University of Birmingham
Research at Birmingham

Threatened and extinct island endemic birds of the world

Matthews, Tom; Wayman, Joseph P. ; Cardoso, Pedro; Sayol, Ferran; Hume, Julian P; Ulrich, Werner; Tobias, Joseph A.; Filipa, Soares; Thébaud, Christophe; Martin, Thomas E.; Triantis, Kostas A.

DOI:
10.1111/jbi.14474

License:
Other (please specify with Rights Statement)

Document Version
Peer reviewed version

Citation for published version (Harvard):
Matthews, T, Wayman, JP, Cardoso, P, Sayol, F, Hume, JP, Ulrich, W, Tobias, JA, Filipa, S, Thébaud, C, Martin, TE & Triantis, KA 2022, 'Threatened and extinct island endemic birds of the world: distribution, threats and functional diversity', *Journal of Biogeography*, vol. 49, no. 11, pp. 1920-1940. https://doi.org/10.1111/jbi.14474

Link to publication on Research at Birmingham portal

Publisher Rights Statement:
This is the peer reviewed version of the following article: T J Matthews et al. ‘Threatened and extinct island endemic birds of the world: Distribution, threats and functional diversity’, Journal of Biogeography, 2022, which has been published in final form at DOI: 10.1111/jbi.14474. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. This article may not be enhanced, enriched or otherwise transformed into a derivative work, without express permission from Wiley or by statutory rights under applicable legislation. Copyright notices must not be removed, obscured or modified. The article must be linked to Wiley’s version of record on Wiley Online Library and any embedding, framing or otherwise making available the article or pages thereof by third parties from platforms, services and websites other than Wiley Online Library must be prohibited.

General rights
Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of ‘fair dealing’ under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy
While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

Download date: 20. Apr. 2024

Article Type: Synthesis

Threatened and extinct island endemic birds of the world: distribution, threats and functional diversity

Thomas J. Matthews[1,2*], Joseph P. Wayman[1], Pedro Cardoso[3,2], Ferran Sayol[4,5], Julian P. Hume[6], Werner Ulrich[7], Joseph A. Tobias[8], Filipa C. Soares[9], Christophe Thébaud[10], Thomas E. Martin[11,12] and Kostas A. Triantis[13]

[1]GEES (School of Geography, Earth and Environmental Sciences) and Birmingham Institute of Forest Research, University of Birmingham, Birmingham, B15 2TT

[2]CE3C – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group and Universidade dos Açores – Depto de Ciências Agráriase Engenharia do Ambiente, PT-9700-042, Angra do Heroísmo, Açores, Portugal.

[3]Laboratory for Integrative Biodiversity Research (LIBRe), Finnish Museum of Natural History Luomus, University of Helsinki, Finland

[4]CREAF, Centre for Ecological Research and Applied Forestries, Cerdanyola del Vallès, Catalonia, 08193, Spain

[5]Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, UK

[6]Bird Group, Department of Life Sciences, Natural History Museum, Akeman Street, Tring HP23 6AP, UK

[7]Department of Ecology and Biogeography, Nicolaus Copernicus University, Toruń, Poland

[8]Department of Life Sciences, Imperial College, London, Ascot, United Kingdom

[9]Centre for Ecology, Evolution and Environmental Changes (cE3c), Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal

[10]Laboratoire Évolution and Diversité Biologique, CNRS-IRD-Université Toulouse 3 Paul Sabatier, UMR 5174, Toulouse, France

[11]Operation Wallacea, Wallace House, Old Bolingbroke, Spilsby, UK

[12]Wild Planet Trust, Paignton Zoo, Totnes Road, Paignton, UK

[13]Department of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University of Athens, Athens GR-15784, Greece.

*Address for correspondence (Tel: +0044 12141 58388; E-mail: txm676@gmail.com)

ABSTRACT

Aim: The world's islands support disproportionate levels of endemic avian biodiversity despite suffering numerous extinctions. While intensive recent research has focused on island bird conservation or extinction, few global syntheses have considered these factors together in combination with morphological traits and functional diversity. Here, we provide a global summary of the status and ecology of extant and extinct island birds, the threats they face, and the implications of species loss for island functional diversity.

Location: Global.

Taxon: Birds.

Methods: We provide a review of the literature on threatened and extinct island birds, with a particular focus on global studies that have incorporated functional diversity. Alongside this, we analyse IUCN Red List data in relation to distribution, threats and taxonomy. Using null models and functional hypervolumes, in combination with morphological trait data, we assess the functional diversity represented by threatened and extinct island endemic birds.

Results and main conclusions: We find that almost half of all island endemic birds extant in 1500 CE are currently either extinct or threatened with extinction, with the majority of threatened extant species having declining population trends. We also found evidence of 66 island endemic subspecies extinctions. The primary threats to extant island endemic birds currently are agriculture, biological resource use, and invasive species. While there is overlap between the hotspots of threatened and extinct island endemics birds, there are some notable differences, including that the Philippines and Indonesia support a substantial number of threatened species but have no recorded post-1500 CE bird extinctions. Traits associated with threatened island endemic birds are large body mass, flightlessness, aquatic predator, omnivorous and vertivorous trophic niches, marine habitat affinity, and, paradoxically, higher dispersal ability. Critically, we find that threatened endemics i) occupy distinct areas of beak morphospace, and ii) represent substantial unique areas of the overall functional space of island endemics. We caution that the loss of threatened species may have severe effects on the ecological functions birds provide on islands.

Key words: birds, conservation, functional traits, hypervolumes, island biogeography, IUCN Red List, null modelling, threats

INTRODUCTION

Islands are fascinating study systems where a range of ecological and evolutionary theories have been developed and tested (Whittaker & Fernández-Palacios, 2007; Warren et al., 2015; Whittaker et al., 2017; Matthews & Triantis, 2021). A wide range of island systems exist (Matthews, 2021), but here we are focused solely on true marine islands (i.e., islands of land in the sea). It is also widely acknowledged that island biodiversity is acutely and disproportionately threatened as a result of a wide range of human actions, many of which interact, including habitat loss, hunting, the introduction of non-native species and anthropogenic climate change (Steadman, 1997; Whittaker & Fernández-Palacios, 2007; Szabo et al., 2012; Spatz et al., 2017; Graham et al., 2017; Leclerc et al., 2018; Veron et al., 2019; Russell & Kueffer, 2019; Fernández-Palacios et al., 2021). Island birds have been particularly hard hit, with many of the classic examples of extinction being island endemic birds, including the dodo of Mauritius, the giant moa of New Zealand, the Hawaiian honeycreepers, and the elephant birds of Madagascar (Hume, 2017). Much of the empirical work on threatened and extinct island bird species has been undertaken with a focus on specific regions or island groups (e.g., Duncan et al., 2002; Duncan et al., 2013; Steadman, 2006; Boyer, 2008; Boyer & Jetz, 2014; Hume et al., 2018; Steadman & Franklin, 2020), with less systematic combined evaluations of threatened and extinct species undertaken at the global scale (but see Pimm et al., 2006; Leclerc et al., 2018).

Previous global evaluations of threatened and / or extinct island birds have also generally not incorporated multiple functional traits (exceptions include Leclerc et al., 2020b; Fromm & Meiri, 2021; Marino et al., 2022). Even fewer have incorporated multiple *continuous* traits that are important for understanding why particular island species are more vulnerable to extinction and thus the design of effective conservation strategies (Şekercioğlu et al., 2004; Cardillo et al., 2005; Chichorro et al., 2019). This is largely because continuous functional trait data are hard to collect, particularly for extinct species. However, specifically for birds, recent advances (e.g., Sayol et al., 2020, 2021; Soares et al., 2021, 2022; Tobias et al., 2022; Triantis et al., 2022) have sourced and synthesised extensive functional trait data for extant and extinct island birds at the species level. The collection of these data now allows for more in-depth analyses of avian functional diversity – the morphological and ecological characteristics that influence fitness and the effects of organisms on the environment – on islands (Tobias et al., 2022). For example, using recently assembled datasets of traits for extinct bird species, Sayol et al. (2021) and Soares et al. (2022) found that avian extinctions on certain island groups have resulted in large reductions in functional diversity.

Our aim here is to provide the first global evaluation of both extinct and threatened island birds simultaneously, including assessment of threats and their causal drivers, and evaluation of the functional diversity represented by these species. This synthesis is particularly pertinent given the large number of relevant studies published on the topic over the last five years. Our objectives are three-fold: to 1) provide a review of the literature on threatened and extinct island endemic birds, with a particular focus on functional diversity; 2) undertake an overview of island endemic bird species in terms of their distribution, taxonomy and threat status; and 3) provide a statistical evaluation of the individual traits, and overall functional space, of threatened and extinct island endemic birds, with comparison to their non-threatened counterparts. As such, this synthesis combines a review of the literature with a range of different analyses. In regard to the latter, we focus on all of the world's bird species (11,162 extant and extinct species based on BirdLife's taxonomy) and bring together multiple databases to provide a comprehensive global evaluation of both threatened and extinct island endemic species simultaneously. First, we utilise the International Union for Conservation of Nature and Natural Resources' (IUCN) Red List, which provides an extinction risk assessment for almost all the world's bird species (IUCN, 2021a). Second, we source data on multiple functional traits for extant and extinct species, including nine continuous morphological measurements for all the world's extant bird species from the recently published AVONET trait database (Tobias et al., 2022). We also provide and summarise a novel global dataset of endemic island bird subspecies extinctions. Together, these investigations provide the most up-to-date overview of the global conservation status of island endemic birds, the threats they face, the traits that drive their extinction risk, and the implications of their loss on island functional diversity.

MATERIALS AND METHODS

Literature review

We searched the literature for published studies on threatened and extinct island endemic birds. This was not a fully comprehensive review of all published studies on the topic (which number in the hundreds if not thousands). Rather, we focused our attention more on recent global and regional analyses, particularly analyses incorporating functional trait data.

Data Collection - IUCN conservation status and threat data

We used the IUCN Red List API (IUCN, 2021a), accessed through the *rredlist* R package (Chamberlain 2020). This allowed us to download the full list of the world's birds (11,162 species) along with their IUCN classification and population trend (i.e., increasing, decreasing, stable or unknown). In the IUCN Red List, each assessed species is classified as being one of Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), or Data Deficient (DD), based on a range of different criteria. As a first step, we removed all species classified by the IUCN as data deficient (n = 50), leaving 11,112 species. We created a threatened group (TH) by combining all species classified as CR, EN or VU (cf. Bennett & Owens, 1997; Carmona et al., 2021). Herein, reference to 'threatened' species relates to this TH group. Twenty-two species are classified as CR but with an additional 'Possibly Extinct' marker (IUCN 2021b); we have kept these as CR as this is their actual current IUCN classification. Information on whether each species was an island endemic was taken from Sayol et al. (2020). Following Sayol et al. an island endemic was defined as any species that only occurs on islands that were not connected to the continent during the last glacial period, when sea levels were up to 120 m lower than the present day. All other species are referred to collectively as non-island-endemics. For each species, we also recorded higher taxonomic information available in the Red List, such as order.

Our main analyses are focused on full species. However, as part of the data collection for this synthesis, we also used a variety of sources (e.g. Szabo et al., 2012; Billerman et al., 2022) to collate data on island endemic subspecies extinctions (data collection methods and resultant dataset presented in Appendices S1 and S2).

For all species classified as threatened island endemics, we used the 'rl_threats' function in the *rredlist* R package to access the IUCN Red List API and compile information on the threats facing each species. The IUCN Red List lists direct threats that "have impacted, are impacting, or may impact" a species and contributed to its listing, and are categorised into 12 broad groups (e.g., biological resource use, pollution, invasive species and diseases, climate change; see Table S1 in Appendix S3 for the full list along with threat group numbers). The 12th group is defined as ‘Other’ and we did not include it in our analyses. For each threat faced by a species, we collected information on threat timing (e.g., Future, Ongoing, Past, Unlikely to Return) and severity (e.g., Negligible declines, No decline, Rapid Declines) (see Table S1) as listed in the IUCN Red List entry for that species.

We also sourced from the IUCN Red List all bird species classified as extinct (*n* = 164) since 1500 CE. For the present study, as there were only five cases, we considered those species classified as Extinct in the Wild as being extinct. Again, for the extinct species, we sourced island endemism data from Sayol et al. (2020) and the wider literature. For each island endemic species (extant and extinct), we also recorded the island group they were endemic to, and the latitude and longitude of the rough centre of this island group. These island groupings were necessarily coarse, given that most species were not endemic to single islands, with some representing whole island countries that are not easily divided (e.g., Philippines), and others particular archipelagos (e.g., Hawaii, Caroline Islands, south New Zealand Outlying Islands).

Going forward, we utilised four main (nested) species datasets in our analyses: 1) all-species dataset (including all extant and extinct birds; *n* = 11,112), 2) extant species dataset (including all extant bird species; *n* = 10,948), 3) all-island endemics dataset (including only extant and extinct island endemic species; *n* = 1,856), and 4) extant island endemics dataset (including only extant island endemic species; *n* = 1,707).

While our main analyses are focused on species that have gone extinct since 1500 CE (as these are the only species included in the IUCN Red List), as part of a separate project (F. Sayol & T. Matthews, unpublished data; see also Sayol et al., 2020) we also compiled data on all island species that are known to have gone extinct in the last 125,000 years. Here, we present an overview of these data in relation to island species.

Data Collection - Functional trait data

In order to analyse functional diversity patterns, we collected trait data related to volancy and body mass for extinct and extant species, and a range of additional morphological and ecological traits for extant birds.

Extant species

We used Sayol et al.'s classifications of volancy (flightless or volant) for each species. Eleven species (including extinct species) were classified by Sayol et al. as weak flyers, and we classified these as flightless. For those species not covered by Sayol et al. we classified species in regard to island endemism and volancy by using a range of literature sources (e.g., the 'Birds of the World'; Billerman et al., 2022).

