Conserving the evolutionary history of birds

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Article Impact Statement

We identify the priority species, orders, groups, countries, and important bird areas for conservation of bird evolutionary history.

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Abstract

In the midst of the sixth mass extinction, limited resources are forcing conservationists to prioritize which species and places will receive conservation action. Evolutionary distinctiveness measures the isolation of a species on its phylogenetic tree. Combining a species' evolutionary distinctiveness with its extinction risk creates a measure called an EDGE score. We use EDGE scores to prioritize the places and species that should be managed to conserve bird evolutionary history. We analyze all birds across species, orders, countries, and important bird areas. We further examine parrots, raptors, and seabirds in depth because these groups are especially threatened and relatively speciose. These three focal groups have greater median threatened evolutionary history than other birds, making them important for conserving bird evolutionary history. Australia, Brazil, Indonesia, Madagascar, New Zealand, and the Philippines are especially critical countries because they have the most threatened evolutionary history for endemic birds and are important for parrots, raptors, or seabirds. We further highlight that increased enforcement of international agreements for the conservation of parrots, raptors, or seabirds is needed because these agreements protect hundreds of millions of years of threatened bird evolutionary history. Decisive action is required to conserve the evolutionary history of birds into the Anthropocene.

Introduction

Humans are causing a sixth mass extinction that appears to be worsening (Ceballos et al. 2010, 2015). Conservation action can prevent extinction (Bolam et al. 2021) and protected areas are

effective conservation tools when properly managed (Watson et al. 2014). Unfortunately, there are large disparities in the availability of resources that national governments allocate for conservation-related activities (McClanahan & Rankin 2016), with many countries not achieving their commitments to the creation and maintenance of protected areas (Watson et al. 2014). Despite laudable goals such as zero extinction (Parr et al. 2009; Funk et al. 2017; Wiedenfeld et al. 2021), insufficient resource allocation forces conservationists to prioritize the taxa and places that might be saved (Bottrill et al. 2008, 2009). Conservation organizations and governments therefore often face the difficult decision of which extinctions to prevent while allowing the remainder to proceed unmanaged.

Biologists frequently use extinction risk (e.g. Red List categories) to rank the conservation priority of species (Temple & Terry 2009; Pleguezuelos et al. 2010; Croxall et al. 2012). Such an approach implicitly assumes that loss of any species represents an equal loss of biodiversity (Redding & Mooers 2006; Isaac & Pearse 2018). Phylogenetic diversity, however, is an evolutionary measure of biodiversity (Faith 1992; Palmer & Fischer 2021) that can be used to further refine conservation priorities (Faith 2009) and thereby improve efficiency to address conservation concerns provided finite resources. Phylogenetic diversity is generally correlated with morphological diversity (Owen et al. 2019) and ecosystem function (Cadotte et al. 2008; Gravel et al. 2011; Cadotte 2013). Evolutionary distinctiveness is the relative contribution of a species to phylogenetic diversity (Isaac et al. 2007), or isolation of a species relative to its branch length within its phylogenetic tree (Jetz et al. 2014). Prioritizations based on evolutionary distinctiveness assume that loss of more distinct species or lineages is worse than the loss of others. Thus, when setting conservation priorities among species and places, evolutionary isolation can arguably sometimes outweigh extinction risk (Isaac & Pearse 2018).

Evolutionary diversity accumulates over millions of years, yet can be lost quickly and is currently under increasing threat (Davis et al. 2018; Bellard et al. 2021). Conservation prioritizations that employ evolutionary distinctiveness measures are therefore gaining momentum. The International Union for the Conservation of Nature (IUCN) adopted a resolution calling for the conservation of species with "high evolutionary significance" (IUCN 2012) and consequently created a Phylogenetic Diversity Task Force. The Intergovernmental Science-Policy Platform for Biodiversity and Ecosystem Services (IPBES) adopted the status of phylogenetic diversity as an indicator for multiple components of Nature's Contributions to People (Díaz et al. 2019). The United Nations' Convention on Biological Diversity's draft Post-2020 Global Biodiversity Framework includes both phylogenetic diversity and an index of evolutionary distinctiveness and global endangerment (i.e. EDGE score (Isaac et al. 2007)) to track the status of global biodiversity (Secretariat of the Convention on Biological Diversity 2021).

