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DATA ARTICLE

AVOTREX: A Global Dataset of Extinct Birds and Their Traits

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ABSTRACT

Motivation: Human activities have been reshaping the natural world for tens of thousands of years, leading to the extinction of hundreds of bird species. Past research has provided evidence of extinction selectivity towards certain groups of species, but trait information is lacking for the majority of clades, especially for prehistoric extinctions identified only through subfossil remains. This incomplete knowledge potentially obscures the structure of natural communities, undermining our ability to infer changes in biodiversity across space and time, including trends in functional and phylogenetic diversity. Biases in currently available trait data also limit our ability to identify drivers and processes of extinction. Here we present AVOTREX, an open-access database of species traits for all birds known to have gone extinct in the last 130,000 years. This

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database provides detailed morphological information for 610 extinct species, along with a pipeline to build phylogenetic trees that include these extinct species.

Main Types of Variables Contained: For each extinct bird species, we provide information on the taxonomy, geographic location, and period of extinction. We also present data on island endemicity, flight ability, and body mass, as well as standard measurements of external (matching the AVONET database of extant birds) and skeletal morphology from museum specimens where available. To ensure comprehensive morphological data coverage, we estimate all missing morphological measurements using a data imputation technique based on machine learning. Finally, we provide an R package to graft all extinct species onto a global phylogeny of extant species (BirdTree).

Spatial Location and Grain: Global.

Time Period and Grain: All known globally extinct bird species from 130,000 years ago up until 2024.

Major Taxa and Level of Measurement: Birds (Class Aves), species level.

Software Format: Spreadsheets (.csv) stored in Dryad.

1 | Introduction

Recent years have witnessed a remarkable transformation in the availability of data on species traits (Etard, Morrill, and Newbold 2020; Moura et al. 2024), revolutionising our understanding of biodiversity and ecological processes (Schleuning, García, and Tobias 2023). The emergence of various collaborative efforts has significantly enhanced data availability, leading to the publication of comprehensive species-level trait datasets for vertebrates (Jones et al. 2009; Wilman et al. 2014; Myhrvold et al. 2015; Galán-Acedo et al. 2019; Tobias et al. 2022; Moura et al. 2024) and vascular plants (Kattge et al. 2011, 2020; Tavşanoğlu and Pausas 2018; Weigelt, König, and Kreft 2020). These datasets have stimulated research that has provided valuable insights into the variation in functional diversity across space and time (Díaz et al. 2016; Cooke, Eigenbrod, and Bates 2019; Loiseau et al. 2020; Pigot et al. 2020). Nevertheless, it is increasingly recognised that human impacts have been reshaping Earth's biodiversity, with anthropogenic activities known to have resulted in the extinction of thousands of vertebrate species (Dirzo et al. 2014; Ceballos et al. 2015; Di Marco et al. 2018; Otto 2018; Tollefson 2019; Cooke et al. 2023). Failure to account for extinct species in ecological and macroecological analyses is therefore likely to impair and potentially bias our understanding of the evolution, distribution, and function of biodiversity (González-Suárez, Lucas, and Revilla 2012; Boyer and Jetz 2014; Helmus, Mahler, and Losos 2014; Faurby and Svenning 2015; Triantis et al. 2022; Matthews et al. 2023).

Many bird species have suffered the detrimental consequences of anthropogenic pressures. Iconic extinct birds, such as the Dodo (*Raphus cucullatus*), the Elephant Birds (an entire order with two known genera and three species), and the Moas (an entire order with six known genera and nine species), serve as poignant examples of distinct lineages driven to extinction by human activities. Incorporating information on these extinct species could have important implications for our understanding of biodiversity, from speciation to trait evolution. For example, the frequency of evolution towards flightlessness in birds is underestimated if anthropogenic bird extinctions—many of which involved flightless species—are not included in the analysis (Sayol et al. 2020). Indeed, our understanding of the sensitivity of extant birds to different threats indicates that species vulnerability to extinction is strongly shaped by their functional traits: for example, large-bodied and long-lived species tend to be more threatened (Owens and Bennett 2000; Bird et al. 2020; Chichorro et al. 2022; Matthews et al. 2022). The link between traits and sensitivity suggests that future species loss will involve the non-random extinction of bird species, resulting in a disproportionate loss of functional diversity (Ali et al. 2023). However, our current understanding is based largely on studies of extant species, and the question of how extinction risk is related to traits needs to be revisited in the context of data from extinct species.

It is now widely acknowledged that current macroevolutionary and macroecological patterns are impacted by recent species extinctions. For example, island systems are known to have suffered a disproportionate number of extinctions (Whittaker, Fernández-Palacios, and Matthews 2023). These losses have impoverished insular avian radiations (Illera et al. 2024), decreased the functional alpha (Sobral, Lees, and Cianciaruso 2016; Sayol et al. 2021) and beta-diversity (Soares et al. 2022) of islands and archipelagos, and changed the form of the island diversity–area relationship (Matthews et al. 2023). Despite attempts to include extinct bird species and their traits in island biodiversity analyses (Sobral, Lees, and Cianciaruso 2016; Sayol et al. 2021; Matthews et al. 2022, 2023; Soares et al. 2022; Triantis et al. 2022), trait information for extinct birds remains highly scattered and is mainly available only for well-studied archipelagos (Sobral, Lees, and Cianciaruso 2016; Sayol et al. 2021; Heinen et al. 2023). As a result, most studies to date have focused on particular regions or systems, and a comprehensive global dataset of anthropogenic bird extinctions and their traits is still lacking.

