomy of BirdLife International (BirdLife International and HBW 2019) including 755 bird species native to Australia but excluding introduced species and vagrants (i.e. core taxa; Australia 2022). For ultrataxa, we followed Garnett and Baker (2021) in including 1,302 taxa. See all data used for the analyses in supplementary online material.

#### Response variables

Global and national extinction risk assessments were based on the IUCN Red List Criteria (IUCN 2012; IUCN Standards and Petitions Committee 2019). Categories applied to each taxon for each decade were assessed retrospectively in 2020 and broadly follow Garnett and Baker (2021) but in some instances were subsequently revised to reflect more recent data (see supplementary online material and Berryman *et al.* 2024). We categorised species or ultrataxa as threatened (value '1') if they were assessed as meeting the IUCN Red List Criteria for Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) in 2020, or

retrospectively in 1990, 2000, and 2010 (Garnett and Baker 2021; supplementary dataset). None of the species or ultrataxa were assessed as Data Deficient (DD) or Not Evaluated (NE). A value of '0' was assigned to taxa considered Near Threatened (NT) or Least Concern (LC).

Extinct (EX) taxa were excluded from the models to keep the focus on extant birds across the subsequent analyses (they are not considered 'threatened' by the IUCN Red List Criteria), and because they were missing from the phylogenetic trees (see below). We analysed all Extinct (EX) taxa separately by comparing their collective traits to extant ultrataxa in 2020 by using means and analysis of variance (ANOVA). All analyses were performed in R Statistical Software (v4.2.2; R Core Team 2022).

### Explanatory variables

Numerous characteristics are hypothesised to be associated with an increased risk of extinction in birds (Bennett *et al.* 2005). We focused here on biological characters shown elsewhere to be linked to extinction risk (Bennett *et al.* 2005; Croxall *et al.* 2012; Olah *et al.* 2016). We selected such variables from the standardised dataset of Garnett *et al.* (2015) for Australian birds based on expert opinion (Table S1), tested them with the 'corrplot' R package (Wei and Simko 2021), and calculated Variance Inflation Factor (VIF) values with the 'car' R package (Fox and Weisberg 2019). Based on the correlogram (Figure S1a), we removed variables with  $0.5 < \text{Pearson's } r < -0.5$  that correlated with higher number of other variables. We kept nine variables, including uniqueness, mass, brain mass residual, clutch size, generation length, island endemism, feeding locations, food types, and feeding in agriculture, which all had VIF values  $< 5$  (Figure S1b). We normalised the variables of mass, clutch size, and generation length using natural logarithms.

### Statistical modelling

#### Species

In the species-level analyses, to control for the effect of phylogenetic relatedness among species in the models, we used phylogenetic trees of 719 bird species native to Australia (Jetz *et al.* 2014). Since these trees are generated with pseudo-posterior distribution (Rabosky 2015), to account for potential uncertainties in the branch lengths and nodes separating species, we downloaded 1,000 possible phylogenetic trees of these species from the birdtree.org dataset (Ericson stage 2 backbone). For the analysis, we excluded all Extinct species (7–8 in each decade) and an additional 29 species for which

phylogenetic information was missing from the dataset. Since these species were not represented on the trees, their phylogenetic dependence could not have been accounted for in the models. For each of the 1,000 phylogenies, we performed a phylogenetic generalised linear mixed model (PGLMM) using the *pglmm\_compare* function of the 'phyr' R package (Ives *et al.* 2020; Li *et al.* 2020). Our response variable represented whether a species was considered threatened or non-threatened. For each explanatory variable (Table S1), we report the average estimates of the regression coefficients (B), z-scores for the fixed effects regression coefficients (Z), and the *p*-values, accounting for phylogenetic relatedness. For each model, we report the average random effects variances for nested random effects (*s*<sub>2</sub>) with standard deviation (SD). We also report the coefficient of determination of each model ( $R^2_{pred}$ ), computed from the variance between observed and predicted values, with the 'rr2' R package (Ives and Harmon 2019).

#### Phylogenetic consensus tree

In order to visualise the most important predictors of extinction risk on a single phylogeny tree, we created a 50% majority-rule consensus tree with Geneious (Kearse *et al.* 2012), using the same 1,000 trees downloaded from birdtree.org. For each branch, we report the clade credibility value (consensus support of the given node, as a percentage) in the online version. At each branch tip, we visualised data of the most significant explanatory variables. We generated the phylogeny figures using iTOL v6 (Letunic and Bork 2021).

