

## RESEARCH ARTICLE

## Animal Functional Traits

# Bird extinctions threaten to cause disproportionate reductions of functional diversity and uniqueness

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## Abstract

1. Human activities are driving rapid defaunation of Earth's ecosystems through increasing rates of extinction. However, the ecological consequences of species loss remain unclear, in part due to the limited availability of high-resolution functional trait data.
2. To address this, we assess how predicted extinctions will reshape avian functional diversity quantified using a multidimensional trait space, or morphospace, reflecting variation in eight key morphological traits closely linked to ecological function across 9943 (>99%) extant bird species.
3. We show that large regions of this morphospace are represented by very few species and, thus, vulnerable to species loss. We also find evidence that species at highest risk of extinction are both larger and functionally unique in terms of ecological trait dimensions unrelated to size, such as beak shape and wing shape.
4. Although raw patterns suggest a positive relationship between extinction risk and functional uniqueness, this is removed when accounting for phylogeny and body mass, indicating a dominant role for clade-specific factors, including the combination of larger average body size and higher extinction risk in the non-passerine clade.
5. Regardless of how a threat is related to uniqueness, we show using simulations that the loss of currently threatened bird species would result in a greater loss of morphological diversity than expected under random extinctions.
6. Our results suggest that ongoing declines of threatened bird species may drive a disproportionately large loss of morphological diversity, with potentially major consequences for ecosystem functioning.

## KEYWORDS

extinction, functional redundancy, functional traits, hypervolume, morphological diversity, threatened species, trait space, uniqueness

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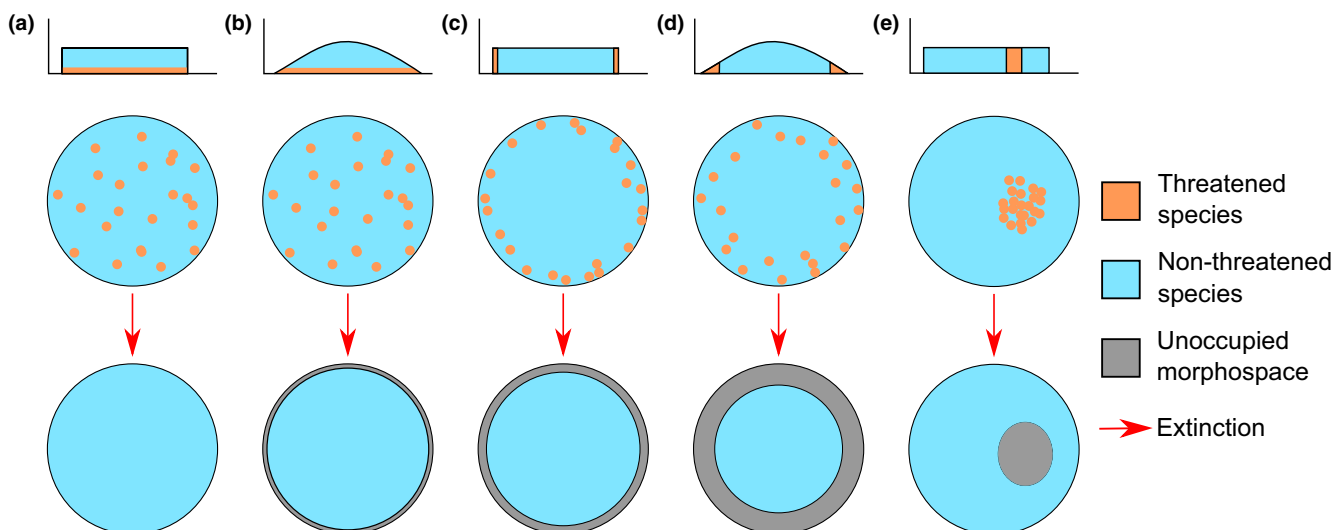
## 1 | INTRODUCTION

Over recent decades, a combination of threats, including habitat loss, invasive species, climate change and pollution, have resulted in a dramatic loss of biodiversity worldwide (Pereira et al., 2012). Current species extinction rates are up to 100 times higher than the background rate (Barnosky et al., 2011; Ceballos et al., 2015) with some estimates suggesting that a million species are threatened with extinction by human activities (Díaz et al., 2019). It is often proposed that such drastic declines in biodiversity may compromise the functioning and stability of the natural ecosystems on which human societies depend (Mace et al., 2012; Newbold et al., 2016; Rockström et al., 2009). However, while it is well established that high levels of biodiversity promote both the productivity and resilience of ecosystems (Hooper et al., 2005; Petchey, 2000), understanding how global species losses will impact ecological function remains a major challenge.

The contribution of species to ecological function is to a large degree determined by their traits. Thus, metrics of functional diversity (FD)—which incorporate both the number of species and the differences between them—may provide a more mechanistic understanding of the ecological impacts of extinction than changes in species richness alone (Cadotte et al., 2011; Carmona et al., 2021). In particular, the loss of functionally unique species—that is, species with distinct functional traits associated with unique functional roles—is expected to have a greater impact on ecosystem function than the loss of species with less distinctive functional traits, which can more easily be replaced by species performing similar functional roles (Violle et al., 2017). These outcomes are most easily quantified

in a morphological trait space, or morphospace, a mathematical representation of multidimensional trait variation where each axis represents values of a particular trait (or combination of traits), and each point represents a species (Mitteroecker & Huttegger, 2009; Thompson, 1917). Within this framework, the consequence of extinction for the loss of FD depends both on species distributions throughout the morphospace and how extinction risk varies with respect to the position of species within this space (Figure 1).

When both species and threat are uniformly distributed across morphospace, extinction is effectively random, resulting in an even “thinning” of morphospace as the density of species declines throughout, but without necessarily causing any loss of FD (Figure 1a). Two scenarios could result in losses of FD occurring more rapidly than under this optimistic scenario (Figure 1b,c). One possibility, is that some areas of morphospace, including the outer boundary, may have low trait redundancy because most species are clustered around central optima (e.g., Díaz et al., 2016) or because other processes cause trait space to be empty. In this case, even random extinction will lead to a decline in FD as the sparsely populated edges of morphospace contract inwards (Walker, 1992) (Figure 1b). Another possibility is that species are uniformly distributed across morphospace, but species losses are non-random so that functionally unique species at the edges of morphospace are more likely to be removed (Figure 1c). These scenarios are not mutually exclusive. A combination of both high functional uniqueness and threat among species at the edge of morphospace will cause FD to decline even more rapidly (Moullot et al., 2013) (Figure 1d). A final possibility is that threat is clustered within morphospace (Figure 1e), in which case extinction may produce an unoccupied internal region or “hole”.



