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LETTER

AVONET: morphological, ecological and geographical data for all birds

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Abstract

Functional traits offer a rich quantitative framework for developing and testing theories in evolutionary biology, ecology and ecosystem science. However, the potential of functional traits to drive theoretical advances and refine models of global change can only be fully realised when species-level information is complete. Here we present the AVONET dataset containing comprehensive functional trait data for all birds, including six ecological variables, 11 continuous morphological traits, and information on range size and location. Raw morphological measurements are presented from 90,020 individuals of 11,009 extant bird species sampled from 181 countries. These data are also summarised as species averages in three taxonomic formats, allowing integration with a global phylogeny, geographical range maps, IUCN Red List data and the eBird citizen science database. The AVONET dataset provides the most detailed picture of continuous trait variation for any major radiation of organisms, offering a global template for testing hypotheses and exploring the evolutionary origins, structure and functioning of biodiversity.

KEYWORDS
avian traits, continuous variables, data integration, ecomorphology, functional diversity, macroecology, macroevolution, trait-based ecology

INTRODUCTION

Functional traits—the morphological and ecological characteristics that influence organismal performance or fitness—have driven innovation in the field of ecology for the last two decades (McGill et al., 2006; Violle et al., 2007). Preliminary analyses of functional trait variation across lineages or within species assemblages have led to the development of influential models and metrics in a range of fields, including macroevolution (FitzJohn, 2010), community ecology (Petchey & Gaston, 2002) and ecosystem science (Suding et al., 2008). Perhaps, the most alluring factor that draws researchers from these different fields to functional traits is the hope they offer of moving beyond species to a more mechanistic understanding of ecosystem structure and function (Cadotte et al., 2011; Díaz et al., 2013; Funk et al., 2017; Hooper et al., 2002; Tilman et al., 1997). Another recurring theme is the idea that functional traits can help us to devise a quantitative framework for understanding and predicting ecological communities (Schleuning et al., 2020; Winemiller et al., 2015). However, unlocking the true potential of functional traits is highly dependent on comprehensive sampling at the species level, whereas coverage remains patchy for all major taxonomic groups, particularly for continuous morphological traits (Cernansky, 2017; Kohli & Jarzyna, 2021).

Progress to date in amassing trait data has been weighted towards plant systems, partly because of the fundamental importance of plants to critical ecological functions (Funk et al., 2017), and also because plant traits are relatively easy to access and measure. International initiatives for data sharing and synthesis are relatively advanced for plants, and plant trait data are therefore readily available to the scientific community at a global scale (Kattge et al., 2020). However, while these datasets have provided insightful tests of theory, including the mechanisms underlying community assembly (Mayfield & Levine, 2010), species coexistence (Kraft et al., 2008) and the scaling from traits to ecosystems (Enquist et al., 2015), it is difficult to know whether these results can be applied more generally to non-plant systems. The same caveat applies to many fundamental trait-based concepts designed from a plants-only perspective (Suding et al., 2008).

Plant functional ecology has flourished, yet trait datasets of plants are nonetheless patchy in terms of species and trait coverage at a global scale. Out of roughly 352,000 flowering plant species, the TRY database currently contains fewer than 60,000 species (17%) with 10 or more traits (Kattge et al., 2020). This creates problems for analytical approaches that assume coverage is complete, including phylogenetic comparative analyses and evolutionary models. Missing species in partially sampled trait datasets can radically alter the trait structure of communities and the fit of evolutionary models, reducing predictive power and restricting studies to a biased sample of well-known clades (Kohli & Jarzyna, 2021; Weiss & Ray, 2019). The main obstacle to the completion of species sampling for plant traits is the sheer diversity of plants themselves. One solution for the next generation of trait-based models in ecology and evolutionary biology is to switch some attention to vertebrate clades containing a more manageable number of species. In any case, a catch-up phase for animal trait databases

is a high priority because this would open up research into a range of novel questions. For example, integration across animal and plant trait data may provide the key to understanding complex trophic interaction networks at the heart of ecological processes, such as nutrient and energy transfer, seed dispersal, pollination and predation (Bartomeus et al., 2016; Harfoot et al., 2014; Schleuning et al., 2015).

A brief history of animal functional ecology

To date, the most prominent species-level trait datasets published for animals at a global scale—PanTHERIA (Jones et al., 2009), EltonTraits (Wilman et al., 2014) and the amniote database (Myhrvold et al., 2015)—have focused mainly on life history and ecological traits for the world's mammals, birds and reptiles. These datasets have been highly influential, yet the only complete continuous morphological trait data presented in each case is body mass. Body mass has long been the mainstay of ecological and evolutionary research, but it provides only limited information about ecological niches and trophic interactions (Bender et al., 2018; Pigot et al., 2020). Moving beyond body mass in animal functional ecology has proved challenging, with most progress made in the validation and compilation of avian traits (Tobias et al., 2020).

The study of avian morphological traits helped to inspire core theoretical concepts in ecology and evolutionary biology, from adaptive radiation and ecological speciation (Darwin, 1859), to the mechanisms underlying community assembly (Diamond, 1975) and large-scale biodiversity gradients (MacArthur, 1972). In the last two decades of the twentieth century, the field of ecomorphology rose to prominence in avian ecology (Bock, 1994; Leisler & Winkler, 1985; Miles & Ricklefs, 1984; Ricklefs & Travis, 1980), laying the foundations for all recent research into avian functional traits (see Figure 1). Most of the focus has been on beak size and shape, given the apparent association of beak traits with dietary niche and resource competition (Cooney et al., 2017; Pigot & Tobias, 2013). Some studies focusing on smaller spatial or taxonomic scales have reported only weak predictive power for avian morphological traits, including beaks (Bright et al., 2016; Miller et al., 2017; Weeks et al., 2020). However, other recent analyses have shown that a more holistic combination of morphological traits can predict avian trophic niches or interactions far more powerfully than either body mass or beak shape alone (Pigot et al., 2020).