#### Ultrataxa

We also conducted analyses on the ultrataxon-level dataset, because this is the taxonomic level typically used for conservation management of Australian birds (e.g. DCCEEW 2023). Szabo *et al.* (2012a) found similarity between the indices for species and ultrataxon datasets in Australia, but analysis at this level can reveal some important traits correlating with extinction risk. We fitted a generalised linear mixed-effects model (GLMM) using the *glmer* function of the 'lme4' R package (Bates *et al.* 2015). The response variables were derived from the Australian Red List categories, and the same explanatory variables were used as in the PGLMM (Table S1). Since an ultrataxon-level phylogenetic tree was not available for all Australian birds, here we used the taxonomic families as a random effect to control for phylogeny. For each explanatory variable, we report the estimates of the regression coefficients (B), z-scores for the fixed effects regression coefficients (Z), and the chi-square *p*-values. For each model, we report the average variance ( $V \pm \text{SD}$ ) and the coefficient of

determination ( $R^2_{pred}$ ). For better comparability, we repeated the GLMM models on the species-level dataset.

### Changes over time and across groups

We repeated both the PGLMM and GLMM models for data in 1990 ( $n_{PGLMM} = 719$  species;  $n_{GLMM} = 1,274$  taxa), 2000 ( $n_{PGLMM} = 719$ ;  $n_{GLMM} = 1,272$ ), 2010 ( $n_{PGLMM} = 718$ ;  $n_{GLMM} = 1,271$ ), and 2020 ( $n_{PGLMM} = 718$ ;  $n_{GLMM} = 1,271$ ).

We also ran the GLMM models on the most species-rich bird taxa separately at species- and ultrataxon-level, including passerines (Passeriformes;  $n_{sp} = 340$ – $341$  species;  $n_{ut} = 714$ – $717$  taxa), parrots (Psittaciformes;  $n_{sp} = 56$ ;  $n_{ut} = 102$ ), shorebirds (Charadriiformes;  $n_{sp} = 91$ ;  $n_{ut} = 107$ ), and seabirds (Sphenisciformes, Procellariiformes, and Suliformes;  $n_{sp} = 89$ ;  $n_{ut} = 100$ ) for each decade.

