



CONTRIBUTED PAPERS

Conserving the evolutionary history of birds

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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 globally endangered status creates an EDGE score. We use EDGE scores to prioritize the places and species that should be managed to conserve bird evolutionary history. We analyzed all birds in all countries and important bird areas. We examined parrots, raptors, and seabirds in depth because these groups are especially threatened and relatively speciose. The three focal groups had greater median threatened evolutionary history than other taxa, making them important for conserving bird evolutionary history. Australia, Brazil, Indonesia, Madagascar, New Zealand, and the Philippines were especially critical countries for bird conservation because they had the most threatened evolutionary history for endemic birds and are important for parrots, raptors, and seabirds. Increased enforcement of international agreements for the conservation of parrots, raptors, and 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.

KEYWORDS

bird of prey, EDGE score, evolutionary distinctiveness, important bird area, parrot, raptor, seabird

Resumen

En medio de la sexta extinción masiva, los recursos limitados están obligando a los conservacionistas a priorizar cuáles especies y lugares recibirán acciones de conservación. La peculiaridad evolutiva mide el aislamiento de una especie con respecto a su árbol filogenético. La combinación entre la peculiaridad evolutiva de una especie y su estado de conservación mundial genera un puntaje EDGE. Usamos estos puntajes para priorizar los lugares y especies que se deben gestionar para conservar la historia evolutiva ornitológica. Analizamos todas las especies de aves en todos los países y áreas de importancia ornitológica. Estudiamos a profundidad a los psitácidos, rapaces, y aves marinas por el nivel de amenaza que enfrentan estos grupos y porque cuentan con muchas especies. Estos tres grupos tuvieron una mayor mediana de historia evolutiva amenazada que los demás taxones, por lo que son de suma importancia para la conservación de la historia evolutiva ornitológica. Australia, Brasil, Indonesia, Madagascar, Nueva Zelanda y las Filipinas fueron países particularmente críticos para la conservación de las aves pues cuentan con la mayor historia evolutiva amenazada de aves endémicas y son localidades importantes para nuestros tres

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grupos focales. Se requiere de un incremento en la aplicación de los acuerdos internacionales para la conservación de los psitácidos, rapaces y aves marinas ya que estos acuerdos protegen cientos de millones de años de historia evolutiva ornitológica. Se necesitan acciones decisivas para conservar la historia evolutiva de las aves en el Antropoceno.

Palabras Clave:

área de importancia ornitológica, aves marinas, peculiaridad evolutiva, psitácidos, puntaje EDGE, rapaces

【摘要】

重引入顶级捕食者是生态系统恢复的重要方法,同时也是一项挑战。灰狼 (*Canis lupus*) 在1900年左右在日本灭绝,此后,日本一直缺少顶级捕食者。目前,野生有蹄类动物的数量正在增加,对农业和森林造成了破坏。这引发了研究者和非政府组织持续争论是否应重引入灰狼,以促进高生物多样性的生态系统进行自我调节。我们在全中国范围内进行了一次调查,分析了日本公众对灰狼重引入的态度。我们向全国88,318名公民发出了在线调查问卷。在12,028名受访者中,除去那些回答无效、不完整或不具有资格的受访者,我们获得了7,500份回答并进行了分析,这些受访者在日本公民重要的社会人口属性方面具有代表性。不同意重引入灰狼的受访者 (39.9%) 多于同意的受访者 (17.1%),还有许多受访者 (43.0%) 不能下定论。结构方程模型显示,风险认知影响了公众态度,意味着人们对灰狼袭击的威胁感知越明显,就越不可能支持灰狼重引入。相反,因野生动物价值观而对灰狼产生的态度(如“我喜欢狼”),以及对灰狼生态作用的信念(如控制鹿的数量)积极影响着公众对于灰狼重引入的态度。那些对灰狼重引入持积极态度的人表现出参与支持灰狼重引入行动的意向。我们的结果表明,传播与灰狼生态作用有关的信息并培养人们更多的互助心态有助于积极推动日本公众对灰狼重引入的支持。

