Article

Global Distribution and Conservation of Evolutionary Distinctness in Birds

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Summary

Background: Integrated, efficient, and global prioritization approaches are necessary to manage the ongoing loss of species and their associated function. "Evolutionary distinctness" measures a species' contribution to the total evolutionary history of its clade and is expected to capture uniquely divergent genomes and functions. Here we demonstrate how such a metric identifies species and regions of particular value for safeguarding evolutionary diversity.
Results: Among the world's 9,993 recognized bird species, evolutionary distinctness is very heterogeneously distributed on the phylogenetic tree and varies little with range size or threat level. Species representing the most evolutionary history over the smallest area (those with greatest "evolutionary distinctness rarity") as well as some of the most imperiled distinct species are often concentrated outside the species-rich regions and countries, suggesting they may not be well captured by current conservation planning. We perform global cross-species and spatial analyses and generate minimum conservation sets to assess the benefits of the presented species-level metrics. We find that prioritizing imperiled species by their evolutionary distinctness and geographic rarity is a surprisingly effective and spatially economical way to maintain the total evolutionary information encompassing the world's birds. We identify potential conservation gaps in relation to the existing reserve network that in particular highlight islands as effective priority areas.
Conclusions: The presented distinctness metrics are effective yet easily communicable and versatile tools to assist objective global conservation decision making. Given that most species will remain ecologically understudied, combining growing phylogenetic and spatial data may be an efficient way to retain vital aspects of biodiversity.

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Introduction

The planet is in the midst of an extinction crisis [1]. Conservation of individual species is one important response [2–4], but limited resources necessitate prioritization [5]. Some species have particular aesthetic, functional, or evolutionary attributes such that their extinction would represent especially important losses. One such attribute distinguishing species is "evolutionary distinctness" (ED), a measure of how isolated a species is on its phylogenetic tree [6]. Highly distinct species may express nonrandom phenotypes [7] and represent uniquely divergent genomes (see e.g. [8]). Moreover, sets of evolutionarily distinct species are expected to encompass a large proportion of the parental clade's total phylogenetic diversity (PD; [9]). This attribute may be important because PD [10] is a good predictor of ecological assemblage function [11–15]. However, it is not known whether considering evolutionary distinctness to guide prioritization of threatened species effectively safeguards total evolutionary information [10] or, critically, whether it can guide spatially efficient conservation planning.

For many understudied taxa, phylogenetic information is accruing much more rapidly than ecological information. Therefore, integrating phylogenetic data into prioritization metrics for species and areas may offer an efficient way to protect and maintain ecosystem function in a rapidly changing world [5, 16–18]. Here, we make use of a new distribution of dated phylogenies ([19]; see Experimental Procedures) for the class Aves to address these questions and perform the first fully quantitative phylogenetically and geographically integrated conservation assessment for all 9,993 recognized species of birds worldwide. Specifically, we (1) identify and map the world's most evolutionarily distinct species and test hypotheses about their evolution and biogeography; (2) assess the association between distinctness, threat, and range size; (3) describe a new species-level metric that integrates evolutionary distinctness and range restriction; (4) assess the potential for such species metrics to minimize the potential loss of evolutionary information in a spatially efficient manner; and (5) identify key conservation gaps for imperiled evolutionary information. Our approach identifies how spatially and phylogenetically informed prioritization can maximize the extent of the tree of life that can persist into the future.

Results and Discussion

Variation in Avian Evolutionary Distinctness

We measured the isolation of a species on its phylogenetic trees as its evolutionary distinctness (ED) metric (see Table 1), fully accounting for the branch lengths in addition to nodes separating species, and summarized it over 10,000 phylogenetic trees (see Experimental Procedures). We found that ED is distributed very unevenly among species and is highly right skewed, with the median bird species harboring ~6.2 MY (million years) of ED (Figure 1A inset; min 0.8 MY, max 72.8 MY; see also Figure S1 and Table S1 available online and http://www.birdtree.org and http://www.mol.org/projects/ED). ED scores vary little among different tree calibrations representing a range of current expert opinions regarding

Table 1. Glossary of Terms

Term	Definition	Units Used
PD (phylogenetic diversity)	Sum of all lengths of all branches in a defined phylogenetic tree.	time (e.g., MY)
ED (evolutionary distinctness)	A species-level measure representing the weighted sum of the branch lengths along the path from the root of a tree to a given tip (species). Identical to and sometimes referred to as the fair proportion (FP) metric [9]. Note that the ED of all species in a tree sums to PD.	time (e.g., MY)
EDGE (Evolutionary Distinct and Globally Endangered)	A metric combining distinctness and extinction risk. We used the formulation from [16]: ln(ED + 1) + GE*ln(2), where GE is a rank scalar ranging from 0 (IUCN Red List designation "Least Concern") to 4 (IUCN Red List designation "Critically Endangered").	–
EDR (evolutionary distinctness rarity)	ED divided by a species' global geographic range size.	time per range area (e.g., MY/10,000 km^2)
Total EDR	Summed EDR of all species co-occurring in a given location (e.g., grid cell).	time per range area (e.g., MY/10,000 km^2)

the treatment of fossil data (Figure S1). The summed ED of all species is equal to the total PD of all birds (i.e., median 77,150 MY), and the top 10% most evolutionarily distinct species disproportionately represent approximately one-third of that total. ED varies widely, with high- and low-ED species found throughout the avian tree of life (Figure 1A). ED shows moderate levels of phylogenetic clustering (strength of phylogenetic signal of the top 10% highest-ED species measured as mean $D = 0.283$, standard deviation = 0.015, where D approaching zero is consistent with strong phylogenetic inertia; see Experimental Procedures). Nine-primaried oscines and most passerine clades contain more low-ED (phylogenetically redundant) species than other parts of the tree, especially some species-poor nonpasserine groups. This is consistent with the higher overall diversification rate previously observed in passerines and the noted increases at the base as well as throughout this clade [19, 21, 22].