**FIGURE 1** Potential impacts of extinction on functional diversity. Species traits can be plotted in multivariate space using principal component scores to form a multidimensional shape, or morphospace. The top row shows a cross section of morphospace; lower rows show two-dimensional views of morphospace, before (middle) and following (bottom) the extinction of threatened species (orange points). Species extinctions may occur randomly so that morphospace is thinned but remains the same size (a) or undergoes contraction due to low trait redundancy due to low trait redundancy at the periphery (b). Alternatively, extinction can occur non-randomly, preferentially removing species towards the periphery causing larger contractions in morphospace size (c), an effect that can be further exaggerated if trait redundancy is lower at the periphery (d). Numbers of extinctions are equal in (c) and (d), but contraction of morphospace is greater in (d). Finally, if extinction is clustered internally, it can create a ‘hole’ in morphospace (e).

Despite these clear predictions, our understanding of the effect of ongoing and future global species losses on FD has been hampered by the limited availability of high-resolution functional trait data across large numbers of species (Tobias & Pigot, 2019), particularly in animals, where progress in functional trait ecology has lagged behind that of plants (Díaz et al., 2016; Tobias et al., 2022).

One possible solution to limited trait data has been to use phylogenetic diversity (PD) as a surrogate for differences in functional traits (Jetz et al., 2014). However, the strength of the relationship between PD and FD remains debated (Mazel et al., 2018) and PD may be a relatively poor surrogate of ecological function in general (Pigot et al., 2020). The main alternative adopted by numerous studies is to estimate FD using the restricted set of traits typically available at large scales, including body size and coarse categorical data on life history and ecology (e.g., Carmona et al., 2021; Cooke et al., 2019, 2020; Jetz et al., 2014; Oliveira et al., 2020; Pollock et al., 2017; Toussaint et al., 2021). These analyses consistently report that predicted extinctions will reduce avian FD to some degree. However, aggregating species into these simplified categories may vastly underestimate functional variation and overestimate functional redundancy (Kohli & Jarzyna, 2021; Pigot et al., 2020), thus offering only limited insight into the functional consequences of species gains or losses.

To provide a more nuanced perspective on the ecological implications of the current biodiversity crisis, we estimate the impact of bird extinctions on FD. Birds offer a useful study system because they perform a broad array of services that regulate and stabilise ecosystems, including predation, pollination, seed dispersal, and scavenging (Pigot et al., 2020; Şekercioğlu, 2006; Şekercioğlu et al., 2004). Moreover, variation in these roles across species can now be quantified using detailed measurements of ecomorphological traits, including beaks, wings, tails and legs (Tobias et al., 2022). These traits describe important dimensions of ecological diversity, from trophic level (herbivore, omnivore, carnivore, scavenger) and diet (frugivore, nectarivore etc.) to more subtle variation in behavioural foraging strategy (Pigot et al., 2020). In contrast to the kinds of categorical data on ecological function used previously (e.g., Carmona et al., 2021; Cooke et al., 2019, 2020; Oliveira et al., 2020; Toussaint et al., 2021), these continuous traits provide more precise information about the variety of functional roles performed by species. For example, within a given ecological niche category, such as insectivores or frugivores, differences in beak dimensions provide key information on the size and type of prey and fruit items consumed (Bovo et al., 2018; Bregman et al., 2016; McFadden et al., 2022). In theory, extinction could have widely different impacts on FD—and hence the provision of these services—depending on where species losses tend to occur in relation to overall morphological variation (Figure 1).

To understand the potential functional impact of species extinctions, we first describe the distribution of 9943 (>99%) extant bird species in a unified morphospace. We assume that this morphospace represents ecological niche space, with different dimensions defined by axes of variation in functional traits (Blonder, 2018;

Blonder et al., 2014), in accordance with Hutchinson's (1957) view of the niche as an  $n$ -dimensional hypervolume. The size of this global avian hypervolume provides a measure of FD (functional richness) and the variety of ecological functions species perform (Fonseca & Ganade, 2001; Griffin et al., 2009; Hoehn et al., 2008; Petchey & Gaston, 2006; Pigot et al., 2020). The density within the hypervolume captures morphological distinctness or functional uniqueness—species with unique traits, found in sparsely occupied parts of the hypervolume are expected to have lower functional redundancy than species in densely packed regions of the hypervolume. Given the expected importance of non-random patterns of extinction for FD loss, we test the relationship between functional uniqueness and extinction risk, based on species' current threat status from the IUCN Red List.

We then quantify the effects of potential future extinctions on avian FD by calculating the reduction in hypervolume size in response to simulated extinction of currently threatened birds. We compare this projected reduction in FD with the expected loss of FD that would arise if the same number of species were removed at random with respect to extinction risk. Given that body size is a well-established predictor of extinction risk in birds (Gaston & Blackburn, 1995; Jetz & Freckleton, 2015), we repeated our analysis including or removing the effects of body size. This allowed us to identify the effects of additional trait dimensions that are critical in describing the ecological functions provided by birds, and that may also be subject to non-random patterns of FD loss. Through these analyses, we aim to determine whether future extinctions are likely to disproportionately reduce avian FD because they are biased towards the periphery of morphospace or sufficiently clustered to produce holes within the hypervolume (Figure 1).

## 2 | MATERIALS AND METHODS

### 2.1 | Functional traits and morphospace

To compile information on avian morphological traits, we used the AVONET dataset (Tobias et al., 2022). We used the version of the dataset containing mean trait values from Pigot et al. (2020), focusing on eight morphological characters (1) beak length measured from tip to skull along the culmen, (2) beak length measured from the tip to the anterior edge of the nares, (3) beak depth, (4) beak width, (5) tarsus length, (6) wing length from carpal joint to wingtip, (7) secondary length from carpal joint to tip of the outermost secondary and (8) tail length (Table S1). These traits have a well-established association with avian foraging and dietary niches (Lederer, 1975; Miles & Ricklefs, 1984; Pigot et al., 2016) and have been shown to predict trophic niches at global scales (Pigot et al., 2020). We excluded kiwis (*Apteryx*) because they are extreme outliers with some traits that cannot be measured (e.g. wing and tail dimensions). The final sample contained 9943 bird species, representing more than 99% of the world's avian diversity. Traits were measured from an average of 5.3 (1–158; median = 4) individuals per species, including live birds

and museum specimens. For 38 species, traits were inferred from a closely related species—either a sister species or congener—with near-identical morphological traits (see Tobias et al., 2022 for details, including all surrogate species).