【翻译:胡怡思;审校:聂永刚】

关键词: 猛禽,重要鸟区,鸚鵡,猛禽,海鸟,EDGE指数,演化独特性

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 (Funk et al., 2017; Parr et al., 2009; 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 (Croxall et al., 2012; Pleguezuelos et al., 2010; Temple & Terry, 2009). Such an approach implicitly assumes that the loss of any species represents an equal loss of biodiversity (Isaac & Pearse, 2018; Redding & Mooers, 2006). 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, 2013; Cadotte et al., 2008; Gravel et al., 2011). Evolutionary distinctiveness is the relative contribution of a species to phylogenetic diversity (Isaac et al., 2007), or the isolation of a species relative to its branch length within its phylogenetic tree (Jetz et al., 2014). Prioritizations based on evolutionary distinctiveness assume that the 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 (Bellard et al., 2021; Davis et al., 2018). 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 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 phylogenetic diversity and an index of evolutionary distinctiveness and global endangerment (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. The score indicates a species' quantitative conservation priority and can be used for ranking. EDGE scores thus increase along with evolutionary distinctiveness and extinction risk. The methodology to calculate EDGE scores was recently revised and is now more intuitive (Gumbs et al., 2023). Under the new method, a score 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). We also examined the evolutionary history and threatened evolutionary history of endemic birds per country to delineate the evolutionary history for which each country is responsible for conserving in the wild. We performed our 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 & Rolek, 2020; McClure et al., 2018), and seabirds (Dias et al., 2019; Spatz et al., 2017). Twenty-eight percent of parrots, 20% of raptors, and 31% of seabirds are threatened with extinction, compared with 13% across all birds (BirdLife International, 2023a). We focused on these three groups to demonstrate how our method can be used to help prioritize and target ongoing conservation.

METHODS

Calculating evolutionary distinctiveness and EDGE scores

For our taxonomy, we used BirdLife International's Handbook of the Birds of the World 5.0 (Birdlife International, 2020) and matched it to the phylogeny of Jetz et al. (2012, 2014) based on the Hackett backbone (further described below). We examined 9645 species. We randomly sampled 1000 trees from the available distribution of phylogenies to adequately capture uncertainty in phylogenetic relationships and node ages (Jetz et al., 2014; Thomas et al., 2013). 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 1000 phylogenetic trees that contained all valid species (1343 imputed species). For imputation, we followed earlier approaches to insert missing species into their genus along the existing phylogenetic branches (Cox et al., 2022; Forest et al., 2018; Gumbs et al., 2023) with the `congeneric.impute` function in 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 among 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 (Gumbs et al., 2023; Redding et al., 2014). 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 1000 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 used to direct conservation action (Gumbs et al., 2018).

EDGE scores have been calculated for birds (Gumbs et al., 2018; Jetz et al., 2014); however, we used the updated EDGE method that provides a more robust and comparable prioritization of evolutionarily distinct species for application to conservation (Gumbs et al., 2023). The updated 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 (Gumbs et al., 2023; Steel et al., 2007), which was missing from the original EDGE metric. This increases the priority of species from clades in which 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 high variability in extinction risk (i.e., unlikely to lose deep branches of the tree, e.g., Anseriformes).

With the updated EDGE metric (EDGE2), the evolutionary distinctiveness of a species is multiplied by its probability of extinction, where the evolutionary distinctiveness of species i is given as:

$$ED_i = TBL_i + \sum_{j=2}^{n_i} \left(L_{i,j} \times \prod_{k \in C_{i,j} - \{i\}} p_k \right), \quad (1)$$

where TBL_i is the terminal branch length of species i , $L_{i,j}$ is the sum of the lengths of all internal branches connecting species i to the root of the phylogenetic tree; p_k is the product of the probability of extinction 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 in Figure 1a,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 million years (MY), so we assigned 50% of that branch to species A. Following this, the evolutionary distinctiveness of species A is $5 +$