Geographically, the distribution of ED is also clustered (Figures 2A and 2B), and the world's top 1,000 (i.e., top 10%) ED species are particularly prevalent in the isolated landmasses of Australia, New Zealand, and Madagascar, as well as in Africa and southern South America. Due to insufficient phylogenetic information, uncertainty in ED is high in parts of Africa, Southeast Asia, and Australia (Figure S2), but not enough to affect the major trends we identified (compare Figure S2 with Figure 3). The tropics have previously been suggested as "museums" for ancient or relictual lineages [23]. ED provides an approximate measure to test the "museum hypothesis." Although the cause (extinction of recent relatives or lack of speciation) is ambiguous, high-ED species have relatively ancient recorded speciation events and do not have many recent close relatives. In contrast, low-ED species are characterized by recent divergences and are clearly not relictual. We found that top ED membership does not show any strong trend with the latitudinal midpoint of ranges (median p = 0.27, f(p < 0.05) = 19/100). Similarly, Northern versus Southern Hemisphere location has no effect (p = 0.46, f(p < 0.05) = 5/100), and, in contrast to recently rapidly diversifying lineages [19], there is also no strong Eastern versus Western Hemisphere difference in top ED (p = 0.24, f(p < 0.05) = 24/100).

Regions with high current prevalence of top ED species are those where evolutionarily distinct species have originated, or immigrated to, and remained. A separate consideration of nonpasserines (4,027 species) and passerines (5,966 species, derived from within nonpasserines) allows a more nuanced interpretation of geographic variation (Figure 3). Although they have similar geographic patterns of overall species richness (Figure 3A; $r_S = 0.90$, N = 12,778), the two groups show contrasting patterns of richness when considering the proportion of top 10% high-ED species in each grid cell (Figures 3C and 3D; $r_S = 0.13$). In passerines, top ED species are most prevalent on the large islands of Australasia and Southeast Asia, consistent with their hypothesized region of origin and the subsequent diversification and dispersal of oscines northward and westward [22, 24]. Distinct passerine and nonpasserine lineages show geographic concordance only in North Africa, the Middle East, and Madagascar, providing support for these arid biomes being associated with processes leading to evolutionarily distinct lineages.

A high coincidence of peaks in species richness and high prevalence of top ED species combined with limited distributional changes over time would support the idea of relictual lineages highlighting regions that have accumulated species richness over time, for example due to age or climatic stability [25–27]. Although there is a general trend for areas with higher species richness to also contain more top 10% ED species (Figure 2C), there is no association between species richness and the relative prevalence of high-ED species (scored as the proportion of all species that are in the top 10% of ED species: nonpasserines: $r_S = 0.15$, passerines: $r_S = -0.03$), at least at this spatial grain of analysis. The only notable exception is lowland South America, where radiations such as the tinamous contribute to high top ED prevalence of nonpasserines. Indeed, places where top ED species are prevalent today are predominantly not those with many very recent and rapid radiations, measured as proportion of bottom 10% ED species in a grid cell (nonpasserines: $r_S = -0.47$, passerines: $r_S = -0.34$ [19]). On the contrary, an almost fully inverted geographic pattern (Figures 3E and 3F) instead suggests that the same factors (e.g., extensive Quaternary habitat change at high latitudes) that promote recent diversification have negative effects on species persistence (cf. [28]). At our scale of analysis, mountains, often hypothesized to be a safe harbor for ancient lineages [27–29], show no relationship with high top ED prevalence (grid cell mean elevation as predictor: nonpasserines: $r_S = 0.04$, passerines: $r_S = 0.05$). This is supported by a comparative analysis using median elevation across species' global ranges as predictor (Figure 4A).