For all 10,948 extant species (island endemics and non-island-endemics), we sourced additional trait data from the AVONET trait database (Tobias et al., 2022). This included several categorical and continuous traits linked to avian resource use, trophic level, foraging, behaviour and dispersal. The categorical traits were: habitat affinity (e.g., forest, marine, grassland), trophic level (i.e., carnivore, herbivore, omnivore, scavenger; we excluded scavenger from these analyses due to the low numbers of island scavengers – 0.2% of the total extant species and no island endemics), and trophic niche (e.g., ten categories including frugivore, invertivore, nectarivore). To reduce the number of habitat categories, we combined coastal, riverine and wetland habitat categories into a single wetland category, forest and woodland into forest, and grassland and shrubland into grassland. For the few (<100 out of ~11,000) species with missing trait data (i.e. habitat and trophic data), we used information from the wider literature to make informed decisions on the missing values. Eight species in the IUCN Red List were not in AVONET (either recent splits or newly described species);

for these we used the trait values of the species each was split from (i.e. the sister species). Continuous traits included eight morphological measurements (beak length along the culmen, beak length to nares, beak width, beak depth, tarsus length, wing length, first secondary length and tail length), body mass, and the hand-wing index (HWI, a measure of dispersal ability; see Sheard et al., 2020). See Tobias et al. (2022) for more details on all traits.

Extinct species

For all extinct species, we sourced volancy data from Sayol et al. (2020). We also compiled data on body mass using a range of published sources. As a first step, we checked two primary data sources for body mass values: Birds of the World (Billerman et al., 2022), and a recent analysis of island birds including extinct species (Triantis et al., 2022). Birdlife International's data zone (Birdlife International, 2021) was also checked. For the majority of extinct species, body mass values were not available and thus we used those three sources, in addition to Hume (2017), to identify the closest extant relative for each extinct species, and used its body mass value, with some adjustments when the closest relative was known to be bigger or smaller (e.g., see Triantis et al., 2022). Additional studies were used for certain species (e.g., emu species, Hume & Robertson, 2021). In general, these sourced values only represent coarse estimates of extinct species body mass and should only be used in future analyses with this in mind.

Null model analyses

To determine whether i) island endemic bird species in general, ii) specific orders of island endemic birds, and iii) island endemic species with certain traits, were more likely to be classified as threatened or to have gone extinct than expected by chance, we ran a series of null model analyses, each one based on 9,999 iterations. While it would theoretically be possible to use direct quantitative tests (e.g., tests of equal proportions or contingency analysis) to compare the proportion of island endemics with non-island-endemics in terms of categorical traits, we decided to use a null model approach for all traits (categorical and continuous) to ensure a consistent method was applied, and to allow easy visualisation of the strength of effects. As the null distributions were often slightly skewed (i.e., non-normal), we instead used an alternative to the typical standardised effect size (SES) approach. Our effect size (ES) approach (Lhotsky et al., 2016; Matthews et al., 2020a) works by calculating the empirical probability (*P*) that the observed value is less than expected using the formula:

$$P = \frac{length(null < obs) + \frac{length(null = obs)}{2}}{n + 1},$$

where *null* is the vector of null distribution values, *obs* is the observed value, and *n* is the number of null model iterations (here *n* = 9,999). This empirical probability was then probit transformed (see Lhotsky et al., 2016) using the *VGAM* R package (Yee, 2010) to obtain the ES value. To ensure an empirical probability of 0 or 1 is not returned (as these values cannot be probit transformed), the observed value (*obs*) is added to the vector of null values (hence the *n* + 1 term). ES values greater than 1.96 (probit of roughly 0.975) or less than -1.96 (probit of roughly 0.025) can be considered to be significantly greater or less than expected by chance, based on an alpha level of 0.05. It should be noted that, while the theoretical ES range is between minus and positive infinity, the actual achievable range will depend on *n*: minimum *P* = 0.5 / (*n* +1) and max *P* = (*n* + 0.5) / (*n* + 1). With an *n* of 999, this equates to a maximum ES value of +- 3.29, while for *n* = 9,999 the equivalent value is +- 3.891.

In regard to the null models themselves, for (i), we randomly sampled (without replacement) the total number of extant and extinct island endemic species (*n* = 1,856) from the all-species dataset, and recorded the number of CR, EN, VU, TH and EX species in each sample (i.e., five null distributions were created).

In regard to (ii), to ensure an interpretable number of orders was used, we focused on the 13 orders that included more than 150 species in the all-species dataset. Using the all-island endemics dataset, we calculated the number of island endemic species classified as CR, EN, VU, TH and EX. For each of these five cases, we then randomly sampled this number of species (irrespective of IUCN status or order) from the all-species dataset and recorded the number of species belonging to each of the 13 orders. We repeated the analysis but instead randomly sampling from the all-island endemics dataset (i.e. switching from a global species pool to an island endemics species pool).

In regard to (iii), separate null model analyses were run for each of seven traits: volancy, HWI, habitat affinity, body mass, trophic level, trophic niche (we focused on the seven most species-rich trophic niches as the remaining three contained very few island endemics) and beak morphology. For beak morphology, we took the four beak traits (length to culmen, length to nares, width, depth; log-transformed) for all extant species and conducted a PCA to obtain four orthogonal axes. We then subsetted the 530 threatened island endemics and built a hypervolume using these four axes and the method outlined in detail below ('Functional morphospace comparison' section; here we used a 'svm.gamma' parameter of 1.2 to provide a tighter wrap to the data), using the total volume of this hypervolume as our measure of beak morphology; here 999 null iterations were used as the process was much more time-consuming. For the null modelling, for each trait separately, we randomly sampled the number of threatened island endemic species (*n* = 530) from the species pool and, using this sample, calculated either the number of species in the different trait categories, the median HWI or body mass, or the volume of the beak hypervolume. We ran the analyses twice, using two different species pools: the extant species dataset (*n* = 10,948) and the extant island endemics dataset (*n* = 1,707); the latter constraining the pool to island endemic species only. In the case of volancy and body mass, we also tested whether more or fewer extinct island endemic species were flightless than expected by chance, and if median body mass of extinct species was significantly different than expected, by sampling the observed number of extinct island endemic species (*n* = 149) from the all-species dataset (*n* = 11,112) or the all-island endemics dataset (*n* = 1,856).

Individual trait differences between threatened and non-threatened island endemics

To more explicitly compare individual traits between threatened island endemics (TEs) and non-threatened island endemics (NTEs), we directly compared body mass, HWI, beak morphology, habitat (forest, grassland, marine and wetland) and trophic niche (same seven niches used in the null models). For beak morphology, we took the first two axes from the PCA undertaken on just the four beak traits (described above). Here, all four beak traits had a positive loading on PC1 (i.e. it is a measure of beak size; 84% of total variance), while PC2 described the trade-off between beak length, and width and depth (13%). Continuous traits were compared between the two species groups using Wilcoxon Rank Sum tests, while categorical traits were tested using chi-square tests.

Functional morphospace comparison

As a further analysis of threatened island endemic functional diversity, we compared the overall functional space occupied by threatened and non-threatened island endemics. For this, we used the eight continuous morphological functional traits and body mass for all 10,943 extant bird species. This is five less than the full number of extant species as it was necessary to remove the five kiwis [*Apteryx spp.*] as they represent extreme functional outliers in regard to wing and tail length (see Pigot et al., 2020) and including them distorted the resultant functional spaces. These species were not removed for the separate beak morphospace analyses as they were not outliers with respect to the beak traits. All nine traits were log-transformed (cf. Pigot et al., 2020), and scaled to have a mean of zero and unit variance. We ran a PCA on these nine traits (for the 10,943 species) using the ‘prcomp’ function from the *stats* R package, and extracted the first five PCA axes (we did not scale the PCA axes). We focused on the first five PCA axes only as they explained 98% of the total variance and, more importantly, it is recommended that hypervolumes be constructed using as few dimensions as required (Mammola & Cardoso, 2020). PCA axis 1 (77% of variation) was positively associated with all measurements (i.e. an overall size axis), PCA2 (9%) described the trade-off between beak size vs. tail, tarsus and wing length, PCA3 (5%) the trade-off between beak width and depth vs. beak length, PCA4 (4%) the trade-off between tarsus length and tail length, and PCA5 (2%) the trade-off between wing length, and tail and tarsus length.

Using the five PCA axes, we built kernel density hypervolumes using the *BAT* R package (Cardoso et al., 2015) and the one-class support vector machine method (SVM, Blonder et al., 2018). We used SVM as it has been previously shown to work well for building avian functional morphospace (e.g., Cooke et al., 2019), we are confident the functional outliers in our data represent the true boundaries (Blonder et al., 2018), and we wanted the hypervolume to represent a ‘tight wrap’ to the data. When using SVM, we increased the default ‘svm.gamma’ parameter to 0.8 while keeping the ‘svm.nu’ parameter at its default value of 0.01. These values were found to generate sensible looking spaces that produced relatively tight (but not restrictive) wraps to the data; however, we also tested a range of other values (see Appendix S4 and Tables S2 and S3). We used the default samples per point values.

We built separate hypervolumes for (i) non-threatened island endemics (‘NTE’) and (ii) threatened island endemics (‘TE’). We then calculated pairwise hypervolume dissimilarity (Btotal; Jaccard-family) between NTEs and TEs using the ‘kernel.beta’ function and the *BAT* R package (Mammola & Cardoso, 2020; see also Ulrich et al., 2017 for discussion of a similar metric). We partitioned the overall Btotal (Jaccard-family) into replacement (Brepl) and net difference in amplitude (Brich) components. We also calculated the unique portion of combined functional space occupied by each individual hypervolume, as their unique volume divided by the total volume (i.e., the union of the two in the pair). We tested whether the observed Btotal and unique portion values were significantly smaller or larger than expected by randomly classifying 1,702 (the number of observed island endemics, minus the five kiwi species) of the full set of extant global bird species as island endemics, and then randomly classifying 526 of these as threatened, and re-calculating the metrics. This was repeated 999 times to create null distributions for each metric. We repeated the null modelling using the extant island endemics dataset (again minus the kiwis) as the species pool. Given PCA1 explained 77% of the variation in traits and was an overall size axis, we also repeated the hypervolume analyses using body size corrected traits. For this, we ran eight simple linear regressions with a given morphological trait as the response and body mass (both log-transformed) as the predictor; the residuals from each model were then used as the new trait. With the scaled residual traits and body mass, we re-ran the PCA and hypervolume calculations. All analyses were undertaken using R (Version 4.1.0; R Core Team, 2019). The hypervolume null models were run across two 20-core 128GB clusters (~1,500 core-hours). The R code and data used are available on GitHub ("txm676/islandbirds").

RESULTS

Overview of threatened and extinct island endemic birds

In regard to the review of the published literature, Table 1 provides an overview of 29 studies focused, at least in part, on threatened and/or extinct island birds, particularly those that included some element of functional trait analysis. We draw on many of these studies in the 'Discussion' section below.

In regard to the analysis of the IUCN Red List data, compared to non-island-endemics, there were relatively high numbers of island endemic bird species in each of the four most severe

IUCN Red List categories (i.e., EX, CR, EN and VU, Fig. 1a), and the proportion of threatened and extinct species was much higher for island endemics than non-island endemic species (Fig. 1b). Eight percent of island endemic species (known to be present in 1500 CE; *n* = 149) are classified as extinct by the IUCN, compared to 0.002% of non-island-endemics. Across all extant island endemic species, 31% (*n* = 530) are classified as threatened; the same proportion for non-island-endemic species is 10%. Figure 2 provides order-level summary information on the percentage of threatened species, both for all species and just island endemics. Fig. 2 provides further evidence that, for almost all avian orders, the proportion of island endemics that are threatened / extinct is (often much) larger than the proportion of all species that are threatened / extinct. Of the 530 threatened island endemic species, 371 have decreasing population trends, 38 are increasing, with 97 stable and 24 unknown population trends. Thirty-nine Critically Endangered endemic species (35% of all endemic CR species) have a total global population size of less than 50 individuals. We also found evidence of 66 island endemic subspecies extinctions (or likely extinctions) (Appendices S1 and S2).

In regard to threats (in the species' IUCN listings) faced by threatened island endemics, when all threat timings and severity levels were included, the threats affecting the most species according to the IUCN Red List were agriculture and aquaculture, biological resource use (e.g., hunting), invasive species and disease, and climate change (Fig. 3). A chi-square test was not significant ($\chi^2 = 29.8$, df = 20, P = 0.07), but analysis of the Pearson's residuals and cell contributions (Fig. S1 in Appendix S5) indicated that there were more CR species threatened by invasive species, and fewer by biological resource use, than expected, and more endangered and fewer vulnerable species threatened by human intrusions and disturbance (e.g. wars) than expected. When only immediate threats causing rapid species declines were included, the patterns were similar with the exception that a lower proportion of species were threatened by climate change and pollution, and no species were threatened by transportation (Fig. 3).

Overview of all known island bird extinctions

Only species that have gone extinct since 1500 CE are included in the IUCN Red List and are thus the focus of our main analyses. However, compiling data on all known bird extinctions over the last 125,000 years reveals approximately 595 bird species have gone extinct, of which 477 (80%) are island endemics (F. Sayol & T. Matthews, unpublished data). Thus, approximately 22% of island endemic bird species, present 125,000 years ago, are known to have been driven extinct.

Threatened and extinct species hotspots

Threatened island endemic species are found on a wide range of island groups across the world, but hotspots include the Philippines, several island groups within Indonesia, Madagascar, Hawaii, the Caribbean, New Zealand, and the Bismarck and Solomon archipelagos (Fig. 4a). Several other Pacific island groups support numerous threatened endemic bird species. A wide range of island groups have also seen species extinctions (Fig. 4b), with the four most affected being the Mascarene Islands (32 extinctions), the Hawaiian Islands (27), New Zealand (13) and the Society Islands (10). Overall, Polynesia and Melanesia, the Caribbean, East Asian islands and the island groups around Madagascar have all seen large numbers of extinctions. The full lists of threatened and extinct island endemic species per island group are provided in Table S4 in Appendix S5.

Null model analyses

There were significantly more extinct, CR, EN, VU and all threatened (TH) island endemic species than expected; all ES and empirical *P*-values were the maximum value (i.e., ES = 3.891; and *P* equivalent to < 0.001) (Fig. S2).