The EDGE score combines evolutionary distinctiveness with extinction probability to assign species a quantitative conservation priority that can be used for ranking. EDGE scores thus increase with both evolutionary distinctiveness and extinction risk. The methodology to calculate EDGE scores was recently revised and is now more intuitive (Gumbs et al. 2023). This revised index is interpreted as potential expected loss in phylogenetic diversity (in millions of years, MY) that could be averted if conservation action prevents the extinction of a given species (Gumbs et al. 2023).

We examined the evolutionary distinctiveness and EDGE scores of all bird species across orders, countries, and important bird areas (IBAs). IBAs are subsets of Key Biodiversity Areas recognized for birds and are considered as globally important for targeted conservation management by protecting unique areas (Smith et al. 2018). We summed evolutionary distinctiveness and EDGE scores separately across every bird species occurring within each country and each bird species triggering an IBA. We hereafter refer to summed evolutionary distinctiveness as 'evolutionary history' and summed EDGE scores as 'threatened evolutionary history'(both measured in MY). We therefore reserve the terms 'evolutionary distinctiveness' and 'EDGE score' for referring to individual species, not summed values. We also examined the evolutionary history and threatened evolutionary history of endemic birds per country, with the resulting values representing the total MY of evolutionary history for which each country is solely responsible for conserving in the wild. To further prioritize species for conservation action, we specifically designate 'EDGE species' as those where we have 95% confidence that their EDGE scores are above the median value across all birds (Gumbs et al. 2023). We performed these analyses across all birds and for three specific speciose groups that contain particularly large proportions of threatened species — parrots (McClure & Rolek 2020; Vergara-Tabares et al. 2020), raptors (McClure et al. 2018; McClure & Rolek 2020), and seabirds (Spatz et al. 2017; Dias et al. 2019). Twenty-eight percent of parrots, 20% of raptors, and 31% of seabirds are threatened with extinction, compared to 13% across all birds (BirdLife International 2023a). These three groups are of interest to the authors and provide an opportunity to

demonstrate how our results can be used to help prioritize and target ongoing conservation efforts.

Methods

Calculating evolutionary distinctiveness and EDGE scores

For our taxonomy we used BirdLife International's Handbook of the Birds of the World v5.0 (Birdlife International 2020), and matched it to the phylogeny of Jetz et al. (2012, 2014) based on the Hackett backbone as further described below, retaining 9,645 species. We randomly sampled 1,000 trees from the available distribution of phylogenies to adequately capture uncertainty in phylogenetic relationships and node ages (Thomas et al. 2013; Jetz et al. 2014). To maximize the inclusion of species and enable effective comparison between clades, we imputed the species missing from the phylogeny, following taxonomy matching, to generate 1,000 phylogenetic trees that comprised all valid species (1,343 imputed species). For imputation, we followed earlier approaches to insert missing species into their genus along the existing phylogenetic branches (Forest et al. 2018; Cox et al. 2022; Gumbs et al. 2023), using the '*congeneric.impute*' function in the R package '*pez*' (Pearse et al. 2015).

Jetz et al. (2012) produced two sets of phylogenies built on different underlying hypotheses of the higher relationships amongst birds, the 'Hackett' and 'Ericson' backbones, that lead to varying topologies deeper in the trees. However, the majority of a species' evolutionary distinctiveness and EDGE score is contributed by branches near the tips, or the terminal branch (the branch connecting a species to all other branches of the tree) alone (Redding et al. 2014; Gumbs et al. 2023). Speciation rate analyses at the tips of trees from the Hackett and Ericson backbones show that these two topologies are highly correlated (Rabosky et al. 2015). We found a strong correlation (r = 0.984) of median terminal branch lengths for each species across 1,000 trees from each backbone. Given that the two phylogenies are highly correlated and unlikely to lead to fundamental differences in conservation prioritization, we elected to use the distribution of phylogenies built on the 'Hackett' backbone to retain consistency with previous EDGE lists employed for directing applied conservation action (Gumbs et al. 2018).

