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LETTER

# Global biogeographic patterns of avian morphological diversity

**Emma C. Hughes**[1] | **David P. Edwards**[1] | **Jen A. Bright**[2] | **Elliot J.R. Capp**[1] | **Christopher R. Cooney**[1] | **Zoë K. Varley**[3] | **Gavin H. Thomas**[1,3]

[1]School of Biosciences, University of Sheffield, Sheffield, UK

[2]Department of Biological and Marine Sciences, University of Hull, Hull, UK

[3]Bird Group, Department of Life Sciences, The Natural History Museum, Tring, UK

**Correspondence**
Emma C. Hughes, School of Biosciences, University of Sheffield, Sheffield, UK, S10 2TN.
Email: echughes1@sheffield.ac.uk

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**Abstract**

Understanding the biogeographical patterns, and evolutionary and environmental drivers, underpinning morphological diversity are key for determining its origins and conservation. Using a comprehensive set of continuous morphological traits extracted from museum collections of 8353 bird species, including geometric morphometric beak shape data, we find that avian morphological diversity is unevenly distributed globally, even after controlling for species richness, with exceptionally dense packing of species in hyper-diverse tropical hotspots. At the regional level, these areas also have high morphological variance, with species exhibiting high phenotypic diversity. Evolutionary history likely plays a key role in shaping these patterns, with evolutionarily old species contributing to niche expansion, and young species contributing to niche packing. Taken together, these results imply that the tropics are both 'cradles' and 'museums' of phenotypic diversity.

**KEYWORDS**
avian biodiversity, community structure, morphological diversity, morphological traits, morphospace, niche expansion, niche packing

## INTRODUCTION

Exploring and understanding global patterns of biodiversity is central for determining its origins and conservation. Numerous hypotheses have been posited to explain how biodiversity has accumulated over geographical space and evolutionary time, with particular focus on how species richness varies across major environmental gradients (Currie et al., 1999; Gaston, 2000; MacArthur, 1965; Rohde, 1992). However, species richness-based metrics of diversity consider all species as equal units, ignoring differences among species in their evolutionary history, morphology or ecological roles, and do not adequately explain community structure or the mechanisms underlying species coexistence (Devictor et al., 2010; Faith, 1992; Purvis & Hector, 2000; Safi et al., 2011; Stevens et al., 2003). One approach to combating these shortfalls is to classify species according to their functional roles (e.g. diet, behaviour or life history), allowing investigation into how species are structured within communities, and the potential historical, environmental and ecological drivers leading to spatial variation in community assembly (Belmaker et al., 2012; Safi et al., 2011).

An alternative to classifying species into functional groups based on scoring of functional roles is to use continuous morphological traits to capture ecologically relevant variation (Jones et al., 2009; Kohli & Jarzyna, 2021; McLean et al., 2021; Oliveira et al., 2017; Pigot et al., 2020; Pigot, Trisos, et al., 2016; Wilman et al., 2014). This is beneficial where behavioural observations are lacking or unavailable for rare or cryptic species, across large geographical scales and for whole taxonomic groups. More generally, recent simulation studies have shown that using coarse grained data can be misleading in studies of species community or assemblage structure and recommend the use of high-resolution continuous data where possible (Kohli & Jarzyna, 2021). Such detailed morphological trait data can capture variation among functional categories (Pigot et al., 2020), providing fine-grained resolution that distinguishes multiple morphologies filling a single functional role and avoids the need to assign species to functional categories. The advent of novel, high-quality datasets of morphological traits for entire classes has advanced understanding of how communities fill multidimensional trait space (i.e. morphospace) (Pigot, Trisos, et al., 2016), how morphological form maps to ecological role and/ or function (Anderson et al., 2011; Bright et al., 2016, 2019; Miller et al., 2017; Navalón et al., 2019; Olsen, 2017; Pigot et al., 2020), and how morphological diversity has evolved and is distributed across the phylogeny (Cooney et al., 2017). Nonetheless, with a few exceptions (McLean et al., 2021; Sheard et al., 2020), we lack good understanding of the biogeographical patterns of morphological diversity at a global scale, and thus of the macroecological factors driving trait diversity both within and across species assemblages. In this study, we use continuously measured morphological traits as a high-resolution approximation of the diversity of ecological roles.

Communities vary in terms of their species richness, and this variation may be associated with ecological 'niche packing' and/or 'niche expansion' (Karr & James, 1975; MacArthur, 1965; Pigot, Trisos, et al., 2016). The packing of niche space occurs because of the finer specialisation of phenotypes or increased overlap in resource use, leading to increased density of species in morphospace over a smaller volume (Karr & James, 1975; MacArthur, 1965; Pigot, Trisos, et al., 2016). Alternatively, species may fill an expanded variety of niches and exhibit dissimilar morphologies, revealed by higher volumes and lower densities of species in morphospace (Pigot, Trisos, et al., 2016). Investigating how species fill morphospace in terms of both the volume and density occupied can therefore inform on the species richness of communities.

Variation in communities' morphological diversity results from a combination of evolutionary and environmental factors that have shaped global patterns of biodiversity accumulation (Safi et al., 2011), leading to the prediction that avian morphological diversity will be distributed unevenly across the globe. For instance, in heterogeneous habitats, species are likely to coexist because of greater availability of niches (Guégan et al., 1998; Kerr & Packer, 1997; Kerr et al., 2001; MacArthur & MacArthur, 1961; Rahbek & Graves, 2001), and we therefore predict that assemblages will occupy morphospace at higher density than in homogeneous habitats. Habitats are also expected to vary with altitude (Davies et al., 2007; Kerr & Packer, 1997; Rahbek & Graves, 2001), with mountainous regions forming important dispersal barriers, centres for recent speciation, and exhibiting high species richness (α-diversity) and turnover (β-diversity) across entire montane slopes (Davies et al., 2007; Graham et al., 2009; Jarzyna et al., 2021; Melo et al., 2009; Voskamp et al., 2017). We expect to find high morphological density, with species filling similar areas in trait space, in areas transcending the largest altitudinal ranges (i.e. mid-montane slopes) because of the packing of niche space of closely related species, both before, and after controlling for species richness.

The influence of ecological limits to species coexistence may be reduced in areas of high productivity as resources are plentiful (Mittelbach et al., 2001; Pigot, Tobias, et al., 2016), potentially supporting many species filling similar roles (i.e. niche packing) that are more finely specialised in their morphology. Equally, if resources are limited, communities may show low morphological density, with species needing to occupy wider ecological niches (Safi et al., 2011). Consequently, we predict the greatest morphological density in highly productive areas, and low morphological density where productivity is poor.

Evolutionary factors also influence the temporal accumulation of biodiversity. Over time, the divergence of species and their traits will shape the accumulation of phenotypic diversity in communities. Species that represent older, more isolated branches – that is, those with higher evolutionary distinctness (Jetz et al., 2014; Redding & Mooers, 2006; Vane-Wright et al., 1991) – may possess phenotypic traits that are unique and so fill otherwise unoccupied areas of trait space (Jetz et al., 2014; Redding et al., 2010). We predict that assemblages with high sums of evolutionary distinctiveness, and therefore representing more total evolutionary history, will have greater phenotypic diversity. These assemblages should contain species that are spread out in morphospace, leading to higher morphological volumes and lower morphological densities.

