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EDITORIAL

A bird in the hand: Global-scale morphological trait datasets open new frontiers of ecology, evolution and ecosystem science

The recent prominence of functional traits in ecological analyses is based on the premise that measurable attributes of an organism's phenotype can take us beyond simple lists of species and closer to valid tests of mechanisms and processes (Cadotte et al., 2011). However, the full potential of trait-based ecology and evolutionary biology is ultimately constrained by incomplete coverage and completeness, particularly in the case of morphological traits (Etard et al., 2020). Filling these gaps in data coverage has proved challenging, with even the best-sampled major taxonomic groups—such as vascular plants—still lacking comprehensive morphological measurements for well over 50% of species worldwide (Hietz et al., 2021; Kattge et al., 2020; Violle et al., 2014). A major step has now been taken towards addressing this challenge with the completion of datasets containing multiple morphological traits for all 11000 bird species (Tobias et al., 2022). The goal of this special issue is to present these data for wider use alongside a series of studies summarising recent advances based on morphological analyses, highlighting their potential application to research and policy.

The most widely used functional traits in macroecological and macroevolutionary analyses are categorical variables, mainly including information on habitat, life-history or diet (Jones et al., 2009; McLean et al., 2021; Wilman et al., 2014). These datasets have been highly influential, yet overall progress has been impeded because many categorical traits are relatively crude and uninformative, reducing their utility as indices of ecological function (Kohli & Jarzyna, 2021). Moreover, they offer an imperfect framework for some statistical models and phylogenetic analyses since many species are assigned the same values and the distance between categories is arbitrary. An obvious solution is to use continuous morphological variables, as these vastly improve the resolution of evolutionary models (Chira et al., 2018) and metrics of community assembly (Blonder et al., 2018; Ricklefs & Travis, 1980). To date, the availability of complete continuous morphological trait datasets has been largely restricted to body mass (Wilman et al., 2014), which is only weakly connected to ecological function (Pigot et al., 2020). A hawk and a duck may share the same body size, for example, but this tells us very little about their functional role in the ecosystem. Analyses based on more detailed compilations of morphological traits have not been possible outside a few well-studied families, leading to a variety of problems including sampling bias and inaccurate evolutionary models (Chang et al., 2020; Mouillot et al., 2021; Tobias et al., 2020).

Birds offer the best opportunity to address the challenge of comprehensive trait coverage for a number of reasons. First, overall species richness (~11,000 species) is far lower than plants, for instance, offering a more achievable target. Second, birds are distributed worldwide across all oceans and terrestrial biomes, where they perform a range of key ecological services (Şekercioğlu, 2006). Third, because of their visibility and appeal, they are the best-studied clade at this global scale, with extensive datasets now available on distribution, abundance, ecology and life history for almost all species (Bird et al., 2020; Callaghan et al., 2021; Sullivan et al., 2014; Tobias et al., 2020; Tobias & Pigot, 2019; Wilman et al., 2014). Fourth, bird morphology offers a classic system for investigating a range of novel ecological questions because their beaks, legs and wings provide insight into trophic interactions, locomotion and dispersal respectively (Dehling et al., 2016; Pigot, Trisos, et al., 2016; Sheard et al., 2020). Indeed, birds are unique in that specific combinations of traits have been shown to predict key functional characteristics, including dietary niche and foraging behaviour, with far greater accuracy than body mass alone (Kennedy et al., 2020; Pigot et al. 2020).

The power of morphological traits to predict ecology was initially established by a series of papers on bird communities from 1960 onwards (e.g. Miles & Ricklefs, 1984). Although these analyses were based on relatively small samples of species (see Tobias et al., 2022, Figure 1), they provided the conceptual foundation for the field of ‘ecomorphology’ (Bock, 1994; Wainwright & Reilly, 1994) which in turn drove the subsequent (post-2000) development of avian functional ecology based on continuous variables. Over the last two decades, several research groups compiled and analysed bird trait datasets of gradually increasing size, initially targeting manageable samples of a few hundred species (e.g. suboscines: Claramunt, 2010; corvides: Kennedy et al., 2016) or local assemblages (e.g. Manu National Park, Peru: Dehling, Fritz, et al., 2014; Pigot, Bregman, et al., 2016), and more recently spanning thousands of species worldwide (e.g. Cooney et al., 2017; Kennedy et al., 2020; Phillips et al., 2018; Pigot et al. 2020). However, these resources have

FIGURE 1 Global bird diversity spans an astonishing variety of phenotypes. This variation in morphological form is closely connected to ecological function because traits such as beaks, wings and legs are shaped by adaptation to particular niche dimensions, including diet, foraging strategy, flight ability and locomotion. The publication in this special issue of detailed morphological measurements for over 90,000 individuals of approximately 11,000 bird species offers a trait-based framework with a wide range of potential applications, from research and teaching to environmental management and policy. Photographs by J.A. Tobias (www.tobiaslab.net/gallery)

until now been fragmented, with raw data largely incompatible and unpublished.