Continental regions with high concentration of range-restricted species, such as mountains, have generally been purported to represent refugia that indicate long-term climatic stability, and where we might expect to see ancient or relictual lineages [30, 31]. However, in birds, the relative proportion of top 10% range-restricted species shows no association with
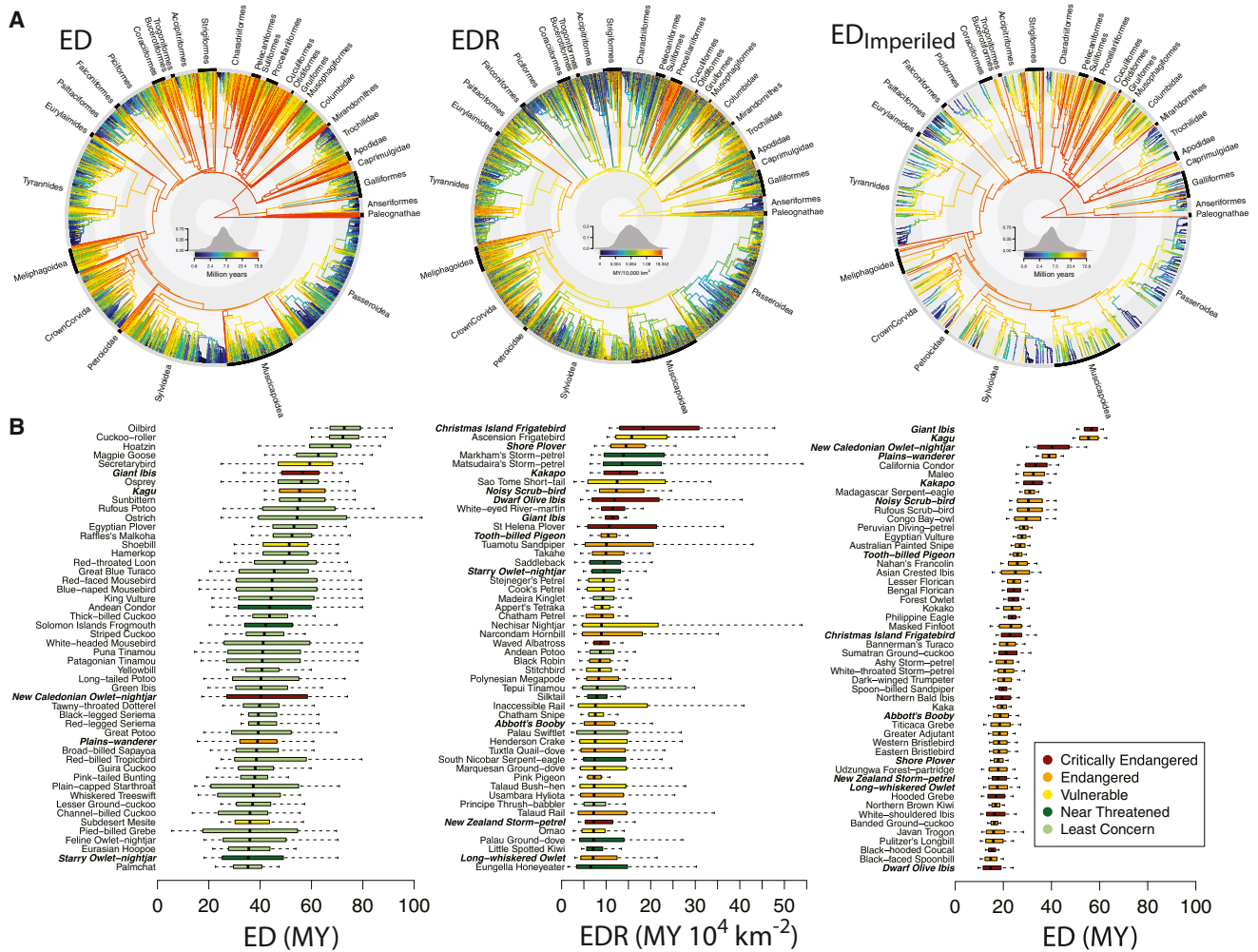
Figure 1. Phylogenetic Distribution and Top-Ranking Species for Phylogenetic Conservation Measures for Birds

Phylogenetic distribution (A) and top 50 species values (B) for evolutionary distinctness (ED, left), evolutionary distinctness rarity (EDR; i.e., ED per unit of species range size, middle), and ED among the 575 most imperiled species (right). In (A), edges are colored for visualization purposes according to ancestral states estimated under Brownian motion using a least-squares algorithm using R package ape [20]. In (B), boxplots show the variation (minimum, 5th percentile, median, 95th percentile, maximum) in metrics among 10,000 trees from the posterior distribution, colors depict 2012 IUCN Red List threat status, and species found in more than one list are highlighted. Our broad tree distribution [19] captures much of the inherent remaining uncertainty in node ages and ED estimates and demonstrates that some comparisons remain too close to call.

that of top 10% ED species in either nonpasserines or passerines ($r_S = 0.05$, $r_S = 0.00$, respectively, with 1,037 island cells excluded; Figures 3G and 3H). Geographically, the identified centers of avian endemism appear associated with select mountain regions and especially with islands, a general trend also seen in other taxa for which small habitat areas and isolation have been cited as key factors supporting high endemism [32]. Although the topographic and bathometric histories of mountains and islands are globally heterogeneous, the geographic pattern of high-ED species is not consistent with islands or elevation facilitating the origination or immigration and persistence of ancient lineages. Species with more than half of their range on islands are less likely to be in the top 10% ED category than those predominantly on mainland (Figure 4C; p = 0.02, f(p < 0.05) = 66/100). Indeed, the geologically young age of many island archipelagos may facilitate extremely rapid, recent divergence [19, 33] and a global trend of low ED of island avifaunas (especially in passerines; see Figures 3D and 3F).