Although previous analyses have calculated original EDGE scores for birds (Jetz et al. 2014; Gumbs et al. 2018), our approach uses the updated EDGE methodology, which advocates for the robust and comparable prioritization of evolutionarily distinct species for conservation action (Gumbs et al. 2023). The new EDGE protocol explicitly incorporates 'phylogenetic complementarity' to reflect that the extinction risk of closely-related species will influence the expected distinctiveness of a given species into the future (Steel et al. 2007; Gumbs et al. 2023), which was missing from the original EDGE metric. This increases the priority of species from clades where all species are threatened (i.e. high likelihood of losing deeper branches of the tree, e.g. Mesitornithiformes), and decreases the priority of species from clades that include species with a higher variability in extinction risk (i.e. unlikely to lose deep branches of the tree, e.g. Anseriformes).

Formally, the new EDGE metric ('EDGE2') multiplies the evolutionary distinctiveness of a species by its probability of extinction, where the evolutionary distinctiveness of species i is given as:

$$ED_{i} = TBL_{i} + \sum_{j=2}^{n_{i}} \left(L_{i,j} \times \prod_{k \in C_{i,j} - \{i\}} p_{k} \right)$$

Where TBL_i is the terminal branch length of species *i*, plus the sum of the lengths of all internal branches $L_{i,j}$ connecting species *i* to the root of the phylogenetic tree, with these lengths multiplied by the product of the probability of extinction p_k of each species *k* that comprise the set of all species $C_{i,j}$ descended from the corresponding branch (see Gumbs et al. 2023 for a detailed discussion of EDGE metrics).

In the hypothetical example of Figure 1 (A-B), species A's evolutionary distinctiveness is determined not only by its unique terminal branch of 5 MY, but also by the fact that its sister species, species B, has a 0.5 probability of becoming extinct (Figure 1B). Therefore, species A has a 50% chance of being responsible for their shared internal branch of 10 MY, and so we assign 50% of that branch to species A. Now, the evolutionary distinctiveness of species A is 5 + (10 * 0.5) = 10 MY. The EDGE score under the new protocol is then the amount of species A's evolutionary distinctiveness we expect to lose due to that species becoming extinct, which is calculated by multiplying the evolutionary distinctiveness of the species by its extinction risk (Figure 1). For species A in our example, where its extinction risk (global endangerment; GE) is 0.2, this would be 10 MY * 0.2, so EDGE = 2 MY. This 2 MY is the amount of expected loss of evolutionary history we can avert with conservation action.

When we look at two real-world examples, the kea (*Nestor notabilis*, Fig. 1C-D) and the Philippine eagle (*Pithecophaga jefferyi*; Fig. 1E-F), we see how the extinction risk of closely-related species will influence the evolutionary distinctiveness of the focal species. The

kea receives a large proportion of its evolutionary distinctiveness score from the internal branches it shares with the kākā (*N. meridionalis*) and kākāpo (*Strigops habroptilus*) due to both species being threatened (Vulnerable and Critically Endangered, respectively) and the three species sharing relatively long branches of the tree. Conversely, the Philippine eagle receives > 99% of its evolutionary distinctiveness solely from its terminal branch, due to it sharing its first internal branch with eight eagle species, five of which are Least Concern on the Red List.

We quantified extinction risk following the new EDGE protocol, where each IUCN Red List category has a median extinction risk, between 0 and 1, around which there are bounds of uncertainty from which we can draw values to incorporate extinction risk (median values: Critically Endangered = 0.97, Endangered = 0.485, Vulnerable = 0.2425, Near Threatened = 0.12125, Least Concern = 0.060625; see Figure 1 in Gumbs et al. 2023 for full distribution). We then repeated our EDGE calculations across the 1,000 phylogenetic trees, for each tree selecting a new extinction risk value from the bounds of uncertainty for the given Red List category for each species. This approach allows for comparison with other taxonomic groups and facilitates the downstream use of the priority EDGE list by conservation initiatives (see Gumbs et al. (2023) for full details). We defined an 'EDGE species' as a species where the 2.5^{th} percentile of the EDGE score was above the median (0.19) EDGE score for all birds across the world.