Taxonomic order

When using the all-species dataset as the species pool, there were always significantly fewer passerines (perching birds) and Piciformes (including woodpeckers and barbets) than expected by chance within all five categories of species (EX, CR, EN, VU and TH), and Caprimulgiformes (nightjars and hummingbirds) in all except CR. There were significantly more Columbiformes (pigeons and doves) in all categories, Psittaciformes (parrots) in all except EN, and Gruiformes (including cranes, crakes and rails) in all except CR and EN (Fig. 5). A number of other orders were also significantly over (e.g., Strigiformes – owls) and under (e.g., Galliformes – game birds) represented in certain IUCN Red List status categories (Fig. 5). The Anseriformes (waterfowl) were overrepresented amongst extinct species. Using the all-island endemics dataset as the pool resulted in more conservative results (Fig. S3), particularly in regard to the CR and EN threat status groups, where the only significant result was fewer threatened passerines than expected by chance. All ES and empirical *P*-values are provided in Table S5.

Functional traits

In terms of traits, and when using all extant species (or the all-species dataset for the extinct species analyses) as the species pool, there were significantly more threatened and extinct flightless island endemic bird species than predicted by the null models (Fig. 6). Observed threatened island endemic median HWI and body mass were both significantly higher than expected given the null models (Fig. 6). Median body mass of extinct species was also significantly larger than expected. There were significantly more forest and marine, and fewer grassland, threatened island endemics than expected given our null model. There were significantly more aquatic predator, omnivorous and vertivorous threatened island endemic species than expected, while there were fewer granivorous, invertivorous and nectivorous species (Fig. 6). None of the trophic level categories were significant. For beak morphology, the volume of the hypervolume built using the beak traits of threatened island endemics was significantly larger than expected given the null model. Using only island endemic species as the pool resulted in broadly similar results (Fig. S4). The main differences related to habitat; for the island pool analyses there were significantly fewer threatened forest species (compared to significantly more for the all-species pool), significantly more wetland species (compared to non-significance for the all-species pool) than expected, and no significant difference for grassland species. All ES and empirical *P*-values are provided in Tables S6 and S7.

Individual trait differences between threatened and non-threatened island endemics

Body mass (larger average for threatened species), HWI (larger average for threatened species) and beak morphology PC1 (larger average for threatened species, meaning larger average beak size) all significantly differed between threatened and non-threatened island endemic species (Wilcoxon test *P*-values all < 0.01) (Fig. 7), while beak morphology PC2 did not ($P = 0.32$). For the categorical traits, the chi-square tests were significant for both habitat ($\chi^2 = 84.4$, $P < 0.001$) and trophic niche ($\chi^2 = 52.5$, $P < 0.001$); Fig. 7 indicates that threatened island endemic species contained a lower proportion of forest, grassland, invertivorous and nectivorous species, and a higher proportion of marine, wetland, aquatic predator and vertivorous species, than non-threatened species. These findings largely match with those presented in Figures 6 and S4.

Comparing functional morphospaces using hypervolumes

When comparing the hypervolumes of non-threatened island endemics (‘NTE’) with threatened island endemics (‘TE’), overall dissimilarity (Btotal) was moderate (0.45; zero representing identical, and one representing completely dissimilar, assemblages), with the largest unique portion of the combined hypervolumes represented by TEs (26% of the union of the two hypervolumes) compared to NTEs (20%). Brepl (0.38) comprised a larger portion of Btotal than Brich (0.07) (Fig. 8). The hypervolume for TEs (volume = 52.6) was larger than that for NTEs (48.0). When using the global extant species pool, the null modelling indicated that, while the observed overall Btotal was not significantly different than expected, the unique portion represented by non-threatened island endemics was significantly lower, and the unique portion represented by TEs significantly larger, than expected by chance (Fig. 8). Equivalent findings were observed when using the extant island species pool (Fig. S5). When using body size corrected traits, Btotal was similar (0.56), and TEs represented an even larger unique portion of combined hypervolumes (43% vs. 15% for NTEs). The main difference was that Brepl (0.28) and Brich (0.29) comprised similar fractions of Btotal (see Appendix S5 for the full results).

DISCUSSION

Overall conservation status of island endemic birds

In the present study, we have combined a review of the published literature (see Table 1) with an analysis of various data sources in order to provide an overview of the conservation status of the world's island endemic bird fauna. One disheartening observation is that 8% (n = 149) of island endemic species classified by the IUCN have gone extinct since 1500, which is orders of magnitude larger than the extinction rate for continental bird species over the same time period (Pimm et al., 2006). These results align with several previous studies reporting that island species have suffered disproportionate numbers of extinctions (Pimm et al., 2006; Whittaker & Fernández-Palacios, 2007; Szabo et al., 2012; Loehle & Eschenback 2012; Whittaker et al., 2017; Sayol et al., 2020; Fromm & Meiri, 2021; see also Table 1). Another alarming finding is that almost half of all island endemic birds (that were known to be extant in 1500 CE) are either extinct or threatened with extinction. This number is also a considerable underestimate. First, it does not include species that went extinct as a result of human actions prior to 1500 CE. Pre-1500 CE human communities are known to have caused a large number of avian extinctions on islands through hunting, the introduction of non-native species and habitat loss (Milberg & Tyrberg, 1993; Steadman, 2006; Whittaker & Fernández-Palacios, 2007; Boyer, 2008; Szabo et al., 2012; Duncan et al., 2013; Hume, 2017; Russell & Kueffer, 2019; Sayol et al., 2020; Soares et al., 2021, 2022; Table 1). Indeed, we found evidence of at least 307 pre-1500 CE island endemic extinctions (i.e. the 8% extinct figure increases to 22% if we include all known island endemic bird extinctions). Second, the number of extinct island endemics is likely an underestimate as some species classified by the IUCN as extant are likely extinct, given the time since they were last seen (Pimm et al., 2006; Butchart et al., 2018). Indeed, the IUCN applies a "Possibly Extinct" marker for some Critically Endangered species in this category. For example, the endemic New Caledonian rail (*Gallirallus lafresnayanus*) has not been conclusively reported since the 19th century, but unconfirmed reports since mean the species is still classified as CR. Overall, there are estimated to be 20 island endemic bird species that have not been seen for more than fifty years (Martin et al., 2022). That being said, there are some famous cases of bird species being rediscovered after not having been reported for decades (so called 'Lazarus species'). For example, the black-browed babbler (*Malacocincla perspicillata*; although not technically an island endemic based on the definition used here) was recently re-discovered in the rainforests of Borneo after not having been reported for 172 years (Akbar et al., 2021). Third, it is very unlikely that the fossils of all, even recently extinct, species driven extinct by humans have been discovered and, as Pimm et al. (2006; see also Duncan et al., 2013) argue, we should in fact report our numbers as species that are *known* to have gone extinct since 1500 CE. Finally, it is worth noting that these estimates do not include endemic subspecies extinctions, about which much less is known historically. We found evidence of 66 likely island endemic subspecies extinctions, including four from continental islands (i.e. technically not island endemics based on our definition employed here), one (San Benedicto rock wren) that went extinct from natural causes (volcanic eruption), and some from islands that have not suffered known full species extinctions (e.g. Cyprus). The data also indicate that island extinctions extend to families not otherwise represented in summaries of extinct species (e.g. Paridae). Interestingly, some extinct subspecies belong to otherwise wide-ranging species, often with broad ecological niches (e.g. *Columba palumbus maderensis*), indicating that the inherent vulnerabilities of island endemics extend beyond those possessing high evolutionary isolation and ecological specialization.

While there was overlap between the threatened and extinct hotspot maps, there were some notable differences (Fig. 4). For example, the Philippines and Indonesia have seen no post-1500 CE extinctions of island endemic species, but support large numbers of threatened species, while the Mascarenes suffered a larger number of extinctions than remain as threatened species, indicating perhaps that the majority of the most sensitive endemic species have already been lost (see also Johnson & Stattersfield, 1990). These differences could be due to one or a combination of the i) larger number and size of islands in the Philippines and Indonesia buffering endemics from extinction to a certain extent, ii) better knowledge of extinctions (e.g., higher density of fossil excavations) in the Mascarenes and the fact that several areas of the Philippines and Indonesia are relatively understudied, or iii) focus here only on post-1500 CE extinctions. It should also be noted that this analysis does not include subspecies extinctions, and only relates to species classified as Extinct by the IUCN. The Philippines in particular has seen extinctions of numerous subspecies (n = 8), including the Cebu white-bellied woodpecker (*Dryocopus javensis cebuensis*), endemic to the island of Cebu in the Philippines and not seen for over 50 years. In addition, various full species endemic to these island groups have also not been convincingly reported for decades, and, as discussed above, are possibly extinct despite still being classified as CR by the IUCN. These include the Sulu bleeding-heart (*Gallicolumba menagei*), a species that has no confirmed records for over 100 years.

In terms of threatened species, the Philippines was the ‘hottest’ hotspot, with almost double the number of threatened species of the second ranked hotspot (Hawaii). However, the comparison with other island groups is slightly unfair given that, for ease, we considered the Philippines as a single archipelago despite its size. Regardless, what can be said with certainty is that the biogeographic region encompassing the Philippines, Malaysia, Indonesia and Papua New Guinea, a region known to support large amounts of threatened biodiversity (Johnson & Stattersfield, 1990; Mittermeier et al., 2011), is home to a substantial number of threatened island endemic birds (Fig. 2) and is thus an essential focal point for future avian island conservation efforts.

Threats and variation in sensitivity between orders

Our analyses build on the findings of previous studies to highlight that the main threats to island endemic bird species are agricultural expansion, introduced species and biological resource use (e.g., hunting) (Table 1; Johnson & Stattersfield, 1990; Spatz et al., 2017; Leclerc et al., 2018, 2020b; Russell & Kueffer, 2019; see Lees et al., 2022, for a review of threats to all bird species), with climate change expected to become an increasingly prevalent threat going forward (e.g., see Leclerc et al., 2020a, for a vulnerability assessment of island endemic mammals and future climate change). There is a large literature on the impacts of introduced species on island species, in particular the loss of many endemic seabirds and ground-nesting birds due to predation from introduced cats and rats (Bellard et al., 2016; Spatz et al., 2017; Richards et al., 2021; Marino et al., 2022). Our analyses indicate that CR species in particular are threatened by introduced species, highlighting the urgency required to deal with this issue on many islands before it is too late. While also an issue in continental systems, the effects of biological resource use, and especially hunting, are particularly acute on islands due to the small population sizes of many island endemics coupled with the small nature of the island themselves and thus lack of refugia (Steadman, 2006; Whittaker & Fernández-Palacios, 2007; Matthews et al., 2020b). While all the aforementioned drivers are detrimental when occurring in isolation, we found that many species are affected by more than one driver and it is likely that certain drivers will interact in a multiplicative fashion (Holdaway & Jacomb, 2000). For example, the loss and degradation of natural habitat opens up areas for introduced species to more easily spread through the landscape (Johnson & Stattersfield, 1990). One important thing to highlight is that habitat loss and fragmentation, known to be primary drivers of species loss across taxa (Haddad et al., 2015), are not included as specific threats by the IUCN but are instead incorporated within multiple different threats (e.g., agricultural expansion).

When using all global species as the species pool, our analysis of taxonomic orders found that certain orders of island endemic birds are particularly threatened, such as those including pigeons, crakes and rails, parrots and owls. These orders tend to contain species that possess particular traits that place them at risk of extinction, including flightlessness and large body size, and in the case of parrots, colourful feathers that put them at the risk of collectors (Boyer, 2008; Spatz et al., 2017; Lévêque et al., 2021). Interestingly, the results for Gruiformes (which includes the rails) were non-significant for Critically Endangered and Endangered species, which could indicate that the most sensitive species have already gone extinct; further evidence for this is provided in Figure 5 which shows that more Gruiformes have gone extinct since 1500 than expected based on our null model.

We also found that the orders including pigeons, rails, parrots and ducks have suffered disproportionate numbers of island extinctions (see Szabo et al., 2012; see also Steadman, 2006 and Lévêque et al., 2021, for discussions on island rail extinctions). Pigeons and rails are one of the small groups of birds known to be substantially negatively impacted by both introduced species and habitat loss (Owens & Bennett, 2000), which likely partly explains this observation. As outlined above, these species also possess traits that make them very vulnerable to human activities, such as hunting and species introduction. In fact, perhaps no other group better illustrates the colossal loss of island birds than the Columbidae (pigeons and doves). Hume (2017) lists 47 Columbidae taxa (note this includes certain taxa listed by the IUCN as CR but for which no confirmed records have been reported for decades) that are known to have gone extinct due to human actions (both pre- and post-1500 CE), almost all of which were island species, including four turtle doves (*Nesoenas*), a range of flightless taxa such as the dodo (*Raphus cucullatus*), the St Helena pigeon (*Dysmoropelia dekarchiskos*) and numerous ground doves (*Alopecoenas*), four blue pigeons (*Alectroenas*), and four imperial pigeons (*Ducula*). Of the few non-island species, the passenger pigeon (*Ectopistes migratorius*) is perhaps the most famous. Interestingly, many relatively small islands were historically able to support surprising numbers of endemic pigeons, although this is no longer the case. For example, Henderson Island in the South Pacific, an island of only 37 km^2 and a maximum height of 33 m, once supported four pigeon species, three of which (the Henderson imperial pigeon *Ducula harrisoni*, Henderson archaic pigeon *Bountyphaps obsoleta*, and ground dove *Pampusana leonpascoi*) have been driven extinct (Hume, 2017).