Here, we address this shortfall and present the AVOTREX database, a comprehensive repository of species-level traits for all known extinct bird species ($n = 610$) worldwide covering the period from 130,000 years ago to the present day. The database provides valuable information on geographical location, island endemicity, and 10 species-level traits, including flight ability, body mass, and standard measurements of eight external traits (including beak, tarsus, wing, and tail length). These eight morphological measurements match AVONET, a recently published trait database of all extant birds (Tobias et al. 2022). The AVOTREX dataset also includes 22 skeletal measurements, which help to infer external morphological trait values for species with subfossil remains. To infer missing trait values, we use recent advances in machine learning techniques to integrate measurements from different sources (i.e., skeletal and skin material), together with taxonomic information. Additionally, AVOTREX provides a pipeline for constructing phylogenetic trees including both extant and extinct birds. Based on its breadth and functionality, we hope that AVOTREX will allow a more realistic quantification of phylogenetic and functional diversity loss.

2 | Methods

All the datasets cited throughout the text are available in the AVOTREX (v. 1.0) Dryad repository (https://doi.org/10.5061/dryad.zgmsbcckk).

2.1 | Known Extinct Bird Species

We compiled a list of all known bird extinctions that have occurred over the last 130,000 years ("Avotrex_taxonomy_v1" dataset). This includes all extinction events that have been recorded since modern humans began to migrate out of Africa and spread across the globe (i.e., from the Late Pleistocene onward). We updated an existing list of 581 species (Sayol et al. 2020) by compiling data from published monographs and books (Steadman 2006; Turvey 2009; Hume 2017). To update this inventory, we undertook a literature search in Google Scholar combining a list of geographical terms + avian OR bird + extinct OR fossil. The list of geographical terms included continents (Asia, Africa, etc.), oceans (Pacific, Atlantic, etc.) and main island regions (Macaronesia, Melanesia, etc.). We then screened titles and abstracts to identify sources reporting extinct bird species. Cited references within all sources were also screened to identify further relevant literature.

Our final dataset only includes species that became extinct since the onset of the last Pleistocene interglacial period (130,000 years ago), which is determined by their presence in more recent fossil deposits or by contemporary records of the species. Each species was given a unique identifier ("sp_id") to allow tracability across dataset versions (i.e., potential taxonomic changes). Considering the date of extinction (or last record), each species was classified using a set of status codes: "EX"—species that went extinct after 1500 CE (Common Era) that are documented by the International Union for Conservation of Nature (IUCN); "EH" (from "Extinct Historic")—species that went extinct after 1500 CE but that are not yet included in the IUCN Red List (primarily undescribed extinct species); "EP" (from "Extinct Prehistoric")—older extinctions, from 130,000 BP to 1500 CE, that are believed to have been caused by anthropogenic impacts; "EPU" from "Extinct Prehistoric Uncertain"—older extinct species (i.e., pre-1500 CE extinctions) that may have gone extinct as a result of natural causes not related to human impacts (e.g., natural climatic change) (Supporting Information Methods–Section 1). All post-1500 CE extinctions (i.e., EX and EH) are believed to relate directly or indirectly to human impacts. Finally, we included the five bird species that are considered to be extinct in the wild ("EW") in the IUCN Red List. We also included one Critically Endangered species (*Gallirallus lafresnayanus*) that is considered possibly extinct (CR(PE)), as its trait data were not available in previous datasets (Tobias et al. 2022).

For species that are not yet formally described, we denoted them with the tentative genus followed by "sp." and the location of the species (e.g., *Bubo*_sp_Eivissa). This type of labelling allowed us to differentiate between undescribed species within the same genus. In cases where two undescribed species with the same genus were found in the same location, we added a numerical identifier (e.g., *Tyto*_sp_Latangai_1) or an adjective (e.g., *Zapornia*_sp_Hawaii_Small) to distinguish them, following the original publication sources. Some undescribed species are not assigned to a genus, so we named these by family instead (e.g., Columbidae_sp_Buka_1). For each species, we provided the taxonomic order, family, and genus, following the IUCN/Birdlife taxonomy. Our list only includes species for which there is sufficient evidence that they once existed; this generally means that physical remains (skeletal and/or skin material) for all species in our database have been found. However, there are three species where physical remains have not been found, but that were included in the database because they are based on trustworthy accounts by naturalists: (i) a blue pigeon from Réunion (*Alectroenas*_sp_ Réunion), presumably a close relative to other *Alectroenas* species from Mauritius and Rodrigues (Hume 2013); (ii) the Réunion Fody (*Foudia delloni*), presumably a close relative of other *Foudia* from Mauritius and Rodrigues (Cheke and Hume 2018); and (iii) a duck from St. Paul island (*Anas*_sp_StPaul), Indian Ocean, presumably a close relative of the Amsterdam duck from Amsterdam island (*Anas marecula*) (Olson and Jouventin 1996).