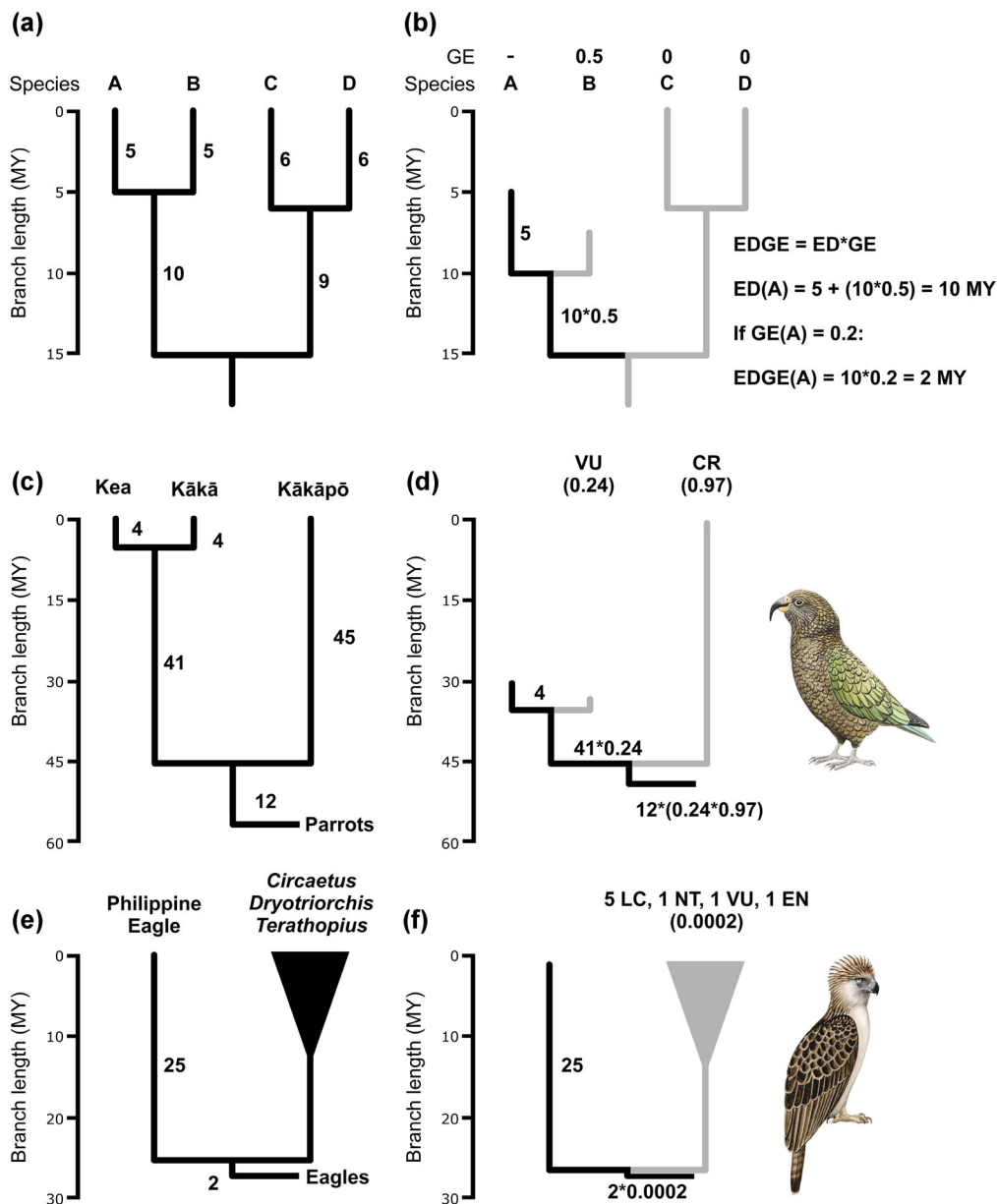


FIGURE 1 Calculation of evolutionarily distinct and globally endangered (EDGE) scores: (a) a hypothetical phylogenetic tree for four species (A–D) (numbers beside branches, branch lengths in millions of years [MY]); (b) evolutionary distinctiveness under the updated EDGE protocol for species A when the probability of extinction (global endangerment [GE]) of species B is 0.5 and GE of species C and D is 0 as determined by summing the black branches (where branch length is multiplied by the GE of all descendant species excluding species A) (There is a calculation of evolutionary distinctiveness [ED] and EDGE scores when GE of species A is 0.2 in the text.); (c) phylogenetic tree for the clade including the kea (*Nestor notabilis*); (d) evolutionary distinctiveness (ED) for the kea; (e) phylogenetic tree for the clade, including the Philippine eagle (*Pithecophaga jefferyi*); and (f) evolutionary distinctiveness for the Philippine eagle. Illustrations by Bryce W. Robinson.

(10 * 0.5) = 10 MY. The EDGE score under the new protocol is then the amount of species A's evolutionary distinctiveness expected to be lost 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, whose 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 that can be averted through conservation.