Despite the historical emphasis on ecomorphology, most trait-based studies using this conceptual framework still focus on a few well-sampled clades, including ovenbirds (Tobias et al., 2014), tanagers (Drury et al., 2018) and corvoid passerines (Kennedy et al., 2020). In

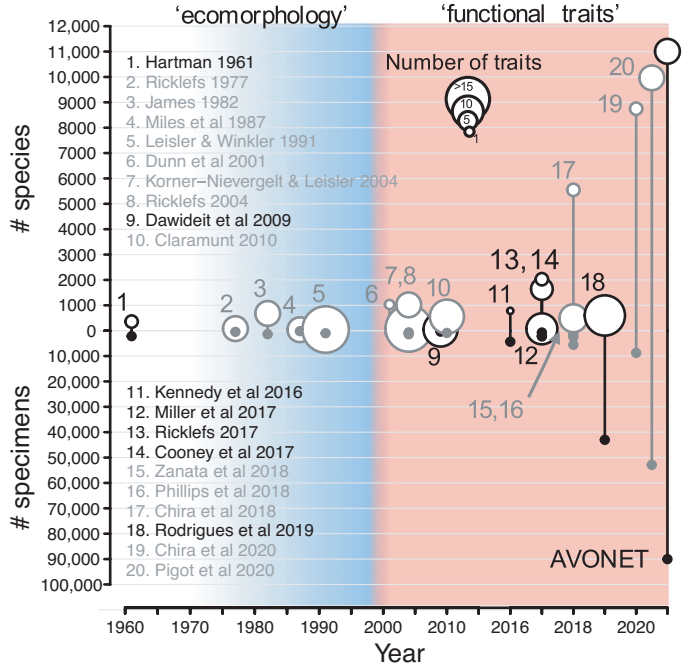

FIGURE 1 The sampling of avian morphological traits over time. The number of species (above x axis) and the number of specimens (below x axis) measured for landmark studies along with their year of publication is indicated by the vertical bars. Each bar indicates the maximum number of species and specimens measured for any trait. The number of traits in each study is represented by circle sizes (continuous from 1 to 15, with examples shown in the legend). Studies openly providing raw trait data are indicated in black. AVONET contains the raw specimen-level data for Pigot et al. (2020), along with substantial expansion in coverage of both species and specimens-per-species. To provide historical context, coloured time periods correspond roughly to interest in 'ecomorphology' (blue) and 'functional traits' (red). Citations for studies not used in the main text are provided in the Supplementary Material

addition, many trait-based analyses testing ideas relating to community assembly, ecosystem function or responses to land-use change are focused on local study systems containing a few hundred species at most (Bregman et al., 2016; Dehling et al., 2016; Pigot et al., 2016). All datasets presenting compilations of avian morphological traits were similarly restricted in geographical or taxonomic sampling until 2017 (Figure 1). Since then, a series of global analyses (e.g. Chira et al., 2018, 2020; Cooney et al., 2017) have included data from many more species, but relatively few measurements per species of a limited number of traits (Figure 1). The recent publication of macroevolutionary analyses by Pigot et al. (2020) marked another step-change in scale, with comprehensive species-level sampling and deeper individual sampling of multiple morphological traits. However, all these datasets have limited utility for research because they present measurements summarised as principal components aligned with the BirdTree taxonomy (Jetz et al., 2012).

In this paper, we provide a global overview of the AVONET database, a compilation of individual-level trait measurements for all the world's bird species. AVONET contains the raw trait data used by Pigot et al. (2020), focusing on the same set of phenotypic traits with well-established connections to diet, dispersal and locomotion (Pigot et al., 2016, 2020; Sheard et al., 2020; Figure 2, Supplementary Dataset 1). To improve intraspecific sampling, we added measurements taken from a further 37,150 individual birds—a 71% increase (Figure 1). To improve interoperability with external datasets, we also averaged all traits at the species level according to three alternative taxonomic treatments—BirdLife International, eBird and BirdTree (Supplementary Dataset 1). We hope this removes a major obstacle to future analyses, allowing integration with IUCN Red List data and geographical range maps, as well as eBird citizen science data (Sullivan et al., 2014) and the global bird phylogeny (Jetz et al., 2012). The AVONET database represents a collaborative effort by specimen collectors, museum workers and field ornithologists over many decades. In the spirit of the Open Traits network (Gallagher et al., 2020), the data are released for use by the wider research community, in conjunction with additional information describing the ecology and geographical context of all bird species.

MATERIALS AND METHODS

Morphological traits

External morphological traits were measured from live individuals and preserved museum skins. For each individual, we measured nine traits (generally to the nearest 0.1 mm): four beak measurements, three wing measurements, tarsus length and tail length (see Figure 2 and Supplementary Dataset 1 for details). Traits were selected for the information they provide about ecological niches. The beak is the primary apparatus used by birds to capture and process food, while morphological differences in wings, tails and legs are related to locomotion, providing insight into the way birds move through their environment and forage for resources (Leisler & Winkler, 1985; Miles & Ricklefs, 1984; Pigot et al., 2020; Ricklefs & Travis, 1980). We targeted four individuals