2.2 | Biogeography and Island Endemicity

For each extinct species, we recorded whether the species was an island endemic ("insular") or not ("continental"). An island endemic was defined as a species exclusively found on an island or a group of islands not connected to any continent during the last glacial maximum (when sea levels decreased to approximately 120 m below the current levels) (Siddall et al. 2003). For continental extinct species (i.e., non-island endemics), we recorded the terrestrial biorealm in which they were found (Nearctic, Neotropical, Palearctic, Afrotropical, and Australasia). For island endemics, we recorded the archipelago (i.e., the island group) to which the species was endemic, as well as the biorealm of the island / archipelago (Arctic, Temperate Northern Atlantic, Temperate Northern Pacific, Tropical Atlantic, Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, and Southern Ocean), following the Marine Ecoregions of the World system (Spalding et al. 2007).

2.3 | Morphological Traits and Trait Imputation

2.3.1 | Data Acquisition

We recorded the flight ability of each species as fully volant (1), a weak flyer (0.5) or flightless (0), based on author descriptions. We also gathered information on eight external morphological measurements (in mm) commonly used in the avian literature, all of which are included in the AVONET database (Tobias et al. 2022). These comprise four beak measurements (depth, width, length from culmen, and length from nares), two wing measurements (total wing chord length and Kipp's distance [length from the tip of the first secondary feather to the tip of the longest primary]), tarsus length and tail length (Figure 1). The external morphological measurements were taken from preserved skins of specimens in natural history collections ("RawData_D1" dataset) or from literature sources ("RawData_D2"). We also obtained body mass (g) for extinct birds from the literature ("RawData_D5" dataset). Any missing data on external morphological measurements (i.e., because only subfossil or skeletal remains exist) were imputed (outlined in the next section). To inform the imputation process, we also included skeletal measurements. To this end, we collected data for 22 linear skeletal measurements from museum specimens ("RawData_D3") and the literature ("RawData_D4"). The skeletal measurements include the same four beak measurements (depth, width, length from culmen, and length from nares), and three measures for the hindlimbs and forelimbs (total length, proximal width, and distal width for each bone) (Figure 1). As the imputation method requires that each species has at least one trait measurement, for some species with no measurements for any of the traits ($n = 66$ species), we inferred body mass based either on qualitative descriptions in the literature (i.e., reported to be a similar size to a specific close relative) or skeletal proportions (i.e., 10% larger than a relative based on femur measurements) ("RawData_D6"). Where this was not possible due to a lack of information, we used the median body mass of congeneric species ($n = 40$), or confamilial species ($n = 12$) when the genus has not yet been determined.

To further inform the imputation of missing data, we sourced morphological trait data for the same eight external morphological measurements (and body mass) for all extant species from AVONET (Tobias et al. 2022). Kiwis (*Apteryx* spp.) lack external wings and tails (Billerman et al. 2020). For this reason, they are given arbitrary values of 0.1 for all wing and tail measurements in AVONET but in our case we changed wing chord length and tail length to NA prior to imputation. In addition, to improve the power of the algorithm in imputing external morphological measurements from skeletal data, for 289 extant bird species from a diverse array of taxonomic groups (95 different families from 32 orders), we measured the same 22 linear skeletal traits on museum specimens ("RawData_D7"). We complemented these data with skeletal information on 436 extant species from the literature ("RawData_D8").

2.3.2 | Trait Imputation

Trait imputation is a powerful approach for filling missing values and facilitates more robust downstream analyses. Imputation increases representation and sample size and, consequently, the statistical power of analyses, while reducing bias and error (Penone et al. 2014; Taugourdeau et al. 2014; Kim, Blomberg, and Pandolfi 2018; Stewart et al. 2023). Hence, we performed trait imputation to achieve complete trait coverage and facilitate potential future analyses, such as functional diversity analyses (Stewart et al. 2023). We used Bayesian hierarchical probabilistic matrix factorization (BHPMF) implemented in the R package 'BHPMF' (Schrodt et al. 2015). This method uses a machine learning algorithm to impute missing entries within a species trait matrix. BHPMF is an extension of probabilistic matrix factorization that leverages the taxonomic hierarchy of the data as a proxy for the phylogenetic signal in the traits. BHPMF has proven to be a robust approach that simultaneously incorporates the taxonomic trait signal and the correlation amongst traits (Schrodt et al. 2015). In our case, we used the complete trait matrix, including all collected traits (the eight external morphological measurements, 22 skeletal measures, body mass, and flight ability) of both extant and extinct species. We also included four levels of taxonomic information (infraclass/superorder [Palaeognathae, Galloanserae, and Neoaves], order, family, and genus) to aid in inferring trait gaps based on similarities due to shared evolutionary histories. Although the algorithm fills all data gaps, our main objective was to infer external morphology (i.e., skin traits) to provide standard measurements for all extinct species (Figure S3). We ran the imputation with log-transformed values for all continuous traits for 1000 iterations. Our final trait database includes the original trait values where available and the median value from the imputed trait values for the cases where data were missing. The only exception are the moa (order: Dinornithiformes), for which the values for wing length were manually set to 0.1 (following the approach used in the AVONET database, e.g., in the case of kiwis) as there is evidence that this group lacked any wing bones (Edwards et al. 2024).