Trait values were first log-transformed and scaled to have mean of 0 and standard deviation of 1. A logarithmic scale is appropriate because a given unit change in the log-transformed trait corresponds to a constant proportional increase in size. These morphological traits are strongly correlated, so we performed a principal component analysis (PCA) to identify independent axes of trait variation. However, we also repeated our analyses without log transforming the morphological data to test whether results were sensitive to data transformation (see Tables S2–S5 for variance explained by PCs and the associated PC loadings).

A previous analysis of the same trait dataset that we use (Pigot et al., 2020) showed that at least four PC axes are required to classify major functional dimensions of the avian hypervolume, including trophic level, resource type (e.g., insects or fruit) and acquisition mode (e.g. the behavioural strategy used to obtain food, including aerial foraging, sallying from a perch, or walking on the ground). Therefore, we first use a morphospace defined by PC axes 1–4. As found in previous analyses of similar data (Pigot et al., 2020; Trisos et al., 2014), the dominant axis (PC1) is strongly related to size (Figure S1; Pearson's correlation coefficient with log body mass =  $-0.92$ ). To account for body size effects, we also created a morphospace using PC axes 2–5, which represent dominant axes of shape variation.

## 2.2 | Constructing hypervolumes

To describe the avian hypervolume, we estimated the probability density of the multidimensional trait data using a thresholded kernel density estimate (Blonder, 2016a; Blonder et al., 2014), in line with previous analyses in other taxonomic groups (Echeverría-Londoño et al., 2018; Oliveira et al., 2020). This method places a kernel—a distribution with a specific bandwidth and shape—around each observation, then sums the kernels to produce an estimate of the overall probability density. The bandwidth is used to determine whether the region between points is occupied (when the distance between two points is less than the bandwidth) or unoccupied. Regions with density above a certain threshold value define the shape of the hypervolume, and the size of the resultant hypervolume provides a measure of FD. In this case, points within the hypervolume are species, and the probability density at each point reflects the number of other species with similar trait values, providing a measure of functional uniqueness (Blonder, 2016b)—that is, a low probability density indicates high functional uniqueness.

To assess whether there were empty areas within the morphospace, we compared the observed hypervolume to an estimate of potential FD, defined as the volume of a convex hull enclosing all species' traits (Blonder, 2016a). The convex hull includes all possible interior linear combinations of traits given the observed extreme values and is a baseline expectation for the trait combinations that

could exist within a certain extreme range. This expectation reflects the assumption that, in morphospace, a hypothetical species could feasibly occupy an intermediate position with respect to any two other extant species. If extant species are unevenly distributed in trait space, mainly occupying a relatively small proportion of the convex hull, extinctions in sparsely occupied areas would result in large losses of FD.

For each analysis, we used a Gaussian kernel. The bandwidth (0.168 units) was determined using a Silverman estimator applied to the entire trait dataset (Silverman, 1986). The Silverman estimator minimises the mean integrated square error under the assumption the data are univariate normal, and is calculated as  $1.06 \times sd(X) \times m^{-1/5}$ , where  $X$  is the data and  $m$  is the number of observations. We used this bandwidth for all analyses which ensured that the quantification of morphospace occupancy was consistent across hypervolumes. To assess the size of the avian hypervolume in each analysis, we used the volume of the hypervolume at a quantile value of 1.0, that is, including all of the probability density.

## 2.3 | Extinction risk

We assumed that species classified as Threatened or Near-threatened under IUCN Red List criteria have an elevated risk of extinction. We use Red List classifications (HBW & BirdLife International, 2017) rather than more sophisticated metrics of extinction risk (e.g. Andermann et al., 2021), because our analyses are based on a binary classification and because the available models estimating extinction risk have some methodological drawbacks (see Supplementary material). We categorised species as either non-threatened ( $n = 7745$  species, including 7700 Least Concern [LC] and 45 Data Deficient [DD]) or threatened ( $n = 2198$  species, including 182 Critically Endangered [CR], 408 Endangered [EN], 705 Vulnerable [VU] and 903 Near Threatened [NT]) (HBW & BirdLife International, 2017). Species classified as NT are 'close to qualifying' for threatened status under one or more Red List criteria or 'likely to qualify ... in the near future' (IUCN, 2012). These species still have relatively small or declining populations and/or small geographical range size but do not yet meet the criteria for the CR, EN or VU categories. To assess whether our results were influenced by grouping NT species together with species facing more immediate risk of extinction, we repeated our analysis using an alternative classification with NT species categorised as non-threatened. A factorial combination of these two threat groupings, with analysis of raw and log-transformed traits as well as inclusion/exclusion of PC axis 1 (as described above) resulted in eight different hypervolume configurations (Table S6).

## 2.4 | Effect of functional uniqueness on threat status

We calculated functional uniqueness as the probability density at the location of each species within a hypervolume constructed using

PC axes 2–5. We excluded PC axis 1 for this section of the analysis because it largely reflects variation in body size, a well-established predictor of extinction risk (Carmona et al., 2021; Gaston & Blackburn, 1995; Jetz & Freckleton, 2015; Ripple et al., 2017), whereas we are explicitly interested in functional uniqueness that cannot simply be explained as variation in body size. We examined the relationship between threat status and functional uniqueness using Bayesian binary-response linear mixed models with a probit link. Unless otherwise stated, all the following models are Bayesian linear models implemented in the R package MCMCGLMM (Hadfield, 2010).

To test the hypothesis that functionally unique species are at elevated risk of extinction, we fitted a univariate model of threat status with functional uniqueness as the only predictor. This univariate model could potentially be confounded by two factors. First, species traits are phylogenetically non-independent because closely related species often share similar traits due to shared ancestry. Second, high functional uniqueness may in part be associated with unusually small or large body size, both of which are traits linked to increased extinction risk (Ripple et al., 2017). To address the first issue, we controlled for phylogenetic non-independence by fitting replicate models using the Jetz et al. (2012, 2014) phylogeny, based on the backbone topology of Hackett et al. (2008). To address the second issue, we fitted three additional models to account for the effects of body mass. First, we included log-transformed body mass as a predictor of extinction risk alongside functional uniqueness, in a non-phylogenetic model. Next, we ran a model simultaneously accounting for both body mass and phylogenetic non-independence. Finally, we fitted a model to test for a positive relationship between functional uniqueness and body mass.

In each case, two replicate models were run for 2,000,000 iterations with a burn-in of 200,000 and a thinning interval of 2000. We assessed model convergence using the Gelman-Rubin statistic (Gelman & Rubin, 1992) in the R package CODA (Plummer et al., 2006). We also ensured that model trace plots were stable and showed no trends in parameter estimates (which would indicate failure to converge).