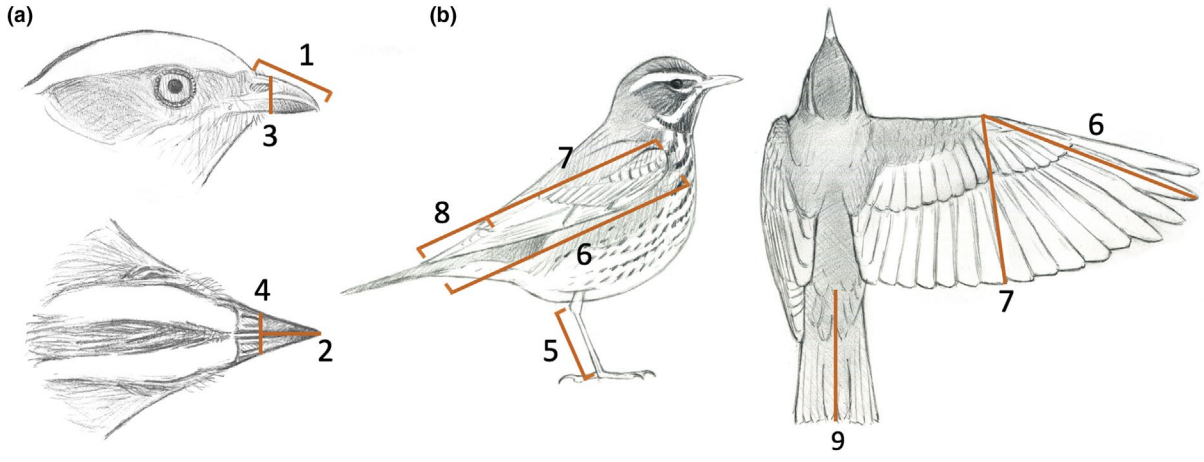

FIGURE 2 Diagram of linear measurements of avian morphology presented in AVONET. (a) Resident frugivorous tropical passerine (fiery-capped manakin, *Machaeropterus pyrocephalus*) showing four beak measurements: (1) beak length measured from tip to skull along the culmen; (2) beak length measured from the tip to the anterior edge of the nares; (3) beak depth; (4) beak width. (b) Insectivorous migratory temperate-zone passerine (redwing, *Turdus iliacus*) showing five body measurements: (5) tarsus length; (6) wing length from carpal joint to wingtip measured on the unflattened wing; (7) secondary length from carpal joint to tip of the outermost secondary; (8) Kipp's distance, measured directly or calculated as wing length minus first-secondary length; (9) tail length. Protocols for measuring these traits are provided in Supplementary material. AVONET also includes body mass, and Hand-wing index (calculated from 6 to 8), making 11 traits in total. Illustration by Richard Johnson

(two of each sex) as our minimum sample wherever possible. Further data for these traits were added by merging independent datasets, excluding data measured in a substantially different way. The final version contains measurements from 90,020 individual birds with an average of 8.1–9.0 individuals per species (variable depending on taxonomy; Table S1). All raw data and species averages are provided in Supplementary Dataset 1.

In addition to direct measurements, we also calculated the hand-wing index (HWI), a metric of flight efficiency and dispersal ability in birds (Claramunt, 2021). Although a global HWI dataset following BirdTree taxonomy has been published previously (Sheard et al., 2020), we update HWI scores to reflect additional sampling under the BirdTree taxomomy, and provide species averages aligned with BirdLife and eBird species lists. Finally, we also update published body mass data for 1985 species, either by inferring from close relatives or, in the case of 716 species, from literature, fieldwork and museum specimen labels (Supplementary Material). In many of these cases, previously published mass data had been inferred with low accuracy on the basis of predictive models (Wilman et al., 2014), so AVONET provides a much-improved body mass dataset for the world's birds.

Data curation

We included a series of checks to identify and remove errors before merging trait datasets (Supplementary Material). To assess the potential influence of observer biases, we collected duplicate measurements from 4799 individual specimens of 3421 species measured by 64 different people. We then used mixed effects models to assess concordance between independent measures of the same trait. To assess whether trait data were significantly different in museum specimens versus live samples, we compared measurements for 962 species with both types of data.

Taxonomic classification

Taxonomic classification is in constant flux, particularly in birds (Garnett & Christidis, 2017), causing major problems for compilers and users of functional trait datasets. To facilitate integrative analyses, we average our trait data according to three different taxonomic treatments differing by roughly 1000 species: BirdLife International (2020), 10,999 species; eBird (Clements et al., 2021), 10,661 species; and BirdTree (Jetz et al., 2012), 9993 species. Most extant BirdLife species (n = 8949, 81.4%) are one-to-one matches with BirdTree species. This leaves roughly a fifth of species with imperfect matches across these two datasets. In many cases, BirdTree species have been split into multiple BirdLife species, such that traits are averaged across smaller numbers of specimens-per-taxon, with specimens reallocated among newly split species. This can lead to variation in trait averages even when taxonomic names are the same (see Supplementary Material). Levels of matching are similar between BirdLife and eBird versions. To facilitate navigation between datasets, we created crosswalks between them (Supplementary Dataset 1). We also included Avibase ID where possible to provide a more stable resolution of taxonomic concepts over time (Lepage et al., 2014).

Geographical sampling

All individual birds measured by field teams were assigned to the country in which sampling localities were situated. For museum data, we identified the country where each specimen was collected based on the label. For specimens with no locality data, we assigned them to their respective countries in the case of single-country endemics. Where possible, we matched the transcription with country names and boundary data aligned with country shapefiles published by the World Resources Institute (https://github.com/wri/wri-bounds, accessed on 14/10/2020). Further details of methods for identifying localities and assigning specimens to countries are given in Supplementary Material.

Ecological categories

For each species, we used the information on proportional dietary categories used by Pigot et al. (2020) to score the proportion of diet obtained from three trophic levels (herbivore; carnivore; scavenger). Herbivores represent primary consumers; carnivores (including invertivores) represent secondary and tertiary consumers. Following Pigot et al. (2020), we assigned all species to nine trophic niches (frugivore; granivore; nectarivore; terrestrial herbivore; aquatic herbivore; invertivore; vertivore; aquatic predator; scavenger) encompassing major resource types utilised by birds. Our scoring of species diets is primarily based on data from Wilman et al. (2014), extensively updated and re-organised (Tobias & Pigot, 2019; Supplementary Material).

Next, we classified each species into five lifestyles (or domains) according to their predominant locomotory niche while foraging: aerial, insessorial, terrestrial, aquatic and generalist. This is a separate dimension to diet inasmuch as species eating fish may be aquatic (e.g. pelican), aerial (e.g. tern), terrestrial (e.g. heron) or insessorial (e.g. kingfisher). Insessorial denotes a perching lifestyle, including arboreal species, but also any species habitually perching on other substrates, including cliffs or manmade structures. Further explanations of all ecological categories are given as metadata (Supplementary Dataset 1).

Biogeographical variables

For the BirdLife dataset, species geographical range maps were obtained from Birdlife International. We selected breeding and resident ranges in areas where the species is coded as extant and either native or reintroduced. Mapping species under the BirdTree taxonomy dataset often required the combination of maps for multiple BirdLife species to form an expanded range map for a single BirdTree species (Supplementary Dataset 1). We did not generate new maps for the eBird dataset which can be integrated directly with citizen-science locality data and a suite of spatial research tools (Sullivan et al., 2014).