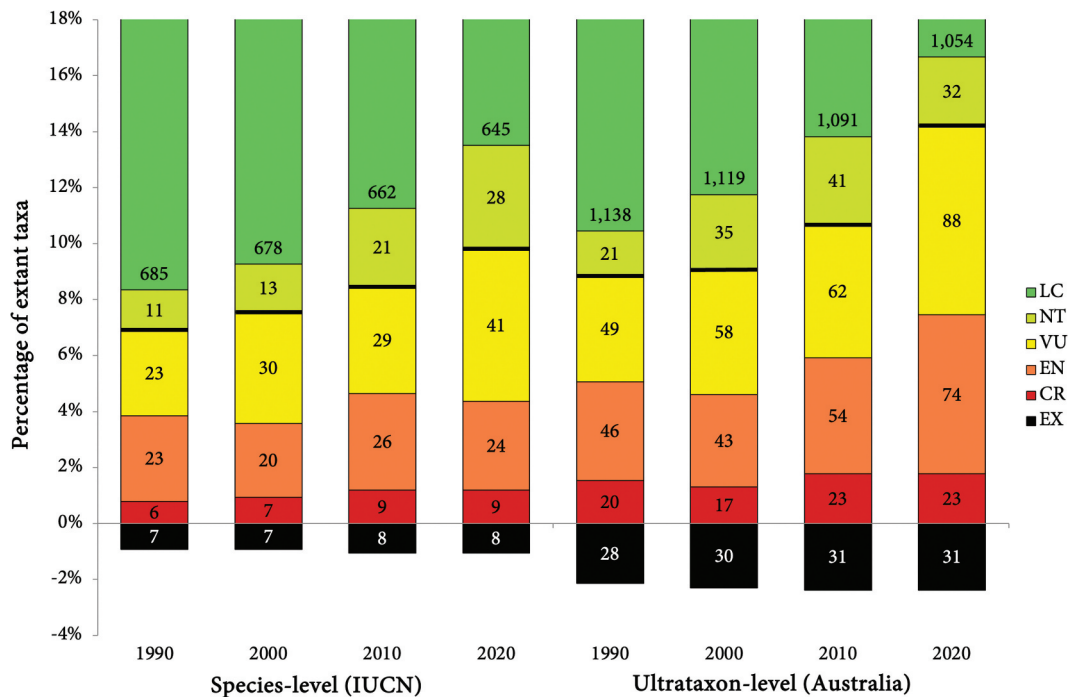
## Results

In 2020, 9.9% (74 species) of the 747 extant bird species were threatened with extinction, and eight species were judged to be Extinct (Figure 1). At the ultrataxon-level, there were 1,271 bird taxa (species and/or subspecies) extant in Australia in 2020, of which 14.6% (185 taxa) were threatened with extinction, and an additional 31 taxa were assessed as Extinct (Figure 1). In previous

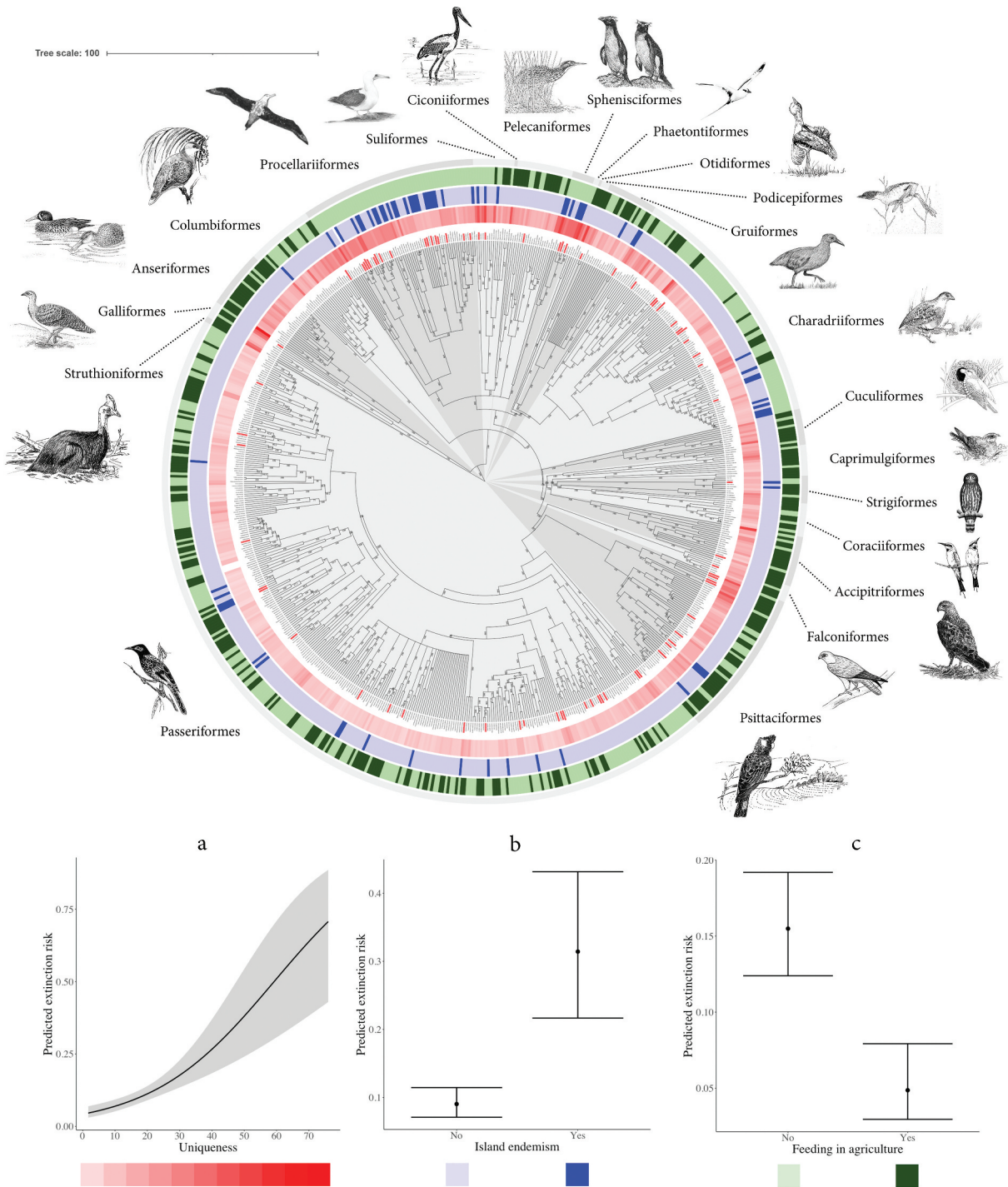
assessment windows, retrospectively updated with the current categories and criteria (IUCN 2012), threatened birds summed 52 species and 115 ultrataxa in 1990, 57 species and 118 ultrataxa in 2000, and 64 species and 139 ultrataxa in 2010 (Figure 1).