To assess whether specific clades were driving the observed relationship between functional uniqueness and species threat status, we fitted standard generalised linear models of threat status and deleted each taxonomic order in turn (function *glm* in package *STATS*; R Core Team, 2019). If a particular clade of birds was primarily responsible for the relationship between functional uniqueness and threat status, then its exclusion would change this association. The only clade removal that produced a change in the relationship detected between functional uniqueness and species threat status involved passerines (Passeriformes). Based on this finding, we fitted two non-phylogenetic univariate models, one for passerines ( $n = 5941$ ) and another for non-passerine species ( $n = 4002$ ).

We further explored the role of functional uniqueness and body mass in promoting extinction risk at different taxonomic levels by

fitting non-phylogenetic models for all bird orders and for all passerine families (each model: 1,000,000 iterations, 100,000 burn-in, 1000 thinning interval). We restricted analyses to clades in which (i) model trace plots show no trend, and (ii) effect sizes were estimable for both functional uniqueness and mass. For models of clades with only two species, two fixed effects cannot be estimated, therefore these models were excluded.

In all models described above, both body mass and raw probability density values were log-transformed and scaled to have a mean of zero and variance of 1. To aid interpretation, we multiplied the transformed probability density by  $-1$  so that lower values represented low uniqueness (probability density is higher for species with redundant morphology). Rescaling of variables facilitates model convergence. For linear models, we report Bayesian 'p-values' (pMCMC) and the 95% highest posterior density interval (95% HPD).

## 2.5 | Simulating species loss

To assess the likely functional impacts of species loss, we simulated the extinction of threatened bird species from the total pool of extant bird species. Applying the standard method adopted in numerous previous studies (e.g. Baiser et al., 2018; Davies & Yessoufou, 2013; Purvis et al., 2000; Sayol et al., 2021; Vamosi & Wilson, 2008), we constructed one hypervolume for all extant species and then a second hypervolume after simulating the removal of all threatened species. We repeated this process for each of the eight hypervolume configurations described above, testing for the presence of unoccupied regions or holes in each hypervolume. We then compared the decrease in hypervolume size after removal of threatened species to a null distribution generated by removing an equivalent number of randomly selected species, calculating the loss of FD, and then repeating this process 1000 times. If predicted extinctions are random with respect to species traits, we should find no significant difference between the observed decline in FD and the null distribution. Conversely, if the reduction in FD is larger than expected under the null model, this would suggest that threatened species tend to be functionally unique or relatively more common near the edges of morphospace (Figure 1).

To explore the potential consequences for ecosystem function in the context of key ecological processes, we constructed hypervolumes for herbivores ( $N = 2773$ ), omnivores ( $N = 1615$ ), carnivores ( $N = 5535$ ) and scavengers ( $N = 20$ ). Trophic level classifications were obtained from AVONET (Tobias et al., 2022). We then removed threatened species (CR, EN, VU, NT;  $N_{\text{herbivore}} = 656$ ,  $N_{\text{omnivore}} = 318$ ,  $N_{\text{carnivore}} = 1209$  and  $N_{\text{scavenger}} = 15$ ) for each trophic level and compared the size of the hypervolume before and after simulated extinction.

All analyses were performed in R > 3.5.1 (R Core Team, 2019). The R package HYPERVOLUME 2.0.12 (Blonder et al., 2014, 2018) was used to construct hypervolumes and estimate their sizes. Phylograms were plotted with the Interactive Tree of Life (itol.embl.de) (Letunic

& Bork, 2007). Silhouettes used in figures are from PhyloPic ([www.phylopic.org](http://www.phylopic.org)); citations for each image are in the supplementary material.

### 3 | RESULTS

#### 3.1 | The structure of the avian hypervolume

The first five PCs used to describe the avian morphospace account for over 98% of the variance in the original traits (Tables S2 and S3). The first axis (PC1) was highly correlated with body size ( $r = -0.92$ , Figure S1), capturing most of the size-related variance in all measured traits. In our main analyses, we removed PC1 to limit the influence of body size, focusing only on PCs 2–5, which account for 22% of the variance, producing a hypervolume capturing shape variation rather than size differences. Plots of the remaining four PCs show that species cluster by clade, indicating that morphology is phylogenetically conserved and thus the position of species in morphospace is influenced by evolutionary history (Figure 2a).

We found that species density in the avian hypervolume is highest near the centre of morphospace and declines gradually towards the periphery (Figure 2b). In addition, we found that just over a third (38%) of the hypothetically available morphospace (the convex hull) is occupied by extant species (Figure 3, Table S7), indicating that large portions of the avian morphospace are currently unoccupied. This emptiness reflects the concave nature of the occupied region of morphospace, rather than the existence of any discrete internal “holes”.

#### 3.2 | Effect of functional uniqueness on threat status

A univariate Bayesian linear model showed that functional uniqueness is positively associated with extinction risk across all birds (Figure S2a,i, Table S8). This positive relationship confirmed that extinction removes more FD than expected under random species loss because morphologically distinctive (i.e. functionally unique) species are more likely to be threatened than species with more redundant combinations of traits.

The effect of functional uniqueness on species threat status was not significant when we accounted for phylogenetic non-independence and/or body size (Figure S2b–d, Table S8). Despite our measure of functional uniqueness being derived from a hypervolume constructed without the PC axis most correlated with body size (PC1), we found that functional uniqueness increased with body size (pMCMC = 0.001, 95% HPD interval: 0.29–0.33), suggesting that larger species tend to be morphologically unique in attributes other than size. When separate models were fitted for passerines and non-passerines, the relationship between body size and functional uniqueness was positive for passerines and negative for non-passerines (Table S9).

Comparison of univariate models subsetted by the two major clades revealed that the positive relationship between threat status and functional uniqueness does not hold within either passerines or non-passerines, which together make up all birds. In isolation, both clades show a negative effect of functional uniqueness on threat status (Figure S2e,f,i), although non-passerines tend to be both more unique (Figure S3) and more threatened than passerines.