To provide an integrated resource with broad utility, managers of different bird trait datasets have joined forces to merge their work into AVONET, a compendium of morphological, ecological and geographical data for all bird species published as the flagship article of this special issue (Tobias et al., 2022). AVONET was inspired by the success of the TRY plant trait database, a potent catalyst of high-impact research in ecology and ecosystem science over the last decade (Kattge et al., 2020). To maximise the likelihood of a similar positive impact, and to align with Open Science principles (Gallagher et al., 2020), AVONET is released as individual measurements of specimens as well as species averages, without restrictions on data access.

To some degree, the publication of AVONET marks an endpoint a personal journey. My fascination with bird traits began in the 1980s as a schoolboy walking the tidelines and powerlines of Northumberland in search of corpses for dismembering. I owe a belated debt of thanks to my mother for abiding with bedroom shelves full of skulls and cabinets loaded with malodorous wings and tarsi. But the story of AVONET extends far wider than that, and deeper in time. The completion of this first iteration—AVONET 1.0—is a truly international effort, with vital expertise and data contributed by 115 authors based at 106 institutions in 30 countries. The most important shifts in momentum occurred when the project was joined by colleagues managing their own extensive trait datasets, including Santiago Claramunt (Uruguay), Matthias Schleuning and Susanne Fritz (Germany), Carsten Rahbek (Denmark), Gavin Thomas (United Kingdom) and Gustavo Bravo (Colombia).

A common denominator among these major datasets is their reliance on museum specimens. Across AVONET as a whole, most specimens were measured at the Natural History Museum, London and the American Museum of Natural History, New York, with smaller samples from a further 76 collections (see Tobias et al., 2022, Fig. 4). Indeed, the project would not have been possible without the contributions of countless museum curators, field assistants and specimen collectors since the mid-1800s, some luminaries among them, including Charles Darwin, Alfred Russell Wallace, Ernest Shackleton and John James Audubon, all of whom prepared specimens subsequently measured for trait data. Ultimately, given the key importance of well-preserved specimen material for trait-based ecology, AVONET is a monument to the museum community and the crucial service it provides to scientific research and human society in general (Suarez & Tsutsui, 2004).

Many sources of information were distilled to provide the first detailed summary of morphological, ecological and geographical data contained in AVONET. Using this resource, anyone can now extract traits, ecology and spatial context for any avian taxon or assemblage—indeed, even for the entire radiation of extant birds. The data can be used to fit models, test hypotheses, or to calculate biodiversity metrics, including various dimensions of functional diversity. Comprehensive data improve the validity of these methods and increase the scale at which they can be applied. For example, tests of evolutionary models can be executed not only on well-sampled clades (e.g. Drury et al., 2018; Tobias et al., 2014) but also across far wider tracts of the avian phylogenetic tree (Crouch & Tobias, 2022). Similarly, methods using traits to quantify niche differences among species are no longer limited to smaller samples (e.g. Pigot & Tobias, 2013) and can now be applied across all birds (Drury et al., 2021; Freeman et al., 2022; Pigot et al., 2018).

A unique feature of AVONET is that trait data are presented in alignment with three alternative taxonomic treatments: BirdLife International, Clements and BirdTree (Tobias et al., 2022). In theory, this will be a major time-saver for users, facilitating integration with published geographical range maps and IUCN Red List data, eBird citizen-science data (Sullivan et al., 2014) and the global bird phylogeny (Jetz et al., 2012). Interoperability across these datasets allows an array of research questions to be addressed in novel ways. The following sections summarise recent progress in applying AVONET data across different research fields along with a horizon-scan of emerging opportunities.

MACROEVOLUTION AND GENOMICS

Although the current global BirdTree (Jetz et al., 2012) is far from perfect and urgently requires an update, it has nonetheless provided a valuable tool for phylogenetic analyses. Recent studies combining AVONET traits with phylogenies downloaded from BirdTree or elsewhere have explored an array of evolutionary topics, including the role of species interactions (e.g. McEntee et al., 2018), ecology (e.g. Crouch & Tobias, 2022) and geographical context (e.g. Benítez-López et al., 2021) in driving phenotypic evolution. With the rapid ongoing improvement of avian phylogenies and the associated toolkit of evolutionary models, AVONET trait data offer an unparalleled template for future analyses of this kind. In particular, there is scope for a new wave of studies focused on intraspecific variation and sex differences, both of which are made possible by the open release of underlying raw measurements for over 90,000 individual birds.