To evaluate the imputation algorithm's efficacy in inferring external morphology under different scenarios of missing data, we conducted leave-one-out cross-validation tests using a subset of species with known external morphology and skeletal data (> 75% coverage for both types of data, $n = 306$ species). In the first cross-validation test, we assessed the accuracy of inferring external morphology solely from skeletal data by applying the imputation algorithm after first removing all external morphology data for each species at a time. In the second cross-validation test, we repeated the same process but first removed both external morphology and skeletal data per species. We evaluated the predictive performance of the models (comparing the observed to the predicted values) with three goodness of fit measures using the *gof* function ('hydroGOF' R package (Zambrano-Bigiarini 2020)): Spearman's rank correlation, cross-validated R^2, and percent bias.

2.4 | Construction of Phylogenetic Trees Incorporating Both Extant and Extinct Birds

In order to construct comprehensive phylogenies including both extant and extinct bird species, we utilised the 'BirdTree' phylogenies of extant birds (Jetz et al. 2012) as our initial taxonomic framework. We then developed a pipeline to graft each extinct bird species in our database onto a given BirdTree phylogeny. This pipeline has been integrated into the newly developed 'avotrex' R package v.1.3.0 (See Supporting Information Methods–Section 2).

Amongst the species in our database, 12 extinct species were already included in the BirdTree taxonomy. For the remaining 598 extinct species, we used information on their taxonomic