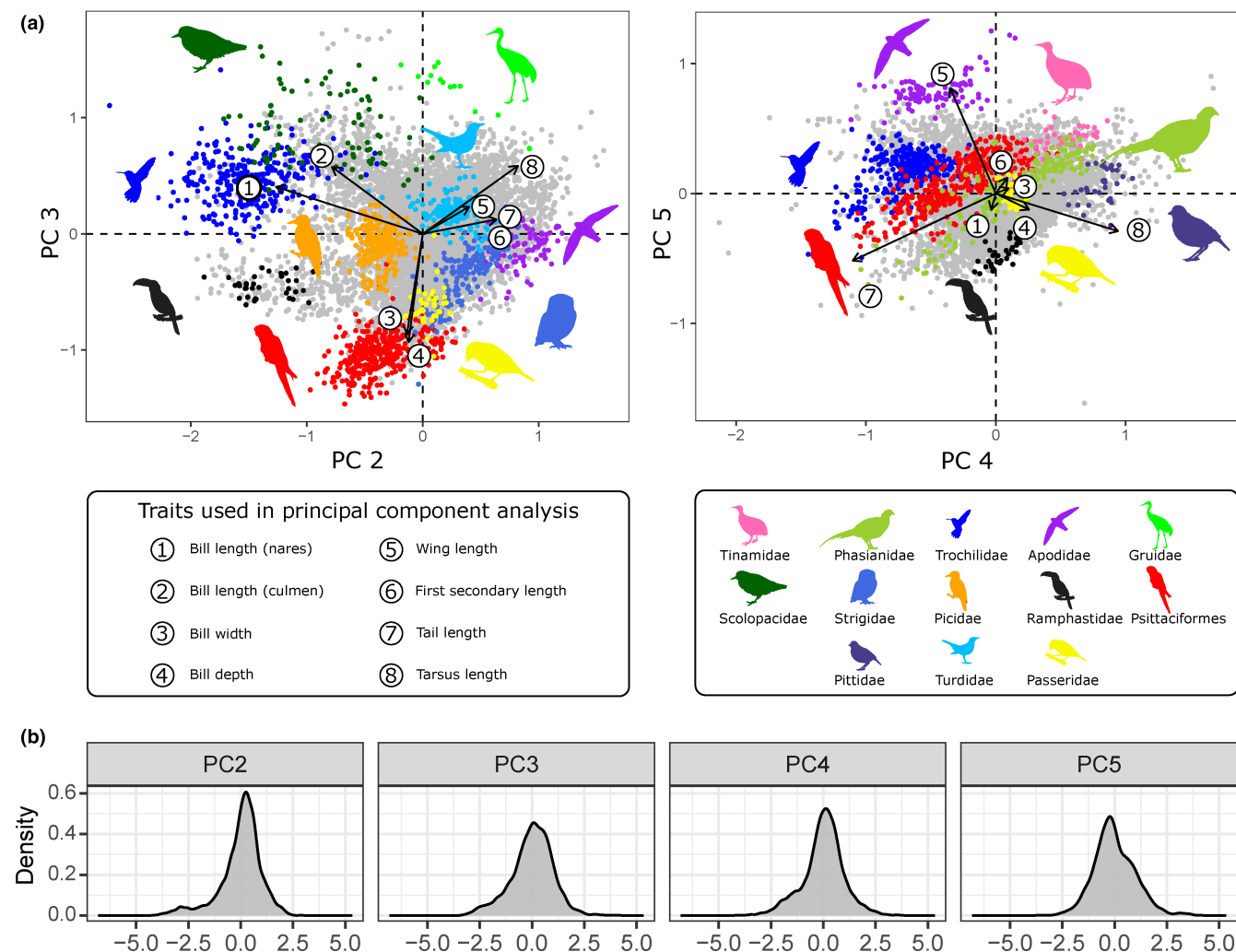
After accounting for body size in separate models for passerines and non-passerines, we again found contrasting results for the two major clades (Figure S2g,h,j, Table S8). Elevated functional uniqueness is associated with decreased extinction risk for passerines (trend, pMCMC = 0.06, 95% HPD:  $-0.14$ – $0.00$ ) but increased risk for non-passerines (pMCMC = 0.02, 95% HPD:  $0.01$ – $0.18$ ). When we further explored our results in the context of different taxonomic groups using multivariate Bayesian linear models, we found that the presence and direction of a significant effect of functional uniqueness on threat status were highly variable across all orders of birds (Figure S4) and among passerine bird families (Figure S5).

#### 3.3 | Consequences of extinction

Under a hypothetical scenario in which all threatened and near-threatened species (22.1% of extant birds,  $n = 2198$ ) became extinct, we found that their loss resulted in a 12.3% reduction in avian FD (Figure 4). This degree of contraction is substantially higher than expected under random species extinction ( $9.1 \pm 0.5\%$ , Figure 4, Table S7; the post-extinction hypervolume was in the lowest 2.5% of the null distribution). Simulated extinction did not create large internal holes in avian morphospace (all internal holes were less than 1% of the occupied morphospace) suggesting that the contraction of FD was caused by a further thinning of species density in peripheral morphospace. Plotting the relative numbers of threatened and near-threatened species across morphospace confirmed that they have a greater tendency to be found near the edges of morphospace than non-threatened species (Figure 5). The results of simulated extinctions were robust to alternative threat status definitions. Results were also qualitatively similar when morphological traits used for PCA were untransformed, suggesting that our findings are not sensitive to log transformation of trait data (Table S7). Simulated extinction within trophic levels also resulted in substantial decreases in FD (Figure 4).

### 4 | DISCUSSION

Our analyses show that functional uniqueness predicts species threat status at a global scale in birds. This relationship is at least partly driven by the tendency of threatened species to be more commonly found in the periphery of avian morphospace than at the core, relative to non-threatened species. Using simulations, we also show that projected future losses of threatened species would result in a greater reduction of morphological diversity than expected under random extinctions.



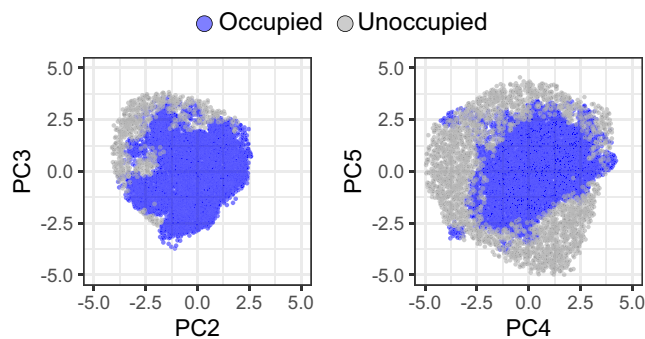
**FIGURE 2** The morphospace of extant birds ( $n = 9943$  species). (a) Principal component loadings of eight morphological traits for principal components 2–5, capturing variation in beak and body shape. Silhouettes indicate 13 clades selected as exemplars; colour-matched data points show the position in morphospace for each species within these clades. Grey points show all other birds. The clustered distribution of related species in morphospace suggests strong phylogenetic signal in trait combinations. (b) Species are clustered near the centre of trait space for all axes of morphospace used in our analyses, indicating that redundancy declines towards the periphery of morphospace.