The geographic restrictedness, or range size, of species is a key correlate of past and projected extinction risk [34, 35]. High-ED species have been suggested to have both large and small ranges [36, 37], and a negative correlation between ED and range size would make high-ED species of immediate conservation concern. For all birds, we found that the lack of geographic concordance between range restrictedness and top ED extends more generally to a cross-species comparison of geographic breeding range size and avian ED, and that top ED species are not geographically more restricted than others (Figure 4B); in fact, the top 10% ED species have slightly larger ranges than lower-ED species (p = 0.00, f(p < 0.05) = 85/100). Given the positive correlation between ED and species age, this very scattered relationship between ED and range size (Figure 4B) does not strongly support a simple age-area association [38], at least when, as here, island species are included, and instead supports the view of geographic range dynamics as complex and multicausal [37].
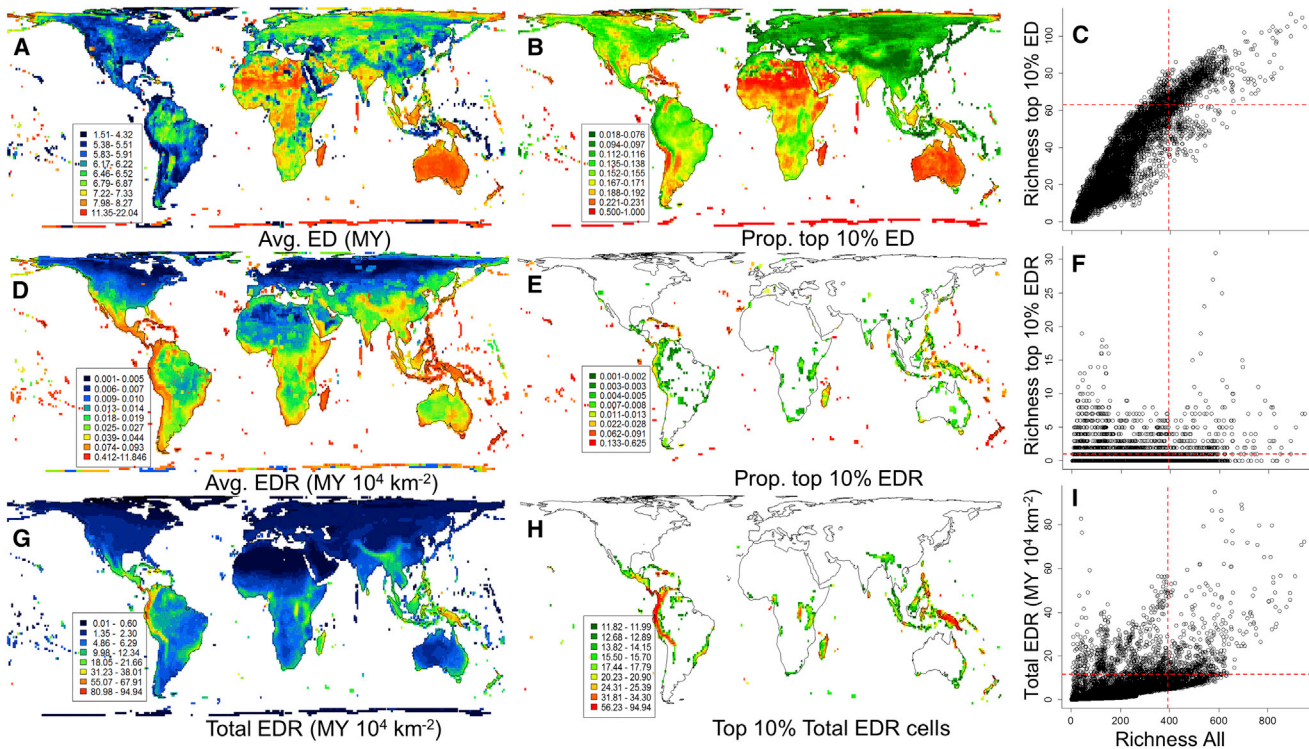
Figure 2. Geographic Variation in Evolutionary Distinctness and Evolutionary Distinctness Rarity for Birds

(A–C) Evolutionary distinctness (ED).

(D–I) Evolutionary distinctness rarity (EDR).

Averages (A and D) provide (geometric) mean grid cell assemblage values (of medians across 10,000 trees) accounted for range size. Proportions (B and E) give the prevalence of top 10% species in a cell. Total EDR (G–I) is the summed EDR of all species occurring in an assemblage for all (G) and the top 10% (H) grid cells. Scatterplots relate the number of top 10% ED (C) and EDR (F) species and total EDR (I) with the total species richness across all grid cells. Dashed red lines in scatterplots mark the top 10% quantiles of each axis (e.g., for the x axis, the most species-rich 1,268 of all 12,680 grid cells) to highlight the congruence among top-ranked x and y cells. Congruence values (defined as the intersection of top 10% cells of x and y divided by the top 10% cell count of x) are: ED (C): 971/1,268 = 0.77; average EDR (F): 174/1,268 = 0.14; total EDR (I): 470/1,268 = 0.37. Grid cells are 110 × 110 km (see Experimental Procedures).

Conservation of Evolutionarily Distinct Species

The world's top 50 most evolutionarily distinct bird species (Figure 1B) include widely distributed and common species such as the osprey and the ostrich (which may be even more distinct; see [39]), well-known oddities such as the hoatzin and the shoebill, and lesser-known, range-restricted species such as the New Caledonian owlet-nightjar and the Solomon Islands frogmouth. They also include species such as the oilbird (South America), cuckoo roller (Madagascar), and hoatzin (South America) with terminal branches that link them to the remainder of the extant avian tree prior to the Cretaceous-Paleogene boundary (>65 MY; see PE or "pendant edge" score in Table S1). Notable also are members of small or monotypic families that might have been expected to but did not make this top list. Passerines are represented by only three species (broad-billed sapayoa, pink-tailed bunting, and palmchat), while in members of other ancient passerine lineages such as lyrebirds, scrubbirds, and New Zealand wrens, ED values are reduced from partial redundancy with close sister species. Monotypic families such as the ibisbill, olive warbler, bristlehead, emu, and limpkin are in the top 300 ED group but have sufficiently close relatives to not rank higher. This illustrates the limits of a taxonomy-based identification of evolutionary distinctness, even in well-studied groups such as birds. Even if taxonomy and phylogeny are fully congruent, variation in the species richness of higher taxa, their times of origin, and their interrelationships can all generate taxonomic discrepancies in measures of evolutionary distinctness. Countries with especially high proportional stewardship for the top 50 and the top 10% ED bird species include Australia, Indonesia, Brazil, Peru, Madagascar, Argentina, and New Zealand, most of which also rank exceptionally high for their total bird diversity (Tables 2 and S2). These countries carry a special responsibility for conserving global avian evolutionary information.