Here, we focus on testing these predictions in birds, which exhibit a huge diversity of phenotypes (Cooney et al., 2017; Pigot et al., 2020; Tobias et al., 2020), worldwide distribution across all terrestrial land-masses (Orme et al., 2005), and high-quality phylogenetic and trait data (Cooney et al., 2017; Jetz et al., 2012; Wilman et al., 2014). We use ecologically relevant morphological traits to: (1) map global patterns of avian morphological diversity; (2) identify areas with exceptional levels of morphological diversity; and (3) test the environmental and evolutionary drivers of global avian morphological diversity.

## MATERIALS AND METHODS

All data compilation, analysis and visualisation were conducted in RStudio version 1.3.959 (RStudio Team, 2020) and R version 4.0.2 (R Core Team, 2020). We follow the taxonomy used in the BirdTree phylogeny http://birdtree.org/ (Jetz et al., 2012).

## Morphological trait data

We compiled a dataset of continuous morphological traits that are linked to the ecological niches of birds in a community (Pigot, Trisos, et al., 2016; Sheard et al., 2020).

### Trait compilation

Using a 3D landmark-based beak shape dataset, we extracted coordinates for the bill shape for 8353 species of bird, across 189 (of 194) bird families. 3D scanning, post processing and landmarking were performed using protocols described in Chira et al. (2018) and Cooney et al. (2017). In summary, we took 3D scans of the beaks of museum study skins, using white and blue structured light scanning (*FlexScan3D*). For some families (e.g. nightjars [Caprimulgidae]), many species could not be scanned as they had feathers and/or bristles obscuring parts of the beak, and are therefore underrepresented in our dataset (Figure S1). From these scans, we used landmark-based geometric morphometric analysis to measure bill shape and ran a principal component analysis (PCA) to produce a morphospace capturing the major axes of bill shape variation (see Supplementary Material S1a for further information).

We extracted the first seven axes from the PCA, which accounted for 98.9% of the overall variation in bill shape (Figure S2, Table S1). We calculated centroid size as a measure of bill size for each species in our dataset. For each specimen scanned, we took measurements of wing and tarsus length (mm). Where possible, if these measurements were not taken (e.g. broken tarsus or sewn wings), another specimen or a mean score calculated from multiple specimens was used. Body mass (g) for each species was taken from the EltonTraits database (Wilman et al., 2014). We include centroid size as well as body size because there is substantial variation in beak size that cannot be explained by allometry alone (e.g. raptors, Bright et al., 2016).

### Avian morphological trait space

Next, we constructed a raw morphological trait dataset containing the seven main axes of beak shape variation, and combined them with $\log_{10}$-transformed measurements of body mass, centroid size, wing and tarsus length. Trait data were centred and re-scaled by standardising each to zero mean and unit variance (z-transformation). Finally, we ran a second PCA on this combined dataset and selected the first eight PC axes from the resultant morphospace which represented 96.1% of the variation in traits (Figure 1; Table S1).

## Spatial data

Global distribution maps for all extant and probably extant bird species were obtained from BirdLife International (http://www.birdlife.org/datazone/home). Species breeding and resident range maps were included where these species were classified as native or re-introduced. Whilst these maps may be less accurate and do not incorporate abundance data as more focused surveys, they allow for a much broader scope, and analysis in regions where survey data are not available or sufficiently plentiful. As a result of taxonomic differences, we first matched species names used by BirdLife to the BirdTree phylogeny http://birdtree.org/ (Jetz et al., 2012), and range maps were projected onto a 100 km x 100 km equal area grid under a Behrmann cylindrical equal-area projection (see Supplementary Material S1b for further detail). Species presence or absence in each terrestrial grid cell was recorded. Our final dataset comprised 8353/9993 (83.6%) species, distributed across 15980 assemblages. For each assemblage, species lists and species richness were obtained. Global maps and phylogenetic plots of omitted species can be found in Figures S1 and S3.

## Morphological disparity metrics

Numerous disparity metrics have been proposed to assess how species occupy multidimensional trait space. Using single metrics to quantify multidimensional space occupancy limits the ecological inferences that can be made (Guillerme et al., 2020; Villéger et al., 2008). Therefore, we aimed to select one metric that accurately captured changes in morphospace volume and another that captured changes in density (i.e. how species fill trait space).

To quantify and understand the potential for different metrics to capture such changes in volume and density, we used the function *test.metric* in the R package *dispRity* (version 1.5.0: Guillerme, 2018), following protocols described by Guillerme et al. (2020). Based on simulations of species gains and loss, we selected the metrics (i) sum of variance (Foote, 1992), and (ii) mean distance to nearest neighbour (i.e. the mean Euclidean distance between a species and its nearest neighbour: Foote, 1992). The sum of variance is commonly used as a measure of volume, but it may also capture certain aspects of density (Guillerme et al., 2020) (e.g. a high number of species close to the mean trait value will reduce the sum of variance). Therefore, we define the sum of variance as a measure that captures the spread, or variance, of species in trait space (morphological variance). We decided against using a commonly used, alternative measure of volume, the sum of ranges (Foote, 1992), as it is more sensitive to