Species with higher phylogenetic uniqueness (Figure 2(a)), endemic to islands (Figure 2(b)), and not feeding in agricultural areas (Figure 2(c)) were consistently associated with higher extinction risk at the species-level across all four of the decades analysed (Table 1). When species were analysed with the GLMM models (Table S2), larger brain mass residual was also identified as a significant predictor of extinction risk in 2020 ( $B = 2.75$ ;  $p = 0.005$ ). In passerines, higher uniqueness and island endemism were the most important predictors of extinction risk in all decades, while in 1990 and 2000, smaller brain mass residual was also a significant predictor of extinction (Table S3a). In parrots, island endemism was the only important predictor of extinction across all decades (Table S3b). In shorebirds (Table S3c) and seabirds (Table S3d), we could not find any significant predictors.

At the ultrataxon-level, higher uniqueness, island endemism, and not feeding in agricultural areas were found to be the most important predictors of higher extinction risk across all four time periods (Table 2).



**Figure 1.** Extinction risk of core bird species and/or local subspecies in Australia, derived from BirdLife International's species-level assessments for the 1990–2020 IUCN Red List, and from BirdLife Australia's ultrataxon-level assessments for the same periods. Columns are broken into the percentage of extant taxa per category in each decade, and digits represent the number of taxa per category (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, and CR = Critically Endangered). Thick lines indicate the separation between threatened and non-threatened taxa. Extinct (EX) taxa are displayed below the axis. Given the overrepresentation of LC taxa, the top 82% is not displayed.



**Figure 2.** Consensus phylogeny tree of Australian core bird species (excluding introduced and vagrants) constructed by 50% majority-rule. Inner (and outer) grey shading is used to distinguish the 22 taxonomic orders (Table S3 contains the name of each species in the illustrations and their artists). Threatened (Vulnerable, Endangered, and Critically Endangered) species names are labelled in red. Raw values of (a) uniqueness (inner ring in red), (b) island endemism (middle ring in blue), and (c) feeding in agriculture (outer ring in green), as the most important explanatory variables in 2020 with phylogeny control by phylogenetic generalised linear mixed models (PGLMM), are shown as coloured stripes for each species. Predicted extinction risk of the bird species is plotted for each variable, using the IUCN Red List categories as response ('1' = threatened). Grey ribbon and error bars indicate 95% confidence intervals (CI) around the mean predictions. The zoomable tree is available in colour at <https://itol.embl.de/shared/olahgy>, with values of consensus support (%) on the branches based on the 1,000 trees used in the analyses.

**Table 1.** Predictor variables of the likelihood of Australian bird species being threatened (VU/EN/CR on the IUCN Red List). Results from the phylogenetic generalised linear mixed models (PGLMM) over four decades are provided for the number of species tested (n) as the average random effects variances for nested random effects (s2) with standard deviation (SD), and the coefficient of determination ( $R^2_{pred}$ ). For each explanatory variable, the table includes the means of the estimates (B), the z-scores for the fixed effects regression coefficients (Z), and the p-values (<0.05 are shown in bold). \* normalised by  $\log_e$ .