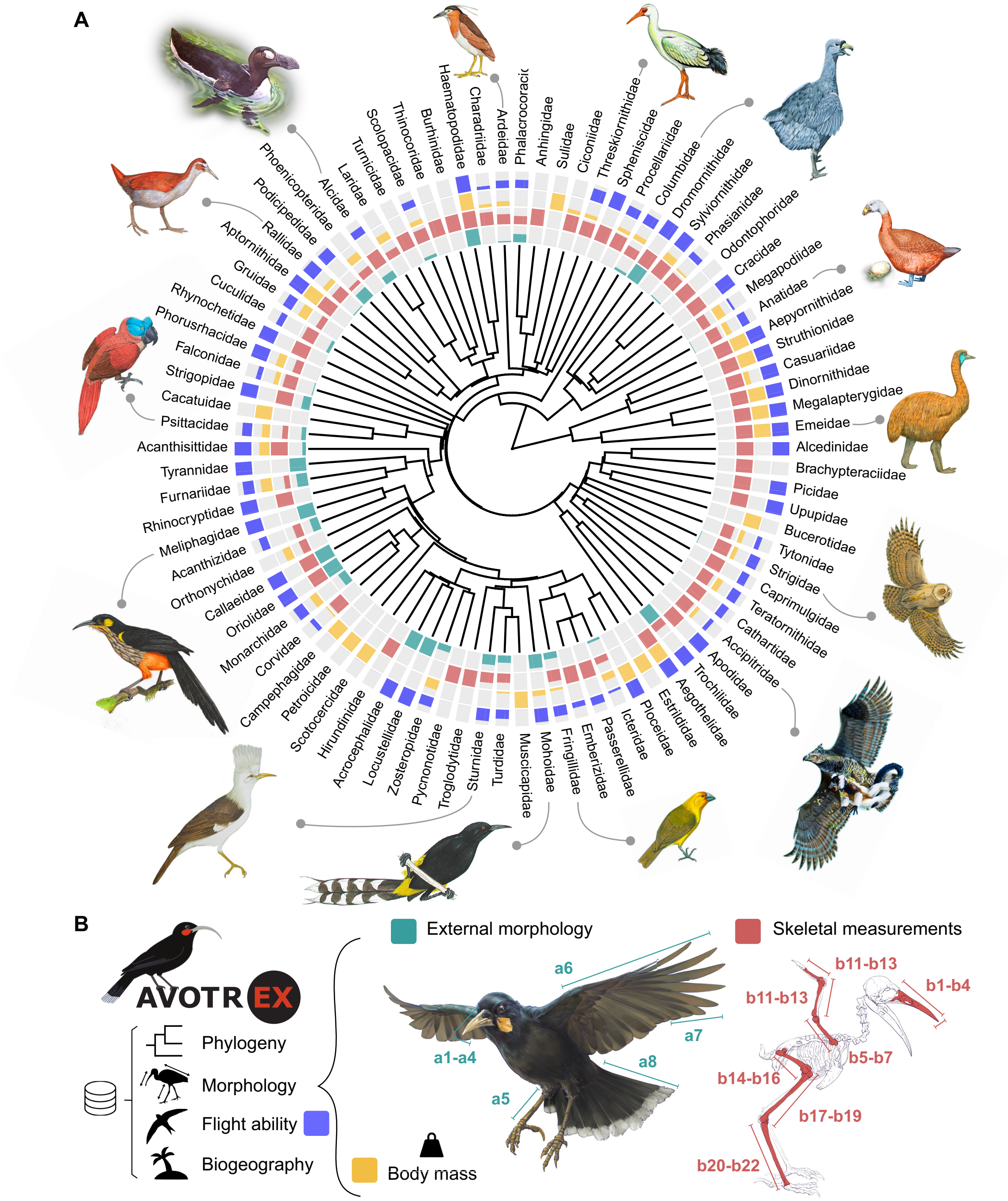

FIGURE 1 | Morphological trait sampling for all bird families included in AVOTREX. (A) A phylogram showing species sampling per family for external morphology (cyan), skeletal measurements (pink), body mass (yellow), and flight ability (dark blue) displayed at the tips. Coloured bars represent the proportion of species within each family (amongst all extinct species) for which there is information for at least one trait in the raw data prior to the imputations. Grey bars represent the proportion of missing information. (B) Types of variables included in the dataset, with a schematic representation of the eight external measurements (a1–a7) and the 22 skeletal measurements (b1–b22) included in the raw dataset. Instead of the Kipp's distance, we show the length of the first secondary (a7), which is the difference between the Kipp's distance and the wing length (a6). The illustrations in A are from Julian Hume, and the Huia illustrations in B are from Pol Serra.

affinities from the published literature to determine their placement within BirdTree. To facilitate the correct placement of each species in the phylogeny, we first identified the corresponding BirdTree Order, BirdTree Family, and BirdTree Genus in the BirdTree taxonomy for each extinct species in our database. For instance, according to the BirdTree taxonomy, all species in the genus *Zapornia* are considered to be *Porzana*. In cases where entire genera, families or orders are extinct, and are not included in BirdTree, the corresponding BirdTree taxonomic level is labelled as "Extinct".

Next, we generated an algorithmic pipeline that inserts each extinct species into a BirdTree phylogeny based on a set of codes and instructions, using the BirdTree taxonomy as a reference. This approach accounts for the uncertainty regarding extinct species placement in the tree, which varies considerably across species (e.g., for some extinct species, an extant sister species is known, while for others, all that is known is the family to which the extinct species belongs). In total, we developed 13 grafting codes (Table S1) that can be classified into five major types, including cases where the extinct species is: (i) added as a sister species (code = "S") to an extant or extinct species already in the tree; (ii) added as a sister to a selected group of species ("SSG"), one ("SGG") or multiple genera ("SGG2"), a family ("SFG") or an order ("SOG") already in the tree; (iii) placed randomly within a group of species ("RSG"), a genus ("RGG"), a group of genera ("RGG2"), or a family ("RFG"); or (iv) made sister to a randomly chosen genus from a pre-defined group of genera ("RSGG") or a randomly selected genus within a pre-defined family ("RSGG2"). Finally, the "AP" code denotes the 12 extinct species that are already present in BirdTree. In our database, each species was assigned one of these 13 codes (Table S1), along with any additional information required for the grafting (e.g., the identity of the sister species to graft to, or a list of species for "RSG").

To graft the extinct species onto the BirdTree phylogenies, our algorithm uses the *bind.tip* function from the 'phytools' R package (Revell 2012) to create a new branch at a specified position along an existing branch. Given the limited knowledge of divergence times for most extinct species, we randomly placed an extinct species at a point along the target branch, either connecting to the tip (in the case of sister species) or to the common ancestor of all species within a given clade (e.g., genus, family, group of species). To avoid unrealistically short branches, by default the functions in the 'avotrex' R package ("PER" argument) truncate the branch by a fifth of its length at either end before randomly selecting a point for grafting. For a small number of species, the grafting was constrained to always occur at a fixed point along a branch (by default, the quarter point from the rootward node, but this can be changed by users) (Supporting Information Methods–Section 3).

The algorithm operates on the extinct species phylogeny database (available in the 'avotrex' R package). It is necessary to graft a number of the extinct species in a specific order (Supporting Information Methods–Section 4). For example, three avian orders are entirely extinct: Aepyornithiformes (elephant birds), Dinornithiformes (moa), and Gastornithiformes (giant flightless fowl). For these, the first representative of each order was assigned the code "SOG" and grafted onto the tree as a sister order, before adding the rest of the species within the extinct order. Aepyornithiformes were made sister to Apterygiformes (Mitchell et al. 2014; Grealy et al. 2023), Dinornithiformes to Tinamiformes (Mitchell et al. 2014), and Gastornithiformes to Galliformes (Worthy et al. 2017). The extinct family Sylviornithidae was considered to be within Galliformes, but sister to all other species in the order (Worthy et al. 2016, 2017).