Using BirdLife and BirdTree maps, we extracted range size (km^2), longitude (of range centroid) and three latitudinal variables (maximum, minimum and centroid). See Supplementary Material for details of mapping methods used to generate these data. We included maximum and minimum latitude because these values may be important in studies of latitudinal gradients, constraints or climatic effects. Note that range size based on interpolated range polygons tends to over-estimate the true extent of occurrence (Jetz et al., 2008). To map morphological traits, we extracted species ranges onto an equal area grid (Behrmann projection) with a resolution of 110 km (≈1° at the equator).

RESULTS

Repeatability of morphological measurements

When all repeated trait measurements were pooled regardless of measurement protocol used, data were highly concordant among individual measurers (Figures S1 and S2), indicating that different methods produce comparable measurements of the traits included in our dataset. Repeatability (R) scores differed across traits (GLM: $F = 523{,}963$, Df = 7, $p < 0.0001$; Table S4) suggesting that some trait measurements are more repeatable than others. For example, estimated variation in beak width was relatively high (6.6%; Figure S1), suggesting low repeatability arising from the use of different trait definitions by contributors (see Supplementary Material). Nonetheless, the overall concordance of trait data collected by different measurers was high for all traits (R = 0.928–0.996; Table S4). When we analysed variance separately for duplicate pairs measured using the AVONET protocol (n = 277), we found that they usually had higher correspondence (Figure S3) than duplicates for which at least one measurement was taken using a different protocol (n = 4527; Figure S4). While this suggests that repeatability improves when measurement protocol is standardised, the effects are marginal and only found in some traits. Finally, we found only minor differences when comparing measurements taken on museum specimens and live samples (Figure S5) suggesting that data from different sources can be pooled (Supplementary Material).

Species coverage

Discounting duplicate measurements, we compiled morphological trait data from 90,020 individual birds, including previously unpublished raw data from 75,287 museum specimens and 11,424 living individuals. We added further measurements from 556 museum specimens and 2753 living individuals published in previous data papers (Supplementary Dataset 1). Overall, morphological trait sampling was conducted by 153 researchers, of which 88 used the AVONET protocol (see Supplementary Material). In addition, we integrated several unpublished trait datasets including morphological traits of 37,150 individual birds measured using alternative protocols by 65 researchers.

In total, 99.4% (n = 89,434) of measured individual birds were included in all three datasets (BirdLife, eBird and BirdTree), with the remaining 0.6% (n = 586) appearing in 1–2 datasets. The AVONET database greatly increases coverage and availability of morphological trait data for birds in comparison with previous studies (Figure 1; Table S1). All morphological traits are now sampled for 95.7–96.8% species under BirdLife; 96.4–97.1% under eBird; and 99.4–99.7% species under BirdTree (percentages varying by trait; see Table S2). Regardless of taxonomy, 100% of avian families are sampled, with species-level sampling near-complete for most families, particularly for the BirdTree dataset (Table S1; Figure 3). The few remaining undersampled families are either small (low species richness), particularly when subject to recent taxonomic splitting (e.g. ostriches), or difficult to collect (e.g. owls; Figure 3; Table S3). At the species level, sampling was uneven according to specimen availability, with some common species sampled intensively and rarer species falling short of the targeted four individuals (Figure 3).

The AVONET dataset currently lacks direct measurements of any trait for 351 species under BirdLife, 308 species under eBird and 26 species under BirdTree. An additional 56–193 species have data missing for one or more traits, depending on the taxonomy used (Table S3). We fill these gaps using inference by identifying the closest relative with the most similar ecology and morphology (often this was the parent species in the case of daughter species arising from taxonomic splits). We highlight inferred traits and the surrogate species from which inferences were made (Supplementary Dataset 1) to allow future users to decide whether to include inferred trait data. Their decision may vary with context since, on the one hand, data inferred by this method may invalidate evolutionary models, but on the other hand they can refine models of community assembly wherein the inclusion of like-for-like proxies is better than deleting species