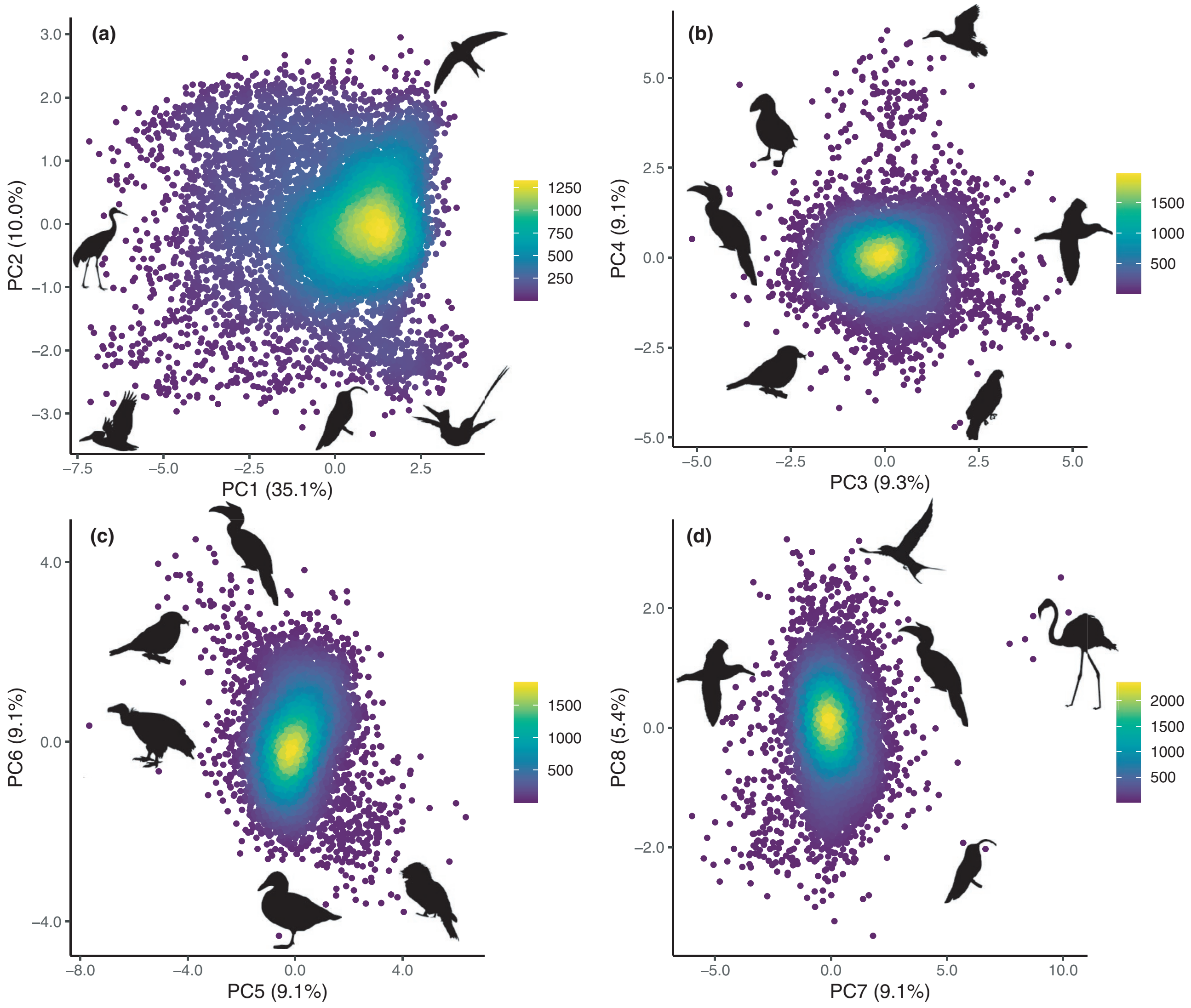

**FIGURE 1** Scatterplots showing the first eight principal components of morphological traits, and the proportion of variance represented by each. The scale bar shows the number of neighbouring points within one standard deviation of the Euclidean distance of each species to all other species across both axes for each scatterplot. Points were coloured with yellow being where species are most numerous, and purple least numerous. PC1 is dominated by size metrics, with high values corresponding to small body mass, tarsus, wing and bill (centroid) size, and the largest species falling at negative values. PC2 captures the main variation of beak shape, going from long, pointy bills at the negative end of the spectrum, to wide, short bills at the positive end. The remaining PCs capture more nuanced variation in beak shape (Figure S2). All silhouettes are in the public domain, and were downloaded from PhyloPic.org.

outliers (Guillerme et al., 2020). The mean distance to nearest neighbour quantifies the density of species packing in morphospace (morphological density). Both metrics were calculated for each unique assemblage using the *dispRity* R package (version 1.5.0: Guillerme, 2018).

## Assemblage evolutionary distinctiveness

We downloaded 100 complete species-level phylogenetic trees based on the Hackett backbone (Hackett et al., 2008) from http://birdtree.org/ (Jetz et al., 2012). For each tree, we calculated an evolutionary distinctiveness score for each species in the phylogeny ($n$ = 9993), using the 'equal splits' derivation (Redding & Mooers, 2006) in the *evol.distinct* function in the R package *picante* (version 1.8.2: Kembel et al., 2010). 'Equal splits' divides each branch length by the daughter species it represents, giving a value for each species of the amount of evolutionary time each embodies. For each community, evolutionary distinctiveness scores for all species present were summed. This was done for each of the 100 trees, and a mean value was taken giving an 'assemblage evolutionary distinctiveness' score for each community.

## Null models

To test whether the morphological variance, density and assemblage evolutionary distinctiveness of each assemblage deviated from expected given the observed species richness, we constructed null models based on two different species pools. Firstly, we used a global species pool where any species from the entire dataset could be drawn. Secondly, we used a species pool where draws were restricted to phylogenetically distinct regional pools in order to avoid sampling from largely historically independent assemblages (Figure S4). To do this, we followed the protocol outlined by Holt et al. (2013) and defined 13 unique phylogenetic regions that have distinct evolutionary histories (Section S1c). Null models for each grid cell were calculated using both species pools, enabling us to capture regional effects under a global species pool, and more local effects when using a phyloregional species pool.

For each unique species richness value, 1000 null communities were generated and morphological variance and density were calculated. For each of the 100 sets of evolutionary distinctiveness scores, 1000 null communities were generated, and assemblage evolutionary distinctiveness was calculated. To assess the difference between the observed (variance, density, assemblage evolutionary distinctiveness) and simulated (null) biodiversity values, we calculated the standardised effect size (SES) for each assemblage: A positive SES value indicates a higher biodiversity value than expected based on null simulations, while a negative SES indicates a lower value. Exceptional values of morphological variance, density and assemblage evolutionary distinctiveness were those that showed statistically significant deviation from expected (+/− 2).

## Environmental correlates

For each grid cell, we extracted environmental variables that we predicted are associated with geographical variation in morphological diversity: main habitat type (Buchhorn et al., 2020), the number of unique habitats (Shannon's index) (Buchhorn et al., 2020), altitudinal range (Fick & Hijmans, 2017) and gross primary productivity (GPP) (Zhang et al., 2017) (see Section S1d for full details).

## Predicting patterns of morphological diversity

We fitted generalised least squares (GLS) models using the function *gls* in the R package *nlme* (version 3.1–149: Pinheiro et al., 2020) with either morphological variance$_{\mathrm{SES}}$ or morphological density$_{\mathrm{SES}}$ (calculated using both global and phyloregional species pools) as response variables. Species richness, assemblage evolutionary distinctiveness$_{\mathrm{SES}}$, GPP, habitat heterogeneity, altitudinal range and habitat type were included in the full model as predictor variables, with additional models fitted where the categorical variable habitat type was dropped or included alone (Table S2).

We log$_{10}$-transformed the variables species richness, GPP, habitat heterogeneity and altitudinal range. To allow for non-linear relationships between our response and predictor variables, we included both linear and quadratic terms of the numeric predictor variables in our models. To account for spatial autocorrelation, all models were fitted with either exponential, gaussian or spherical correlation structures, using spatial information from longitudinal and latitudinal cell centroid values. We used Akaike Information Criterion scores (AIC) to select the best-fitting models for each dependent variable, with the models with the lowest AIC scores considered to be most well-supported (Table S2). Due to computational limits, the 15,277 terrestrial grid cells were split into 25% subsets using a chequerboard approach, where every fourth terrestrial grid cell was included (e.g. set A: 1,5,9… etc.). All models were run on each of the four subsets (Table S2).

# RESULTS

## Avian morphospace

Variation in avian morphological traits is distributed such that the majority of species occupy a dense core in the centre, with more extreme forms found towards the edges of morphospace (Figure 1; Figure S2) (Chira et al., 2018; Pigot et al., 2020). When considering all morphological traits together, 96% of the variation is captured by 8 PCs (Figure 1). PC1 (35% variation) is dominated by size metrics, describing the spectrum from the largest (e.g. cranes [Gruidae]) to smallest (e.g. hummingbirds [Trochilidae]) species.

The major axis of beak shape primarily loads onto the second PC of morphological trait variation, with long pointed bills (e.g. sword-billed hummingbird [*Ensifera ensifera*]) to short, wide beaks (e.g. swifts [Apodidae]). Certain groups of species occupy distinct areas of morphospace that are only apparent on PC axes that themselves account for low total variation, such as waterfowl (Anseriformes) on PCs 5 and 6, and flamingos (Phoenicopteriformes) on PC7 and PC8.