Many of the aforementioned groups are known to be over-represented in threatened birds more generally (Bennett & Owens, 1997), although other bird groups known to be generally threatened (e.g., Galliformes – game birds; Bennett & Owens, 1997) were not found to be over-represented amongst island endemics. This could be due to their general under-representation on islands, likely owing to their lower dispersal ability. Alternatively, it could be due to a lack of representation in the fossil record for these groups. For example, in relation specifically to Galliformes, a recent study described three newly discovered extinct species of quails in Madeira and Cabo Verde (Rando et al., 2020); all three species are believed to have been flightless, likely explaining their extinction after human colonisation of these islands. Across all categories (extinct through to all threatened species), we found that there were fewer passerine species than expected. This could be driven by the fact that non-passerines tend to be larger, with lower reproductive rates, and are thus more at risk of threats such as hunting (Pimm et al., 2006). In addition, the order-level focus will likely have masked patterns at lower taxonomic levels within passerines, such as the Fringillidae (finches) family that includes, amongst others, the Hawaiian honeycreepers (e.g., Fig. 1a), a group that has suffered large numbers of extinctions (Hume, 2017). We also found fewer threatened Piciformes than expected, but this could be biased by the relatively small number of Piciformes on islands (19 extant and extinct island endemics out of a global total of 483 species).

Interestingly, when using the all-island endemics dataset as the species pool (i.e. restricting the pool only to island endemics), some avian orders no longer contained more / less threatened species than expected. This was most notable with Columbiformes, which were no longer significantly different from expected in any of the five threat status categories (Fig. S3). Columbiformes are known to be overrepresented on islands relative to their frequency on the mainland, likely due to their ability to pass through the dispersal and environmental filters necessary to colonise islands (Triantis et al., 2022). This could partly explain the overrepresentation of these species in the threatened and extinct groups when using the all global species pool. Using the all-island endemics dataset as the species pool is arguably a more realistic scenario. However, it is far more conservative than using all the world’s species, as each sample of 530 species represents a relatively large proportion (29%) of the total 1,856 island endemics, and thus each sample will contain a considerable number of actual threatened island endemics. Regardless, these results indicate that accounting for island endemism status in analyses of this type (which several previous analyses were unable to do, e.g. Bennett & Owens, 1997) can influence the results for certain taxonomic groups.

Traits associated with threatened island endemics birds

Our null model analyses of species functional traits revealed that there is a higher proportion of flightless threatened species on islands than predicted. In birds, the increased tendency for island endemics to have lost the ability to fly, most notably in Anatidae, Columbidae and Rallidae, alongside the evolutionary loss of predator avoidance, is often provided as evidence of the vulnerability of island endemic species (Steadman, 2006; Whittaker & Fernández-Palacios, 2007). Flightless species are unable to easily escape predators and are thus particularly at risk from introduced species, a known extinction driver for many island taxa, such as cats and rats, and indeed humans (Table 1; Duncan et al., 2002; Boyer, 2008; Wright et al., 2016; Sayol et al., 2020; Fromm & Meiri, 2021).

Previous studies of threatened birds have found that body size is often *not* a significant predictor of threat status, because different threats tend to target different sized species (Leclerc et al., 2020b); larger-bodied species being more at risk from hunting, while smaller species often being more at risk from habitat loss (Owens & Bennett, 2000, Chichorro et al., 2019). In addition, an analysis of avian extinctions in the Hawaiian Islands found that species that went extinct in prehistoric times (i.e., prior to European contact) tended to be large-bodied, whereas those in historic times (i.e., after European contact) tended to be mid-sized species, possibly because the most vulnerable large-bodied species had already been lost (Bower, 2008). However, in our null model and individual trait comparison analyses, we found that larger-bodied island endemic species were more likely to be threatened and to have gone extinct (see also Fromm & Meiri, 2021, and Soares et al., 2022). This result could illustrate that hunting, which typically targets larger-bodied bird species (e.g., Duncan et al., 2002, 2013), is the most pervasive threat on islands, or it could be that the traits that tend to correlate with body size (low reproductive rates, low rates of population growth, small population sizes, small clutch size, long intervals between clutches, larger home ranges; Gaston & Blackburn, 1995; Bower, 2008) are driving this pattern.

We also observed that threatened island endemics had a higher median hand-wing index (HWI) than expected given our null model (when using both species pools), and average HWI was significantly larger for threatened compared to non-threatened island endemics (Fig. 7). This is surprising given that HWI is positively associated with dispersal ability (Sheard et al., 2020), a characteristic that is believed to negatively correlate with extinction risk. This could be due to the fact that island bird species need to have high enough dispersal ability to reach many islands in the first place (Whittaker & Fernández-Palacios, 2007), a pattern that will then be dampened by the subsequent evolution of flightlessness in many lineages due to the energetic advantages of flightlessness on islands lacking mammalian predators, at least before the arrival of humans (Diamond, 1981; Wright et al., 2016; Sayol et al., 2020). However, the same result was obtained when the null model species pool was restricted to only island endemics, and when comparing threatened and non-threatened island endemics. It is also likely partly related to the high number of threatened seabirds (see Richards et al., 2021), many of which have high dispersal ability but are endemic breeders on only one or two islands; examples include the New Zealand storm petrel (*Fregetta maoriana*) and Mascarene petrel (*Pseudobulweria aterrima*), both Critically Endangered. Indeed, re-running the null model analyses after removing marine species resulted in lower observed HWI values and a closer match between observed values and the null distributions, although the observed values were still significantly larger.

Our null model (Fig. 6) and individual trait comparative (Fig. 7) analyses indicated that there were significantly more threatened island endemic aquatic predators and vertivores than expected, but interestingly fewer invertivores. Invertivores are often listed as being particularly threatened, for example, by habitat loss and climate change (Boyer, 2008; Bowler et al., 2019; Stouffer et al., 2021), although Şekercioğlu et al. (2004) did report that, as a guild, they contained fewer extinction-prone species than average. It is worth noting that invertivores represent the dominant avian trophic niche globally, and this proportion is relatively similar between all bird species (48%) and just island endemic species (44%). There were also fewer threatened island endemic granivore and nectarivore species than expected. One point to bear in mind is that current threatened island species patterns will be biased by the fact that many island species with certain traits that predispose them to extinction will have already been lost (Boyer, 2008; Leclerc et al., 2018). For example, Boyer (2008; see also Carpenter et al., 2020) found that granivores were more susceptible to extinction in Hawaii prior to European contact, possibly due to the specialisation of island endemic birds on specific plant species. If the most vulnerable island endemic granivores have already gone extinct, we would be less likely to observe a significant pattern for threatened species in regard to those granivores that remain. It was not possible to test this idea using the datasets we collated as we did not have trophic niche data for extinct species. However, a recent study by Soares et al. (2022) did determine the primary diet type (invertivore, carnivore, frugivore, granivore, omnivore and herbivore) for 759 native bird species (including 214 extinct species; both pre- and post-1500 CE extinctions) across 74 oceanic islands. Interestingly, a simple analysis of the data in Soares et al. reveals that the proportion of extinct species in each of the six diet categories is roughly similar to the proportion of extant native species in each category (see Table 2), with invertivores being the only group with a greater than 5% difference between extinct and extant species proportion

(26% of extinct species were invertivores compared with 39% of extant species). However, if we look at the proportion of total species in each diet category (i.e., extant + extinct) that have gone extinct from those islands (Table 2), it reveals that fewer invertivores (24% of the total) have gone extinct relative to the other groups, particularly (non-invertivorous) carnivores (41%) and herbivores (48%). Thus, it does appear that invertivores have suffered less relative to birds in other diet groups.

The analysis of Soares et al.'s data, in combination with the findings of our main analyses, highlights how the loss of island endemic species, and potential future loss of threatened species, has likely affected (and will likely affect) key ecosystem functions on islands, including scavenging, nutrient recycling, pollination and herbivory (see several studies listed in Table 1, including Boyer, 2008; Boyer & Jetz, 2014; Heinen et al., 2017; Carpenter et al., 2020). For example, the loss of non-invertivorous carnivores (vertivores), which we also found were more threatened with extinction than expected, can lead to increases in the population sizes of species lower down the trophic pyramid, including species considered pests by humans (Şekercioğlu et al., 2004). As a second example, our analysis of beak morphology indicated that threatened endemics incorporate unique areas of beak morphospace (Fig. 6), particularly larger overall beak sizes (Fig. 7). This is also likely the case for many extinct species given that they tended to be larger and flightless, and thus will have often occupied distinct feeding niches (Sayol et al., 2021). Beak size and shape are linked to a number of ecosystem functions provided by birds, such as seed dispersal, as they are directly related to resource use (Pigot et al., 2020; Tobias et al., 2020). As such, the future loss of these threatened species, coupled with the species already lost to extinction, will likely have severe impacts on many important functions. Indeed, the loss of frugivorous species has been shown to have affected forest regeneration on the islands of Reunion (Albert et al., 2021) and Guam (where all native vertebrate frugivores have been lost, Caves et al., 2013) due to the reduced dispersal of (particularly large-seeded) fruiting plant species (Thébaud & Strasberg, 1997). This issue is particularly pertinent on islands given that the non-avian taxa that also undertake these roles on mainlands (e.g., large non-volant mammals) are often absent from islands (Whittaker & Fernández-Palacios, 2007).

The functional space occupied by threatened island endemic birds

It was apparent that, although comprising fewer species (526 vs. 1176), threatened island endemics occupy a larger volume and distinct areas of morphospace compared to non-threatened endemics (Fig. 8). In addition, these findings are conservative given the highly distinct five *Apteryx* (kiwis) species (four of which are threatened), endemic to New Zealand and located in a completely different part of morphospace to the rest of the world's birds (see also Pigot et al., 2020), were excluded. This finding has potential conservation implications as it indicates that the loss of these threatened island endemics will substantially reduce the functional trait space of island endemic birds (see also Leclerc et al., 2020b; and see Cooke et al., 2019, for similar conclusions regarding bird species in general), which could have knock-on effects on island ecosystem functioning given the aforementioned functional roles birds provide (Şekercioğlu et al., 2004; Dirzo et al., 2014; Lees et al., 2022). This aligns with the recent findings of Sayol et al. (2021; see also Table 1) who, in analysis of extinctions on nine archipelagos, found that extinct species occupied distinct areas of morphospace relative to extant and introduced species. It is worth noting that non-threatened island endemics, many of which are still affected by anthropogenic activities (Fig. 3), also occupy distinct areas of island endemic morphospace. Thus, any future change in the status of these species could also have important implications for island ecosystem functioning.

Future research

Our review and analyses have shown that island endemics are disproportionately threatened with extinction, and represent the large majority of known extinctions, although this situation may now be in the process of changing given the increasing extinction rates observed in continental species (Pimm et al., 2006; Butchart et al., 2018; Lees et al., 2022). As a next step, what is necessary is to move beyond analyses of the numbers / proportions of threatened and extinct island endemics, to a focus on the wider impacts of this species loss. Early work in this area has been revealing, indicating that island bird extinctions have resulted in large declines in functional diversity in specific island regions (e.g., Boyer & Jetz, 2014; Sayol et al., 2021), with the disproportionate loss of particular guilds affecting wider ecosystem processes on islands, such as predation of soil and leaf-litter invertebrates (Boyer & Jetz, 2014), and the aforementioned examples of fruiting tree seed dispersal (Caves et al., 2013; Heinen et al., 2017; Albert et al., 2021). Further research on how extinctions have impacted (and potential future extinctions will impact) specific ecosystem functions will prove rewarding, as will a better understanding of how the functional roles of birds on islands overlap with other taxonomic groups (Heinen et al., 2017; Carpenter et al., 2020; Albert et al., 2021), particularly given some (e.g., non-volant mammals and amphibians) are generally underrepresented on islands. To achieve this, it will be necessary for future studies to focus on a broader range of island species and contexts. Our analyses are focused on island endemics and global extinctions. However, i) island avifaunas comprise varying numbers of non-endemic bird species that also undertake functional roles, and ii) globally extant species may have been extirpated from many individual islands.

Identifying at what point future extinctions of highly threatened species (including birds and other taxa) could result in ecosystem collapse in individual island systems is also an important area of future research, as is the extent to which introduced species may compensate the functional diversity and ecosystem roles lost through extinction on islands (e.g., Sobral et al., 2016; Carpenter et al., 2020; Sayol et al., 2021; Soares et al., 2022). For example, in an evaluation of seed predation in New Zealand, the Mascarenes and Hawaii, Carpenter et al. (2020; see Table 1) found that, while introduced birds (including many game bird species) and mammals were functionally similar to some of the avian seed predators that have gone extinct on the islands following human arrival, many extinct species have no functional equivalents, which will likely impact this particular ecosystem function. For example, the extinct moa-nalo, a group of large flightless Anatidae that were endemic to Hawaii and capable of destroying the largest seeds in the Hawaiian flora, have no functional equivalents among the numerous introduced Hawaiian birds. Some introduced mammals in Hawaii can also destroy the largest seeds, but they do so in a different way and with varying consequences on seed dispersal (Carpenter et al., 2020). To take another example, looking at the overall functional diversity of birds on nine archipelagos, Sayol et al. (2021) found that, while introduced species had often compensated for the loss of extinct species in terms of species numbers, they did not fill the gap left by extinctions in terms of overall functional diversity. Soares et al. (2022) found similar patterns in an analysis of birds on 74 oceanic islands. Similar research in other island groups and for other taxa and ecosystem functions is clearly warranted.

Another outstanding question of interest in regard to island birds and ecosystem functioning relates to the prevalence of functional extinction. Many island endemic birds are still extant, and thus still included in analyses of island functional diversity, but are present in such low numbers that it is unlikely they contribute in any meaningful way to ecosystem processes. For example, the Cebu flowerpecker (*Dicaeum quadricolor*) is endemic to the Philippines and had an estimated population size of only 60-70 mature individuals in 2005 (Billerman et al., 2022). Indeed, we found that 35% of all endemic CR species had a global population size of less than 50 individuals. Analyses of the contribution of these ‘functionally extinct’ species to overall island functional diversity are thus warranted. Linked to this, it would be useful (for many reasons) to determine which of those island endemic species that have not been recorded for decades are in fact extinct (Martin et al., 2022). This is not a straightforward task, given the remote nature of most of the islands in question, and the fact that many are uninhabited. However, initiatives such as the ‘Search for Lost Birds’ (supported by Re:wild, American Bird Conservancy, and BirdLife International) which helps fund and organise expeditions to search for such ‘lost’ species should provide vital information in this regard.