For two real-world examples, the kea (*Nestor notabilis*) (Figure 1c,d) and the Philippine eagle (*Pithecophaga jefferyi*) (Figure 1e,f), it is evident how the extinction risk of closely related species affects 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 kākāpō (*Strigops habroptilus*) because both species are threatened (vulnerable and critically endangered, respectively) and the three species share relatively

long branches of the tree. Conversely, the Philippine eagle receives > 99% of its evolutionary distinctiveness from its terminal branch because it shares its first internal branch with eight eagle species, five of which are least concern on the IUCN Red List.

We quantified extinction risk following the updated EDGE protocol, in which each IUCN Red List category has a median extinction risk from 0 to 1, around which there are bounds of uncertainty from which one 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; Figure 1 in Gumbs et al., 2023 contains a full distribution). We then repeated our EDGE calculations across the 1000 phylogenetic trees. For each tree, we selected a new extinction risk value from the bounds of uncertainty for the given red-list category for each species. This approach allowed for comparison with other taxonomic groups and facilitated the downstream use of the priority EDGE list by decision makers (details in Gumbs et al., 2023). We define *EDGE species* as those for which the 2.5th 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 in 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 in 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 in 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 in a country if the species was in the country during any part of the year and excluded occurrences described as vagrant. Species were considered endemic to a single country when they occurred 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 identification of 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 km²), or biome-restricted species

or the area contains at least 1% of the global population of congregating species (Hole et al., 2009).

We summed scores for all birds and summed them separately for parrots, raptors, and seabirds. Parrots consisted of all species in Psittaciformes ($n = 403$ species). Raptors were all species ($n = 561$) in Accipitriformes, Cathartiformes, Falconiformes, Strigiformes, and Cariamiformes (McClure et al., 2019). We used the list of seabirds provided by BirdLife International's website (datazone.birdlife.org), which included a subset of species from nine orders (Anseriformes, Charadriiformes, Gaviiformes, Pelecaniformes, Phaethontiformes, Podicipediformes, Procellariiformes, Sphenisciformes, and Suliformes) (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 the 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 represented the bootstrapped median difference between our focal groups and all other birds outside the respective focal group. Values >0 thus represented situations in which a focal group had greater values than all other Aves, whereas values <0 represented situations in which a focal group has lesser values than all other Aves. There was a difference between focal groups and all other birds when the range from the 2.5th to the 97.5th percentiles of bootstrapped iterations excluded zero. We performed analyses 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 (Figures 2–5) (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 was the giant ibis (*Thaumatibis gigantea*), followed by the kākāpō and the plains-wanderer (*Pedionomus torquatus*). The orders with the greatest median evolutionary distinctiveness were Leptosomiformes (cuckoo roller [*Leptosomus discolor*]), Opisthocomiformes (hoatzin [*Opisthocomus hoazin*]), and Eurypygiformes, which consists of the kagus (*Rhynochetos* spp.) and the sunbittern (*Eurypyga helias*) (Figure 2). The orders with the greatest median EDGE scores were Eurypygiformes, Mesitornithiformes (the mesites), and Cathartiformes (Cathartid vultures) (Figure 2). There were 690 EDGE bird species (Appendix S1).