These findings are consistent with studies showing that species losses are likely to cause disproportionate losses of overall FD estimated from relatively crude categorical traits (Carmona et al., 2021; Toussaint et al., 2021). Our analyses confirm that these effects extend to continuous morphological traits, at least in birds. The implication of this finding is that species extinctions may impair ecosystem function more than expected by chance, particularly because the combination of morphological traits used in our analyses reflect fine-scale variation in important ecological niche dimensions including habitat, lifestyle (Tobias et al., 2022), dispersal (Sheard et al., 2020), diet and behavioural foraging strategy (Pigot et al., 2020).

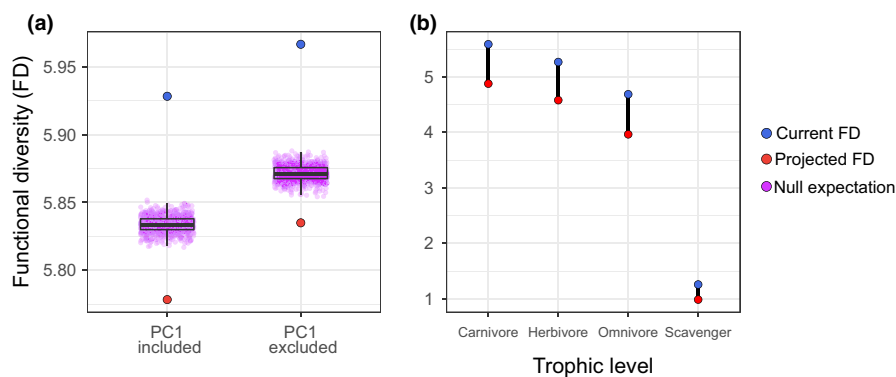
Focusing on the most comprehensive species-level dataset available for any major taxonomic group (Tobias et al., 2022), we show that the avian morphospace has a solid core and sparsely occupied edges, in line with previous analyses (e.g. Pigot et al., 2020) and consistent with a normally distributed multivariate trait space.

Although this type of distribution resembles findings from other taxonomic groups, the avian morphospace tends towards a single central peak in density, whereas some groups are more clearly bimodal (e.g., plants: Díaz et al., 2016) or show multiple peaks (e.g. corals: McWilliam et al., 2018). In addition, we found that much of the hypothetically available morphospace (the convex hull) is not occupied by extant birds, with the gaps perhaps indicating infeasible or inefficient biological strategies (Raup & Michelson, 1965). Alternatively, many possible trait combinations may not be found in extant species because they have yet to evolve or else have been removed by past extinctions (Blonder, 2016a). For example, the extirpation of large flightless species by humans (Duncan et al., 2002) may have created part of the hole we detected, although many such lineages—including moas, elephant birds and dodo—are so distinctive they would almost certainly have extended beyond the outer limits of current morphospace.

The packing of most extant bird species within a small central region of trait space means that the edges of morphospace have decreased functional redundancy relative to the core. Combined with the tendency for threatened species to be found near the sparsely filled edges of morphospace, this clustering of extant bird species makes FD inherently sensitive to impending extinctions. The steep reduction in avian FD that we detect demonstrates a greater vulnerability of FD than anticipated from the loss of species richness alone. This disproportionately high loss of FD is due to the contraction of



**FIGURE 3** Large areas of avian morphospace are unoccupied relative to the convex expectation (all possible interior linear combinations of traits given the observed extreme values). Plots show a slice through four-dimensional avian morphospace ( $n = 9943$  extant species) constructed using principal component (PC) axes 2–5, capturing variation in eight measurements of beak and body shape for 9943 extant species of birds. This version of morphospace with PC1 excluded minimises effects of body size, which is the dominant axis of variation. Points show uniformly random points generated for both the observed hypervolume and convex expectation. Two-dimensional slices through morphospace show points where values lie between  $-0.5$  and  $0.5$  for all PCs except the two focal axes, i.e., the slice is through the middle of the axes. We do this because unoccupied space forms a shell around a core of densely occupied space, masking the underlying patterns.



**FIGURE 4** (a) After extinction of threatened species, functional diversity (FD, measured as the log-transformed hypervolume size [original unit standard deviation to the fourth power]) is lower (red points) than current FD (blue points). Extinction also results in significantly lower FD than the null expectation (boxplots and purple scatterplots). Null distributions were generated by simulating the extinction of 2198 randomly selected species (the same number of species that are currently threatened) and repeating this 1000 times. Results are consistent regardless of whether FD is calculated using the size-related principal component (PC1) and are robust to different threat classifications (Supplementary materials). (b) Substantial decreases in FD are also seen within carnivores, herbivores, omnivores and scavengers, indicating that loss of FD has widespread effects across trophic levels.

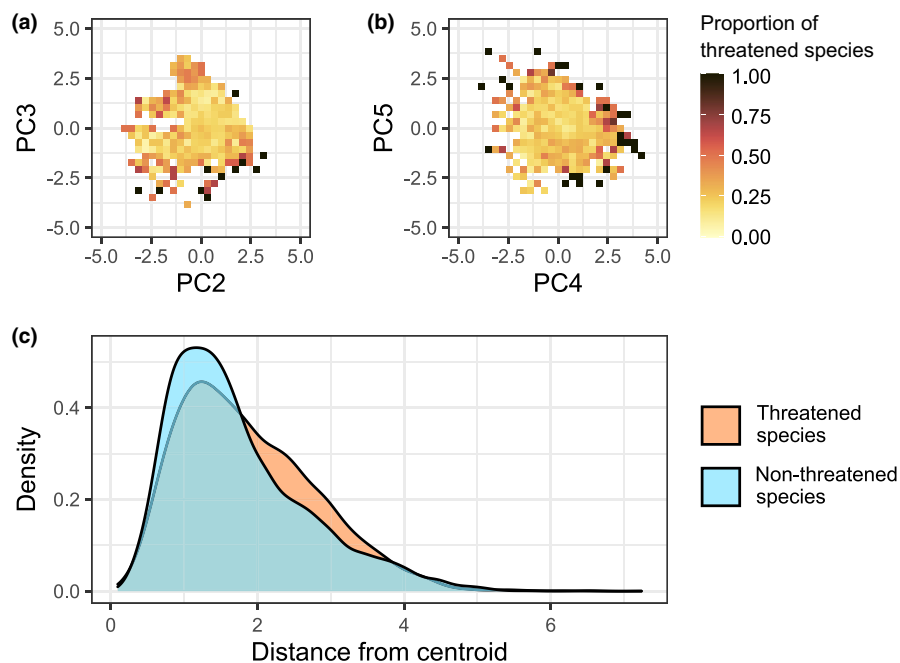
occupied morphospace rather than the creation of internal holes, suggesting that, while the global avian morphospace is highly sensitive to predicted extinctions, the core of this morphospace is much more resilient.