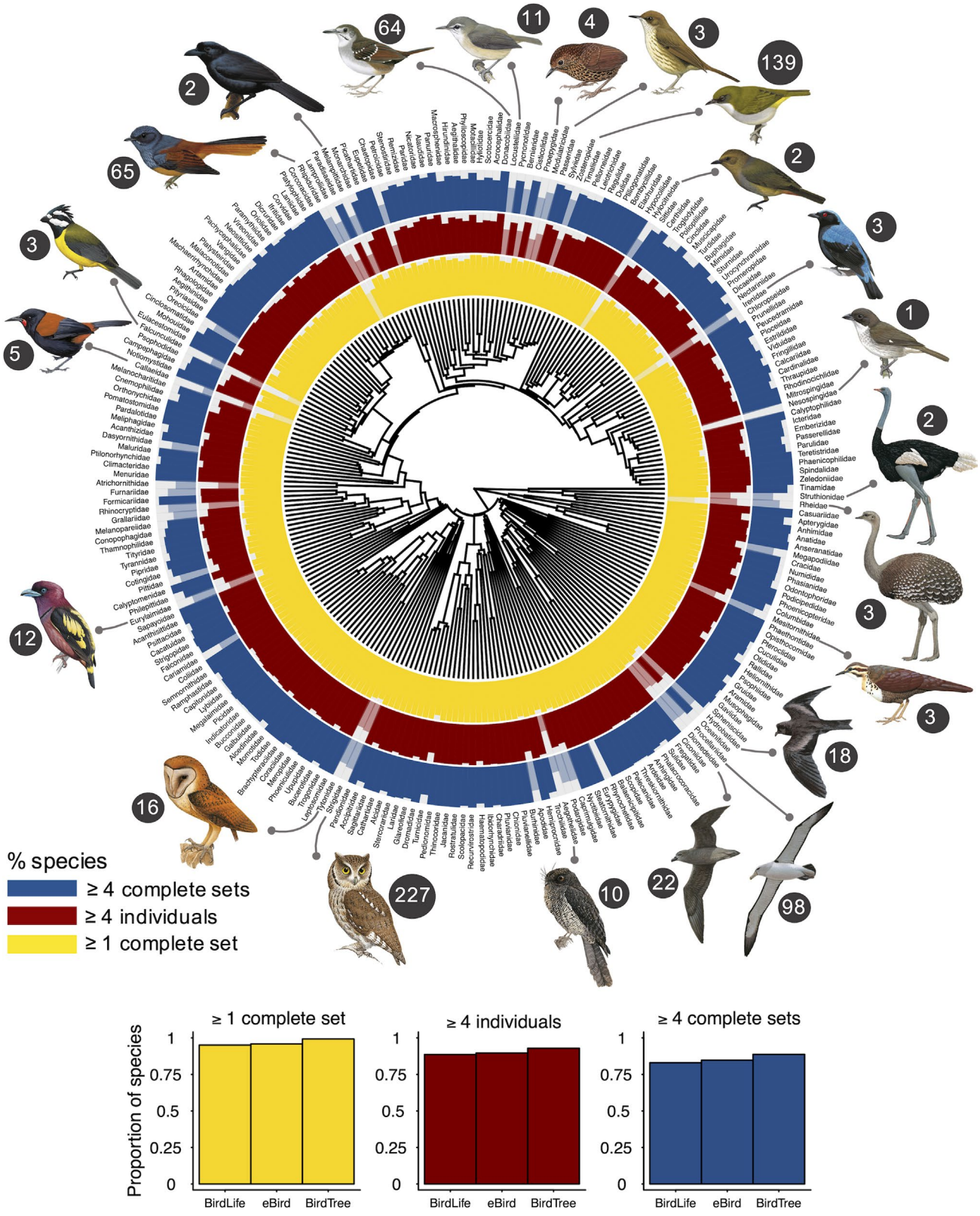

FIGURE 3 Morphological trait sampling for all bird families. AVONET contains 718,662 individual trait measurements, all of which are used to calculate species averages. However, sampling per species varies across families depending on taxonomy. Upper phylogram shows sampling under BirdLife International (11,009 species in 243 families). Families where sampling completeness is below 75% indicated by lighter shading. Most families with lower sampling are species poor (numbers in black circles show species richness). Lower panels show that sampling improves under more conservative taxonomic treatments of eBird (10,661 species in 249 families) and BirdTree (9993 species in 194 families). Coloured bars indicate the proportion of species in each family measured to different levels of completeness. 'Complete set' means a full set of all 9 core morphological traits (not necessarily from the same individual). 'Individuals' means any individual bird with one or more traits measured

altogether. Our rationale for using proxies rather than phylogenetic inference is presented in the Supplementary Material.

Geographical sampling

The 75,843 specimens contributing measurements to this dataset are held in 78 institutional or private collections in 31 countries worldwide (Figure 4). There is a strong bias to the Global North, particularly Europe and North America. Further coordinated sampling of museum collections is most urgently required in Africa and across much of Asia. Pooling across both museum and field data, we were able to assign 77,245 (85.8%) of 90,020 sampled individuals to a specific source country, leaving 12,775 (14.2%) unassigned. Mapping these countries of origin, and overlaying with species geographical ranges, revealed that our morphological traits have been sampled from populations in 206 administrative units, including 181 sovereign countries. Given the preponderance in our dataset of specimens from the Natural History Museum, London, it is no surprise to see a relatively high sampling in regions associated with the former British empire, including South and East Africa, India, Malaysia, Australia and New Zealand (Figure 5b,c). Other regions of dense sampling are North America, Brazil and China, while the main targets for future sampling are in Central and West Africa, the Middle East and North Asia (Figure 5b,c).

Intraspecific trait variation

Previous analyses based on earlier versions of this dataset indicate that most variance in trait values occurs among (98.25%) rather than within (1.75%) species (Pigot et al., 2020), suggesting that species are a valid sampling unit for bird traits at large taxonomic scales. This contrasts with the situation in plant traits, which typically

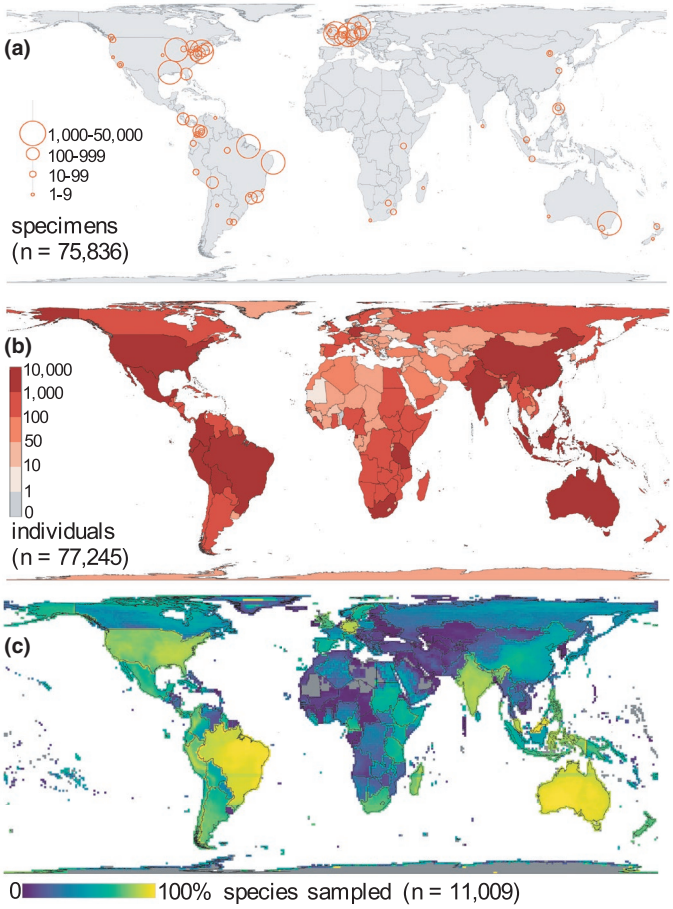

FIGURE 4 Geographical distribution of morphological data sampling. (a) Location of collections sampled (n = 78 museums or scientific collections in 31 countries), with the number of specimens per collection indicated by bubble size (excluding seven specimens from unknown museums). Sampling of live-caught and released individuals (n = 14,177) is not shown. (b) The number of individual birds sampled from each of 206 administrative units (181 countries), combining museum and field sampling (removing cases not assignable to administrative units). Darker colours indicate a larger number of specimens; specimens lacking precise information on the country of origin (n = 12,775) are not included. (c) The completeness of species sampling in each 100 km grid cell. Colours show the proportion of species present in that cell with specimens sampled from the same country in which the cell is located; warmer colours indicate higher proportions. Species presence was mapped as the portion of the species range occurring within the country, because the specimen is unlikely to have originated from outside the natural range