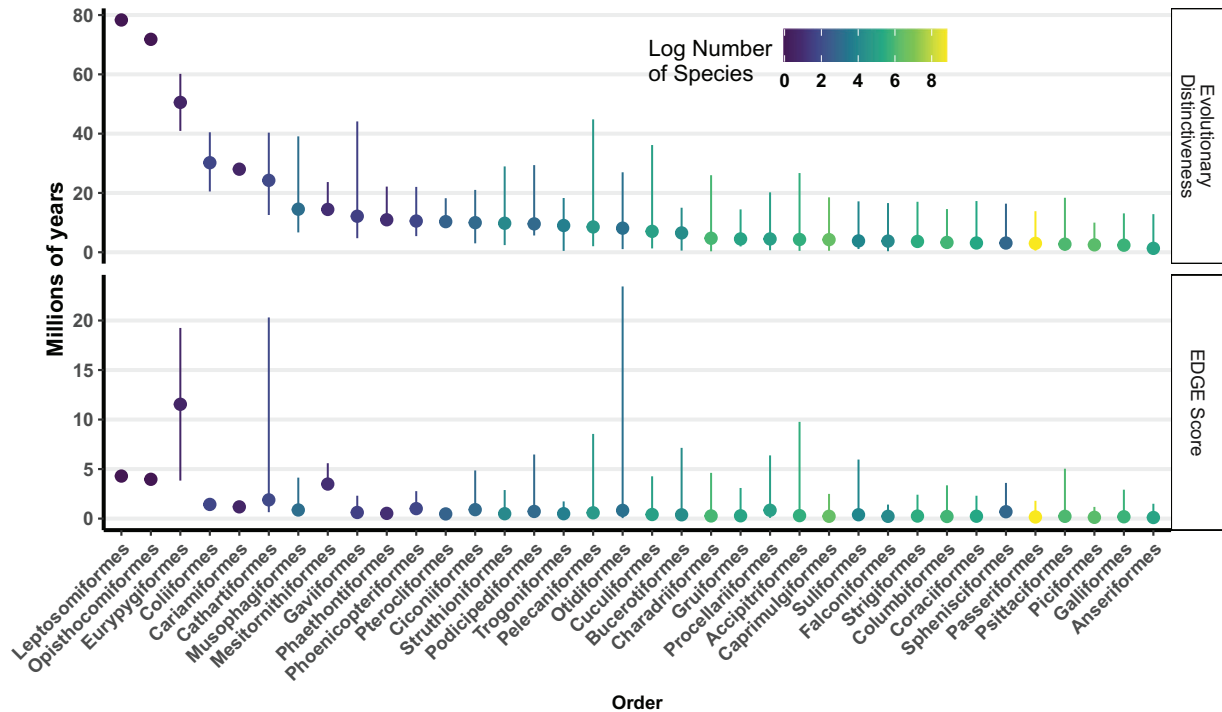


FIGURE 2 Variation in the number of species, evolutionary distinctiveness, and evolutionary distinctive and globally endangered (EDGE) scores per bird order (points, median; lines, 2.5th and 97.5th percentiles of evolutionary history and threatened evolutionary history).

Geographically, Peru, followed by Colombia and Indonesia, contained the greatest bird evolutionary history (Figure 4 & Appendix S2). Indonesia, Brazil, and Colombia possessed the most threatened evolutionary history (Figure 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 have been 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%) (Figure 5). Africa contained 69 of the 100 IBAs with the most evolutionary history and 31 of the IBAs with the most threatened evolutionary history (Figure 5). The IBA with 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 100 IBAs with the most overall and threatened evolutionary history, respectively (Figure 5). Malaysia contained 25 and 32 of the 100 IBAs with the most overall and threatened evolutionary history, respectively (Figure 5 & Appendix S3). The IBA with the most threatened evolutionary history and the greatest number of EDGE species was the Mulu-Buda Protected Area in Malaysia. We highlighted the 100 most important IBAs for simplicity; the

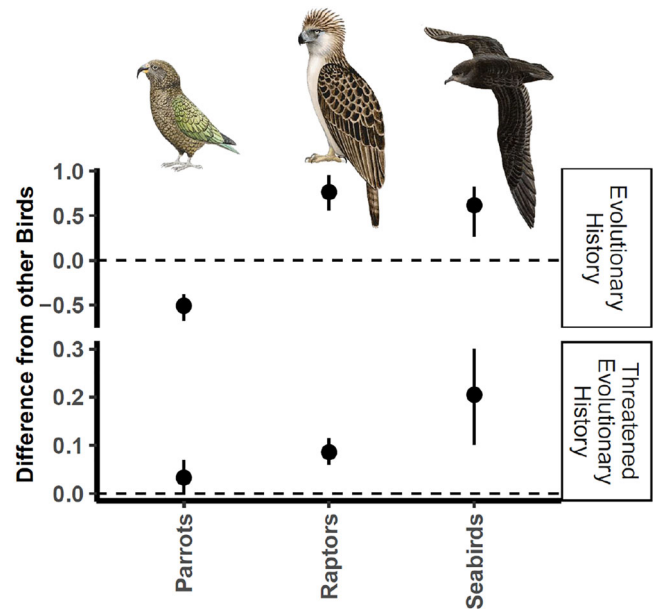


FIGURE 3 Evolutionary distinctiveness and evolutionary distinctive and globally endangered (EDGE) scores for parrots ($n = 403$ species), raptors ($n = 561$), and seabirds ($n = 363$) compared with all other birds (total 10,984 species) (points, medians; vertical lines, 95% confidence intervals of the difference in evolutionary distinctiveness values or EDGE scores between a given bird taxon and the rest of class Aves, positive values indicate groups with values higher than the rest of the class; negative values indicate groups with values lower than the rest of the class; dashed horizontal line indicates no difference between the given taxon and the rest of class Aves). Illustrations by Bryce W. Robinson.