Analyzing evolutionary distinctiveness and EDGE scores

We examined the median, 2.5th, and 97.5th percentiles of evolutionary distinctiveness and EDGE scores per order. We calculated the millions of years of bird evolutionary history contained within each country by summing the evolutionary distinctiveness of each species per country. We

similarly examined the amount of expected loss of phylogenetic diversity that could be averted with conservation action by summing EDGE scores across all species in a country. We also determined which countries contained the greatest average evolutionary distinctiveness and EDGE scores per bird species. We determined the species present within each country following BirdLife International and Handbook of the Birds of the World (2021). Our goal was to determine which countries have the most responsibility to protect the evolutionary history of birds, not to identify spatial hotspots within countries. BirdLife International lists 245 political units including countries and territories. Such territories include special administrative regions, dependent territories, and various subnational administrative and political entities. We refer to all these political units as 'countries' for simplicity. We considered a species to occur within a country—and thus for that country to be responsible for the conservation of a species—if the species occurred within the country during any part of the year, while excluding those identified as vagrant to a given country. Species were considered as currently endemic to a single country when occurring only in that country or in the High Seas across the entire year.

We similarly summed evolutionary distinctiveness values and EDGE scores per trigger species of each IBA (BirdLife International 2022). A species can trigger an IBA if it contains significant populations of one or more threatened (i.e. Vulnerable, Endangered, or Critically Endangered), restricted-range (global range $< 50,000 \text{ km}^2$), or biome-restricted species; or the area contains at least 1% of the global population of a congregatory species (Hole et al. 2009).

We summed scores for all birds, and separately for parrots, raptors, and seabirds. Parrots consisted of all species within the order Psittaciformes (n = 403 species). Raptors were all

species (n = 561) within the orders Accipitriformes, Cathartiformes, Falconiformes, Strigiformes, and Cariamiformes (McClure et al. 2019) and we used the list of seabirds provided by BirdLife International's website (<u>datazone.birdlife.org</u>), which included a subset of species from nine orders (Anseriformes, Charadriiformes, Gaviiformes, Pelecaniformes, Phaethontiformes, Podicipediformes, Procellariiformes, Sphenisciformes, and Suliformes; n = 363 species).

We bootstrapped the median evolutionary distinctiveness and EDGE scores for parrots, raptors, and seabirds separately. Then, we bootstrapped the same medians for all birds except parrots, then except raptors, and finally except seabirds. This bootstrapping was performed by randomly drawing evolutionary distinctiveness and EDGE scores from the groups with replacement and calculating the median for each of 10,000 iterations. We next subtracted each iteration of the bootstrapped medians of parrots, raptors, and seabirds from the associated medians of all other birds. This measure thus represents the bootstrapped median difference between our focal groups and all other birds outside the respective focal group. Values greater than zero thus represent situations where a focal group has lesser values than the rest of Class Aves, whereas values less than zero represent situations where a focal group has lesser values than the rest of Class Aves. We considered there to be a difference between focal groups and all other birds if the range between the 2.5th and 97.5th percentiles of bootstrapped iterations excluded zero. We performed analysis in R (R Core Team 2022).

Results

All birds

We found great heterogeneity in evolutionary distinctiveness and EDGE scores among species, orders, groups, countries, and IBAs (Figs. 2, 3, 4, 5; Appendix S1). Evolutionary distinctiveness ranged from 78.64 MY for the oilbird (*Steatornis caripensis*) to 0.06 MY for the Indian spot-billed duck (*Anas poecilorhyncha*; Appendix S1), which also had the lowest EDGE score. The species with the greatest EDGE score is the giant ibis (*Thaumatibis gigantea*), followed by the kākāpō and the plains-wanderer (*Pedionomus torquatus*). The orders with the greatest median evolutionary distinctiveness are Leptosomiformes (the cuckoo roller [*Leptosomus discolor*]), Opisthocomiformes (the Hoatzin [*Opisthocomus hoazin*]), and Eurypygiformes, which consists of the kagus (*Rhynochetos* spp.) and the sunbittern (*Eurypyga helias*; Fig. 2). The orders with the greatest median EDGE scores were Eurypygiformes, Mesitornithiformes (the mesites), and Cathartiformes (Cathartid vultures; Fig. 2). There were 690 EDGE bird species (Appendix S1).