Finally, there are a lack of continuous functional trait data for extinct species, which is understandable given that many extinct island bird species are only known from a small number (sometimes a single set) of sub-fossil remains (Steadman, 2006; Hume, 2017). Aside from further fossil excavations, which are evidently required but are also time and resource intensive, the development and testing of alternative approaches for estimating extinct species trait data is required. For example, this could include identifying and using the closest extant relative (Triantis et al., 2022), and machine learning techniques (Fromm & Meiri, 2021) and related trait imputation methods (Sayol et al., 2021; Marino et al., 2022).

Overall, we have shown that the world has lost a substantial number of island endemic bird species (and sub-species) due to anthropogenic activities, including many highly distinctive species with unique functional roles. Worryingly, if current trends continue, we can expect the loss of many more, with concomitant reductions in functional diversity. In this way, island birds can be seen as being representative of island biodiversity more generally (Whittaker et al., 2017), highlighting the necessity of increasing conservation activity in island environments.

ACKNOWLEDGEMENTS

A large proportion of the analysed data was provided through the IUCN Red List’s API. The hypervolume computations described in this paper were performed using the University of

Birmingham's BlueBEAR HPC service. John Mittermeier provided information on the ‘Search for Lost Birds’ initiative. Ferran Sayol was supported by the postdoctoral fellowship program Beatriu de Pinós (2020 BP 00067, Government of Catalonia). No permits were needed to carry out this work.

DATA AVAILABILITY STATEMENT

The data are available on DRYAD (https://doi.org/10.5061/dryad.9w0vt4bjn). The code is available on GitHub (txm676/islandbirds).

AUTHOR CONTRIBUTIONS

TJM, JPW, FS, JPH, JAT, FCS, CT, TEM and KAT collected the data; TJM analysed the data with input from PC, FS, and WU; TJM led the writing, and all authors contributed to the writing and interpretation of the results.

REFERENCES

Akbar, P. G., Nugroho, T. W., Suranto, M., Fauzan, M. R., Ferdiansyah, D., Trisiyanto, J. S., & Yong, D. L. (2021). No longer an enigma: rediscovery of Black-browed Babbler Malacocincla perspicillata in Kalimantan, Indonesia. *Journal of Asian Ornithology, 37*, 1-5.

Albert, S., Flores, O., Baider, C., Florens, F. B. V., & Strasberg, D. (2021). Differing severity of frugivore loss contrasts the fate of native forests on the land of the Dodo (Mascarene archipelago). *Biological Conservation, 257*, 109131.

Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters, 12*, 20150623.

Bennett, P. M., & Owens, I. P. F. (1997). Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London. Series B: Biological Sciences, 264*, 401–408.

Billerman, S. M., Keeney, B. K., Rodewald, P. G., & Schulenberg, T. S. (2022). Birds of the world. Retrieved from https://birdsoftheworld.org/bow/home

Birdlife International. (2021). Birdlife data zone. Retrieved from http://datazone.birdlife.org/home

Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L., & Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science, 305*, 1955–1958.

Blonder, B., Babich Morrow, C., Maitner, B., Harris, D. J., Lamanna, C., Violle, C., . . . Kerkhoff, A. J. (2018). New approaches for delineating n-dimensional hypervolumes. *Methods in Ecology and Evolution, 9*, 305–319.

Bowler, D. E., Heldbjerg, H., Fox, A. D., de Jong, M., & Böhning-Gaese, K. (2019). Long-term declines of European insectivorous bird populations and potential causes. *Conservation Biology, 33*, 1120–1130.

Boyer, A. G. (2008). Extinction patterns in the avifauna of the Hawaiian islands. *Diversity and Distributions, 14*, 509–517.

Boyer, A. G., & Jetz, W. (2014). Extinctions and the loss of ecological function in island bird communities. *Global Ecology and Biogeography, 23*, 679–688.

Butchart, S. H. M., Lowe, S., Martin, R. W., Symes, A., Westrip, J. R. S., & Wheatley, H. (2018). Which bird species have gone extinct? A novel quantitative classification approach. *Biological Conservation*, *227*, 9–18.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., . . . Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science, 309*, 1239–1241.

Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT - Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution, 6*, 232–236.

Carmona, C. P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., . . . Toussaint, A. (2021). Erosion of global functional diversity across the tree of life. *Science Advances, 7*, eabf2675.

Carpenter, J. K., Wilmshurst, J. M., McConkey, K. R., Hume, J. P., Wotton, D. M., Shiels, A. B., . . . Drake, D. R. (2020). The forgotten fauna: native vertebrate seed predators on islands. *Functional Ecology, 34*, 1802–1813.

Caves, E. M., Jennings, S. B., HilleRisLambers, J., Tewksbury, J. J., & Rogers, H. S. (2013). Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. *PloS ONE, 8*, e65618.

Chamberlain, S. (2020). rredlist: 'IUCN' Red List Client. R package, Version 0.7.0. Retrieved from https://cran.r-project.org/web/packages/rredlist/index.html

Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation, 237*, 220–229.

Cooke, R. S. C., Eigenbrod, F., & Bates, A. E. (2019). Projected losses of global mammal and bird ecological strategies. *Nature Communications, 10*, 2279.

Diamond, J. M. (1981). Flightlessness and fear of flying in island species. *Nature, 293*, 507–508.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science, 345*, 401–406.

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology, 7*, 214.

Duncan, R. P., & Blackburn, T. M. (2007). Causes of extinction in island birds. *Animal Conservation, 10*, 149–150.

Duncan, R. P., Blackburn, T. M., & Worthy, T. H. (2002). Prehistoric bird extinctions and human hunting. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 269*, 517–521.

Duncan, R. P., Boyer, A. G., & Blackburn, T. M. (2013). Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proceedings of the National Academy of Sciences, 110*, 6436–6441.

Fernández-Palacios, J. M., Kreft, H., Irl, S. D. H., Norder, S., Ah-Peng, C., Borges, P. A. V., . . . Drake, D. R. (2021). Scientists' warning – the outstanding biodiversity of islands is in peril. *Global Ecology and Conservation, 31*, e01847.

Fromm, A., & Meiri, S. (2021). Big, flightless, insular and dead: characterising the extinct birds of the Quaternary. *Journal of Biogeography, 48*, 2350–2359.

Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Gaston, K. J., & Blackburn, T. M. (1995). Birds, body size and the threat of extinction. *Philosophical Transactions: Biological Sciences, 347*, 205–212.

Graham, N. R., Gruner, D. S., Lim, J. Y., & Gillespie, R. G. (2017). Island ecology and evolution: challenges in the Anthropocene. *Environmental Conservation, 44*, 323–335.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., . . . Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances, 1*, e1500052.

Heinen, J. H., van Loon, E. E., Hansen, D. M., & Kissling, W. D. (2017). Extinction-driven changes in frugivore communities on oceanic islands. *Ecography, 41*, 1245–1255.

Holdaway, R. N. (1999). Introduced predators and avifaunal extinction in New Zealand. In R. D. E. MacPhee (Ed.), *Extinctions in near time: causes, contexts, and consequences* (pp. 189–238). New York: American Museum of Natural History.

Holdaway, R. N., & Jacomb, C. (2000). Rapid extinction of the moas (Aves: Dinornithiformes): model, test, and implications. *Science, 287*, 2250–2254.

Hume, J. P. (2017). *Extinct birds*. London: Bloomsbury.

Hume, J. P., Martill, D., & Hing, R. (2018). A terrestrial vertebrate palaeontological review of Aldabra Atoll, Aldabra Group, Seychelles. *PloS ONE, 13*, e0192675.

Hume, J. P., & Robertson, C. (2021). Eggs of extinct dwarf island emus retained large size. *Biology Letters, 17*, 20210012.

IUCN. (2012). *IUCN Red List categories and criteria, Version 3.1, second edition* (Vol. 2021). Gland, Switzerland: IUCN.

IUCN. (2021a). IUCN Red List of threatened species. Version 2021-2. Retrieved from www.iucnredlist.org

IUCN. (2021b). Summary statistics. Retrieved from https://www.iucnredlist.org/statistics

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature, 491*, 444–448.

Leclerc, C., Courchamp, F., & Bellard, C. (2018). Insular threat associations within taxa worldwide. *Scientific Reports, 8*, 6393.

Leclerc, C., Courchamp, F., & Bellard, C. (2020a). Future climate change vulnerability of endemic island mammals. *Nature Communications, 11*, 4943.

Leclerc, C., Villéger, S., Marino, C., & Bellard, C. (2020b). Global changes threaten functional and taxonomic diversity of insular species worldwide. *Diversity and Distributions, 26*, 402–414.

Lees, A. C., Haskell, L., Allinson, T., Bezeng, S. B., Burfield, I. J., Renjifo, L. M., . . . Butchart, S. H. M. (2022). State of the world's birds. *Annual Review of Environment and Resources, 47*, doi: 10.1146/annurev-environ-112420-014642

Lévêque, L., Buettel, J. C., Carver, S., & Brook, B. W. (2021). Characterizing the spatio-temporal threats, conservation hotspots and conservation gaps for the most extinction-prone bird family (Aves: Rallidae). *Royal Society Open Science, 8*, 210262.

Lhotsky, B., Kovács, B., Ónodi, G., Csecserits, A., Rédei, T., Lengyel, A., . . . Botta-Dukát, Z. (2016). Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *Journal of Ecology, 104*, 507–517.

Loehle, C., & Eschenbach, W. (2012). Historical bird and terrestrial mammal extinction rates and causes. *Diversity and Distributions, 18*, 84–91.

Mammola, S., & Cardoso, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods in Ecology and Evolution, 11*, 986–995.

Marino, C., Leclerc, C., & Bellard, C. (2022). Profiling insular vertebrates prone to biological invasions: what makes them vulnerable? *Global Change Biology, 28*, 1077-1090.

Martin, T. E., Bennet, G. C., Fairbairn, A., & Mooers, A. O. (2022). ‘Lost’ taxa and their conservation implications. *Animal Conservation*. DOI: 10.1111/acv.12788

Matthews, T. J. (2021). On the biogeography of habitat islands: the importance of matrix effects, noncore species, and source-sink dynamics. *The Quarterly Review of Biology, 96*, 73–104.

Matthews, T. J., Rigal, F., Kougioumoutzis, K., Trigas, P., & Triantis, K. A. (2020a). Unravelling the small-island effect through phylogenetic community ecology. *Journal of Biogeography, 47*, 2341–2352.

Matthews, T. J., Leidinger, L. K. T., & Cabral, J. S. (2020b). The effect of species extinctions on island biogeographic patterns. *Ecological Research, 35*, 372–381.

Matthews, T. J., & Triantis, K. (2021). Island biogeography. *Current Biology, 31*, R1201–R1207.

Milberg, P., & Tyrberg, T. (1993). Naïve birds and noble savages - a review of man-caused prehistoric extinctions of island birds. *Ecography, 16*, 229–250.

Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. In F. E. Zachos & J. C. Habel (Eds.), *Biodiversity hotspots: distribution and protection of conservation priority areas* (pp. 3–22). London: Springer.

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface, 14*, 20170213.

Owens, I. P. F., & Bennett, P. M. (2000). Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences, 97*, 12144–12148.

Papworth, S. K., Rist, J., Coad, L., & Milner-Gulland, E. J. (2009). Evidence for shifting baseline syndrome in conservation. *Conservation Letters, 2*, 93–100.

Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., . . . Tobias, J. A. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology & Evolution, 4*, 230–239.

Pimm, S., Raven, P., Peterson, A., Şekercioğlu, Ç. H., & Ehrlich, P. R. (2006). Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Sciences, 103*, 10941–10946.

R Core Team. (2019). R: a language and environment for statistical computing (Version 3.4.3): R foundation for statistical computing, Vienna, Austria. Retrieved from https://www.R-project.org/

Rando, J. C., Alcover, J. A., Pieper, H., Olson, S. L., Hernández, C. N., & López-Jurado, L. F. (2019). Unforeseen diversity of quails (Galliformes: Phasianidae: Coturnix) in oceanic islands provided by the fossil record of Macaronesia. *Zoological Journal of the Linnean Society, 188*, 1296–1317.

Richards, C., Cooke, R. S. C., & Bates, A. E. (2021). Biological traits of seabirds predict extinction risk and vulnerability to anthropogenic threats. *Global Ecology and Biogeography, 30*, 973-986.

Russell, J. C., & Kueffer, C. (2019). Island biodiversity in the Anthropocene. *Annual Review of Environment and Resources, 44*, 31–60.

Sayol, F., Cooke, R. S. C., Pigot, A. L., Blackburn, T. M., Tobias, J. A., Steinbauer, M. J., . . . Faurby, S. (2021). Loss of functional diversity through anthropogenic extinctions of island birds is not offset by biotic invasions. *Science Advances, 7,* eabj5790.

Sayol, F., Steinbauer, M. J., Blackburn, T. M., Antonelli, A., & Faurby, S. (2020). Anthropogenic extinctions conceal widespread evolution of flightlessness in birds. *Science Advances, 6*, eabb6095.

Şekercioğlu, Ç. H., Daily, G. C., & Ehrlich, P. R. (2004). Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences, 101*, 18042–18047.

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., . . . Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications, 11*, 2463.

Soares, F. C., Leal, A. I., Palmeirim, J. M., & de Lima, R. F. (2021). Niche differences may reduce susceptibility to competition between native and non-native birds in oceanic islands. *Diversity and Distributions, 27*, 1507–1518.

Soares, F. C., de Lima, R. F., Palmeirim, J. M., Cardoso, P., & Rodrigues, A. S. L. (2022). Combined effects of bird extinctions and introductions in oceanic islands: decreased functional diversity despite increased species richness. *Global Ecology and Biogeography,* DOI: 10.1111/geb.13494

Sobral, F. L., Lees, A. C., & Cianciaruso, M. V. (2016). Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. *Ecology Letters, 19*, 1091–1100.

Spatz, D. R., Zilliacus, K. M., Holmes, N. D., Butchart, S. H. M., Genovesi, P., Ceballos, G., . . . Croll, D. A. (2017). Globally threatened vertebrates on islands with invasive species. *Science Advances, 3*, e1603080.