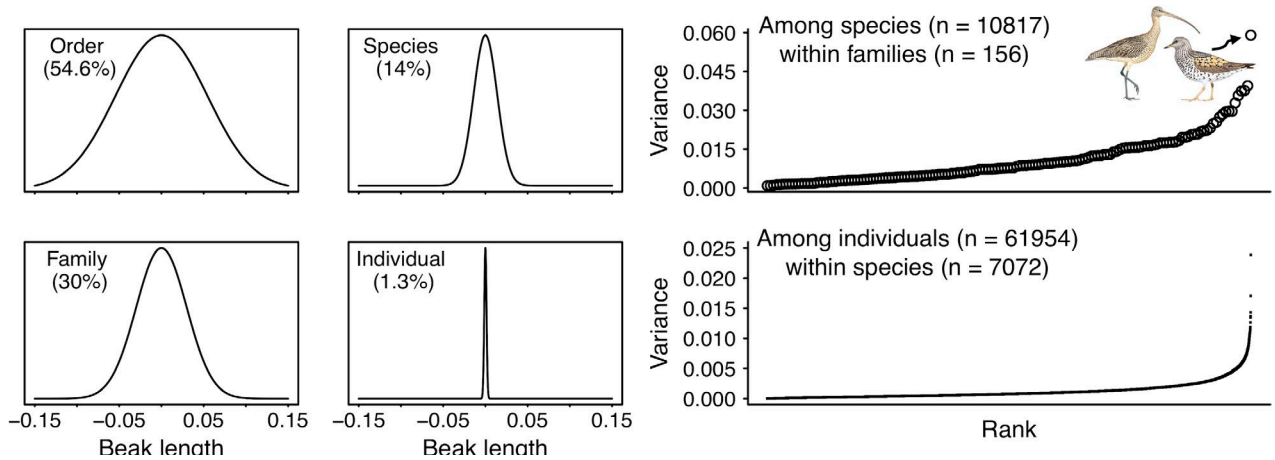

FIGURE 5 AVONET presents raw morphological data for 90,020 individual birds at an average of 8.1–9.0 individuals per species (varying by taxonomy), providing a foundation for a new generation of studies investigating or accounting for intraspecific variance. This figure illustrates how variance is partitioned for a key morphological trait (beak length). Left-hand panels show that most variance is explained at higher taxonomic levels (orders, family and species), whereas intraspecific (individual) variation is contrastingly low, supporting the use of species averages in comparative studies. Curves are normal distributions based on SD; percentages (%) show proportion of variance at each level. Right-hand panels show beak length variance within families and within species (restricting to families with >5 species and species with >5 individuals measured; note different axis scales in upper and lower panel). Sequential ranks show a 'hockey-stick' distribution with examples of the most extreme outlier family (Scolopacidae) illustrated. Extreme within-species values for beak variance may reflect polymorphism or, in some cases, measurement error

vary within species according to local conditions (light, soil chemistry, hydrology, etc.). Since the publication of Pigot et al. (2020) we have added multiple parallel datasets, increasing intraspecific sampling by 71%, rising from around 5.0 individuals per species to 9.0 individuals per species. In tandem, coverage by sex has increased to an average of 3.0 females, 4.6 males and 1.4 unsexed individuals per species (BirdTree dataset; Table S1). Using this expanded sample, and partitioning morphological variation among taxonomic levels, we show that almost all variance can be explained at the level of order, family and genus, whereas intraspecific variance is comparatively small (Figure 5). We conclude that the use of species average trait values is appropriate at a range of taxonomic scales in birds, although we note that much higher levels of inter- and intraspecific variance are detected for some traits in a minority of taxonomic groups (Figure 5).

Macroecological patterns of trait variation

We focus here on presenting an overview of the AVONET data rather than testing particular hypotheses. To illustrate potential uses of the data, we plotted macroscale geographical and ecological patterns for three key traits—HWI, tarsus length and beak length (Figure 6). At a global scale, spatial patterns show that HWI increases towards the poles, indicating strong variation in dispersal ability across latitudes and in relation to particular lifestyles. Relative tarsus length increases in less vegetated biomes (i.e. steppes, grasslands and deserts), reflecting adaptation to a more terrestrial lifestyle. Relative beak length shows a mirror image to this pattern, with increases in well-vegetated regions, including tropical rainforests. Definitions for relative beak and tarsus length are given in Figure 6. Previous work has shown the tight link between avian morphological traits and trophic niches (Pigot et al., 2020), whereas these patterns additionally reveal strong geographical trends in conjunction with a geographical clustering of different lifestyles. Our data also pinpoint certain trait syndromes. For example, species with aerial lifestyles have the shortest tarsi but the highest HWI, in line with their adaptation for frequent flight (Figure 6).

DISCUSSION

Our understanding of biodiversity is ultimately limited by the availability of data in a few critical areas, including species geographical distributions (the so-called 'Wallacean shortfall') and traits (the 'Raunkiæran shortfall'; Hortal et al., 2015). AVONET goes a long way towards addressing these shortfalls by summarising a complete set of morphological trait measurements, along with discrete ecological and geographical variables, for all extant species of birds. This resource provides a foundation for theoretical tests and technical innovations in ecology, evolution and conservation biology, yet also highlights the need for further sampling at the intersection of Wallacean and Raunkiæran shortfalls, where many gaps remain in the intraspecific and geographical sampling of bird traits.