## Global distributions of morphological diversity

Avian morphological diversity is unevenly distributed globally (Figure 2). New Zealand, Patagonia and the Atacama Desert contain assemblages with high values of morphological variance, where species occupy large areas of trait space. Low values of morphological variance are found along the species-rich mountain ranges of the Himalayas and Andes, and the species-impoverished Sahara and Arabian Peninsula (Figure 2a). Areas around the Sahara and Arctic contain communities where nearest neighbour

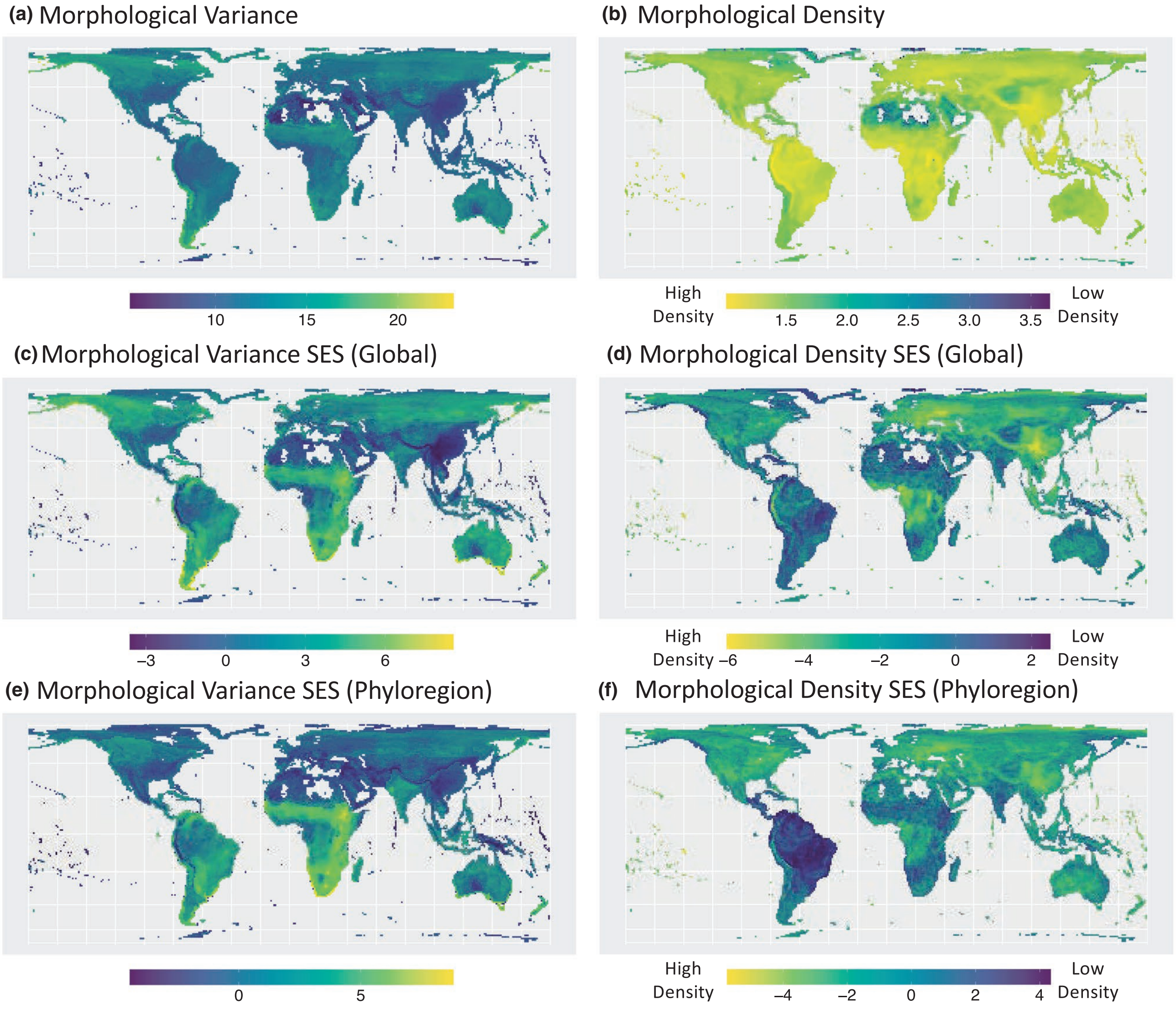

**FIGURE 2** (a) Morphological variance (sum of variances) and (b) morphological density (mean nearest neighbour distance) for 8352 bird species across 15980 terrestrial 1 degree grid cells under Behrmann projection. Standard effect sizes (SES) for each variable were calculated from global (c,d) and phyloregional (e,f) species pools.

distance is high, suggesting low morphospace density. Assemblages containing species that are particularly clustered in morphospace (high morphospace density) are found along the Andean and Himalayan mountains, African rift valley and some oceanic islands (Figure 2b).

Communities with the highest assemblage evolutionary distinctiveness are found in the Neotropics, particularly along the Andes and Amazonian basin, African Rift Valley and Himalayas. Low assemblage evolutionary distinctiveness occurs across the Saharo-Arabian belt, polar regions and island archipelagos (Figure S5b). Overall, spatial patterns of the raw metrics suggest a relationship with species richness (Figure 3; Figures S5a and S6) with, for example, the lowest morphological densities occurring in areas of low species richness (Figure 2b) and the highest assemblage evolutionary distinctiveness communities being those with high species richness (Figure S5b).

## Geographic distribution of exceptional morphological diversity

Observed morphological variance tends to be greater than expected (Figure 3a) for both global, and to a lesser extent for phyloregional pools (Figure S7). These deviations from expectation show strong spatial patterns. We find higher than expected morphological variance along the South American and South Australian coastlines, and in East and South Africa, when using both global and phyloregional pools, highlighting wider assemblage niche breadths (Figure 2c,e). Differences between the species pools arise in the mountains of New Guinea, where

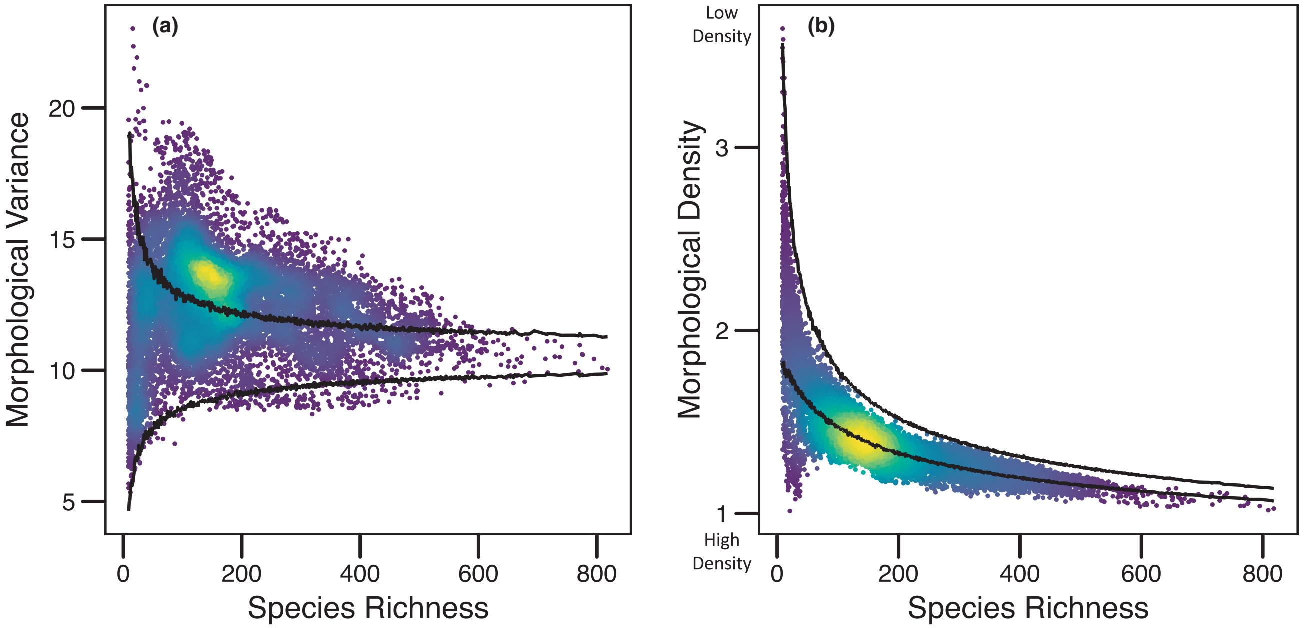

**FIGURE 3** Scatter plots showing the relationship between species richness and (a) morphological variance (sum of variances), and (b) morphological density (mean nearest neighbour distance). Points are coloured according to the number of neighbouring points present to highlight where species are most numerous, with yellow the most and purple the least numerous. The lines show the upper (97.5) and lower (2.5) quantiles calculated across null communities drawn from a global species pool for each value of species richness.

morphological variance is much lower than expected using a phyloregional pool, but not a global pool (Figure 2c,e).