#### 4.1 | Body size effects

One possible explanation for the heightened vulnerability of functionally unique species in our dataset is that animals with extreme body size face a higher risk of extinction (Carmona et al., 2021; Ripple et al., 2017). In general, mass extinctions often target the largest species (Harries & Knorr, 2009; Sallan & Galimberti, 2015), with this so-called “Lilliput Effect” likely to be accentuated in Anthropocene extinction events by factors such as hunting and habitat fragmentation, both of which disfavour species with larger bodies and more extensive area requirements (Estes et al., 2011). Previous analyses have shown that avian body size predicts species threat status (Gaston & Blackburn, 1995; Jetz & Freckleton, 2015) so a relationship between morphological trait uniqueness and extinction risk may not be particularly novel if it is driven by body size effects.

To minimise the impact of body size on our analyses, we calculated functional uniqueness solely from hypervolumes describing variation in shape; that is, we excluded PC1, the only axis of morphospace strongly correlated with body mass. Furthermore, our sensitivity analyses showed that the effect of predicted extinctions on FD was similar regardless of whether we excluded PC1 when quantifying FD, indicating that our results are not primarily explained by the loss of large-bodied species (Figure 4, Table S7). Nonetheless, we found that species with unique shapes are also generally more likely to be larger-bodied, with hummingbirds being a notable exception (Figure S3). This correlation between body size and our size-independent measure of functional uniqueness demonstrates that projected losses of FD are not simply due to a reduction in the range





**FIGURE 5** Distribution of threatened bird species ( $n = 2198$ ) relative to non-threatened species (7745) in a morphospace created from all study species ( $n = 9943$ ). Panels (a) and (b) show that regions far from the centroid of morphospace tend to have more threatened species, whereas non-threatened species are relatively more common near the centroid. Panel (c) shows the density of threatened species and non-threatened species with distance from the centroid. Distance to the centroid is calculated as the Euclidean distance to the mean of the four-dimensional data (PC2, PC3, PC4 and PC5).

of body sizes but also to a narrowing of variation in other important trait dimensions. Thus, our results suggest that future extinctions pose a compound threat for ecosystems because they will drive a contraction in the spectrum of avian body sizes as well as in functional uniqueness of beak and body shapes.

## 4.2 | Effect of functional uniqueness on threat status

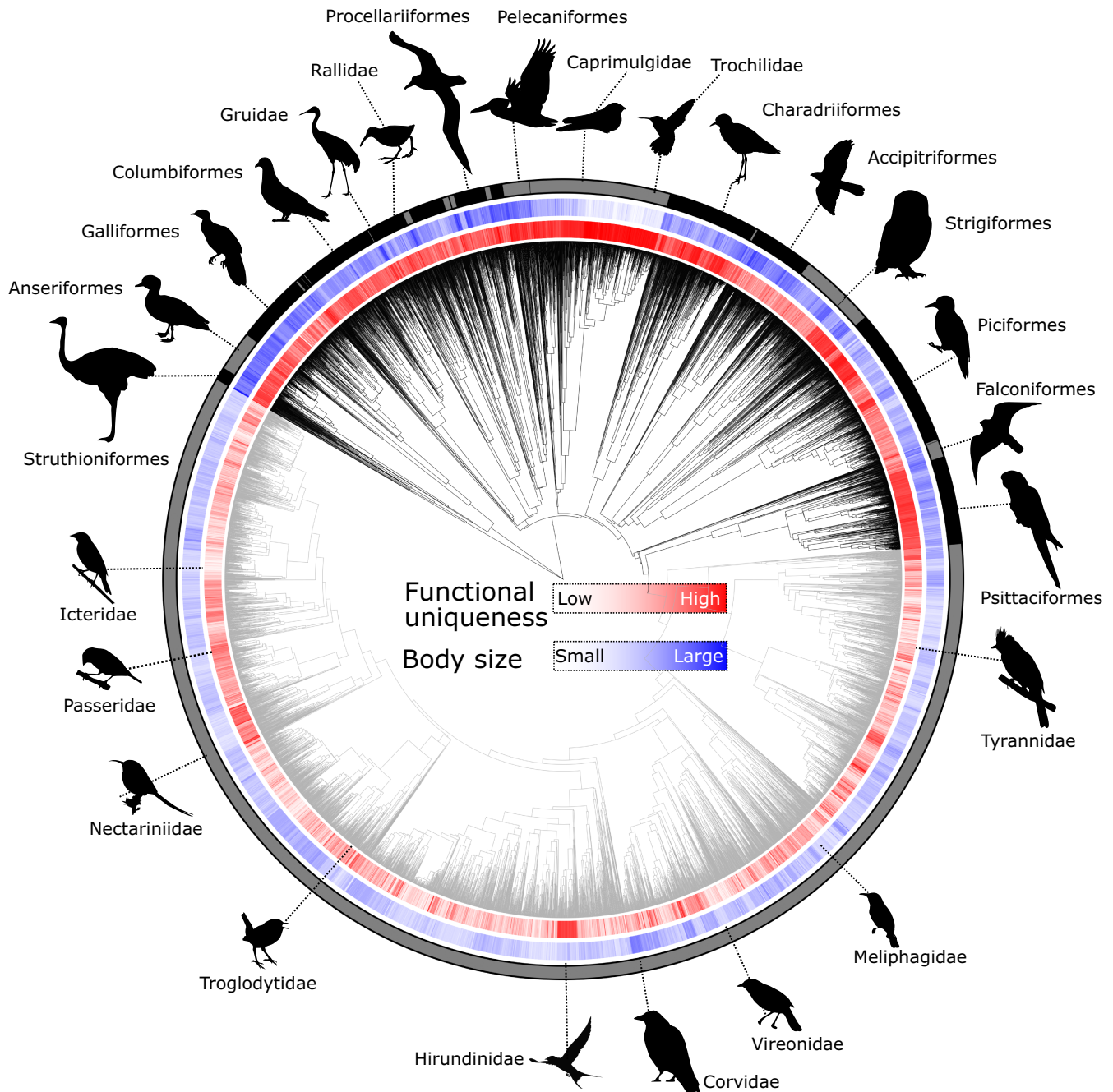
Functional uniqueness positively predicts threat status across all birds. In accordance with this, species with low uniqueness scores are more commonly found in the LC category than in any of the other IUCN threat categories. However, examination of the distribution of functional uniqueness across these threat categories shows that functionally unique species are found in all threat categories (Figure S6). This suggests that while functional uniqueness predicts threat status at a global level, it alone does not predispose species to elevated extinction risk.