We noted above that in birds, high-ED species per se are not geographically more restricted than lower-ED species, which means that they are unlikely to be threatened by shrinking or shifting habitats alone. However, with narrow-ranged species concentrating their ED over a small area, parts of the phylogeny are potentially, and precariously, represented only in restricted areas of the world. Indeed, global change is expected to induce both rapid range extensions and range losses in species, often quite independent of current formal threat categorizations [34], with direct consequences for the spatial concentration and thus potential for global loss of evolutionary information. In this context, we propose a new metric, "evolutionary distinctness rarity" (EDR = ED / species geographic range size), as an integrative, conservation-relevant measure that apportions evolutionary distinctness
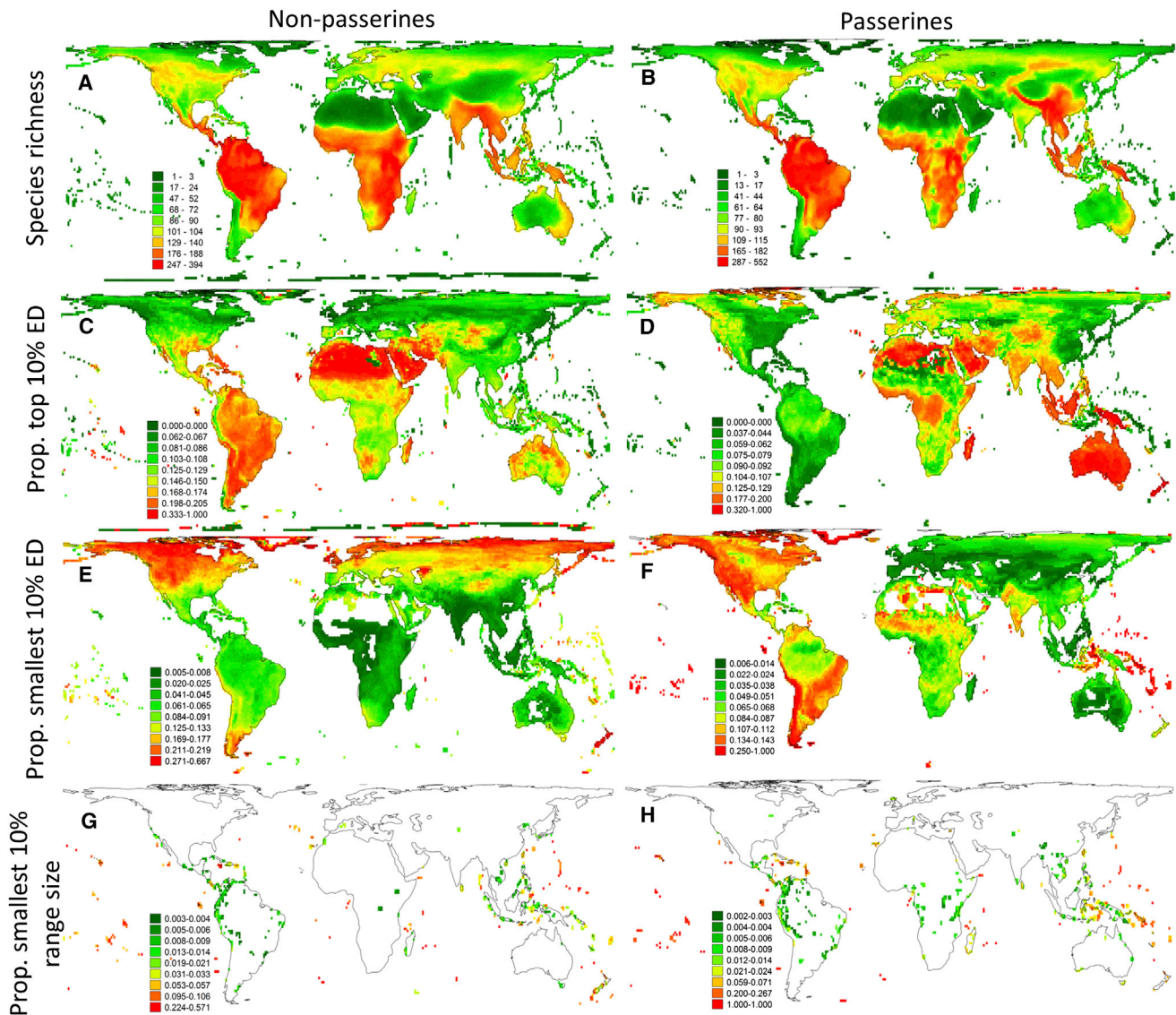
Figure 3. Geographic Patterns of Evolutionary Distinctness for Nonpasserine and Passerine Birds

Maps show the total and relative richness of all (A and B), most evolutionarily distinct (C and D), least evolutionarily distinct (E and F), and geographically most restricted (G and H) bird species. Nonpasserines (4,027 species; A, C, E, and G) and passerines (5,966 species; B, D, F, and H) are shown separately. For more details, see Figure 2.

evenly over a species' occupied regions (e.g., terrestrial grid cells). Unlike related metrics that that are sensitive to multiple members of a clade [40], EDR focuses on the evolutionary distinctness and geographic range dynamics of individual species, e.g., under global change. The distribution of EDR across the avian tree differs strongly from ED (Figure 1), with high-EDR groups ranging from the often (at least in their breeding locations) island-restricted tubenoses (Procellarii-formes) to habitat-restricted suboscine songbird groups. The geographically rarest top ED species include the Christ-mas Island frigatebird (Australia, ED ≈ 22 MY), whose evolutionary information, as in some other seabirds, is restricted to a single 110 × 110 km grid cell, and within it to just a few km², imposing all stewardship for this evolutionary information to a very small site (EDR ≈ 18 MY/10,000 km²). For other species, such as the giant ibis or noisy scrubbird, stewardship and potential exposure to global change extend over several

cells, but their very high ED still places them in the top 50 EDR species.