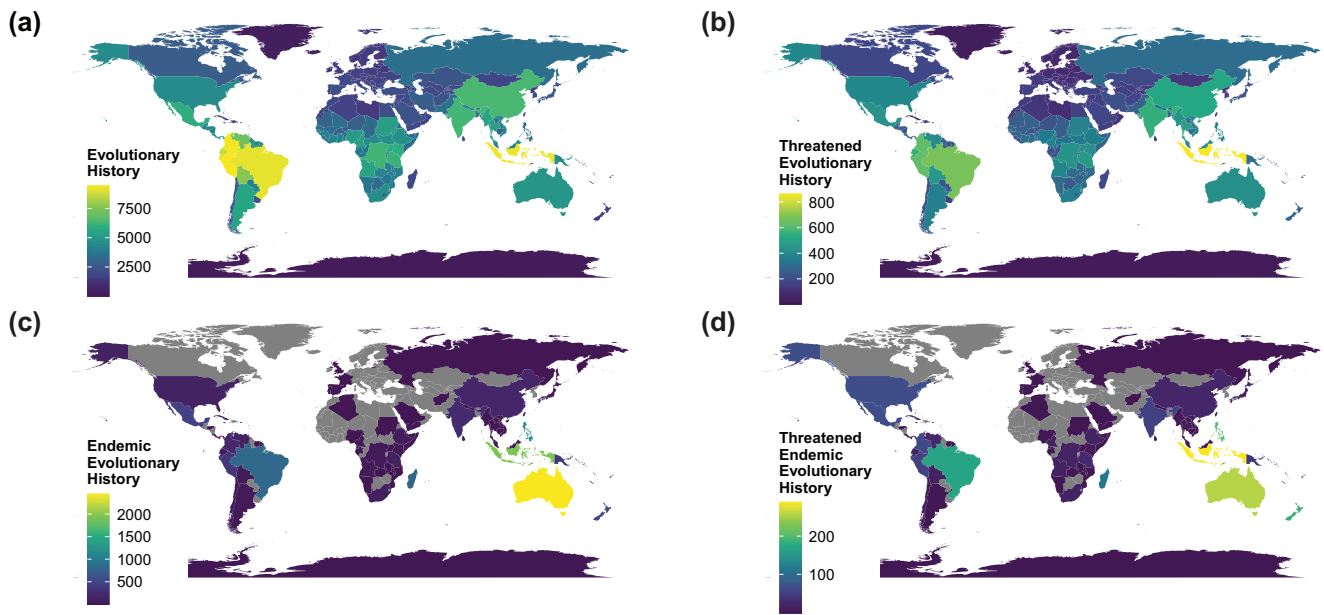


FIGURE 4 Evolutionary history of birds in each country in millions of years: (a) evolutionary history of birds per country, (b) threatened evolutionary history of birds per country, (c) evolutionary history of endemic birds per country, and (d) threatened evolutionary history of endemic birds per country (gray, countries without endemic bird species).

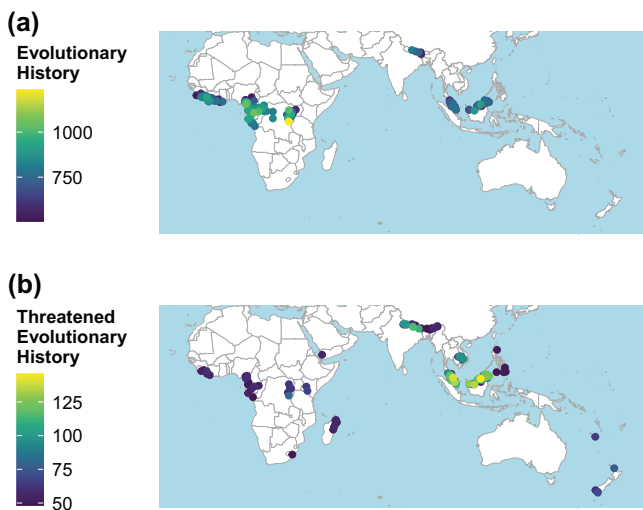


FIGURE 5 Ninety-nine of the 100 most important bird areas (IBAs) with the greatest summed (a) evolutionary history of species triggering an IBA and (b) threatened evolutionary history of species triggering an IBA. One important bird area in Brazil was omitted to better depict the locations of the 99 other IBAs.

full list is 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 were the white-eyed river martin (*Eurochelidon sirintarae*), the Whenua Hou diving-petrel (*Pelecanoides whenuabouensis*), and the Australian painted-snipe (*Rostratula australis*).