Geographically, Peru, followed by Colombia and Indonesia contained the greatest bird evolutionary history (Fig. 4, Appendix S2), and Indonesia, Brazil, and Colombia possessed the most threatened evolutionary history (Fig. 4). The evolutionary history of endemic birds was greatest in Australia, Indonesia, and the Philippines. Similarly, Indonesia, followed by Australia and the Philippines, had the most threatened evolutionary history of endemic birds. The countries with the greatest mean evolutionary distinctiveness were Tokelau, the British Indian Ocean Territory, and Pitcairn. This ranking may be affected by country size and species richness, so these countries may not bear much responsibility for evolutionarily distinct species with large ranges beyond their borders. The countries with the greatest mean EDGE score were New Zealand, New Caledonia, and Samoa (Appendix S2). The 100 IBAs with the greatest overall and threatened evolutionary history almost exclusively occurred in the Eastern Hemisphere (99%; Fig. 5). Africa contained 69 of the top 100 IBAs with the most evolutionary history and 31 of the top 100 IBAs with the most threatened evolutionary history (Fig. 5). The IBA harboring the most evolutionary history across all birds was the Itombwe Mountains of the Democratic Republic of the Congo. Asia contained 30 and 62 of the top 100 IBAs with the most overall and threatened evolutionary history, respectively (Fig. 5). Malaysia was the country containing most of the top 100 IBAs for overall (25 IBAs) and threatened evolutionary history (32 IBAs; Fig. 5; Appendix S3). The IBA with the most threatened evolutionary history and the greatest number of EDGE species was Mulu-Buda Protected Area, Malaysia. We highlight the 100 most important IBAs for simplicity, but the full list can be found in Appendix S3. There were 33 EDGE species for which no IBA has yet been designated. These species included four parrots, three raptors, and two seabirds (Appendix S1). Of those species, the three that are most important for conserving avian evolutionary history are the white-eyed river martin (Eurochelidon sirintarae), the Whenua Hou diving-petrel (Pelecanoides whenuahouensis), and the Australian painted-snipe (Rostratula australis).

Comparing evolutionary distinctiveness among priority groups revealed that parrots were less evolutionarily distinct on average than the rest of class Aves, whereas raptors and seabirds were more distinct (Fig. 3). All three groups, however, had greater EDGE scores than other birds on average (Fig. 3). These three bird groups also contained disproportionate numbers of EDGE species. Parrots, raptors, and seabirds respectively comprise roughly 4%, 5%, and 3% of bird species, yet they comprise approximately 8%, 10%, and 12% of EDGE species. These groups are therefore important for the conservation of bird evolutionary history because they total roughly 12% of all birds yet represent approximately 30% of EDGE species.

Parrots

There are 403 species of parrots, all within the order Psittaciformes. The three parrots with the greatest EDGE scores were the kākāpō, the kākā, and the kea (Appendix S1); species that are all endemic to New Zealand. Australia, Brazil, and Indonesia contain the most parrot evolutionary history, and New Zealand, Brazil, and Australia have the most threatened evolutionary history for parrots (Fig. S1). Regarding endemic parrots, Australia contained the greatest evolutionary history followed by New Zealand and Indonesia (Fig. S1).

All the top 100 IBAs for evolutionary history of parrots occurred in either South America (67 IBAs) or Australasia (33 IBAs; Fig. S2). Regarding threatened evolutionary history, the top 100 IBAs for parrots occurred mostly in Asia (42 IBAs) and Australasia (38 IBAs; Fig. S2). The country with the greatest number of the top 100 IBAs for the evolutionary history of parrots was Brazil (41 IBAs), whereas the Philippines contained the bulk of the top 100 IBAs for threatened evolutionary history (42 IBAs; Fig. S2, Appendix S3). New Zealand contained the 16 most important IBAs for threatened evolutionary history of parrots (Fig. S2; Appendix S3).