Morphological density tends to be greater than expected under a global pool (Figure 3b), but similar to expected when using phyloregional pools (Figure S8). Spatially, we find that for both global and phyloregional species pools, the Andes harbour morphologically dense communities, with species that are more clustered in trait space than expected given species richness (Figure 2d,f). Under a global pool, species occupy morphospace less densely than expected across small areas of the South American lowland tropics, with this pattern extending over greater areas under a phyloregional pool (Figure 2d,f).

We find slightly lower than expected values of assemblage evolutionary distinctiveness for both global and phyloregional null models (Figures S5c,d, S6 and S9). Under a global species pool, assemblages in the tropics and Southern Hemisphere are more evolutionarily distinct than expected based on null simulations, with hotspots in Madagascar, Borneo, tropical central Africa, etc. (Figure S5c). The Andes contain much lower assemblage evolutionary distinctiveness than expected, with younger lineages and/or close relatives dominating (Figure S5c). Patterns are similar under phyloregional pools, but with Australasian assemblages showing expected, rather than greater, assemblage evolutionary distinctiveness (Figure S5d).

We identified areas with combinations of exceptional (+/− 2 s.d) morphological variance, morphological density or assemblage evolutionary distinctiveness. Using global species pools, we find dense packing of species and expected (or lower than expected) variance in SE Asia, tropical West and Central Africa, as well as along the highest terrestrial mountain ranges, the Andes and Himalayas, showing that high richness areas are prone to niche packing (Figure 4a). The Northern Hemisphere is characterised by expected assemblage evolutionary distinctiveness, with species filling expected or high volumes of morphospace, whilst having close neighbours present (Figure S10a,c). Under a phyloregional pool, the Central Highlands of New Guinea are one of few areas in tropical regions with lower morphological variance than expected (Figure 4b), with the western part of the range showing greater assemblage evolutionary distinctiveness than expected, highlighting it as an area with older lineages that are filling similar niches (Figure S10b,d). Oceanic islands tend to hold assemblages with species clustered in smaller volumes of trait space than expected, with many (i.e Galapagos etc.) also containing species representing greater than expected evolutionary distinctiveness (Figure S10b,d).

## Environmental and evolutionary drivers of morphological diversity

Morphological variance$_{\mathrm{SES}}$ (MV$_{\mathrm{SES}}$) is associated with species richness, assemblage evolutionary distinctiveness$_{\mathrm{SES}}$ and altitudinal range, but not with gross primary productivity (GPP), habitat heterogeneity and habitat type (Table S2). Global-pool MV$_{\mathrm{SES}}$ increases strongly before plateauing and subsequently declining with increasing species richness ($p < 0.001$: Figure 5a; Table S3), suggesting a pattern of morphospace expansion followed by packing at high species richness. MV$_{\mathrm{SES}}$ increases

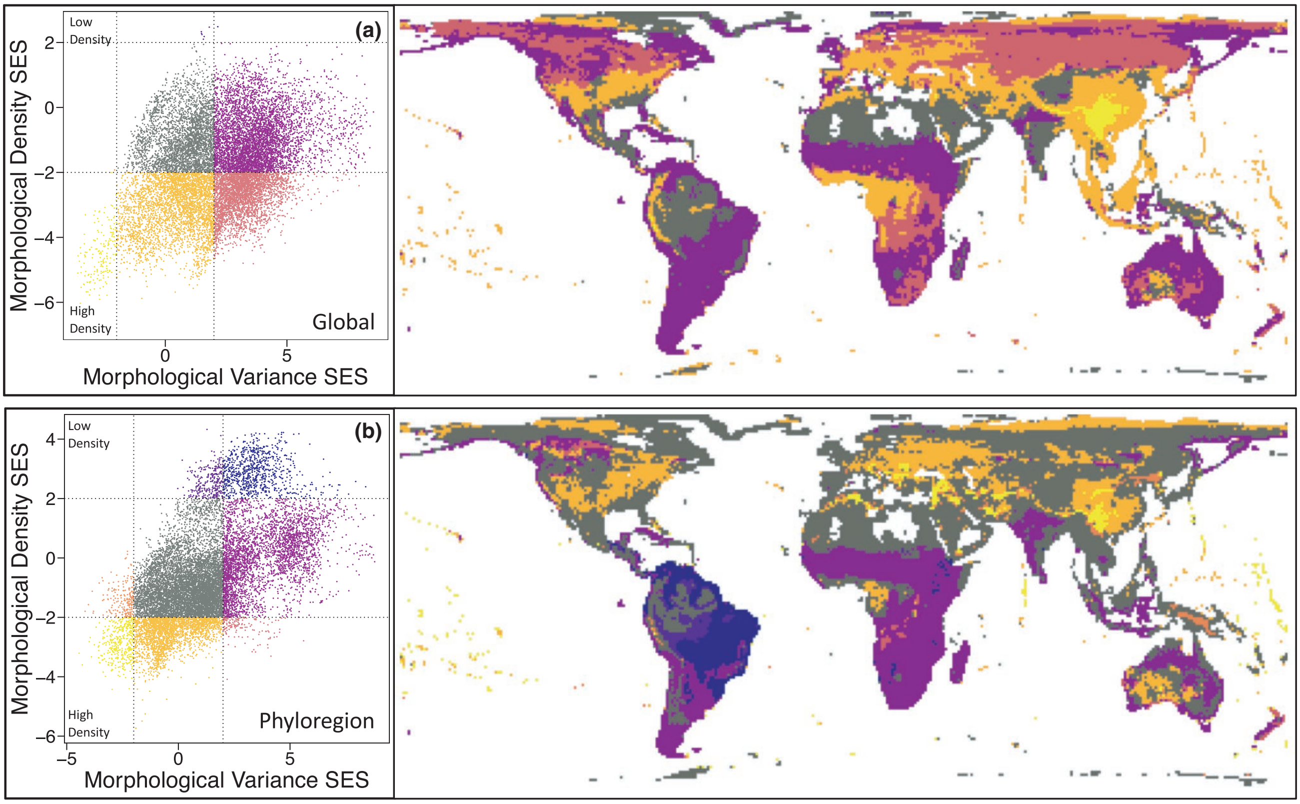

**FIGURE 4** Areas of the globe where the standard effect sizes (SES) of different biodiversity metrics (morphological variance [sum of variances] and morphological density [mean nearest neighbour distance]) show statistically significant deviation from expected (+/− 2) for 8352 bird species across 15,980 terrestrial 1 degree grid cells under Behrmann projection. Combinations of variables are (a) morphological variance$_{SES}$ and morphological density$_{SES}$ where SES was calculated using global species pools, and (b) using phyloregional species pools. The grey colour shows no significant deviation from expected.

linearly with increasing evolutionary distinctiveness$_{SES}$ with the linear term ($p < 0.001$) and not the quadratic term ($p > 0.05$) significant (Figure 5b; Table S3). MV$_{SES}$ initially increases with altitudinal range from low (e.g. lowland plains, upland plateaus) to mid-elevational ranges before decreasing to lower levels where elevational range is greatest (e.g. montane slopes) ($p < 0.001$: Figure 5e; Table S3). We find no association between MV$_{SES}$ and GPP, and an almost flat relationship with habitat heterogeneity for just one subsample of our data (dataset D) ($p < 0.01$ (linear term only): Figure 5d; Table S3). Overall, we find broadly similar results when calculating phyloregional-pool MV$_{SES}$ (Figure 5f–j; Table S3).