Variable	1990 (n = 719)			2000 (n = 719)			2010 (n = 718)			2020 (n = 718)		
	s2 = 0.01 ± 0.01			s2 = 0.01 ± 0.01			s2 = 0.01 ± 0.01			s2 = 0.01 ± 0.01		
	$R^2_{pred} = 0.22$			$R^2_{pred} = 0.26$			$R^2_{pred} = 0.22$			$R^2_{pred} = 0.19$		
	B	Z	p	B	Z	p	B	Z	p	B	Z	p
Uniqueness	0.05	2.79	<b>0.005</b>	0.05	2.91	<b>0.004</b>	0.05	2.71	<b>0.007</b>	0.06	3.34	<b>0.001</b>
Mass*	0.24	1.11	0.266	0.26	1.25	0.212	0.06	0.34	0.736	-0.05	-0.27	0.789
Brain mass residual	0.63	0.38	0.704	0.69	0.42	0.672	0.58	0.39	0.695	2.7	1.87	0.062
Clutch size*	0.26	0.54	0.588	0.44	0.95	0.345	0.61	1.45	0.146	0.23	0.59	0.555
Generation length*	-0.2	-0.29	0.769	-0.06	-0.09	0.925	0.54	0.96	0.339	0.19	0.36	0.718
Island endemism	1.64	4.01	<b>&lt;0.001</b>	1.54	3.77	<b>&lt;0.001</b>	1.27	3.27	<b>0.001</b>	0.92	2.42	<b>0.015</b>
Total feeding locations	0.03	0.08	0.936	-0.1	-0.29	0.775	-0.23	-0.66	0.508	-0.46	-1.47	0.142
Total food types	-0.14	-0.65	0.515	-0.22	-1.02	0.307	-0.14	-0.73	0.464	-0.03	-0.15	0.882
Feeding in agriculture	-1.1	-2.35	<b>0.019</b>	-0.98	-2.17	<b>0.03</b>	-0.92	-2.2	<b>0.028</b>	-0.89	-2.39	<b>0.017</b>

Fewer feeding locations was important for predicting extinction in 2020 only (Table 2). In passerines, island endemism was the most important predictor of higher extinction risk across all four time periods, along with higher uniqueness (except in 2010), while not feeding in agricultural areas (in 1990 and 2000) and larger brain mass residual (in 2020) were important for predicting extinction in certain decades (Table S3a). In parrots, island endemism was the main predictor of higher extinction risk across all decades, while higher uniqueness was only significant in 2020 (Table S3b). In shorebirds, island endemism was also important for predicting extinction over all decades, while larger clutch size and longer generation length were important predictors of extinction risk in 2020 only (Table S3c). In seabirds, only island endemism (in 1990 and 2010) was important for predicting extinction (Table S3d).

The 31 ultrataxa considered Extinct by 2020 were characterised by significantly larger body mass (extinct: mean = 2,554 g ± 1,357 SE, n = 31; extant: mean = 410 g ± 56 SE, n = 1,271; ANOVA: F = 26.93,  $p < 0.001$ ). Over

70% of extinct bird taxa once lived only on islands, which is five times the percentage of extant taxa confined to islands (14%), of which 5% are Critically Endangered, 16% are Endangered, and 16% are Vulnerable.

## Discussion

Currently, Australia has a percentage of threatened bird species (10%) or ultrataxa (15%; Figure 1) that is comparable with the global average (c. 13% of all bird species: BirdLife International 2022). The higher rate of threatened ultrataxa (*vs* species) is consistent with the global patterns of accelerated avian extinction rate at the subspecies-level in recent decades (Szabo *et al.* 2012b). In the current study, in 2020, higher values of uniqueness, island endemism, not feeding in agricultural areas, and to some extent higher brain mass residuals explained the elevated extinction risk in Australian bird species when controlling for phylogeny. These predictors (except the brain mass residual) were equally

**Table 2.** Predictor variables of the likelihood of Australian bird ultrataxa being threatened (VU/EN/CR on the Australian Red List). Results of the generalised linear mixed-effects models (GLMM) are provided for each decade (1990–2020) with the number of ultrataxa tested (n), average variance (V) of the random effects (taxonomic families) ± SD, coefficient of determination ( $R^2_{pred}$ ), estimates (B), z-scores (Z), and chi-square p-values (<0.05 are shown in bold). \*normalised by  $\log_e$ .