Comparing evolutionary distinctiveness among priority groups revealed that parrots were less evolutionarily distinct on average than other Aves, whereas raptors and seabirds were

more distinct (Figure 3). All three groups, however, had greater EDGE scores than other birds on average (Figure 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 in Psittaciformes. The three parrots with the greatest EDGE scores were kākāpō, kākā, and kea (Appendix S1); species that are all endemic to New Zealand. Australia, Brazil, and Indonesia contained the most parrot evolutionary history, and New Zealand, Brazil, and Australia had the most threatened evolutionary history for parrots (Appendix S4). Regarding endemic parrots, Australia contained the greatest evolutionary history followed by New Zealand and Indonesia (Appendix S4).

All the top 100 IBAs for the evolutionary history of parrots occurred in either South America (67 IBAs) or Australasia (33 IBAs) (Appendix S4). Regarding threatened evolutionary history, the top 100 IBAs for parrots occurred mostly in Asia (42 IBAs) and Australasia (38 IBAs) (Appendix S4). 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) (Appendix S4). New Zealand contained the 16 most important IBAs for the threatened evolutionary history of parrots (Appendix S4).

Raptors

There are 561 species of raptors in Accipitriformes, Cathartiformes, Cariamiformes, Falconiformes, and Strigiformes (McClure et al., 2019). The secretarybird (*Sagittarius serpentarius*), Philippine eagle, and California condor (*Gymnogyps californianus*) had the highest EDGE scores. 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 (Appendix S4). Island countries, especially Indonesia, the Philippines, and Madagascar, contained the greatest overall and threatened evolutionary history of endemic raptor species (Appendix S4).

Most of the 100 IBAs with the greatest evolutionary history of raptors occurred in Europe (67 IBAs) (Appendix S4). These IBAs were mostly triggered by the osprey (*Pandion haliaetus*), which has the second-greatest evolutionary distinctiveness of raptors (61.24 MY) but a low extinction risk. Germany contained the most of these IBAs (25). Conversely, the 100 IBAs with the greatest threatened evolutionary history of raptors occurred mostly in Asia (64 IBAs) (Appendix S4); the Philippines contained 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 S4) and require terrestrial breeding sites for reproduction (Dias et al., 2019). Priority seabirds included the Christmas Island frigatebird (*Fregata andrewsi*), the Whenua Hou diving-petrel, and the New Zealand storm petrel (*Fregatta maoriana*) (Appendix S4). The most evolutionary history of seabirds occurred in the United States, Chile, and Mexico (Appendix S4), and the greatest threatened evolutionary history occurred in the United States, New Zealand, and Chile. Only 15 countries had endemic seabird species (Appendix S4). New Zealand, Mexico, and Portugal contained the most evolutionary history, and New Zealand followed by Mexico and Fiji possessed the most threatened evolutionary history among endemic seabirds.

Europe contained the most of the top 100 IBAs for evolutionary history of seabirds (48 IBAs) (Appendix S4), whereas Australasia contained the greatest number of the top 100 IBAs for threatened evolutionary history (25 IBAs) (Appendix S4). Russia (16 IBAs) and New Zealand (24 IBAs) contained the most of the top 100 IBAs for overall and threatened evolutionary history of seabirds, respectively (Appendix S4).

DISCUSSION

Our results reveal priorities for conserving the evolutionary history of birds. The IBAs represent crucial places for bird conservation. Thirty-three EDGE species did 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 (*Eurostopus 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; thus, the places to focus conservation of 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 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 dominated 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 they harbor tend to be evolutionarily distinct within 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 analyses differed from that of Jetz et al. (2014) because they 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 did. 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). The taxon has 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, 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), a raptor with one of the highest EDGE scores. 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 the 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 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). A 2018 assessment showed that 31% of seabirds are threatened with extinction (Dias et al., 2019). The three seabird species with the greatest EDGE scores 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 8000) have ranges that span multiple countries; thus, international collaboration via multinational

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 identified 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 (Raptors MoU) (<https://www.cms.int/raptors/>), which is a nonbinding 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 in 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 also 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 nonprofit organizations, governments, private entities, and Indigenous peoples would be most effective in conserving the evolutionary history of birds.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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