Morphological density$_{SES}$ (MD$_{SES}$) is also associated with species richness, assemblage evolutionary distinctiveness$_{SES}$, altitudinal range and GPP, but not habitat heterogeneity or habitat type (Table S2). We find an initially flat relationship between global-pool MD$_{SES}$ and species richness, before distances between species sharply decrease as species richness increases ($p < 0.001$: Figure 5k; Table S3). Overall, we find a positive relationship between MD$_{SES}$ and assemblage evolutionary distinctiveness$_{SES}$, with species most spread out in trait space where assemblages have the highest assemblage evolutionary distinctiveness given species richness ($p < 0.05$: Figure 5l; Table S3). Species pack more closely in trait space than expected as energy availability (GPP) increases ($p < 0.05$: Figure 5m; Table S3). Assemblages are most packed at flat (e.g lowland plains, upland plateaus) and steep (mid-montane slopes) elevational ranges, with species most spread out at mid-elevational ranges ($p < 0.01$: Figure 5o; Table S3). No relationship between MD$_{SES}$ and habitat heterogeneity was found (Table S3). Under phyloregional pools, we find a contrast in model outputs where species richness is the predictor variable. As species richness increases, species become slightly less clustered in trait space than expected when using datasets B and D ($p < 0.01$ [linear term only]), but for dataset A, we find that species are most clustered in trait space (low MD$_{SES}$) at mid species richness values ($p < 0.05$) (Figure 5p; Table S3).

## DISCUSSION

We present the first global mapping of a comprehensive set of continuous morphological traits, including three-dimensional bill shape data, for 8353 bird species, revealing regions of the world with exceptional relative spread and density of species traits. Our results suggest large-scale geographic variation in the relative importance of niche expansion and niche packing. Density

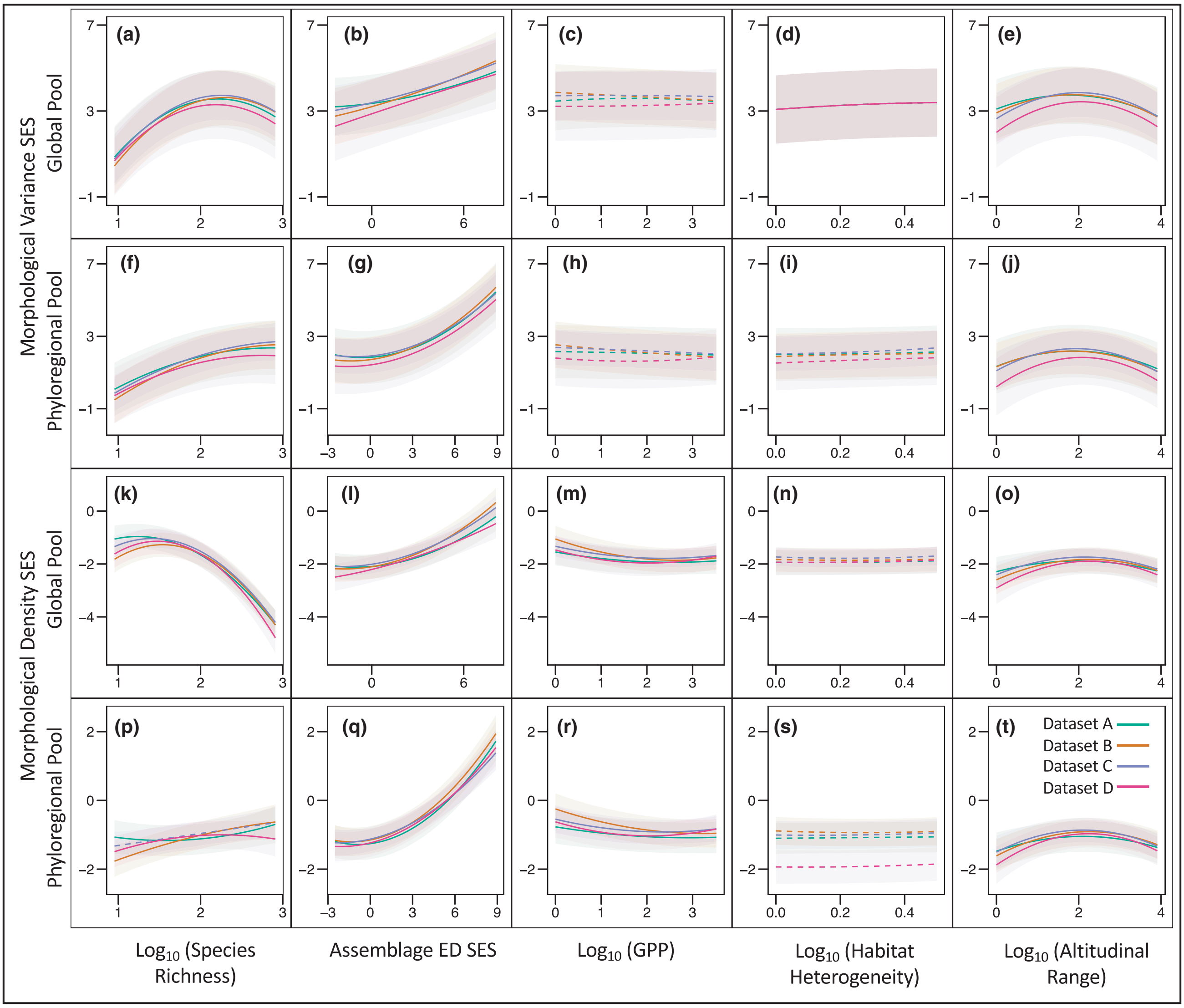

**FIGURE 5** The effect of species richness, assemblage evolutionary distinctiveness (sum of equal splits) SES, gross primary productivity (GPP), habitat heterogeneity (Shannon's index), and altitudinal range on morphological variance (sum of variances) SES [generated from global (a-e) and phyloregional species pools (f-j)], and on morphological density (mean nearest neighbour distance) SES (generated from global (k-o) and phyloregional species pools (p-t)). High values of morphological density represent high mean nearest neighbour distances and therefore low density. Low values of morphological density represent low mean nearest neighbour distances and so high density. All raw variables (i.e. non-SES) are on a $\log_{10}$ scale. The lines represent predicted relationships from the multiple predictor gls models, with solid lines representing significant predictors whereas dotted lines are non-significant. Colours correspond to each 25% data subset (Dataset A = green, B = orange, C = purple, and D = pink).

and variance of morphological trait distributions scale with species richness and evolutionary distinctiveness, whereas only density scales with productivity (albeit weakly). Taken together, we suggest that evolutionary history plays a key role in shaping assemblage composition, particularly through niche expansion, whereas contemporary environment contributes more to niche packing.