Raptors

Raptors consist of 561 species within orders Accipitriformes, Cathartiformes, Cariamiformes, Falconiformes, and Strigiformes (McClure et al. 2019). The three raptor species with the greatest EDGE scores are the secretarybird (*Sagittarius serpentarius*), the Philippine eagle, and the California condor (*Gymnogyps californianus*). The countries with the greatest evolutionary history of raptors were mostly South American, including Bolivia, Colombia, and Peru; whereas countries with the greatest threatened evolutionary history were mostly in Africa, including Kenya, Tanzania, and Uganda (Fig. S3; Appendix S2). Island countries, especially Indonesia, the Philippines, and Madagascar, contained the greatest overall and threatened evolutionary history of endemic raptor species (Fig. S3; Appendix S2).

Most of the top 100 IBAs for the evolutionary history of raptors occurred in Europe (67 IBAs; Fig. S4). These IBAs were mostly triggered by the osprey (*Pandion haliaetus*), which has the second greatest evolutionary distinctiveness of raptors (61.24 MY) but with a low extinction risk. Germany contained the most of those IBAs (n = 25). Conversely, the top 100 IBAs for the threatened evolutionary history of raptors occurred mostly in Asia (64 IBAs; Fig. S4), with the Philippines containing 64% of them (41 IBAs).

Seabirds

There are 363 species of seabirds, all of which require marine environments during at least part of their life cycle (Appendix S1), yet require terrestrial breeding sites for reproduction (Dias et al. 2019). Priority seabirds include the Christmas Island frigatebird (*Fregata andrewsi*), the Whenua Hou diving-petrel, and the New Zealand storm petrel (*Fregetta maoriana*; Appendix S1). The most evolutionary history of seabirds occurred in the USA, Chile, and Mexico (Fig. S5), and the greatest threatened evolutionary history occurred in the USA, New Zealand, and Chile. Only fifteen countries have endemic seabird species (Fig. S5), with New Zealand, Mexico, and Portugal containing the most evolutionary history, and New Zealand followed by Mexico and Fiji possessing the most threatened evolutionary history among endemic seabirds.

Europe contains the most of the top 100 IBAs for evolutionary history of seabirds (48 IBAs; Fig. S6), whereas Australasia contains the greatest number of the top 100 IBAs for threatened evolutionary history (25 IBAs; Fig. S6). Of countries, Russia (16 IBAs) and New Zealand (24 IBAs) contain the most of the top 100 IBAs for overall and threatened evolutionary history of seabirds, respectively (Fig. S6).

Discussion

Our analysis reveals priorities for conserving the evolutionary history of birds. Important Bird Areas represent crucial places for bird conservation. There are 33 EDGE species that do not trigger an IBA. Many of these species presumably do not occur anywhere in sufficient numbers to be trigger species. For example, the Critically Endangered white-eyed river martin has not been observed since 1978, and the New Caledonian nightjar (*Eurostopodus exul*) and Bachman's warbler (*Vermivora bachmanii*) are listed as possibly extinct (BirdLife International 2023a). The stronghold of the Vulnerable Somali ostrich (*Struthio molybdophanes*) is Samburu National Reserve, Kenya (Mutiga et al. 2016). Although this reserve is an IBA, it is not triggered by the Somali ostrich because the species was recognized after the IBA was last assessed in 2001 (BirdLife International 2023a, 2023b). Taxonomic and other updates to BirdLife International's database will likely change the list of EDGE species that do not trigger an IBA. Other EDGE species including the northern ground-hornbill (*Bucorvus abyssinicus*), the South Island takahe (*Porphyrio hochstetteri*), and the Bendire's thrasher (*Toxostoma bendirei*) did not trigger an IBA

and thus the places to focus conservation action for these species are currently poorly delimited. For those EDGE species for which IBAs exist, responsible countries should ensure that those IBAs are managed or protected properly to ensure the persistence of the species for which the IBAs were recognized.

Countries with substantial amounts of unique bird evolutionary history have an increased responsibility to steward such evolutionary information and the benefits it confers (Jetz et al. 2014). Generally, the countries that we have identified as especially important for the conservation of bird evolutionary history are Australia, Brazil, Indonesia, Madagascar, New Zealand, and the Philippines. These countries have the most threatened evolutionary history of endemic birds and are particularly important for parrots, raptors, or seabirds.