Avian genomics is another advancing frontier of evolutionary research, with efforts to sequence the genomes of all extant bird species now well underway (Jarvis, 2016). At the current rate of progress, whole-genome assemblies will soon be sampled for all extant avian genera (>2000), putting birds at the forefront of comparative genomics (Stiller & Zhang, 2019). AVONET data can play a key role in the next phase of this research programme, both in terms of providing traits for genome-wide association studies (GWAS) and predictors in models exploring the drivers of demographic patterns and responses over deep time (Nogués-Bravo et al., 2018).

MACROECOLOGY AND COMMUNITY ECOLOGY

The availability of AVONET trait data allows variation in morphological traits to be mapped and analysed at global scales with reduced sampling bias. The first phase of such analyses included tests of geographical gradients in dispersal-related traits (Sheard et al., 2020) and the role of island colonisation as a driver of predictable trajectories of trait evolution—the so-called ‘island rule’ (Benítez-López et al., 2021). Further studies are needed to explore numerous other putative ecogeographical patterns, such as Bergmann's and Allen's rules, in greater detail. For example, AVONET data open up the possibility of partitioning these effects across different components of phenotype, including trophic, locomotory and dispersal traits.

Quantification of niches via morphology may help trait-based analyses to illuminate the complex mechanisms driving community assembly (McGill et al., 2006; Trisos et al., 2014). In particular, the well-established connection between morphological traits and trophic niches in birds (Pigot et al. 2020) suggests that ecological patterns and processes can be inferred from the trait structure of bird communities. Until recently, a key challenge has been that most approaches for estimating community structure are sensitive to gaps and biases in trait datasets (Blonder et al., 2018; Bregman et al., 2016). This challenge has now been addressed with complex morphometric data based on 3-d scanning of bird beaks for several thousand species (Hughes et al., 2022), while AVONET also provides data sufficiently extensive and comprehensive to estimate the trait structure of communities at any scale, from local sites (e.g. Cannon et al., 2019; Chapman et al., 2018; Trisos et al., 2014) to continental or global assemblages (e.g. Sol et al., 2020; Stewart et al., 2022).

Movement—or dispersal—is another important cross-cutting theme with relevance to many biological questions. The most promising dispersal trait in birds is the hand-wing index (HWI), a metric of wing-shape related to flight efficiency and dispersal ability (Claramunt, 2021; Sheard et al., 2020). AVONET provides calculations of HWI based on two linear wing measurements (wing chord and first secondary length). The first phase of analyses using earlier versions of AVONET data demonstrated the key role of dispersal in shaping patterns of allopatric speciation (Claramunt et al., 2012) and the build-up of alpha diversity worldwide (Pigot et al., 2018; Pigot & Tobias, 2015). Other analyses have used the same HWI data to test ideas in multiple fields, from evolutionary biology (Menezes & Palaoro, 2022; Stoddard et al., 2017) to conservation (Thaxter et al., 2017). The updated summary of HWI for all bird species released in AVONET may prove useful in any phylogenetic model or comparative analysis testing hypotheses related to dispersal, or wherein variation in dispersal needs to be accounted for. For example, HWI can now be used as an index of dispersal to improve the accuracy of models forecasting geographical range shifts of species under future climate change scenarios (Stewart et al., 2022).

Zooming in from assemblage-level analyses to species interactions brings a further set of opportunities into focus. The relationships between morphological traits and key dimensions of avian ecological niches validates the use of trait divergence in studies of range expansion and invasion success among related species. The results of previous analyses are inconclusive, suggesting that trait similarity may either constrain (Pigot & Tobias, 2013) or promote coexistence (Sol et al., 2022) depending on context. Further exploration of this issue is warranted because trait-based metrics of niche similarity and dispersal ability (HWI) may help us to predict the extent of future range shifts and overlaps, a key goal of predictive models in macroecology and biogeography (Tobias et al., 2020).

ENVIRONMENTAL CHANGE

While understanding and forecasting geographical range shifts is a major goal, the morphological traits in AVONET have numerous other potential applications to global change research. Correlative studies sampling across hundreds or thousands of bird species can now investigate whether traits predict responses to climate change (e.g. Neate-Clegg et al., 2021). Similarly, studies applying techniques developed in community ecology have begun to explore how the trait structure and functional diversity of bird assemblages are affected by climate change (Bender et al., 2019; Stewart et al., 2022), urbanisation (Sol et al., 2020), and agricultural expansion (Cannon et al., 2019; Chapman et al., 2018; Rurangwa et al., 2020). Using a trait-based approach can also give important insights into functional turnover between system states. For example, the functional diversity of invasive bird species on oceanic islands does not offset the loss of functional diversity through anthropogenic extinctions (Sayol et al., 2021). Similar questions are ripe for investigation in numerous global-change contexts.