For certain very old clades, grafting species at randomly selected points along branches occasionally resulted in very long terminal branches for extinct species in the clade. To mitigate this issue, where published information was available, we constrained the grafting of species within these clades to occur at a specific time point (Supporting Information Methods–Section 5). The above functionality has all been incorporated within the 'avotrex' R package, with one primary function—*AvoPhylo* –undertaking the grafting. The R package has been designed in such a way that users can (i) generate as many trees as needed, (ii) easily incorporate new extinct species, (iii) modify the codes and instructions provided for extinct species in our database, and (iv) use a different phylogenetic tree as a base if other global bird phylogenies become available. An example of how to install the R package, download the datasets, generate a phylogenetic tree with extinct species grafted on, and plot the resultant tree is provided in the Supporting Information Methods–Section 6. Further information on the package, including the full range of grafting and plotting options, can be found in the package documentation and vignette.

3 | Results

The final complete database including species traits ("**Avotrex_traits_v1" dataset**) comprises 610 extinct species, of which 426 went extinct before 1500 CE (EP + EPU), 178 went extinct after 1500 CE (EX + EH), five are considered extinct in the wild (EW), and one species (*Gallirallus lafresnayanus*) is considered to be Critically Endangered (CR), but possibly extinct. Of the 178 species that were extinct after 1500 CE, 159 (EX) species are officially recognised as extinct by the IUCN and are included in their Red List (IUCN 2022), whereas 19 species (EH) are currently not, but could be included in future Red List assessments once more detailed data are available.

The geographical distribution of extinctions (Figure 2A) is asymmetric. First, most extinctions ($n = 489$, 80%) are island endemics, with far fewer known continental extinctions ($n = 121$, 20%). Indeed, no extinctions at all are known from continental Africa and much of Asia. Second, amongst the different archipelagos with recorded extinctions, Hawaii stands out as possessing the most extinct species ($n = 81$), followed by the Mascarene islands and New Zealand (both $n = 41$). Together, these three archipelagos account for over a quarter (27%) of all known extinctions, whereas there are 16 archipelagos with just one recorded extinct species.

The taxonomic distribution of extinctions (Figure 2B) is also asymmetric. Passeriformes ($n = 136$) and Gruiformes ($n = 111$) have the most recorded extinctions, followed by Anseriformes ($n = 49$) and Columbiformes ($n = 43$). However, considering the current diversity of these groups, Passeriformes extinctions seem to be underrepresented in the dataset (i.e., representing ~60% of extant species but only ~22% of known extinctions, and only 2% of all known passerines are extinct). On the other hand, Gruiformes (particularly Rallidae) have a disproportionate number of extinct species (up to 40% of the known species are extinct), followed by Anseriformes (22% are extinct) and Columbiformes (12% are extinct). Our database also helps to quantify the magnitude of taxonomic diversity loss: three orders of birds (Aepyornithiformes, Dinornothiformes, and Gastornithiformes) and five additional avian families (Aptornithidae [adzebills],