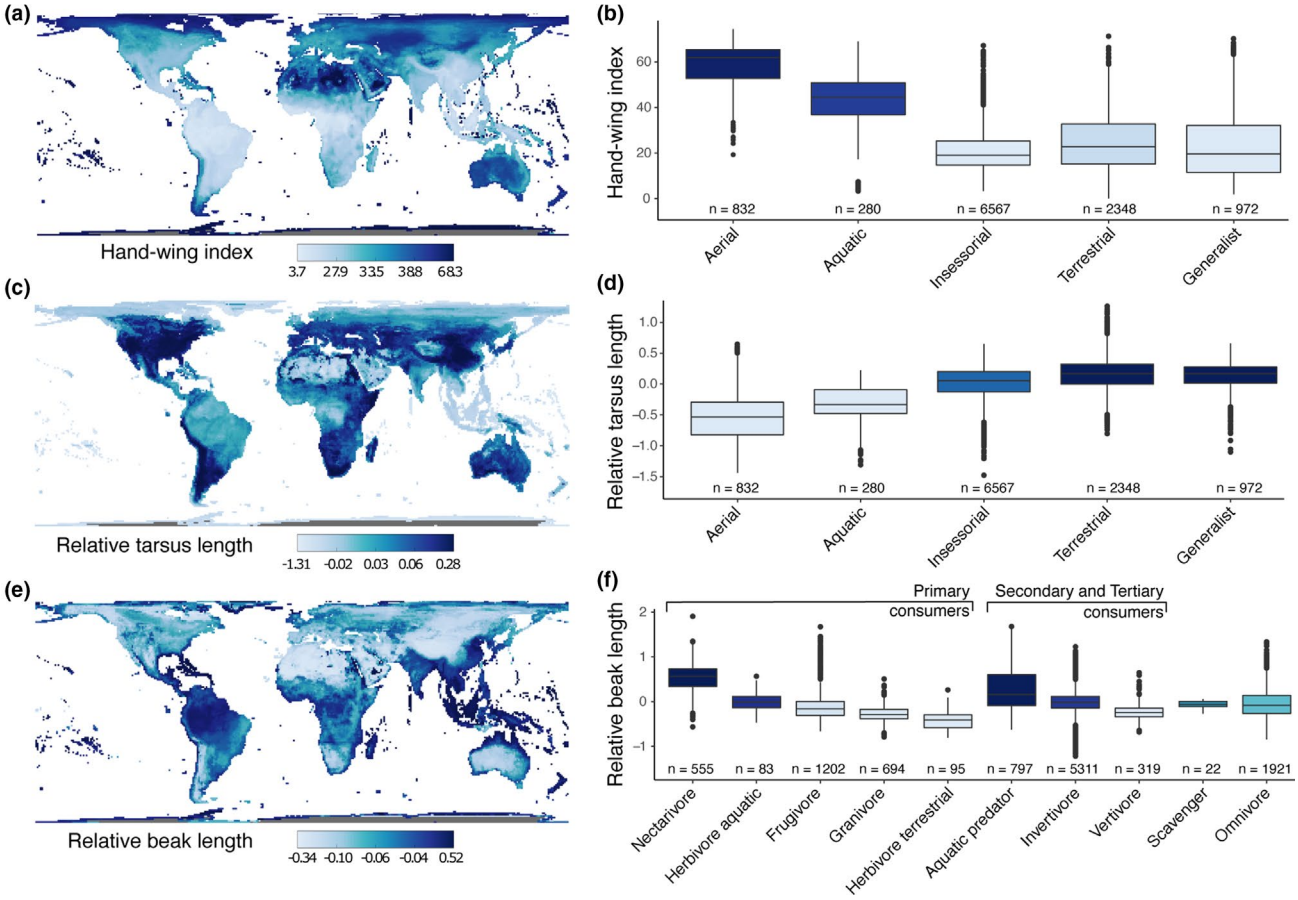

FIGURE 6 Species-level variation in avian functional traits in relation to geography and lifestyle. Hand-wing index (wing elongation) peaks towards high latitudes (a), and in species with aquatic and aerial lifestyles (b); relative tarsus length peaks at mid-latitudes and non-forest regions (c), and in species with terrestrial lifestyles (d); relative beak length peaks in the tropics, including rainforests (e), and in nectar feeders and aquatic predators (f). For maps, median trait values were calculated for 18,709 grid-cell assemblages worldwide. Darker colours indicate larger trait values. Assemblages were delimited by extracting species native resident or breeding distributions (n = 10,964 species for which both trait and geographical range data are available) onto an equal area grid with a cell resolution of ~100 km (Behrmann projection). Relative beak and tarsus length are the residuals of a linear regression of log-transformed tarsus and beak length (mm) against log-transformed body mass (grams). Species in (b,d) are classified according to primary lifestyle (predominant locomotory niche; insessorial = perching lifestyle). Species in (f) are classified according to primary diet following Pigot et al. (2020). Sample sizes (b,d,f) are numbers of species in each category

Our analyses show that morphological trait data in AVONET were sampled from bird populations throughout the world, with intensive sampling in many tropical regions. However, we also show that access to specimens underlying the dataset was distributed very unevenly, with most reference material stored in the collections of North American and European museums (Figure 5a). We hope that the publication of AVONET helps to remove these longstanding biases in access to museum collections by mobilising specimen data for global use.

Morphological traits of animals may fail to fulfil their promise of delivering ecological insights and theoretical advances if their connection to function varies idiosyncratically across evolutionary lineages or if they are uninformative about niche-based processes and interactions (Didham et al., 2016). These concerns are particularly relevant for global datasets wherein species coverage is so high that the set of traits assembled is relatively limited. Fortunately, these potential issues do not appear to undermine the utility of avian morphological traits given they predict trophic niches with remarkable accuracy (Pigot et al., 2020), including species interactions across trophic levels (Dehling et al., 2016). Moreover, we show that the same traits are also strongly indicative of habitat biomes and primary lifestyle. These results suggest that avian morphology is not only ecologically informative, but that the relationships between form and function are sufficiently general to develop the kind of predictive framework envisaged by Winemiller et al. (2015). Furthermore, we show substantial trait variation within taxonomic groups, lifestyles and diet categories, highlighting the importance of quantitative trait data as a basis for moving beyond the subjective and ultimately coarse categorical data used in most previous analyses of vertebrate functional traits (Kohli & Jarzyna, 2021).