While the first phase of this research has focused on the impact of environmental change on the functional diversity of bird communities, there is increasing awareness that environmental change can also drive changes in the morphological traits of particular species (Ryding et al., 2021). One example is the idea that climate change has consistent effects on avian morphological evolution, including selection for smaller body sizes and longer wings at higher temperatures (Weeks et al., 2020). With the addition of further specimen sampling and metadata, the extensive intraspecific sampling of traits for many species in AVONET should allow a more thorough exploration of these trends, particularly because morphological changes can be tracked over the last two centuries using dated museum specimens.

Another promising line of research involves the quantification of trait–environment relationships. If these are sufficiently consistent then trait-based correlative approaches may be used to forecast functional changes to future biomes or communities (Boonman et al., 2022; Enquist et al., 2015). Similar approaches could be applied to bird trait datasets, or indeed a combination of bird and plant traits, to provide a multi-trophic perspective. Trait-matching across trophic levels can also be used to monitor and predict the effects of environmental change on species interactions key to ecosystem function (Schleuning et al., 2020). The first empirical steps towards this target were taken using local-scale datasets to forecast shifts in the functional relationships between plants and birds under climate change projections (Nowak et al., 2019). Similar analyses are now feasible at a global scale.

BIODIVERSITY CONSERVATION AND ENVIRONMENTAL POLICY

Assemblage-based analyses have begun to incorporate AVONET data to assess how the impacts of anthropogenic threats vary under different landscape contexts, an approach that can help to highlight land-use management practices that minimise ecological damage (Sol et al., 2020). At a global scale, similar approaches reveal an inverse relationship between avian functional diversity and extinction risk, suggesting that strategies to maximise trait diversity in current ecosystems may be effective in preventing extinctions (Weeks et al., 2022). Diversity of morphological traits can even be plugged into multi-level ecosystem models to clarify the impacts of environmental change on ecosystem dynamics (e.g. Purves et al., 2013) and the provision of ecosystem services (e.g. Díaz et al., 2013).

AVONET also paves the way for a rethink about biodiversity indicators. For example, trait diversity in disturbed landscapes can now be compared against undisturbed baselines to assess functional intactness, calculated for overall assemblages or partitioned into different trophic groups delivering key services, such as seed dispersal (by frugivores) and pest control (by invertivores). The morphological diversity of bird communities also provides a foundation for functional indicators of habitat quality and ecosystem health, with untapped potential in commercial or governmental policy settings, for instance as metrics to identify the target and extent of biodiversity offsets (Gamarra et al., 2018) or nature-based solutions to climate change (Seddon et al., 2021). Now that we have the appropriate data in hand, a phase of implementing these methods and testing their outputs is required.

ECOSYSTEM SCIENCE

Among the most ambitious visions for trait-based ecology are those proposing fuller integration of highly resolved functional trait data to provide quantitative indices of ecosystem structure and function (Cadotte et al., 2013; Mouillot et al., 2021; Tilman et al., 1997). For example, linking functional traits with metabolic and allometric scaling may provide the basis for a general theory of biodiversity that can be scaled up to understand and predict ecosystem function (Enquist et al., 2015). These objectives can in theory be brought into closer reach with comprehensive morphological traits. One set of approaches—loosely defined as functional biogeography—involves mapping the geographic distribution of animal form and function across trophic levels (Violle et al., 2014). Another approach uses trait matching among species to explore key ecosystem processes mediated by various kinds of interaction networks, including trophic interactions, such as those connecting producers (e.g. plants) and consumers (e.g. birds). Previous analyses have demonstrated or assumed trait matching at the local scale (Bregman et al., 2016; Dehling, Töpfer et al., 2014; Dehling et al., 2016), while AVONET data now allows such patterns to be explored globally (e.g. McFadden et al., 2022). Finally, as ecological network and plant trait datasets improve, combining these resources with AVONET data provides an opportunity to apply and develop new methods for assessing trait-based patterns and correlations over large spatial scales in a multi-trophic context (Albrecht et al., 2018; Wilkes et al. 2020).