Our use of global and phyloregional pools reveals the broad role of evolutionary history in shaping global assemblage structure. Tropical biodiversity hotspots, including the highland tropical Andes (Jarzyna et al., 2021), much of the central African tropics, and Indo-Malayan archipelago are densely packed compared to the global pool but not when compared to phyloregional faunas. In the same regions, variance follows global expectations but is higher than expected under the phyloregional null model. Such patterns would be expected if these hyper-diverse regions are both ‘museums’ where old species persist, and ‘cradles’ of diversity, where speciation rates are high (Gaston & Blackburn, 1996; Jablonski et al., 2006; McKenna & Farrell, 2006; Rolland et al., 2014). For instance, if morphological divergence is closely related to species age, surviving lineages will lead to greater morphospace volumes, and in addition, high numbers of closely-related young species will cause the denser packing of niche space in the tropics. In contrast, oceanic islands retain high density irrespective of the species pool. Collectively these patterns imply a lasting imprint of distinct evolutionary and biogeographic histories on assemblage structure.

Areas of the Northern temperate regions tend to be more densely packed than expected, mirroring findings from smaller areas in the temperate lowlands using mostly categorical traits (Jarzyna et al., 2021). We also find a tendency for temperate assemblages to have higher morphological variance than expected under a global pool null model. Although it is difficult to directly infer the ecological drivers of community assembly using cell assemblage-based methods alone (Blanchet et al., 2020), our results hint that habitat filtering may contribute more to temperate, especially Northern Hemisphere regions, in shaping assemblage structuring. The observed pattern can only arise if morphospace is occupied by clusters of morphologically similar species, but where these clusters are spaced apart from one another. This would lead to high density within clusters, and high variance (the clusters are spread out across morphospace). This observation fits previous findings that standardised mean distance to centroid (functional dispersion) is greatest for birds in temperate and polar biomes (Cooke et al., 2019). Communities in the temperate and polar regions contain many species that migrate south during the Northern winter, with the remaining species likely to possess combinations of traits that allow survival over the harsh winter months (e.g. ecological guilds such as granivores and scavengers: Carnicer & Díaz-Delgado, 2008) leading to increased niche packing in these areas of morphospace.

The importance of evolutionary history for assemblage structure is further supported by our analyses of predictors of morphological diversity. Morphological diversity is expected to correlate strongly with species richness (Safi et al., 2011), as adding species must increase either volume or density. However, even after controlling for species richness using null models, we still find that species richness is a strong predictor of both morphological density and volume. Compared to both global and phyloregional models, morphological volume increases with species richness, suggesting niche expansion, before plateauing at high levels of species richness. This leads to increasing functional redundancy in species-rich regions (Oliveira et al., 2016). In contrast, and only for global models, niche space is exceptionally densely packed in areas of high species richness. This implies that niche packing becomes dominant in hyper-diverse assemblages, and mirrors findings that the similarity of bird species functional roles is highest in species-rich areas (Cooke et al., 2019).

Alongside species richness effects, we also find that assemblages with greater than expected evolutionary distinctiveness have both high variance and lower density in morphological space. This is consistent with the expected link between phylogenetic diversity and morphological diversity (Faith, 1992; Mazel et al., 2018; Safi et al., 2011) and suggests that niche expansion reflects phylogenetic history and the presence of more evolutionarily distinct species in hyper-diverse assemblages. In contrast, the combined increase in density with richness but decline with evolutionary distinctiveness implies that the packing of species in hyper-diverse assemblages is not a reflection of time since divergence. Instead, density, but not volume, increases with productivity. We suggest that assemblage morphospace expansion is driven by the accumulation of evolutionarily old lineages whereas packing is potentially the result of stable and productive environments supporting morphologically similar and evolutionarily young species. However, we note that the effects of productivity on morphological diversity are comparatively weak and therefore this interpretation ought to be treated with caution.

In addition to evolutionary history and productivity, we find some support for the expectation that heterogeneous habitats contain more niches, and can support morphologically more similar species, than homogenous ones (Kerr et al., 2001; Rahbek & Graves, 2001). As altitudinal range increases, morphological density decreases and volume increases, as species fill more niches resulting in a peak at mid-altitudinal ranges. The subsequent decline of morphological volume and increasing morphological density as species cluster in trait space at high altitudinal ranges (i.e. mid-montane slopes), is likely attributable to the high richness (α-diversity) (e.g. Davies et al., 2007) and turnover (β-diversity) (Graham et al., 2009) of closely related species (Voskamp et al., 2017), characteristic of such areas.

In our study, trait data were not available for all species, and biases in sampling could exist both phylogenetically and spatially (Figures S1 and S3) (Etard et al., 2020). For instance, certain groups, particularly those with rictal bristles or feathers obscuring the bill (e.g. nightjars and allies [Caprimulgiformes]), are under-represented because we were not able to obtain complete 3D bill scans. Globally, assemblages contain an average of 94% of species, with no assemblage containing less than 70% of species. Spatially, high richness areas are more likely to contain the greatest numbers of species with missing trait data, although these tend to be species from represented families with similar morphologies. We suggest, based on the phylogenetic (Figure S1) and spatial (Figure S3) structure of the missing data, that our analyses are unlikely to be strongly biased by missing data. We also suggest that the most likely impact of missing data is an underestimation of niche packing in high richness areas and a weaker relationship with productivity, although this is untested.

In conclusion, our work reveals novel insights into the structure and drivers of avian assemblages. We argue that evolutionary history plays a key role in shaping assemblage structure notably with evolutionarily old species contributing to niche expansion, and evolutionarily young species contributing to niche packing in the tropics. We further suggest that tropical niche packing is facilitated by high productivity and potentially, though not directly tested here, the long-term stability of the tropics.

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## AUTHORSHIP

E.C.H., D.P.E. and G.H.T. conceived the ideas and designed the methodology; E.C.H., J.A.B., E.J.R.C., C.R.C., G.H.T. and Z.K.V. collected data from museum specimens and designed analytical protocols for producing the beak shape dataset; E.C.H. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

The data and code supporting the results are available in the University of Sheffield's ORDA repository, provided by figshare: https://doi.org/10.15131/shef.data.16733224

## ORCID

*Emma C. Hughes* https://orcid.org/0000-0003-4682-6257
*David P. Edwards* https://orcid.org/0000-0001-8562-3853
*Jen A. Bright* https://orcid.org/0000-0002-9284-9591
*Christopher R. Cooney* https://orcid.org/0000-0002-4872-9146
*Gavin H. Thomas* https://orcid.org/0000-0002-1982-6051

## REFERENCES

Anderson, P.S.L., Friedman, M., Brazeau, M.D. & Rayfield, E.J. (2011) Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature*, 476, 206–209.

Belmaker, J., Sekercioglu, C.H. & Jetz, W. (2012) Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography*, 39, 193–203.

Blanchet, F.G., Cazelles, K. & Gravel, D. (2020) Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23, 1050–1063.

Bright, J.A., Marugán-Lobón, J., Cobb, S.N. & Rayfield, E.J. (2016) The shapes of bird beaks are highly controlled by nondietary factors. *Proceedings of the National Academy of Sciences*, 113, 5352–5357.

Bright, J.A., Marugán-Lobón, J., Rayfield, E.J. & Cobb, S.N. (2019) The multifactorial nature of beak and skull shape evolution in parrots and cockatoos (Psittaciformes). *BMC Evolutionary Biology*, 19, 104.