Islands dominate the list of countries with the greatest mean evolutionary distinctiveness and EDGE scores (Appendix S2). Baiser et al. (2018) found that islands contain lower bird phylogenetic diversity than expected by chance. Therefore, islands have relatively homogenous avifauna, but the birds that they harbor tend to be evolutionarily distinct within Class Aves. Put differently, the avifauna of a given island might consist of closely related members of isolated and distinct groups. Conservation on islands is important for many bird species (Tershy et al. 2015) including for parrots (Jackson et al. 2015), raptors (McClure et al. 2020; Pizzarello & Balza 2020), and especially seabirds (Jones et al. 2016; Spatz et al. 2017; Holmes et al. 2019). Our results suggest that islands represent opportunities where conservation action over a relatively small area can affect great average evolutionary diversity (Holmes et al. 2019).

We built on past research comparing bird evolutionary history among countries (Jetz et al. 2014). Our analysis differs from that of Jetz et al. (2014) because their study did not use the new approach for calculating EDGE, and instead mostly focused on weighting distinctiveness by range size, which is but one aspect of extinction risk. Further, Jetz et al. (2014) did not specifically test for differences among our focal groups of birds or examine IBAs as we have here. Despite these differences in focus and methodology, the countries and species highlighted by each analysis are generally similar. Lists of country and species priorities for conserving the evolutionary history of birds have thus not changed much in nearly a decade and are robust to differing methodologies.

Our results highlight three especially imperiled groups: parrots, raptors, and seabirds. Parrots are considered umbrella taxa (Vergara-Tabares et al. 2020) and are generally regarded as a global conservation priority (Olah et al. 2016) with a high proportion of threatened and declining species (McClure & Rolek 2020). The kākāpō had the greatest EDGE score among parrot species and is also likely the most intensively managed (Elliott et al. 2001). Most parrots are forest-dependent species, and habitat loss from deforestation, and removal from the wild for the illegal bird trade are the two greatest threats to parrots (Berkunsky et al. 2017).

Habitat loss and persecution are also the principal threats to the Philippine eagle (Salvador & Ibanez 2006), one of the raptors with the highest EDGE scores in our analysis. Raptors perform ecosystem services, are indicators of biodiversity, and have outsized effects on human health (Markandya et al. 2008; Buechley & Şekercioğlu 2016; Donázar et al. 2016; Natsukawa & Sergio 2022). Twenty percent of raptor species are threatened with extinction (BirdLife International 2023a) and 52% have declining global populations (McClure et al. 2018). The secretarybird has the greatest EDGE score of raptors and is declining at an exceedingly high rate in Kenya mostly outside of protected areas, perhaps owing to habitat alteration (Ogada et al. 2022). This species is in dire need of major conservation action to reverse that trend. Conversely, there are ongoing captive breeding and reintroduction programs for the Philippine eagle (Salvador & Ibanez 2006) and California condor (Snyder & Snyder 2000). Given the importance of these two species to the conservation of bird evolutionary history, continued support of their reintroduction programs is crucial along with efforts to assuage their principal threats—habitat loss and persecution for the Philippine eagle (Salvador & Ibanez 2006) and lead poisoning for the California condor (Finkelstein et al. 2012).

Seabirds are a polyphyletic group that is recognized as a conservation priority (Croxall et al. 2012). The two orders comprising almost half of all seabirds, Procellariiformes (petrels and albatrosses) and Sphenisciformes (penguins), have above-average proportions of threatened species (McClure & Rolek 2020). Indeed, a 2018 assessment found that 31% of seabirds were threatened with extinction (Dias et al. 2019). The three seabird species with the greatest EDGE scores each breed on single islands, making those sites globally important for the conservation of bird evolutionary history. The greatest threats to seabirds are the introduction of non-native terrestrial predators to seabird breeding islands and the incidental mortality caused by fishing gear while at sea (Dias et al. 2019). The threat of invasive species can be remedied by eradicating them from islands, which benefits seabirds and other island biodiversity (Jones et al. 2016). Fishing gear can be modified to reduce the risk of bycatch to many seabirds (Melvin et al.