The geographic patterns of grid-cell average species EDR highlight areas where species ED is particularly geographically restricted (Figures 2C and 2D). As noted above, species are especially range restricted on islands and in montane regions, places that accordingly are home to extremely high average EDR and a strict concentration of the top 10% EDR species. Assemblages with the greatest number of top 10% EDR species include some well-known areas of high species richness, but overall, the coincidence of these different forms of richness is very limited (Figure 2F). Countries with a particularly strong concentration of high-EDR species include Indonesia, Peru, Columbia, and especially New Zealand, which alone and exclusively harbors 11 of the top 50 EDR species world-wide (Tables 2 and S2). The summed total EDR of all species in a cell provides a measure of total evolutionary distinctness
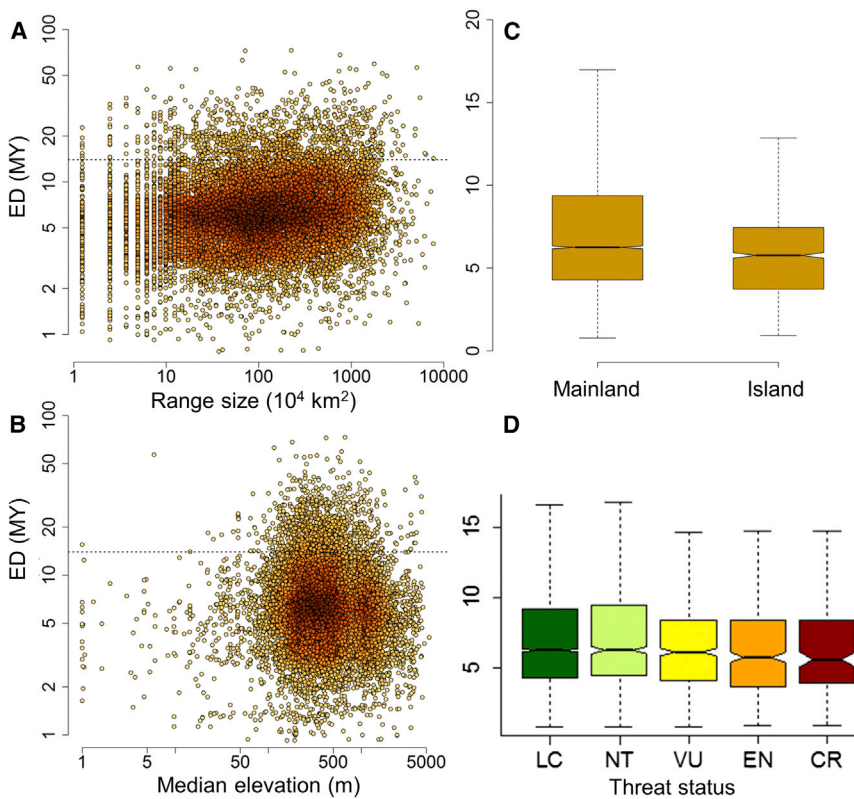
Figure 4. Variation in Evolutionary Distinctness Values across All Birds

Association of ED values of all 9,993 species with breeding range size (A), median elevation of occupied cells (B), island versus mainland status (C), and 2012 IUCN Red List categorization (D). In (A) and (B), dotted horizontal lines identify top 10% ED species and darkness of colors represents density of overlapping points. IUCN categories are LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; and CR, Critically Endangered. Boxplots in (C) and (D) show medians (horizontal line), an approximation of 95% confidence intervals suitable for comparing two medians (notches), 25th and 75th percentiles (boxes), and the most extreme data points that are no more than 1.5 times the length of the box away from the box (whiskers).

restricted to that location. It marks the co-occurrence of geographically restricted high-ED species and transparently flags particularly large amounts of distinct evolutionary information that conservation managers or tourists may encounter there but nowhere else. Under global change, reduction in range size for a species directly translates into increased EDR for that species and increases total EDR for any location where it remains. The high Andes, Madagascar, and New Guinea emerge as important regions for total EDR, but several smaller regions and islands are also highlighted (Figures 2E and 2F). Even though they are by definition associated, hotspots of avian total EDR show little congruence with hotspots of species richness (Figure 2I).

EDR highlights species and regions for which geographic restrictedness alone suggests particular conservation concern under global change. Alternatively, the IUCN Red List's threat listing process provides an existing formal assessment of species extinction threat, and attempts have been made to use Red List categories to produce formal estimates of potential future ED loss and use these for conservation prioritization of "Evolutionary Distinct and Globally Endangered" (EDGE) species [16, 17, 41–43]. We provide the first formal list of EDGE birds in Table S1. The top ten species include the nine highest-ED species that are also assessed as Critically Endangered (giant ibis, New Caledonian owlet-nightjar, California condor, kakapo, Bengal florican, forest owlet, Philippine eagle, Christmas Island frigatebird, and Sumatran ground cuckoo) as well as the Endangered kagu, which has exceptionally high ED (see also Figure 1). The categorical nature and uncertainty surrounding IUCN threat categories, their expected modulation from global change [34, 44], and problems scaling them with actual extinction risk [45, 46] mean that any prioritization scheme

derived from them will require careful and continued monitoring and updating [47]. Nevertheless, the Red List categories present a formalized and operational measure and currently identify a total of 575 bird species as "Imperiled" (which we defined as either Critically Endangered or Endangered).

How does this recognized prioritization of bird conservation urgency and need combine with potential conservation value as measured by ED? An association between taxon age and such assessment-based probabilities of extinction risk has been suggested, linked by stochastic aging of species or a potential connection between extinction risk and the purported specialization of older, "fringe" species [48–50]. Interestingly, Imperiled species show very low levels of phylogenetic clustering (Figure 1; strength of phylogenetic signal of Imperiled species measured as mean $D = 0.887$, standard deviation = 0.009, where D approaching 1 indicates phylogenetic randomness), and ED shows little variation among current-day extinction risk categories according to IUCN (Figures 4D and S3); in this clade, at least, and similarly in mammals [48], evolutionary distinctness is not a surrogate for imperilment (contra [51]). Only four of the top 50 ED species are listed as Imperiled by the IUCN, with a further two as Vulnerable (Figure 1B). Among the 575 Imperiled species, the giant ibis (Southeast Asia) and kagu (New Caledonia) have exceptionally high ED values (ED > 50 MY) and may deserve particular conservation attention. At the other extreme, Imperiled species such as the marsh seedeater (southern South America) or Bolivian spinetail (Bolivia, both with ED ≤ 1.0 MY) are very redundant on the tree of life (see Table S1 for additional metrics, including EDGE [16]).