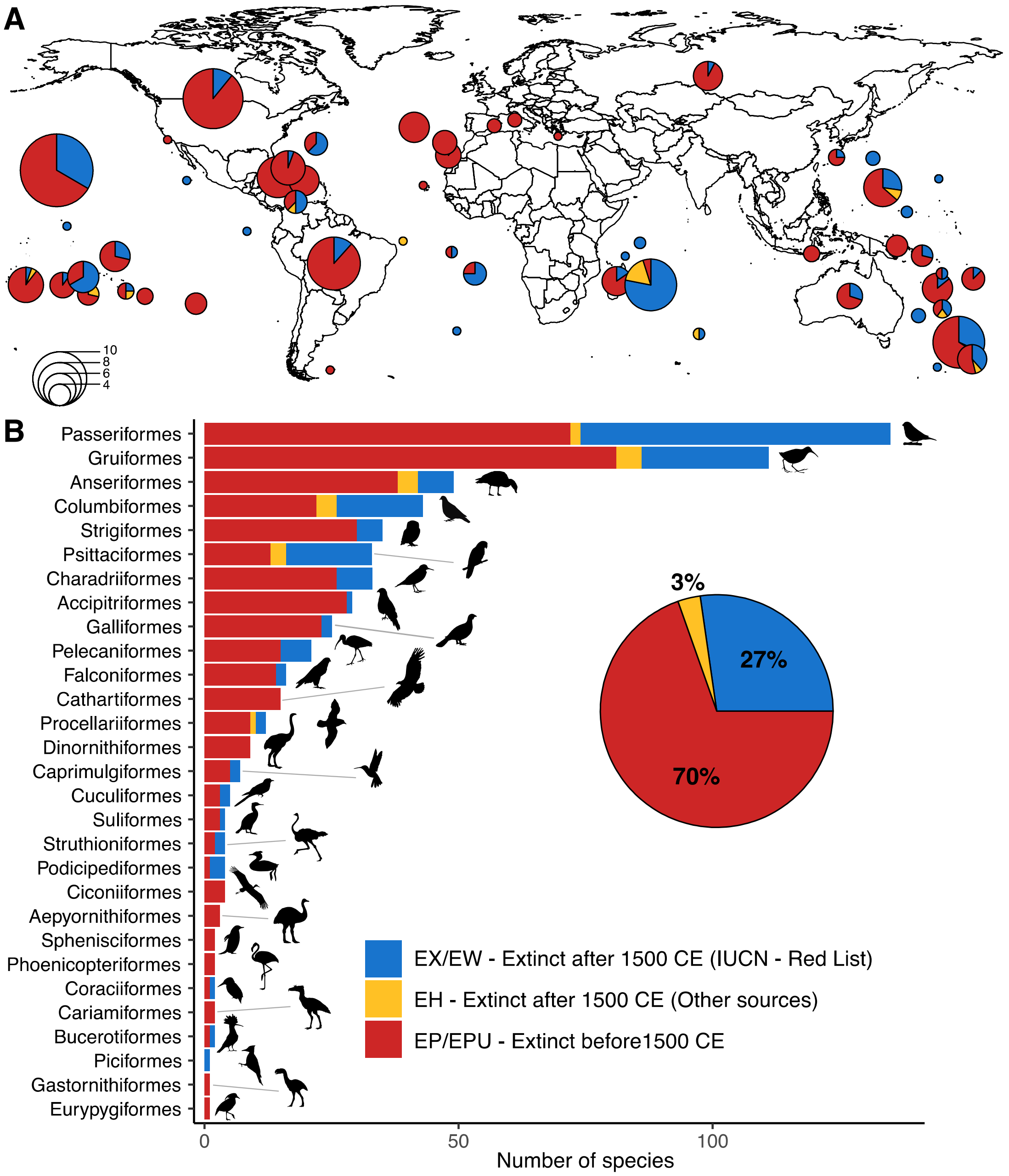

FIGURE 2 | Geographical and taxonomic distribution of extinct birds through time. (A) The global distribution of historical and prehistoric extinct birds is shown by the locations of circles, where the area of the circle represents the total diversity of known extinct species per archipelago and continent. Historical extinctions (EX, after 1500 CE) recorded by IUCN are shown in blue, whereas records from the same period from other sources (i.e., subfossil descriptions, EH) are shown in yellow. Prehistoric extinctions (EP/EPU, <1500 CE) are shown in red. (B) The number of recorded extinct species for each order is shown for each time frame. Original silhouettes are all from PhyloPic.org under Public Domain Dedication 1.0 licences (See collection https://www.phylopic.org/collections/657ad20d-b857-022e-239f-912dbff3873e).

Mohoidae [Hawaiian honeyeaters], Phorusrhacidae [Terror birds], Sylviornithidae, and Teratornithidae [Teratorns]) having gone entirely extinct. In addition, there are at least 87 genera (outside the above-mentioned extinct families and orders) included in our database that are not currently represented by any extant species.

Before imputation, coverage varied across the traits. Although only 103 species (17%) had external morphological data, they have high coverage, with 81 species with complete data on the eight external traits, and an overall coverage of 90% amongst species with at least one measurement (and an average of 7.2 out of 8 traits available; Figure 2B). The most frequently measured external morphological traits were wing length ($n = 102$) and tarsus length ($n = 99$). Skeletal measurements were more sparse, available for 426 species but with a coverage of 34% (average availability of 7.4 out of 22 traits per species; Figure 2B). The most available skeletal traits were the three tarsometatarsus measurements (total length, $n = 260$; proximal width, $n = 215$; distal width, $n = 218$), femur total length ($n = 209$), humerus total length ($n = 200$) and tibiotarsus distal width ($n = 199$). We obtained body mass for about a third of species ($n = 188$, 31% of the total; Figure 2B). The cross-validation analysis shows that our approach can reliably estimate external morphological traits, even if based only on skeletal data (Figure S1) or body mass data (Figure S2).

Twelve species from our database were already present in the BirdTree phylogenies (code AP). For the rest, most species ($n = 482$, 79%), could be precisely placed into the phylogenetic tree. These species were grafted: (i) as sister to an extant or extinct species already in the tree (code S, $n = 246$); (ii) to a randomly selected species from a pre-defined group of species (code RSG, $n = 158$); or (iii) as sister to various taxonomic levels above the species (i.e., sister to an entire genus, sub-family, family or order, codes SSG, SGG, SGG2, SFG, SOG, $n = 78$). The rest of the species ($n = 116$, 19%) had more uncertainty regarding their phylogenetic position.

4 | Discussion

The data presented in AVOTREX confirm that some groups (e.g., Rallidae, Columbidae) are over-represented in the extinction record, potentially reflecting their vulnerability to anthropogenic impacts (Sayol et al. 2020; Matthews et al. 2022). Most of these over-represented groups include multiple island lineages with limited dispersal ability, which may increase their exposure to threats associated with human colonisation (Whittaker, Fernández-Palacios, and Matthews 2023). The information provided in AVOTREX will enable a more thorough investigation of this question. More broadly, it will allow for in-depth analysis of other facets of biodiversity loss beyond species richness–functional and phylogenetic diversity (Sobral, Lees, and Cianciaruso 2016; Sayol et al. 2021; Soares et al. 2022)–as well as enabling the of study natural patterns not biased by human impacts (Sayol et al. 2020; Triantis et al. 2022; Matthews et al. 2023).