The association between functional uniqueness and threat status was not consistent in all our models. First, univariate models revealed a negative relationship between functional uniqueness and threat in both passerines and non-passerines, reversing the positive relationship detected overall. This is an example of Simpson's paradox (Blyth, 1972; Graham et al., 2018) whereby the combination of two subsets of data—in this case, passerines and non-passerines—results in a reversal of the trend seen within the subsets. Taken together, these results suggest that the overall positive relationship between functional uniqueness and threat is driven by major differences between passerines and non-passerines. Second, when mass is taken into account, the relationship between functional uniqueness and extinction risk differs between the two major clades of birds: it is positive in non-passerines, and weakly negative (non-significant) in

passerines (Figure S2g,h,j). This apparent switch in trend implies that those passerines with less distinctive morphology are, on average, more highly threatened. Some of this pattern may be explained by the fact that many threatened passerines are island or montane endemics which are often closely related, and morphologically similar, to non-threatened species.

These contrasting dynamics in passerines and non-passerines may help to explain why the overall relationship between functional uniqueness and species threat status is removed when accounting for phylogenetic relationships and body size. On the one hand, this result suggests that functional uniqueness is only weakly associated with extinction risk at a macroevolutionary scale. On the other hand, it may reflect extensive phylogenetic clustering among different predictors of extinction risk, with high functional uniqueness and high threat status both clustered towards the non-passerine clade, along with large body size (Figure 6). The average size of non-passerine birds (615 g) is substantially larger than the average size of passerines (37 g). Limiting analyses to one clade or the other removes heterogeneity and thus reduces statistical power, while further correcting for phylogeny or body mass may account for several other correlated factors promoting extinction risk.

Despite the inconsistent relationships between functional uniqueness and threat status, the overall association between functional uniqueness and extinction risk is positive at the global level, such that FD declines more rapidly than predicted by random extinction. This link between functional uniqueness and extinction risk may be explained by the effects of ecological specialisation or unusual niches, both of which may reduce population sizes and increase sensitivity of bird species to natural and anthropogenic pressures. A high degree of specialisation to a particular habitat or diet is associated with elevated threat status in birds (Şekercioğlu et al., 2004) presumably because specialised habitats are more easily modified or fragmented, while specialised dietary niches are



**FIGURE 6** The phylogenetic distribution of functional uniqueness across 9943 species of birds worldwide. Non-passerine birds (black branches) tend to be more functionally unique than passerine birds (grey branches) and have larger body sizes. Phylogeny is a time-calibrated tree of 9943 bird species based on a Hackett et al. (2008) backbone and extracted from [www.birdtree.org](http://www.birdtree.org) (Jetz et al., 2012, 2014). Outer ring (alternating black and grey segments) denotes phylogenetic orders. Functional uniqueness is higher in non-passerines than passerines both when including body size and discounting body size effects. These patterns help to explain why our main results appear to be driven by non-passerine birds, which also have higher levels of threat status on average.

liable to disruption through habitat loss and environmental change. Furthermore, specialised organisms with more unique traits will, in theory, be less able to cope with rapidly changing environments than generalist species. Endemic island birds, for example, contribute to the pattern we detect because they are both highly unique in their functional traits and under greater threat of extinction than continental relatives (Matthews et al., 2022).

### 4.3 | Implications for ecosystem functioning

Positive relationships between FD and ecosystem functioning have been shown in a wide range of systems (Cardinale et al., 2012; Díaz & Cabido, 2001; Gagic et al., 2015). Birds are no exception, with diverse avian morphologies reflecting the full spectrum of roles birds play in trophic interactions linked to ecosystem functioning (Pigot

et al., 2020; Tobias et al., 2020). A key implication of this finding is that important attributes of species interaction networks are lost when distinctive species are removed, theoretically reducing the number and variety of seeds dispersed by frugivores (Bovo et al., 2018), and of flowers pollinated by nectarivores (Leimberger et al., 2022). Similarly, removal of distinctive predators may lead to some prey species evading predation, thereby weakening the top-down control of insect or rodent populations (Bregman et al., 2016).

Our finding that the current extinction crisis will target functionally unique bird species suggests that species loss is poised to reduce the breadth of ecological services supplied by birds (Şekercioğlu et al., 2004), potentially impairing the function and resilience of ecosystems. A lower diversity of niche-related traits might reduce the stability and resilience of ecological processes because aggregate systems with a wider spread of characteristics tend to be less volatile than their components—the so-called portfolio effect (Schindler et al., 2015). In ecological systems, part of the reason for this effect is that less distinctive species are more easily replaceable. This might occur, for example, when increases in the geographical range or abundance of organisms with similar traits and trophic niches would compensate for the loss of ecological function—that is, the insurance effect (Yachi & Loreau, 1999). Functionally unique species cannot be replaced so readily, potentially leading to a shortfall in ecosystem function.

It could be argued that our approach exaggerates extinction risk and that many species currently treated as threatened are unlikely to undergo global extinction in the near future. However, many threatened species with surviving populations have nonetheless already become locally extinct over much of their geographical range, or else are becoming so rare as to be considered functionally extinct. Thus, the implications of our results for ecosystem function are relevant regardless of whether predicted extinctions occur or not.

## 5 | CONCLUSIONS

Given that bird morphology datasets are relatively complete, our study provides the most comprehensive assessment of the consequences of anthropogenic extinctions on morphological trait diversity to date. We show that extinctions will most likely prune a large proportion of morphologically and functionally unique species from the avian tree. A similar link between functional uniqueness and extinction risk has been proposed to occur in a range of biological systems, including amphibians, mammals and marine communities (Cooke et al., 2019; McLean et al., 2019; Oliveira et al., 2020; Petchey & Gaston, 2002), as well as in birds, although most direct evidence comes from macroecological studies focused on categorical functional traits (e.g. Carmona et al., 2021; Toussaint et al., 2021). Our analyses build on these findings by showing that extinctions will predominantly remove species with distinctive combinations of morphological traits related to multiple dimensions of ecological and trophic niches (Pigot et al., 2020; Tobias et al., 2020). Such

losses could undermine the functioning and resilience of future ecosystems.

## AUTHORS' CONTRIBUTIONS

Jarome R. Ali, Benjamin W. Blonder and Joseph A. Tobias conceived of the study, Jarome R. Ali and Alex L. Pigot performed data analysis, and all authors contributed to the study design. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data are available via the Figshare Digital Repository of the AVONET database <https://figshare.com/s/b990722d72a26b5bfead> (Tobias et al., 2022).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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