Steadman, D. W. (1997). Human-caused extinction of birds. In M. L. Reaka-Kudla, D. E. Wilson, & E. O. Wilson (Eds.), *Biodiversity II : understanding and protecting our biological resources* (pp. 139–162). Washington DC, USA: Joseph Henry Press.

Steadman, D. W. (2006). *Extinction and biogeography of tropical Pacific birds*. Chicago: University of Chicago Press.

Steadman, D. W., & Franklin, J. (2020). Bird populations and species lost to Late Quaternary environmental change and human impact in the Bahamas. *Proceedings of the National Academy of Sciences, 117*, 26833–26841.

Stouffer, P. C., Jirinec, V., Rutt, C. L., Bierregaard Jr, R. O., Hernández-Palma, A., Johnson, E. I., . . . Lovejoy, T. E. (2021). Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. *Ecology Letters, 24*, 186–195.

Szabo, J. K., Khwaja, N., Garnett, S. T., & Butchart, S. H. M. (2012). Global patterns and drivers of avian extinctions at the species and subspecies level. *PloS ONE, 7*, e47080.

Thébaud, C., & Strasberg, D. (1997). Plant dispersal in fragmented landscapes: a field study of woody colonization in rainforest remnants of the Mascarene Archipelago. In W. F. Laurance & R. O. Bierregaard (Eds.), *Tropical forest remnants: ecology, conservation, and management* (pp. 321–335). Chicago, Illinois: University of Chicago Press.

Tobias, J. A. (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*, 581–597

Tobias, J. A., Ottenburghs, J., & Pigot, A. L. (2020). Avian diversity: speciation, macroevolution, and ecological function. *Annual Review of Ecology, Evolution, and Systematics, 51*, 533–560.

Triantis, K., Rigal, F., Whittaker, R. J., Hume, J. P., Sheard, C., Poursanidis, D., . . . Tobias, J. A. (2022). Deterministic assembly and anthropogenic extinctions drive convergence of island bird communities. *Global Ecology and Biogeography*, DOI: 10.1111/geb.13556

Ulrich, W., Kryszewski, W., Sewerniak, P., Puchałka, R., Strona, G., & Gotelli, N. J. (2017). A comprehensive framework for the study of species co-occurrences, nestedness, and turnover. *Oikos, 126*, 1607–1616.

Veron, S., Mouchet, M., Govaerts, R., Haevermans, T., & Pellens, R. (2019). Vulnerability to climate change of islands worldwide and its impact on the tree of life. *Scientific Reports, 9*, 14471.

Warren, B. H., Simberloff, D., Ricklefs, R. E., Aguilée, R., Condamine, F. L., Gravel, D., . . . Thébaud, C. (2015). Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. *Ecology Letters, 18*, 200–217.

Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: ecology, evolution, and conservation* (2nd ed.). Oxford: Oxford University Press.

Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K., & Triantis, K. A. (2017). Island biogeography: taking the long view of nature's laboratories. *Science, 357*, eaam8326.

Wright, N. A., Steadman, D. W., & Witt, C. C. (2016). Predictable evolution toward flightlessness in volant island birds. *Proceedings of the National Academy of Sciences, 113*, 4765–4770.

Yee, T. W. (2015). *Vector generalized linear and additive models: with an implementation in R*. New York: Springer.

BIOSKETCHES

Tom Matthews is a macroecologist and biogeographer at the University of Birmingham, UK. He is interested in the application of macroecological methods to global environmental change questions, and he has a particular interest in islands and the impacts of human actions on island biodiversity.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

FIGURES

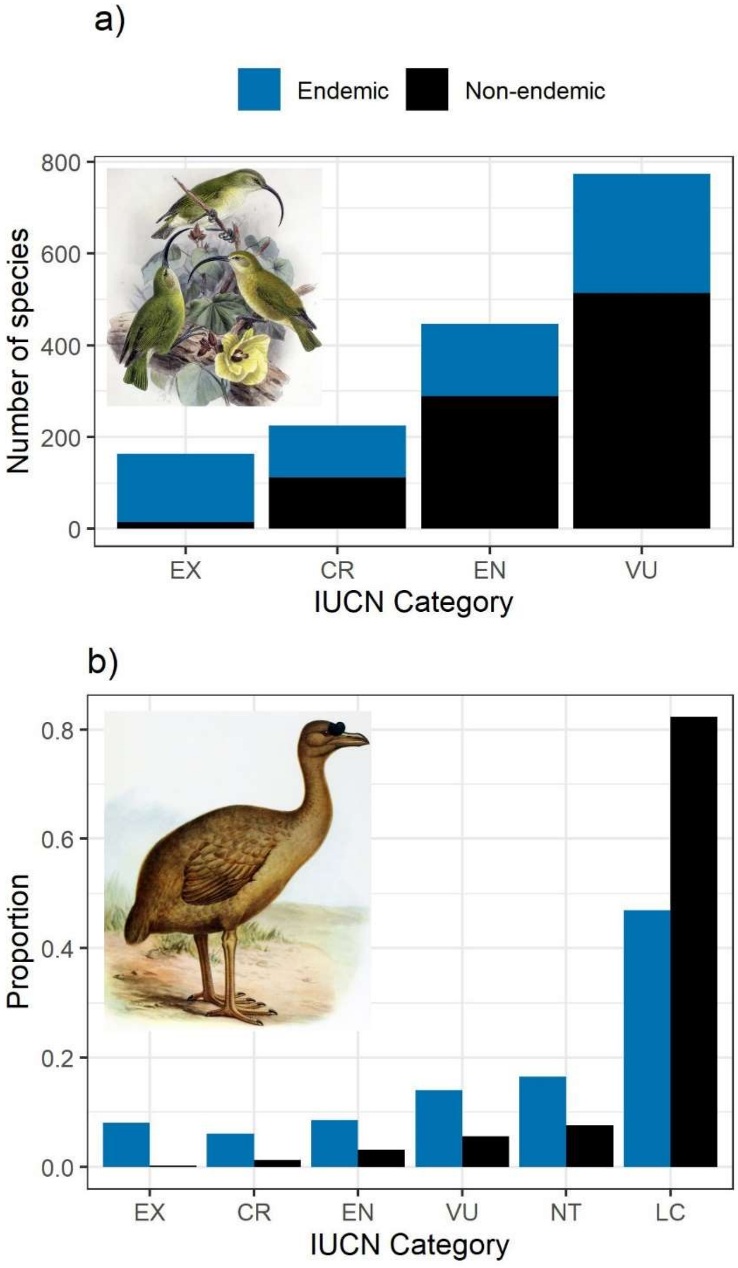

FIGURE 1 a) The number of bird species in four different IUCN Red List categories (EX = Extinct, CR = Critically Endangered, EN = Endangered, and VU = Vulnerable), split by island endemism status (endemic and non-endemic). b) The proportion of species in each category, plus those classified as Near Threatened (NT) and Least Concern (LC). The proportion of island endemic species in each category was calculated relative to the total number of island endemics (1,856), while the non-island-endemics proportions were relative to the total number of non-island-endemics (9,256); both totals included extinct species. The species inset in (a) is a Maui Nui 'akialoa (*Akialoa lanaiensis*), a Hawaiian honeycreeper that was driven extinct by the end of the 19th century (drawn by Lionel Walter Rothschild and John Gerrard Keulemans); the species in (b) is a Rodrigues solitaire (*Pezophaps solitaria*), an

extinct flightless bird that was endemic to the island of Rodrigues, east of Madagascar (drawn by Frederick William Frohawk). Both pictures are in the public domain.

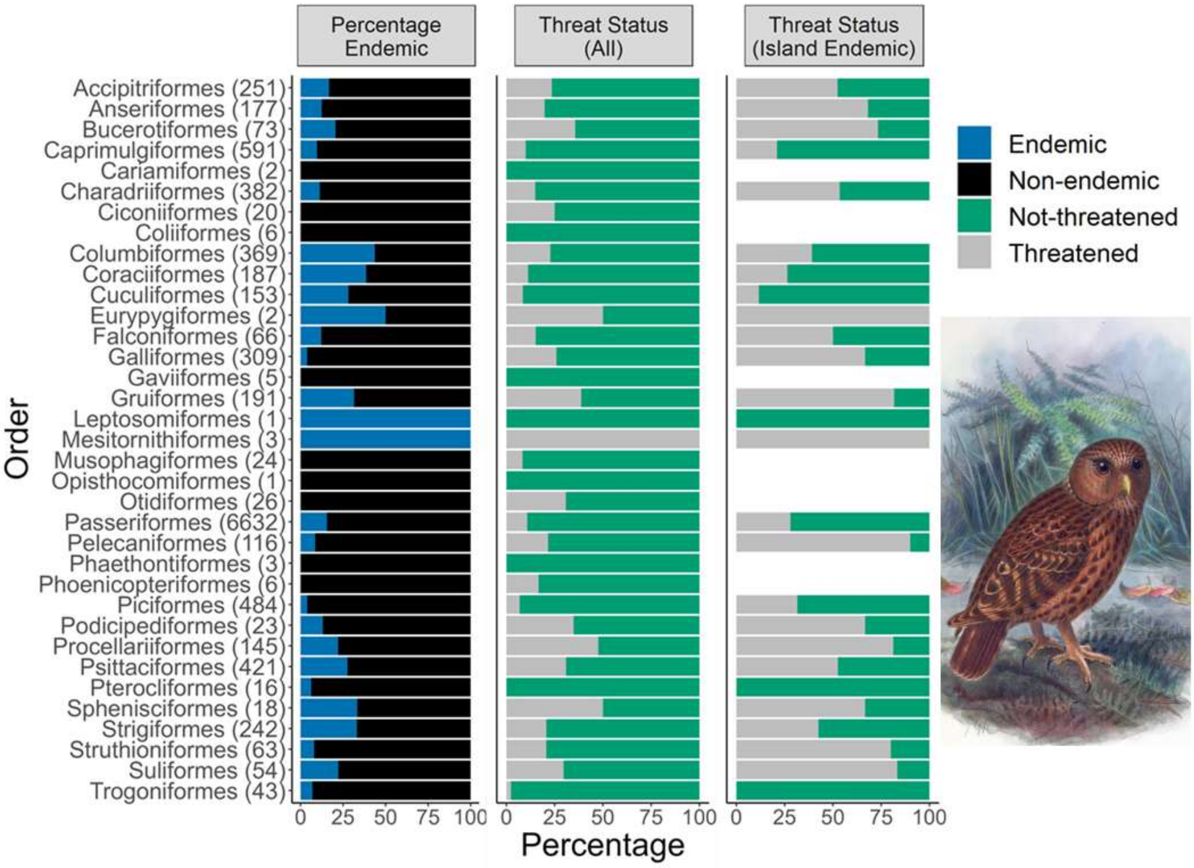

FIGURE 2 The proportion of species (including historically extinct species) in each avian order (n = 36) that are island endemics, and the proportion of all species [Threat (All)] and of island endemics [Threat (Isl.)] that are threatened with extinction / extinct. The numbers in parentheses represent the number of species in each order (11,112 species in total; all values are calculated after the removal of Data Deficient species). The gaps in the furthest right-hand column are orders with no island endemic species. Here, threatened also includes extinct species (i.e., Extinct, Critically Endangered, Endangered and Vulnerable species). The image inset is a laughing owl (*Sceloglaux albifacies rufifacies*; drawn by John Gerrard Keulemans and in the public domain), endemic to New Zealand and driven extinct by introduced species and specimen collecting by the early 20th century.

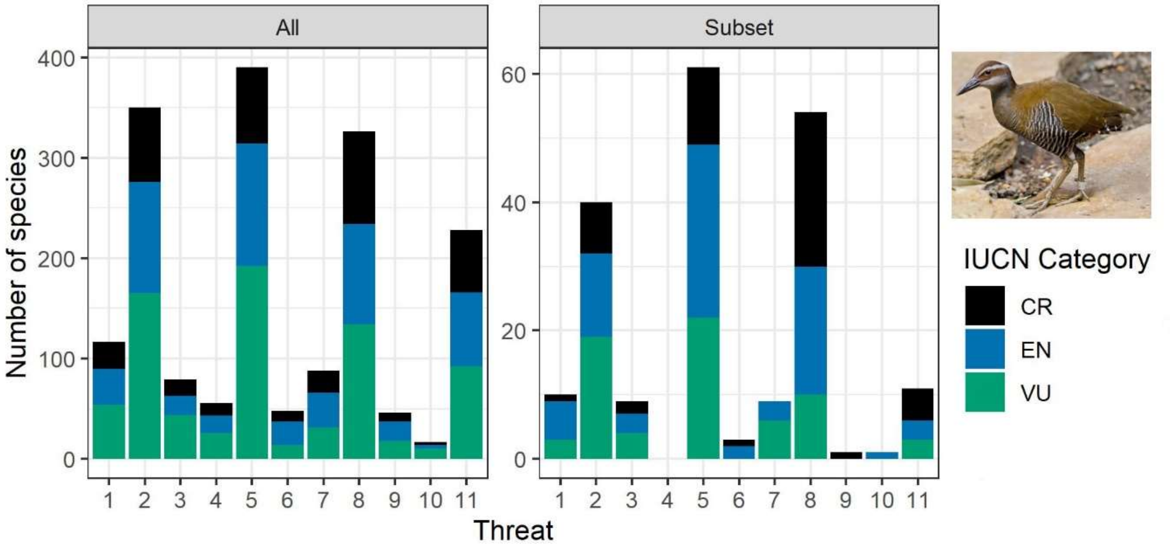

FIGURE 3 The number of island endemic bird species associated with each of 11 threats (see main text) according to the IUCN. The threat numbers correspond to individual threats as listed in Table S1. Threat category 12 (‘other’) has been excluded. The left-hand plot (All) includes all threat listings (i.e., all threat timings and severities). The right-hand plot (subset) only includes threats listed as ‘Ongoing’ and as causing ‘Rapid Declines’ or ‘Very Rapid Declines’. Note that a given species can be associated with more than one threat and thus the numbers in the bars do not sum to the total number of island endemic species (n = 1,856). Note also the different y-axis range in each plot. The species inset is a Guam rail (*Hypotaenidia owstoni*), a species of flightless bird, endemic to the island of Guam. Previously classified by the IUCN as Extinct in the Wild, the species has recently been downgraded to Critically Endangered (only the second time this has happened to a bird species) following a successful reintroduction strategy. Photo by Greg Hume, and is under license: https://creativecommons.org/licenses/by-sa/3.0/deed.en.