2014), and the combination of terrestrial and marine conservation action would benefit a large proportion of threatened seabirds.

Most bird species (nearly 8,000) have ranges that span multiple countries; thus, international collaboration via multi-national conservation agreements is necessary for the conservation of bird evolutionary history. The framework for such international collaboration is already in place for some groups. For example, many of the countries that we identify as important for raptors, specifically, are parties or signatories to the Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia (the 'Raptors MoU';

https://www.cms.int/raptors/), which is a legally non-binding international agreement to conserve migratory raptors throughout Africa and Eurasia. The Raptors MoU covers 93 species that constitute 531 MY of evolutionary history. Signatories to the Raptors MoU commit to implementing such actions as site conservation, legal protection, threat abatement, and population monitoring. However, implementation of such actions is hampered by a lack of political commitment or funding (McClure et al. 2018). Due to the large movements of seabirds, the conservation of these species is generally a shared responsibility of many countries (Beal et al. 2021). Albatrosses and petrels are especially threatened seabirds protected under the Agreement on the Conservation of Albatrosses and Petrels (ACAP) (Cooper et al. 2006). This agreement covers 31 species that constitute 103 MY of evolutionary history. We are aware of no such international agreement specifically targeting parrots, yet over half (53%) of parrot species range across multiple countries, so establishing such an agreement could be an important conservation action.

Many countries that we have highlighted are within the Global South, yet most conservation spending occurs in the Global North (McClanahan & Rankin 2016). Not only should governments in the Global South prioritize conservation spending, but resources in the Global North must be mobilized and allocated more efficiently for conservation efforts abroad, particularly in the tropics (Buechley et al. 2019). Future international collaboration between non-profits, governments, private entities, and indigenous peoples would be most effective in conserving the evolutionary history of birds.

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Figures

Fig. 1. Calculating EDGE scores under the new EDGE protocol. (A) a hypothetical phylogenetic tree for four species, A-D, with branch lengths in millions of years (MY) beside each branch; (B) the evolutionary distinctiveness under the new EDGE protocol for species A, when the probability of extinction (global endangerment; GE) of species B is 0.5, and 0 for species C & D, is measured by summing the black branches, where the branch length is multiplied by the GE of all descendant species excluding species A. Text shows calculation of evolutionary distinctiveness (ED) and EDGE scores when the GE of species A is 0.2. (C) Phylogenetic tree for the clade including the kea (*Nestor notabilis*); (D) evolutionary distinctiveness for the kea.
(E) Phylogenetic tree for the clade including the Philippine eagle (*Pithecophaga jefferyi*); (F) evolutionary distinctiveness for the Philippine eagle. Illustrations by Bryce W. Robinson.



Fig. 2. Variation in the number of species, evolutionary distinctiveness, and evolutionary distinctive and globally endangered (EDGE) scores per bird order. Median (points), 2.5th, and 97.5th (lines) percentiles of evolutionary history and threatened evolutionary history per bird order in millions of years (MY).



Fig. 3. Evolutionary distinctiveness and EDGE scores of parrots (n = 403 species), raptors (n = 561), and seabirds (n = 363) compared to all other birds (total 10,984 species). Points depict medians and vertical lines depict 95% confidence intervals of the difference in evolutionary distinctiveness values or evolutionary distinct and globally endangered (EDGE) scores between a given group and the rest of class Aves. Positive values depict groups with greater values than the rest of class Aves, whereas negative values depict groups with lower values than the rest of the class. The dashed horizontal line at zero references no difference between the groups and the rest of class Aves. Illustrations by Bryce W. Robinson.



Fig. 4. Evolutionary history of birds within each country. A) Evolutionary history of birds per country. B) Threatened evolutionary history of endemic birds per country, and D) Threatened evolutionary history of endemic birds per country. Grey areas represent countries without endemic bird species. All values are in millions of years.



Fig. 5. Important bird areas for the conservation of the evolutionary history of birds. Map of 99 the top 100 important bird areas with the greatest summed A) evolutionary history of trigger species, and B) threatened evolutionary history of trigger species. One important bird area in Brazil was omitted to better depict the locations of the 99 other important bird areas.