Evolutionary Distinctness as a Metric for Conservation Prioritization

Practical conservation management requires identification of least-cost approaches for maximizing conservation outcomes. Under an objective of minimizing global PD loss, how do ED and EDR perform as metrics for a rule-based approach to taxon- and area-based conservation priority setting? Given previous simulation results [9], we predicted that prioritizing among Imperiled bird species using ED would result in

Table 2. Countries with Greatest Evolutionary Distinctness Stewardship

All 9,993 Species

		Top 10% ED	Top 50 ED	Top 10% EDR	Top 50 EDR	All 9,993 (Rank)
1	Australia	96	3	36	3	468 (4)
2	Indonesia	92	2	97	3	821 (2)
3	Brazil	83	6	38	0	925 (1)
4	Papua New Guinea	42	1	37	0	285 (9)
5	Madagascar	35	2	19	1	135 (18)
6	Peru	32	2	46	2	490 (3)
7	United States	32	1	24	1	326 (7)
8	Argentina	28	3	1	0	211 (16)
9	Democratic Republic of the Congo	24	1	6	0	220 (12)
10	Russia	24	1	0	0	214 (15)
11	Colombia	24	2	51	0	426 (5)
12	New Zealand	22	0	50	11	95 (25)
13–229		465	26	594	29	5,377

575 Imperiled Species

		Top 50% ED	Top 50 ED	Top 50% EDR	Top 50 EDR	All 575 (Rank)
1	Indonesia	25	5	20	3	42 (2)
2	Brazil	22	1	20	3	55 (1)
3	New Zealand	21	6	17	9	27 (6)
4	Australia	17	7	7	2	20 (7)
5	Philippines	15	2	11	1	20 (8)
6	India	10	3	4	1	14 (11)
7	United States	10	2	13	2	30 (4)
8	Peru	9	2	13	4	28 (5)
9	Madagascar	8	1	3	0	12 (12)
10	Colombia	8	1	18	0	35 (3)
11	Tanzania	7	1	7	1	10 (16)
12	Mexico	6	0	6	1	17 (10)
13–229		123	19	142	23	265

Countries are selected and sorted by the number of top 10% ED species they harbor among all species (top) and the top 50% ED species among the 575 Imperiled species (bottom). The bottom row in each table combines richness values of the remaining 217 low-ranked countries. The species richness of top ED, top EDR, and all species are weighted among countries by the proportion of each species' global range that they hold and are rounded to integers. Range weighting apportions richness uniquely to each country and ensures that the columns sum to the global total richness for each category. Countries in the top list for both all and Imperiled species are underlined. For the complete list, see Tables S2 and S3.

substantial gains in the total tree preserved and—given the lack of a strong positive association of ED and range size—would conserve more PD over smaller geographic space. We expected EDR-based prioritization to conserve PD with particular spatial efficiency. Importantly, prioritization of Imperiled birds by ED effectively captures total PD (Figure 5A), very closely approaching optimum ("best") complementarity sets [53]. Preferentially conserving the most distinct (highest ED) species leads to more of the tree of life persisting into the future, and proportional PD gain increases as fewer species are given protection. Because EDR prioritizes by spatial extent as well as by distinctness, it is less successful than ED for preserving total PD. All three approaches preserve substantially more PD than random conservation of Imperiled species, and all results are highly similar among the set of trees analyzed and thus robust to topological and branch length uncertainty in the avian tree of life.

However, such a PD-focused prioritization may not be tenable if prioritizing high-ED species necessitates greater area and thus greater resources required for preservation. In order to assess the spatial efficiency of approaches, we identified the minimum set of grid cells (based on 100 runs of simulated annealing in Marxan [52]) required to conserve at least 10% of a species range when species are prioritized by different strategies. We expect this area selection to represent the biogeography of Imperiled species richness and their average ED and total EDR, respectively (Figures 6A, 6C, and 6E). Prioritization based on ED achieves substantially greater

PD gain per area than a random sequence does (and again is indistinguishable from the "best" set; Figure 5B). EDR does even better, producing very rapid gains in total PD for small increments in total area chosen. For example, a goal of saving at least 60% of additional PD under no prioritization among Imperiled species ("random") requires ∼670 cells (and 350 species; Figures 5A and 5B), with cells frequently selected from areas of high Imperiled richness. Prioritization by ED provides the same PD gain with only 480 cells (and 131 species), mostly from areas with high ED (Figures 6C and 6D; see Table 2 for important countries). The frequency of cell selection among optimization runs (a measure of how "irreplaceable" or important cells are for efficiently meeting the conservation goal) indicates a slight shift away from the New World, the Northern Hemisphere, and select islands (with relatively low-ED species), with unchanged or greater emphasis in Africa and Australia. Indonesia, Brazil, New Zealand, Australia, and the Philippines emerge as countries with greatest stewardship in high-ED species (Table 2). Under EDR-based prioritization, only 180 cells (and 261 species) are required to meet the 60% PD conservation goal (Figure 5B). This EDR-based prioritization strategy consistently singles out islands and the Northern Andes as regions that offer greatest PD gain for least conserved area—these are the regions in which Imperiled PD is most spatially restricted and total EDR is highest (Figures 6E and 6F). All of these 180 cells are among the top 10% EDR cells. EDR may thus offer an efficient integrative measure for baseline prioritization of
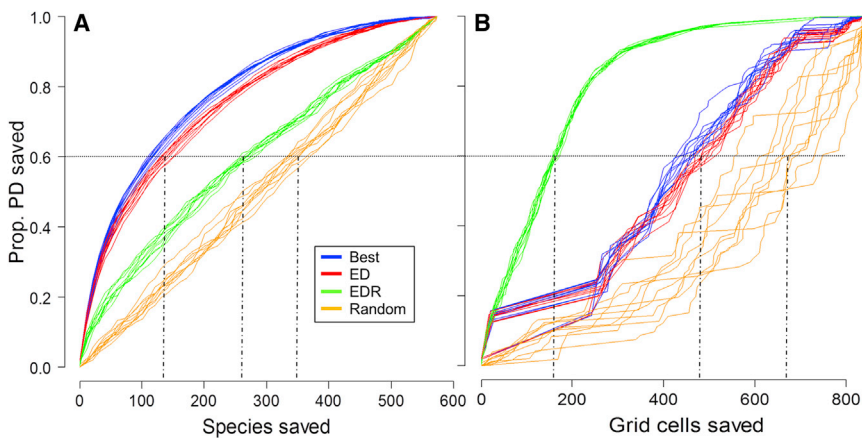
Figure 5. Proportion Gain in Total Phylogenetic Diversity of the World's 575 Imperiled Bird Species under Different Prioritization Scenarios