It is important to acknowledge that the fossil record is incomplete (Blackburn et al. 2004; Pimm et al. 2006; Duncan, Boyer, and Blackburn 2013), and thus many species might have gone extinct without ever having been reported, either because they have not yet been found in the fossil records or because they never left a trace (Duncan, Boyer, and Blackburn 2013; Pimm et al. 2014; Boehm and Cronk 2021). Other bird species have been described but without a clear period of disappearance, obfuscating their potential status as a modern human-era (<130,000 years ago) extinction (e.g., *Shiriyanetta hasegawai*) (Watanabe and Matsuoka 2015). A recent study estimated a total of 788 "hidden extinctions" of birds (Cooke et al. 2023); more than all known extinctions reported here. These estimates, together with known extinctions from other taxa (Faurby et al. 2018; Proios, Cameron, and Triantis 2021), could indicate areas of high priority for paleontological research. With increasing research efforts, more extinct species are likely to be discovered. For instance, in the last few years, at least six new species (all included in AVOTREX) have been described from different paleontological sites, including a ground-thrush from Mauritius (Hume 2022), a raptor from Cuba (Suárez and Olson 2021), three quails from Macaronesia (Rando et al. 2020), and a rail from French Polynesia (Salvador, Anderson, and Tennyson 2021).

Although the most common units of biodiversity loss are species extinctions, numerous subspecies of birds are also known to have been lost (Matthews et al. 2022), such as the recently described Mascarene Booby (Hume 2023). Although we do not include subspecies extinctions in the current version of AVOTREX, we hope to include these data in future to enable a wider quantification of biodiversity loss. Nevertheless, the current species-level dataset can inform us about the disproportionate phylogenetic erosion of some regions above the species level: three orders, five families, and 101 genera of birds are entirely extinct, confirming that previous studies underestimated extinction numbers (Ceballos and Ehrlich 2023). Additionally, the morphological and phylogenetic data provided here will allow future studies to assess phylogenetic and functional diversity loss in more detail. This information will help us to re-evaluate the magnitude of the current extinction crisis (Dirzo et al. 2014; Ceballos et al. 2015), as well as to expand our knowledge regarding different dimensions of biodiversity loss beyond mammals (Faurby and Svenning 2015; Davis, Faurby, and Svenning 2018; Smith et al. 2018), which have been the main focus of past research.

Although the 'avotrex' R package provides a pipeline to generate phylogenies with all known extant and extinct species, we acknowledge the high uncertainty in the exact evolutionary relationships and divergence times for some extinct species. However, the majority of species have relatively well-known affinities, and species with higher uncertainty represent a minority in our database ($n = 116$ species, 19%). In addition, using the package to generate multiple phylogenies for analysis should account for this uncertainty to some extent. Nevertheless, new ancient DNA techniques are rapidly improving our understanding of the phylogenetic relationships of both extant and extinct species (Jarvis et al. 2014; Prum et al. 2015; Oswald et al. 2021; Renom et al. 2021). Future advances in our understanding of the evolutionary relationships of extinct species can easily be incorporated into the 'avotrex' R package.

All the species included in AVOTREX went extinct over the last 130,000 years. The majority of these extinctions are believed to be the consequence of various forms of human impact, including direct hunting (Duncan, Blackburn, and Worthy 2002), release of invasive predators (Blackburn et al. 2004), or habitat destruction (Brooks et al. 2002). However, it is often difficult to disentangle natural from human-caused extinctions, especially for prehistoric extinctions. In our database, we include a variable to specify whether there is evidence suggesting human-driven extinctions; however, in several cases little information is available (See Supporting Information Methods–Section 1).

AVOTREX is a dynamic resource that can be updated whenever extinct bird species are discovered or when new information about species traits and taxonomic affinities becomes available. The pipeline for the construction of the phylogenetic tree has been released as an R package, so that users can readily incorporate new information before future versions of the database are released. By providing functional trait data and phylogenetic relationships for all known extinct birds, AVOTREX provides an essential resource to advance our understanding of the causes and consequences of human-driven extinctions. Earlier versions of this dataset have provided a foundation for an array of studies, including the quantification of functional diversity loss (Sayol et al. 2021; Matthews et al. 2024), the predictors of non-random extinction risk (Martínez-Rubio, Sayol, and Lapiedra 2024) and the resulting biases in biogeographical and evolutionary patterns (Sayol et al. 2020; Matthews et al. 2023; Dufour et al. 2024). We hope that the publication of AVOTREX will continue to spur investigations into avian extinctions, including their implications for the disruption of trophic interactions with plants, both mutualistic (i.e., pollination or seed-dispersal) and antagonistic (i.e., seed predation or herbivory), ancient ecological relationships, and comparisons with patterns of extinction in other taxa.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the datasets presented in this study are available in the AVOTREX (v. 1.0) repository hosted at Dryad (https://doi.org/10.5061/dryad.zgmsbcckk). The "avotrex" R package, that was used to generate phylogenetic trees that include extinct species, is available on CRAN (10.32614/CRAN.package.avotrex).

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Supporting Information

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