EMERGING CHALLENGES AND OPPORTUNITIES

While AVONET 1.0 is an endpoint in some respects, it is also a beginning. Progress towards AVONET 2.0 is underway, with several behavioural and life-history trait datasets nearing completion. There is also plenty of scope for improving morphological trait data. Deeper intraspecific sampling from a wider geographical area is required, along with dates of collection for museum specimens, to investigate and monitor adaptation to changing environments over space and time. Second, future iterations of AVONET should include a wider spectrum of traits, including those correlated with different dimensions of ecological niches, such as light intensity (predicted by eye size; Ausprey et al., 2021) and thermal constraints (predicted by plumage colour or reflectance; Medina et al., 2018). Amassing these data will require a collective effort from the research community and amateur field ornithologists: everyone is welcome to join the next phase of trait measurement by using and expanding the AVONET protocol (see Tobias et al., 2022, Supplementary material).

Two limitations to the morphological trait data in AVONET 1.0 are worth mentioning. First, the traits are quantified using relatively simplistic linear measurements which, for example, may capture the major axes of beak shape (length, width and depth) without accounting for more subtle aspects like curvature. The curvature of beaks is perhaps irrelevant to most macroecological studies but is a key factor in some systems, for example, coevolution between hummingbird beaks and flower corollas (Leimberger et al., 2022). Data on curvature and other beak shape parameters can be accessed using a parallel resource also published openly in this special issue: the Macrobird database containing beak-shape information based on numerous on-screen landmarks of 3-d scans (Hughes et al., 2022). Second, AVONET only contains extant and recently extinct species, with many extinct taxa currently missing. Some progress in addressing this gap has been achieved by measuring traits of extinct island birds (e.g. Sayol et al., 2021) but further efforts are needed to bridge between fossil trait data and extant species, focusing on comparable traits (e.g. tarsus and other skeletal characters).

The traits of extant species compiled in AVONET have already been used as predictors in unexpected ways, such as in analyses asking what characteristics best explain variation in the cultural importance of birds to people (Echeverri et al., 2019). Other creative applications will no doubt arise through integration with rapidly expanding data sources covering a wide range of species-level information. One example is eBird, a citizen-science database providing access to millions of georeferenced bird observations worldwide, allowing fine-grained monitoring of species occurrence and population trends (McEntee et al., 2018; Sullivan et al., 2014). In addition, the interface between trait-based ecology and population biology can now be explored by linking AVONET data with global databases on population parameters and demography (Bird et al., 2020; Salguero-Gómez et al., 2018). A little further off on the horizon, but nonetheless enticing, is the vision of an online ecosystem consisting of interconnected and interoperable trait datasets through which the architecture of trophic connections between plants and animals can be navigated and quantified.

RESEARCH AND TEACHING TOOLS

The morphological data presented in AVONET is based on fieldwork conducted over many decades by thousands of people involved in specimen collecting expeditions and mist-netting surveys. Similarly, the ecological and geographical information is distilled from published observations of thousands of field ornithologists. Building on these efforts, AVONET provides a ready-made template for research and teaching in desk-based or lab-based settings. The preceding sections give some pointers to the breadth of questions that can now be addressed by undergraduate and post-graduate research projects. During recent lockdowns, when field seasons, field training courses, lab practicals and in-person teaching were all put on hold by the Covid-19 pandemic, global-scale bird trait data came into its own, allowing research and teaching to continue from home. Some PhD projects changed tack and morphological trait data provided a basis for redesigned practicals and statistical coursework in undergraduate and masters modules. Among many possible uses, students can test evolutionary or ecological hypotheses using phylogenetic and community assembly models, or even devise strategies for conserving functional diversity. AVONET now gives open access to multi-purpose, lockdown-proof research and teaching materials for anyone with internet access.

CONCLUSIONS

Major advances in avian macroecology and macroevolution were catalysed by the arrival of global maps of all bird ranges (Orme et al., 2006) and a near-complete phylogenetic tree (Jetz et al., 2012), which together allowed general trends to be identified from large datasets. The release of new morphological trait data for all bird species has similar potential to revolutionise models of evolution and community assembly, and to provide a more informative toolkit for understanding and forecasting the response of ecosystems to environmental change (McGill et al., 2006; Tobias et al., 2020). By presenting the first complete summary of morphological trait variation across a diverse global radiation, AVONET takes an important step towards more integrative metrics of ecosystem function (Cadotte et al., 2011; Violle et al., 2014). In conjunction with a range of other trait datasets (e.g. Kattge et al., 2020), these metrics can help to re-invigorate efforts to develop more predictive ecology (Mouquet et al., 2015), and to provide sophisticated biodiversity indices with wide applications in research, corporate strategies, international treaties and policy frameworks (Díaz et al., 2013).

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