Variable	1990			2000			2010			2020		
	n = 1,274; V = 0.46 ± 0.68			n = 1,272; V = 0.41 ± 0.64			n = 1,271; V = 0.6 ± 0.78			n = 1,271; V = 0.84 ± 0.92		
	$R^2_{pred} = 0.17$			$R^2_{pred} = 0.17$			$R^2_{pred} = 0.17$			$R^2_{pred} = 0.17$		
	B	Z	p	B	Z	p	B	Z	p	B	Z	p
Uniqueness	0.05	3.13	<b>0.002</b>	0.05	3.33	<b>0.001</b>	0.04	2.54	<b>0.011</b>	0.03	2.14	<b>0.032</b>
Mass*	0.14	0.97	0.334	0.17	1.18	0.237	0.12	0.86	0.388	0.06	0.47	0.638
Brain mass residual	0.86	0.79	0.428	0.74	0.72	0.473	-0.19	-0.18	0.86	1.55	1.5	0.133
Clutch size*	-0.02	-0.06	0.955	0.05	0.16	0.873	0.2	0.62	0.532	0.19	0.61	0.542
Generation length*	-0.14	-0.32	0.748	-0.14	-0.34	0.733	0.32	0.8	0.421	0.48	1.32	0.186
Island endemism	1.89	7.54	<b>&lt;0.001</b>	1.8	7.27	<b>&lt;0.001</b>	1.75	7.07	<b>&lt;0.001</b>	1.84	8.22	<b>&lt;0.001</b>
Total feeding locations	-0.12	-0.52	0.601	-0.17	-0.75	0.455	-0.28	-1.29	0.198	-0.46	-2.41	<b>0.016</b>
Total food types	-0.15	-0.94	0.345	-0.19	-1.23	0.218	-0.24	-1.61	0.107	-0.16	-1.19	0.235
Feeding in agriculture	-1.16	-3.91	<b>&lt;0.001</b>	-1.1	-3.83	<b>&lt;0.001</b>	-1.08	-3.95	<b>&lt;0.001</b>	-0.87	-3.75	<b>&lt;0.001</b>



important for predicting extinction across all decades analysed both at the species-level (Tables 1 and S2) and the ultrataxon-level (Table 2).

Increased value is sometimes placed on the conservation of evolutionary history, from assigning evolutionary significant units (Moritz 1994) at the local scale, to the Evolutionarily Distinct and Globally Endangered (EDGE) metric at the global scale (Isaac *et al.* 2007). EDGE has been used to generate a priority list of birds (Jetz *et al.* 2014) and inform conservation grant mechanisms (e.g. IUCN 2023). Its adaptation, the WEDGE index (Weighted Endemism and Globally Endangered) has been designed further to rank locations by their biodiversity importance, and shown to outperform previous methods and metrics with similar purposes (Farooq *et al.* 2020). EDGE2 was also developed based on the first EDGE protocol but better dealing with uncertainties and accounting for the effects of closely related species (Gumbs *et al.* 2023). In Australia, although taxonomic distinctiveness is not privileged in conservation legislation or necessarily favoured by the general public, who oppose extinction regardless of the uniqueness of taxa (Garnett *et al.* 2018b), it has been used to develop priorities for conservation among Australian birds (Garnett 1992) and was used to select species in the national Threatened Species Strategy for 2020 (DCCEEW 2022).

In our study, we used uniqueness to characterise the evolutionary distinctiveness of a species or subspecies and found it to be strongly correlated with elevated extinction risk while accounting for phylogeny across the four decades. A recent study also showed a positive relationship between extinction risk and bird species with distinct functional traits associated with unique functional roles (i.e. functional uniqueness) but after controlling for phylogeny and body mass, this correlation disappeared (Ali *et al.* 2023). In our study, higher uniqueness was correlated with higher extinction risk in extant taxa (Figure 2a). We caution, however, that uniqueness itself is unlikely to be a trait that biologically predisposes taxa to elevated extinction risk, and note that it correlated most strongly with mass and generation length (Figure S1a). Both these factors are established predictors of extinction risk, i.e. larger birds with longer generation length are often more likely to be threatened, especially by human hunting and trapping (Cardillo 2003; Bennett *et al.* 2005; Olah *et al.* 2016). Consequently, we suggest (with high confidence) that uniqueness is not a *cause* of increased extinction risk, but the burden of extinction risk appears to disproportionately impact species that have high uniqueness, for reasons we only partially understand. The higher chance of losing more phylogenetically distinctive bird species

is of particular concern because they are often more diverse morphologically (Hughes *et al.* 2022), and their loss may have an elevated impact on ecosystems.