The earliest phase of AVONET development involved different research groups independently collecting smaller subsets of trait data to explore a range of topics

in ecology and evolutionary biology, including adaptive radiation (Claramunt, 2010), character displacement (Tobias et al., 2014), community assembly (Trisos et al., 2014) and the predictive properties of traits in relation to ecological networks (Schleuning et al., 2015). The maturation and integration of these trait datasets into AVONET allows hypotheses to be tested at an ever-larger scale. For example, previous applications of trait-based indices of dispersal focused on avian sister species or individual clades (Kennedy et al., 2016; Pigot & Tobias, 2015) whereas the data are now available for global analyses (Sheard et al., 2020). Similarly, trait-based assessments of the impacts of global change on avian functional diversity have shifted focus from surveys of plots or transects (Bender et al., 2018; Bregman et al., 2015, 2016) to the global scale (Sol et al., 2020; Stewart et al., 2022).

Applications and future directions

Given the visibility and popular interest in birds, we already know more about their distribution and seasonal movement than any other major group of organisms (Tobias et al., 2020). If anything, the pace at which knowledge is accumulating for birds has accelerated over recent years through vast citizen science programmes generating hundreds of millions of distributional data points (La Sorte & Somveille, 2020; McEntee et al., 2018), while efforts are well underway to sequence the genomes of all bird species (Stiller & Zhang, 2019). The scale of these emerging resources suggests that morphological trait data for birds have numerous potential uses and applications. We map out these opportunities in more detail elsewhere, providing a short summary here.

Evolutionary applications span from understanding selection at the level of genes and populations to trait diversification over deep timescales. The opportunity to integrate complete trait information with high-quality genomes now available for hundreds of bird species (Feng et al., 2020) offers a model system for unlocking the genomic basis of adaptation (Stiller & Zhang, 2019). In parallel, AVONET trait data can now support more extensive testing of macroevolutionary hypotheses (e.g. Crouch & Tobias, 2022; Freeman et al., 2022) which have until recently been limited or invalidated by incomplete trait sampling (Drury et al., 2018; Phillips et al., 2018). The availability of comprehensive data will improve models of trait evolution and allow a more thorough examination of how evolutionary processes have led to birds exploring niche space and trait space. Large-scale phylogenetic comparative analyses will also benefit because many of these were previously constrained by the availability of key morphological indices, such as HWI or beak size (Derryberry et al., 2018). In both evolutionary models and comparative analyses, the power of trait-based approaches will increase rapidly as the quality of avian phylogenetic data continues to improve.

In the fields of macroecology and biogeography, AVONET data have immediate uses in quantifying the trophic structuring of diversity gradients (Hanz et al., 2019; Pigot et al., 2016) and understanding the mechanisms of species coexistence and community assembly (Pigot et al., 2018). In the context of ecosystem science, species-level variation can now be applied to understanding the trophic interaction networks regulating key ecological processes, such as insect predation, pollination and seed dispersal (Bender et al., 2018; Schleuning et al., 2015). Comprehensive functional trait data for species delivering these 'services' may, over time, provide valuable insight into the impacts of biodiversity loss on ecosystem function (Tobias et al., 2020).

Avian functional traits, in conjunction with detailed information on bird distribution and movements, provide an opportunity for monitoring and assessing the impacts of global change. Integrating functional perspectives may help make sense of the variation in species responses to change (Bender et al., 2019), enabling the development of more general and mechanistic models of current and future changes in distribution and diversity (Estrada et al., 2016). For instance because the morphological data in AVONET cover different aspects of species ecology, from movement (reflected in wing shape) to feeding (reflected in beak shape), these data can be used to parameterise global range shift models with morphological indices of dispersal and trophic niche structure respectively (Stewart et al., 2022). In addition, trait-based analyses show promise in understanding and predicting the effects of environmental change on trophic interaction networks (Gravel et al., 2016; Schleuning et al., 2020), with implications for the conservation of key ecosystem processes regulated by birds, such as seed dispersal and pest control (Bregman et al., 2015, 2016). In a more general sense, since AVONET data are explicitly aligned with the taxonomy underpinning the IUCN Red List, they will provide a rich seam to explore for conservation biologists wishing to understand the causes and consequences of biodiversity loss (Weeks et al., 2022).

Despite attaining comprehensive species-level coverage, our results reveal uneven representation of avian diversity across and within countries (Figure 5b,c). The next step is to improve intraspecific sampling and geographical coverage for all species—common and rare—to provide a better description of individual trait variation across space and time (Des Roches et al., 2018). Ideally, this will involve continued sampling of historical museum collections, as well as wild individuals mist-netted and released by field projects, to provide the most complete time series and widest spatial sampling. To these ends, we have included missing species to highlight sampling coldspots in Supplementary Dataset 1, and supplied our trait sampling protocol

(Supplementary Materials) to improve the standardisation of morphological trait data for incorporation into AVONET.

CONCLUSIONS

We present a complete description of morphological and ecological trait diversity for all birds (Aves), the largest class of tetrapod vertebrates. The achievement of total species coverage at this scale sets a new standard for morphological trait data. All specimen-level data and metadata are included. Our results confirm that avian traits have distinct associations with diet, environment and lifestyle, offering a framework for testing ecological theory, identifying underlying mechanisms and predicting the response of biodiversity to global change. Although we have focused exclusively on birds, we hope this venture will inspire similar efforts across other animal systems, opening up the possibility of future integration across vertebrate databases.

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AUTHORSHIP

JAT initiated and developed the core dataset and conceived the publication. JAT, MS, GHT and SAF worked on the conceptual framework for the paper. CS coordinated the initial phase of data collection and measured over 10000 specimens. MHCN, NA, HEAM, PAW, SEIJ, CV, AGP, NMM, FMC, VLS, SC, BD, BGF and TPB also collected substantial trait datasets (>1500 specimens measured). LNN, KBG, CR, GHT, SAF and MS coordinated independent trait datasets and helped with merging data. Additional authors contributed smaller trait datasets. AJMD, TLW, RAB, JY, PAW and FS helped with data management and integration of datasets. ALP, AJMD, JY, FS, SAF and JAT conducted analyses and produced figures. JAT wrote the first version of the manuscript with input from MS and ALP. All authors contributed critically to subsequent drafts and gave final permission for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13898.

OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at: https://figshare.com/s/b990722d72a26b5bfead

DATA AVAILABILITY STATEMENT

The AVONET dataset and all code for figures and analyses in this manuscript are archived on Figshare (https://figshare.com/s/b990722d72a26b5bfead).

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