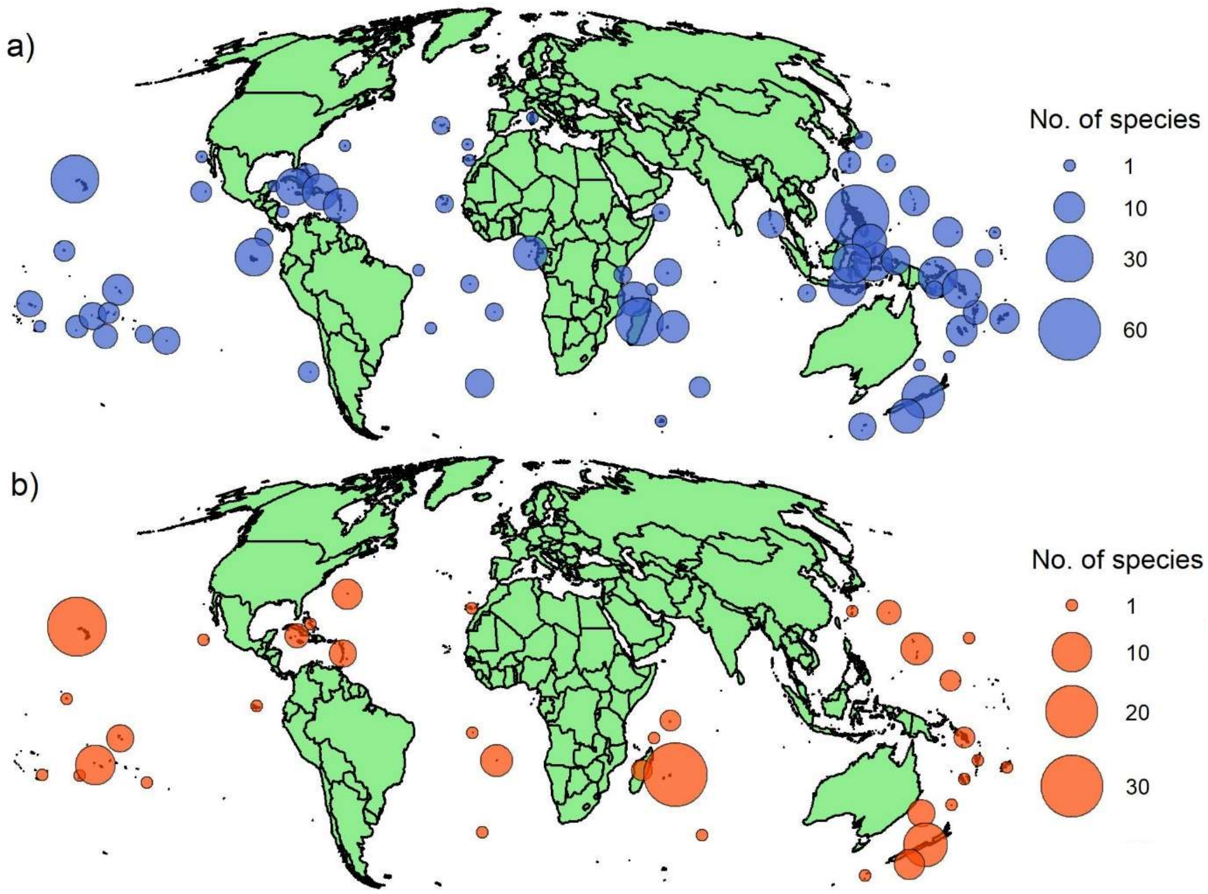

FIGURE 4 Hotspot maps of a) threatened and b) extinct island endemic bird species, according to the IUCN Red List. In (a) all threatened island endemic species (i.e., those classified as Critically Endangered, Endangered, and Vulnerable) are included. Threatened species endemic to multiple island groups were double counted. Only native ranges (i.e., not introduced ranges) were included, and for seabirds, we only focused on islands used for breeding. In (b), only species classified as Extinct by the IUCN are included (i.e., species that went extinct since 1500 CE). Antarctica was cropped out of both maps to save space (no threatened or extinct species were located on Antarctic islands. A Mollweide projection was used.

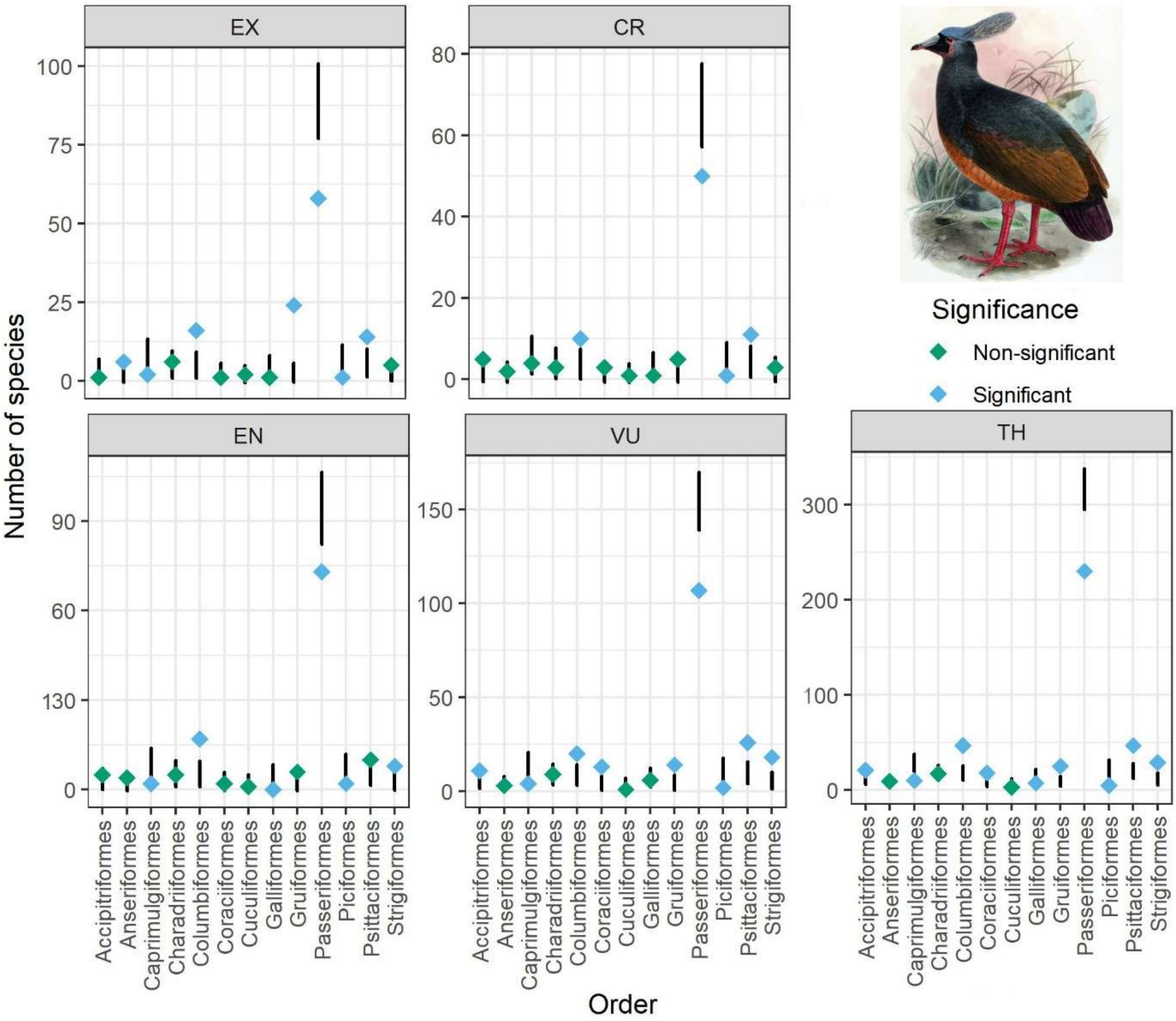

FIGURE 5 Null model results for different bird orders, split by IUCN classification category (see legend of Figure 1). Here, the all-species dataset was used as the species pool. TH represents the number of threatened species classified as CR, EN and VU combined. Only the 13 orders with more than 150 species were used. In each plot, the number of island endemic species with that IUCN classification were randomly sampled from the all-species dataset and the number of sampled species belonging to each of the 13 orders recorded. This process was repeated 9,999 times and the null distributions (black bars) compared with the observed number of island endemic species with that classification in each order (coloured diamonds). Effect sizes were then calculated to determine significance in each case. Note the different y-axis range in each plot. The species inset is a Choiseul crested pigeon (*Microgoura meeki*), an extinct species that was endemic to the Solomon Islands and was driven extinct, likely largely by introduced cats, by the beginning of the 20th century. The picture was drawn by John Gerrard Keulemans and is in the public domain.

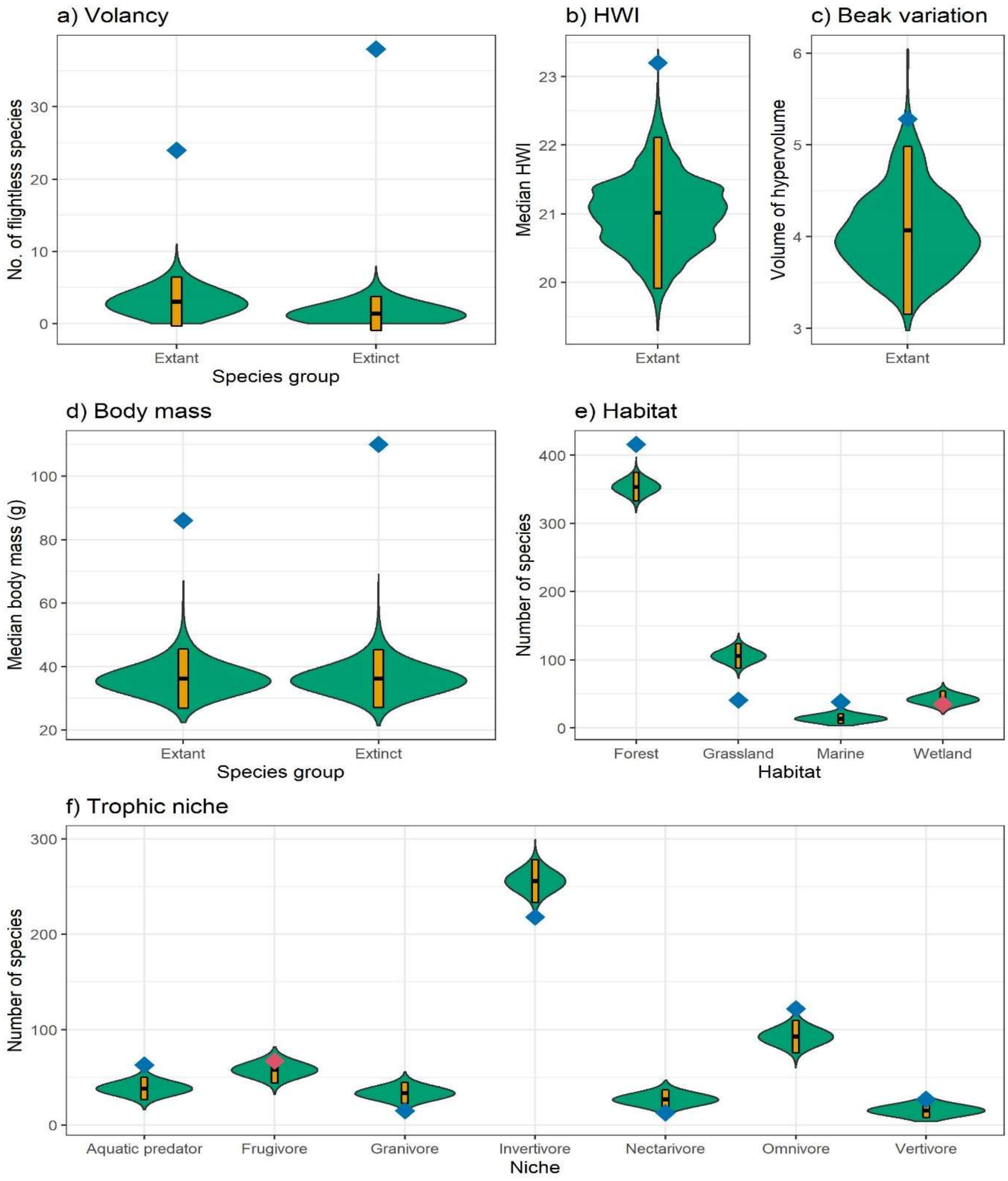

FIGURE 6 Null model results for the six different avian traits. The violin plots show the null distributions based on samples of *n* species from different datasets. In all cases, we randomly sampled the number of threatened island endemics (*n* = 530) from the dataset of all extant species (10,948); in (a) and (d) the number of extinct island endemic species (*n* = 149) sampled from the dataset of all extant and extinct species combined (11,112) was also assessed. Each null model run involved 9,999 iterations, except for (c) where 999 were used. The diamonds show the observed values: blue are significant and red are non-significant cases. The barplots inside the violin plots show the mean of the distribution (black line) and extend to +- 2 standard deviations.