Small range size often corresponds with island endemism (Steadman and Martin 2003), which was significantly correlated with extinction risk in our study (Tables 1 and 2). Island endemism was a significant explanatory factor for elevated extinction risk in a previous study of threatened Australian birds (Garnett 1992). Furthermore, the proportion of island endemics among Extinct taxa was five times higher than among taxa still living in 2020 (Woinarski *et al.* 2024). The main causes of extinction of Australian birds are introduced predators, habitat loss and degradation, and hunting (Woinarski *et al.* 2024). In response to threats, taxa are expected to behave idiosyncratically because of differences in their evolutionary history and other intrinsic biological factors. For instance, species able to take advantage of agricultural landscapes may benefit from anthropogenic habitat changes and be less prone to extinction. Our finding that non-threatened taxa tend to feed more in agricultural areas supports this.

The variation observed in the importance of certain traits explaining extinction risk over the past three decades is probably partly due to the time lags and cumulative effects of continued habitat loss and degradation over time, which in turn influences extinction risk and eventually affects model outcomes when species move between threatened and non-threatened categories. Red List Indices (RLI) were designed to explicitly measure such changes in extinction risk of groups of species (Butchart *et al.* 2004, 2007). In this study, most traits changed significance in 2020 and, to a lesser extent, in 2010 (Tables 1, 2, and S2).

Species groups with shared explanatory characteristics can also change the balance of the tested variables when their extinction risk is reduced. For example, the eradication of non-native mammals on Macquarie Island that was completed in 2014 (Springer 2016; Garnett *et al.* 2018a) led to the downlisting of many island-endemic birds, especially long-lived, low fecundity seabirds. Some of these changes moved subspecies from threatened to non-threatened categories. In this study, while island endemism was a significant explanatory variable of extinction risk for seabirds in 2010, this effect had disappeared by 2020 (Table S3d). The impact of the Macquarie Island restoration is also visible in RLI (Berryman *et al.* 2024). In that assessment, there were six species with a lower extinction risk (mainly petrels), of which half were island endemics. Recent work in some fisheries has also showed encouraging results in reducing seabird bycatch (Melvin *et al.* 2023). These indicate that while underlying biological characteristics

may elevate extinction risk, successful conservation actions are capable of changing the trend.

## Conclusion

Our study confirmed that the main biological characteristics of already Extinct taxa were large body mass and island endemism compared to extant taxa in 2020. Our results suggest that the main underlying biological characteristics of the ongoing declines of threatened Australian bird species and subspecies are high evolutionary uniqueness, island endemism, and an inability to take advantage of agricultural habitats. While island endemism is a well-established contributor to extinction risk, the effect of phylogenetic distinctiveness to bird extinction risk has rarely been shown explicitly (e.g. Jetz *et al.* 2014). Uniqueness is possibly subject to further underlying factors (e.g. body mass and generation length), which should be addressed by future research with well-resolved intraspecific phylogeny. Nevertheless, these findings highlight the importance of phylogenetically informed conservation prioritisation (e.g. WEGE in Farooq *et al.* 2020; EDGE2 in Gumbs *et al.* 2023), as losing evolutionary uniqueness will have major consequences for Australia's bird diversity and can influence ecosystem functioning.

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## ORCID

George Olah  <http://orcid.org/0000-0002-7935-8843>  
 Robert Heinsohn  <http://orcid.org/0000-0002-2514-9448>  
 Alex J. Berryman  <http://orcid.org/0000-0003-1273-7184>  
 Sarah M. Legge  <http://orcid.org/0000-0001-6968-2781>  
 James Q. Radford  <http://orcid.org/0000-0002-6014-0019>

Stephen T. Garnett  <http://orcid.org/0000-0002-0724-7060>

## Data availability statement

The complete dataset used in this study is available as supplementary online material.

The phylogenetic tree is available in zoomable digital version at <https://itol.embl.de/shared/olahgy>.

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