Buchhorn, M., Lesiv, M., Tsendbazar, N.-E., Herold, M., Bertels, L. & Smets, B. (2020) Copernicus global land cover layers—collection 2. *Remote Sensing*, 12(6), 1044.

Carnicer, J. & Díaz-Delgado, R. (2008) Geographic differences between functional groups in patterns of bird species richness in North America. *Acta Oecologica*, 33, 253–264.

Chira, A.M., Cooney, C.R., Bright, J.A., Capp, E.J.R., Hughes, E.C., Moody, C.J.A. et al. (2018) Correlates of rate heterogeneity in avian morphological traits. *Ecology Letters*, 21, 1505–1514.

Cooke, S.C., Bates, A.E. & Eigenbrod, F. (2019) Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology and Biogeography*, 28, 484–495.

Cooney, C.R., Bright, J.A., Capp, E.J.R., Chira, A.M., Hughes, E.C., Moody, C.J.A. et al. (2017) Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature*, 542, 344–347.

Currie, D.J., Francis, A.P. & Kerr, J.T. (1999) Some general propositions about the study of spatial patterns of species richness. *Écoscience*, 6, 392–399.

Davies, R.G., Orme, C.D.L., Storch, D., Olson, V.A., Thomas, G.H., Ross, S.G. et al. (2007) Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B-Biological Sciences*, 274, 1189–1197.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, 13, 1030–1040.

Etard, A., Morrill, S. & Newbold, T. (2020) Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography*, 29, 2143–2158.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10.

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.

Foote, M. (1992) Rarefaction analysis of morphological and taxonomic diversity. *Paleobiology*, 18, 1–16.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, 405, 220–227.

Gaston, K.J. & Blackburn, T.M. (1996) The tropics as a museum of biological diversity: an analysis of the New World avifauna. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263, 63–68.

Graham, C.H., Parra, J.L., Rahbek, C. & McGuire, J.A. (2009) Phylogenetic structure in tropical hummingbird communities. *Proceedings of the National Academy of Sciences*, 106, 19673–19678.

Guégan, J.-F., Lek, S. & Oberdorff, T. (1998) Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, 391, 382–384.

Guillerme, T. (2018) dispRity: a modular R package for measuring disparity. *Methods in Ecology and Evolution*, 9, 1755–1763.

Guillerme, T., Puttick, M.N., Marcy, A.E. & Weisbecker, V. (2020) Shifting spaces: Which disparity or dissimilarity measurement best summarize occupancy in multidimensional spaces? *Ecology and Evolution*, 10, 7261–7275.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J. et al. (2008) A phylogenomic study of birds reveals their evolutionary history. *Science*, 320, 1763–1768.

Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D. et al. (2013) An update of wallace's zoogeographic regions of the World. *Science*, 339, 74–78.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314, 102–106.

Jarzyna, M.A., Quintero, I. & Jetz, W. (2021) Global functional and phylogenetic structure of avian assemblages across elevation and latitude. *Ecology Letters*, 24, 196–207.

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.

Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K. & Mooers, A.O. (2014) Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, 24, 919–930.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L. et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648.

Karr, J. & James, F. (1975) Eco-morphological configurations and convergent evolution in species and communities. In: Diamond, J. & Cody, M.L. (Eds.) *Ecology and evolution of communities*. Boston, MA: Harvard University Press.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.

Kerr, J.T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385, 252–254.

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001) Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences*, 98, 11365–11370.

Kohli, B.A. & Jarzyna, M.A. (2021) Pitfalls of ignoring trait resolution when drawing conclusions about ecological processes. *Global Ecology and Biogeography*, 30, 1139–1152.

MacArthur, R.H. (1965) Patterns of species diversity. *Biological Reviews*, 40, 510–533.

MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, 42, 594–598.

Mazel, F., Pennell, M.W., Cadotte, M.W., Diaz, S., Dalla Riva, G.V., Grenyer, R. et al. (2018) Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications*, 9, 2888.

McKenna, D.D. & Farrell, B.D. (2006) Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences*, 103, 10947–10951.

McLean, M., Stuart-Smith, R.D., Villéger, S., Auber, A., Edgar, G.J., MacNeil, M.A. et al. (2021) Trait similarity in reef fish faunas across the world's oceans. *Proceedings of the National Academy of Sciences*, 118, e2012318118.

Melo, A.S., Rangel, T.F.L.V.B. & Diniz-Filho, J.A.F. (2009) Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, 32, 226–236.

Miller, E.T., Wagner, S.K., Harmon, L.J. & Ricklefs, R.E. (2017) Radiating despite a lack of character: ecological divergence among closely related, morphologically similar honeyeaters (Aves: Meliphagidae) co-occuring in arid Australian Environments. *The American Naturalist*, 189(2), E14–E30.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B. et al. (2001) What is the observed relationship between species richness and productivity? *Ecology*, 82, 2381–2396.

Navalón, G., Bright, J.A., Marugán-Lobón, J. & Rayfield, E.J. (2019) The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution*, 73, 422–435.

Oliveira, B.F., Machac, A., Costa, G.C., Brooks, T.M., Davidson, A.D., Rondinini, C. et al. (2016) Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*, 25(9), 1119–1130.

Oliveira, B.F., São-Pedro, V.A., Santos-Barrera, G., Penone, C. & Costa, G.C. (2017) AmphiBIO, a global database for amphibian ecological traits. *Scientific Data*, 4, 170123.

Olsen, A.M. (2017) Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Functional Ecology*, 31, 1985–1995.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A. et al. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436, 1016–1019.

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

Pigot, A.L., Tobias, J.A. & Jetz, W. (2016) Energetic constraints on species coexistence in birds. *PLoS Biology*, 14(3), e1002407.

Pigot, A.L., Trisos, C.H. & Tobias, J.A. (2016) Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proceedings of the Royal Society B-Biological Sciences*, 283, 20152013.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Morlon, H. & Ackerly, D.D. et al. (2020). *nlme: linear and nonlinear mixed effects models. R package version 3.1-149*. R Core Team.

Purvis, A. & Hector, A. (2000) Getting the measure of biodiversity. *Nature*, 405, 212–219.

R Core Team (2020) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, 98, 4534–4539.

Redding, D.W., DeWOLFF, C.V. & Mooers, A.Ø. (2010) Evolutionary distinctiveness, threat status, and ecological oddity in primates. *Conservation Biology*, 24, 1052–1058.

Redding, D.W. & Mooers, A.Ø. (2006) Incorporating evolutionary measures into conservation prioritization. *Conservation Biology*, 20, 1670–1678.

Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65, 514–527.

Rolland, J., Condamine, F.L., Jiguet, F. & Morlon, H. (2014) Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology*, 12, e1001775.

RStudio Team (2020) *RStudio: Integrated Development for R*. PBC, Boston, MA: RStudio.

Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K. & Diniz-Filho, J.A.F. (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2536–2544.

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

Stevens, R.D., Cox, S.B., Strauss, R.E. & Willig, M.R. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters*, 6, 1099–1108.

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.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect?—Systematics and the agony of choice. *Biological Conservation*, 55, 235–254.

Villéger, S., Mason, N.W. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301.

Voskamp, A., Baker, D.J., Stephens, P.A., Valdes, P.J. & Willis, S.G. (2017) Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds. *Journal of Biogeography*, 44, 709–721.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

Zhang, Y., Xiao, X., Wu, X., Zhou, S., Zhang, G., Qin, Y. et al. (2017) A global moderate resolution dataset of gross primary production of vegetation for 2000–2016. *Scientific Data*, 4, 170165. https://doi.org/10.6084/m9.figshare.c.3789814.v1

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