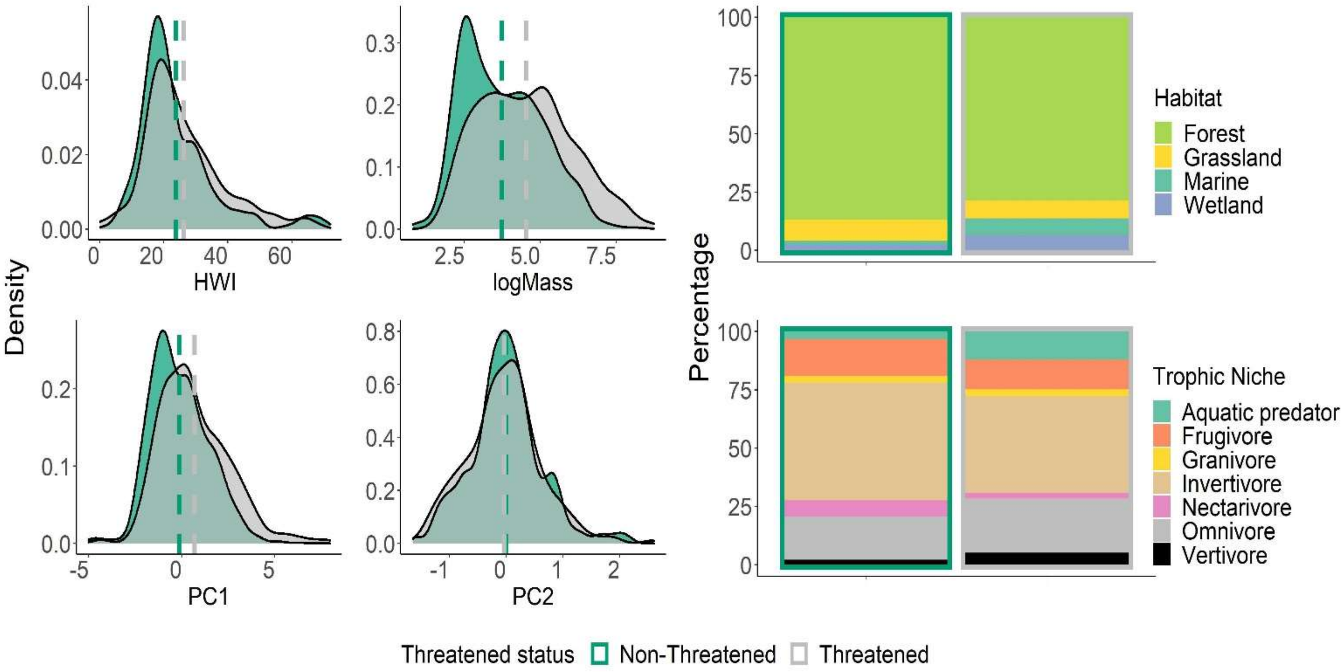

FIGURE 7 Left hand side: density distributions for (clockwise from top left) HWI, body mass (log-transformed), and two measures of beak morphology (PC1 and PC2), split into threatened (n = 530) and non-threatened (n = 1177) island endemic bird species. Dashed lines correspond to the mean of each distribution. The distributions significantly differ (according to Wilcoxon tests) in all but PC2. Right hand side: bar charts show the proportion of each species group represented by different species habitat classifications and trophic niches. Both are significant based on a χ^2 test.

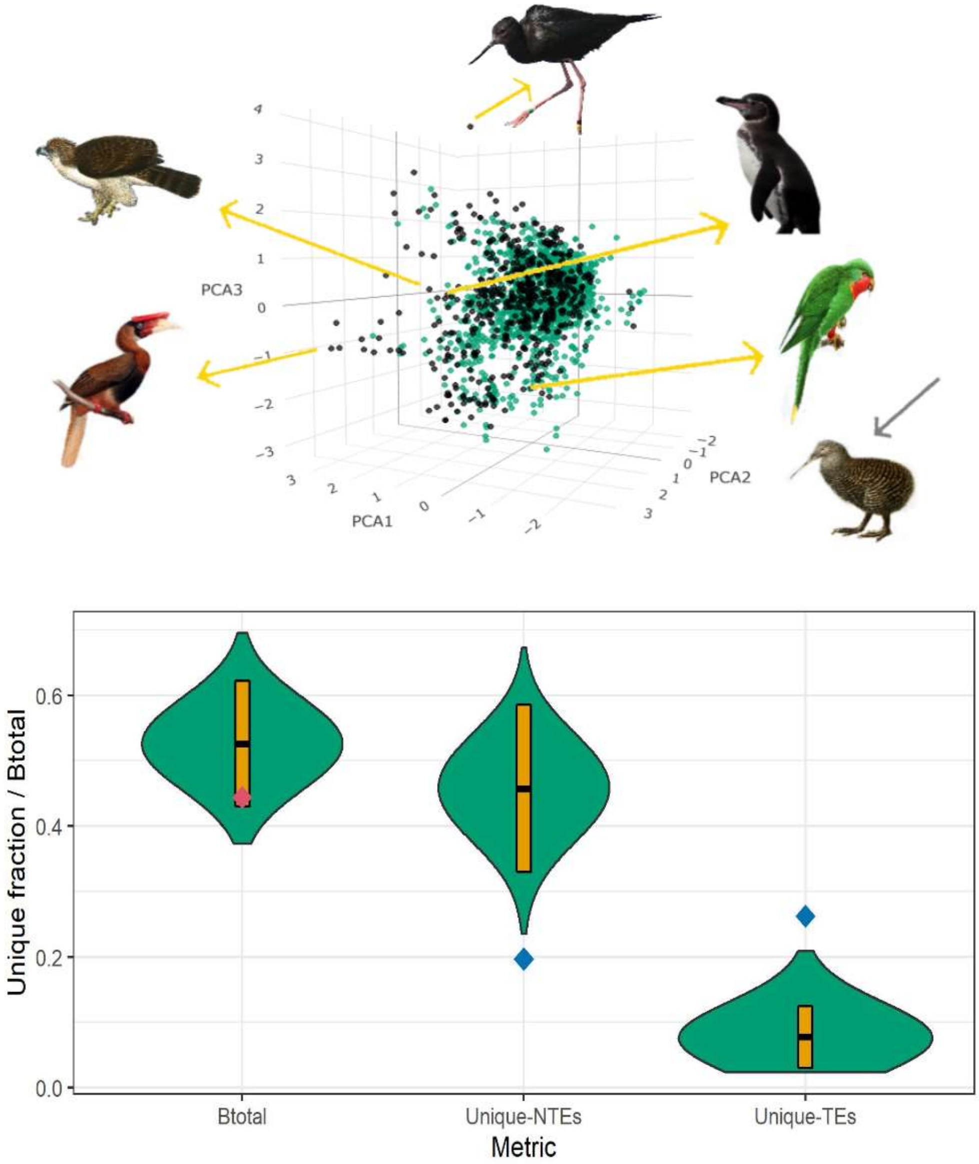

FIGURE 8 Top: functional morphospace of island endemic birds, split by threatened (black dots) and non-threatened (green dots). The yellow arrows highlight specific threatened and relatively functionally distinct island endemic species, from bottom-left in clockwise direction: rufous hornbill (*Buceros hydrocorax mindanensis*; Vulnerable; illustration by Joseph Smit and in the public domain), Philippine eagle (*Pithecophaga jefferyi*; Critically Endangered; image by Henrik Grönvold and in the public domain), black stilt (*Himantopus novaezelandiae*; Critically Endangered; image by Ben-Seabird NZ flickr, under license: https://creativecommons.org/licenses/by-nd/2.0/), Galapagos penguin (*Spheniscus mendiculus*; Endangered; cut from image by Santiago Ron under license: https://creativecommons.org/licenses/by-nd/2.0/), and red-throated lorikeet (*Charmosyna amabilis*; Critically Endangered; illustration by John Gerrard Keulemans and in the public domain). The grey arrow relates to great spotted kiwi (*Apteryx haastii*; Vulnerable; illustration by John Gerrard Keulemans and in the public domain), one of five *Apteryx* (kiwis) species endemic to New Zealand, four of which are threatened, and located in a highly distinct area of morphospace (PCA1 ~ -10, PCA2 ~-9); these species were excluded from the main hypervolume analysis for this reason. Bottom: results of the hypervolume null

modelling comparing threatened island endemics (TEs) with non-threatened island endemics (NTEs). See the main text for details and the legend of Fig. 6 for descriptions of the plot. The two unique components are the unique proportions of the combined hypervolumes represented by each hypervolume individually. The all extant species dataset was used as the species pool.

TABLES

Table 1. An overview of a selection of studies investigating threatened and / or extinct island birds. It is a non-exhaustive summary of studies, with a particular focus on studies undertaken at the global scale and those involving an analysis of functional trait data (bird habitat information classed here as a functional trait).

Study	Geog. scope	Trait data	Main findings
Bellard et al. (2016)	Global	No	60% of post-1500 AD extinctions (majority island endemics) due to alien species.
Blackburn et al. (2004)	Global	No	The probability that a bird species has been lost from each island positively related to number of introduced predatory mammals.
Boyer (2008)	Hawaii	Yes	Prehistoric extinctions involved larger, flightless and ground-nesting species, while historic extinctions involved medium sized species in particular diet niches.
Boyer & Jetz (2014)	Pacific	Yes	Holocene extinctions have substantially affected island avian functional diversity, with some islands supporting five times greater functional diversity prior to arrival of humans.
Carpenter et al. (2020)	New Zealand, Mascarenes and Hawaii	Yes	Prior to human arrival, all seed predation was undertaken by birds, ranging from large, flightless species (e.g., the dodo) to small volant parrots and finches. Many driven extinct by humans, and seed predation now undertaken largely by introduced game birds and mammal species.
Duncan et al. (2002)	New Zealand	Yes	Birds that were hunted to a greater degree by prehistoric humans were more likely to have gone extinct.
Duncan & Blackburn (2007)	NA	No	Link between extinctions and genetic factors, and elevated extinction rates in highly endemic clades and those with large-bodied species.
Duncan et al. (2013)	Pacific	Yes	Flightless, large-bodied and single island endemic species suffered larger extinction rates. Extrapolating, at least 983 non-passerine land birds went extinct after human colonisation of remote Pacific islands.
Fromm & Meiri (2021)	Global	Yes	469 avian extinctions attributable in some way to humans, the majority being island species. Many extinct species found to be flightless, and average body mass of extinct species seven times larger than that of extant species.
Heinen et al. (2017)	Global	Yes	33 islands found to have suffered frugivore extinctions, with large and flightless species having higher extinction probabilities. An average of 34% of the pre-extinction frugivore community lost.
Holdaway (1999)	New Zealand	Yes	Evidence for the extinction of at least 77 breeding bird species on the main New Zealand islands over the last 2000 years.
Hume (2017)	Global	No	Comprehensive compilation of information regarding all human-driven extinct bird species, including many island species.
Johnson & Stattersfield (1990)	Global	Yes	Island endemics are overrepresented in terms of extinctions. Most threatened species are forest birds and, while introduced species were the leading cause of extinctions, the biggest threat was habitat loss.

Leclerc et al. (2018)	Global	No	Cultivation, wildlife exploitation and introduced species reported to be the most significant threats associated with extinct island birds, and to a lesser extent also for threatened birds.
Leclerc et al. (2020b)	Global	Yes	One fifth of island mammal and bird functional diversity supported by threatened species. Cultivation and wildlife exploitation biggest threats for island endemic birds.
Loehle & Eschenback (2012)	Global	No	The majority of mammal and bird extinctions have been on islands, with the extinction being 187 times higher than for continents.
Marino et al. (2022)	Global	Yes	IUCN classified threatened birds represented 29% of total island endemic functional richness, and birds threatened by invasive species (both those classified as threatened and non-threatened) occupied smaller functional spaces than expected given their richness.
Milberg & Tyrberg (1993)	Global	No	Evidence for over 200 prehistoric extinctions, mostly concentrated in particular orders and families (e.g., rails), in addition to evidence of distribution reductions for many extant species.
Pimm et al. (2006)	Global	No	Extinction rates are underestimated due to several reasons. Most human-driven extinctions have been on islands, but future extinctions likely to be continental species.
Richards et al. (2021)	Global	Yes	Threatened seabirds, many of which occur on islands, occupied different areas of trait space to non-threatened species; threatened species were larger, longer-lived and with narrower niche breadths.
Sayol et al. (2020)	Global	Yes	Including extinct species increased total avian richness by 5%, but quadrupled the number of flightless species.
Sayol et al. (2021)	Global	Yes	Introductions have generally not filled the functional gap left by extinct species on islands, and extinctions and introductions have resulted in functional homogenisation across archipelagos.
Şekercioğlu et al. (2004)	Global	Yes	21% of all bird species are threatened with extinction and 6.5% are functionally extinct. Island birds are particularly at risk, but this is due to their small ranges rather than any ‘island effect’.
Soares et al. (2022)	Global	Yes	Although bird species extinctions and introductions combined led to an increase in the average species richness and prevalence of most functional traits per island, the average functional richness and evenness declined.
Spatz et al. (2017)	Global	No	296 highly threatened bird species breed on 1288 islands.
Steadman (2006)	Tropical Pacific	Yes	Overview of extinct birds (primarily land birds) on numerous tropical Pacific islands. Extinctions have impacted biogeographical patterns such as the island species–area relationship.
Steadman & Franklin (2020)	Bahamas	No	Evidence of distributional changes (including extinction) for 69% of species.
Szabo et al. (2012)	Global	No	141 avian species and 138 subspecies gone extinct since 2015; with a majority occurring on oceanic islands. Invasive species the most important extinction driver on oceanic islands, and hunting on continental islands.
Triantis et al. (2022)	Global	Yes	While pre-extinction communities exhibited community convergence, extinctions have strengthened these patterns.

Table 2. The number of native extant and extinct species (pre- and post-1500 CE) from 74 oceanic islands in one of six diet groups. The numbers in parentheses are the proportion across all values in that column (e.g., the proportion of all extinct species that were invertivores). The final column (Prop. Extinct) shows the proportion of total species (extant + extinct) in each diet group that have gone extinct. Data are from Soares et al. (2021). Note that the diet groupings used here differ slightly from those used in our main analyses.

Diet group	Extinct	Extant	Prop. Extinct
Invertivore	56 (0.26)	173 (0.39)	0.24
Carnivore	30 (0.14)	43 (0.10)	0.41
Frugivore	35 (0.16)	69 (0.16)	0.34
Granivore	31 (0.14)	48 (0.11)	0.39
Omnivore	52 (0.24)	101 (0.23)	0.34
Herbivore	10 (0.05)	11 (0.02)	0.48