(A) Proportion of total phylogenetic diversity (PD) preserved, as a function of the number of species selected for conservation by a given metric: best (sets of species offering maximum PD capture in a greedy algorithm), ED, EDR, and random (without consideration of evolutionary distinctness).

(B) Size of the minimum conservation set of grid cells required to protect the species sequentially selected by each metric in (A). This is based on 100 runs of simulated annealing minimum conservation area selection [52] over each of the ten trees and the objective to conserve at least 10% of each selected species' global range. Prioritization of species by ED performs close to best possible, but prioritization by EDR offers spatially more efficient conservation of Imperiled PD. Trends are shown for ten randomly selected trees standardized by the total PD of all 575 Imperiled species (median total PD gain, i.e., proportion PD saved = 1, is 2,764 MY). Dropdown lines indicate species (left) and grid cells (right) required for saving at least 60% of Imperiled PD—see Figure 6 for spatial outcomes.

species whose evolutionary information may be particularly vulnerable to global change and who could be protected over small areas. EDR highlights a group of countries similar to those highlighted by ED (and additionally flags Colombia) as important and efficient targets for safeguarding Imperiled PD (Table 2).

The large majority of the highlighted priority areas are currently only under limited formal protection (Figure 6G). Over 60% of the 180 EDR identified cells have less than 10% of their land protected, well under the Aichi target of 17% [4]. These potential high-priority conservation gaps for geographically rare high-ED species are particularly large for islands, which often are already under particular threat from anthropogenic change [32, 54] and have already lost much of their distinct avifauna [55]. A large number of other factors will need to govern future spatial conservation prioritization, including, among many others, human development pressures [56], reserve effectiveness [57], projected global change [34, 58], species' detailed habitat needs and fine-scale occurrence patterns in relation to parks [59], and non-reserve-based conservation management strategies. But our results highlight how additional protection efforts in only 113 cells (<1% of all land cells) could help safeguard 60% of currently Imperiled avian PD—a remarkable opportunity.

Conclusions

We have illustrated how in birds, often catalysts for human biodiversity attention, ED can fruitfully advance the efficacy of taxonomic and geographic prioritization. ED successfully captures PD in a species-specific manner, and species-level metrics such as ED and EDR support a rigorous yet transparent and efficacious species- and place-based prioritization. With growing and increasingly globally complete data, these metrics are fungible across taxa and combinable with metrics of cultural value, ecological function, or threat status.

We acknowledge that all species-level conservation requires a clear view of what constitutes the entity that is being managed, and different definitions of a species (e.g., via taxonomic "splitting" versus "lumping") will produce different ED metrics (see also [16, 17]). Different fossil calibrations may also affect absolute (and perhaps relative) ED values. However, the ED metric at the basis of our analyses is weighted

by near-present rather than far-past relationships [9] and so should be robust to phylogenetic refinement deeper in the tree of life (e.g., the ED scores from three alternate fossil dating sets have r > 0.98; see Supplemental Experimental Procedures and Figure S1). Finally, many of our species were placed using taxonomic constraints under a simple model of diversification, and new genetic data will lead to tree refinements (see Supplemental Experimental Procedures).

Our framework may offer additional applications, including recreational interest in objectively recognized distinct wildlife that may direct ecotourism and potential conservation attention [60] to high-EDR locations. For instance, species commonly encountered in New Zealand and some other Pacific islands may have an EDR > 5 MY/10,000 km^2, whereas in Northern Eurasia and North America, typical species represent < 0.001 MY/10,000 km^2 (Figures 2C and 2D). For conservation priority setting, the ability of ED-based prioritization to capture total PD is critical. While any particular trait may be phylogenetically labile, PD captures the integrated genotype and phenotype of a lineage and so represents both measured (e.g., present) and unmeasured (e.g., future) function and capacity [10]. Species distinctness metrics highlight both the few species that are very nonredundant on the tree of life and the many species whose feature diversity is shared with many others across large regions. These are attributes that may figure prominently in practical prioritization calculations in the very near future. In the face of global change and limited resources, integration of growing spatial and phylogenetic biodiversity information holds promise for effectively and economically meeting societal biodiversity conservation targets [4].

Experimental Procedures

Data

Our treatment of species follows Jetz et al. [19] and represents a combination of the BirdLife v3 world list and IOC v2.7 list, resulting in a total of 9,993 recognized species (see Table S2 and Supplemental Experimental Procedures). Species distributions were based on noninvasive terrestrial breeding ranges from the literature following [34] and select updates. Following recent validation establishing a reliable presence/absence accuracy of this data to within ~150–100 km [59], we extracted species distributions across a 110 × 110 km equal-area grid in a Behrman equal-area projection, excluding cells with <30% dry land or without offshore islands
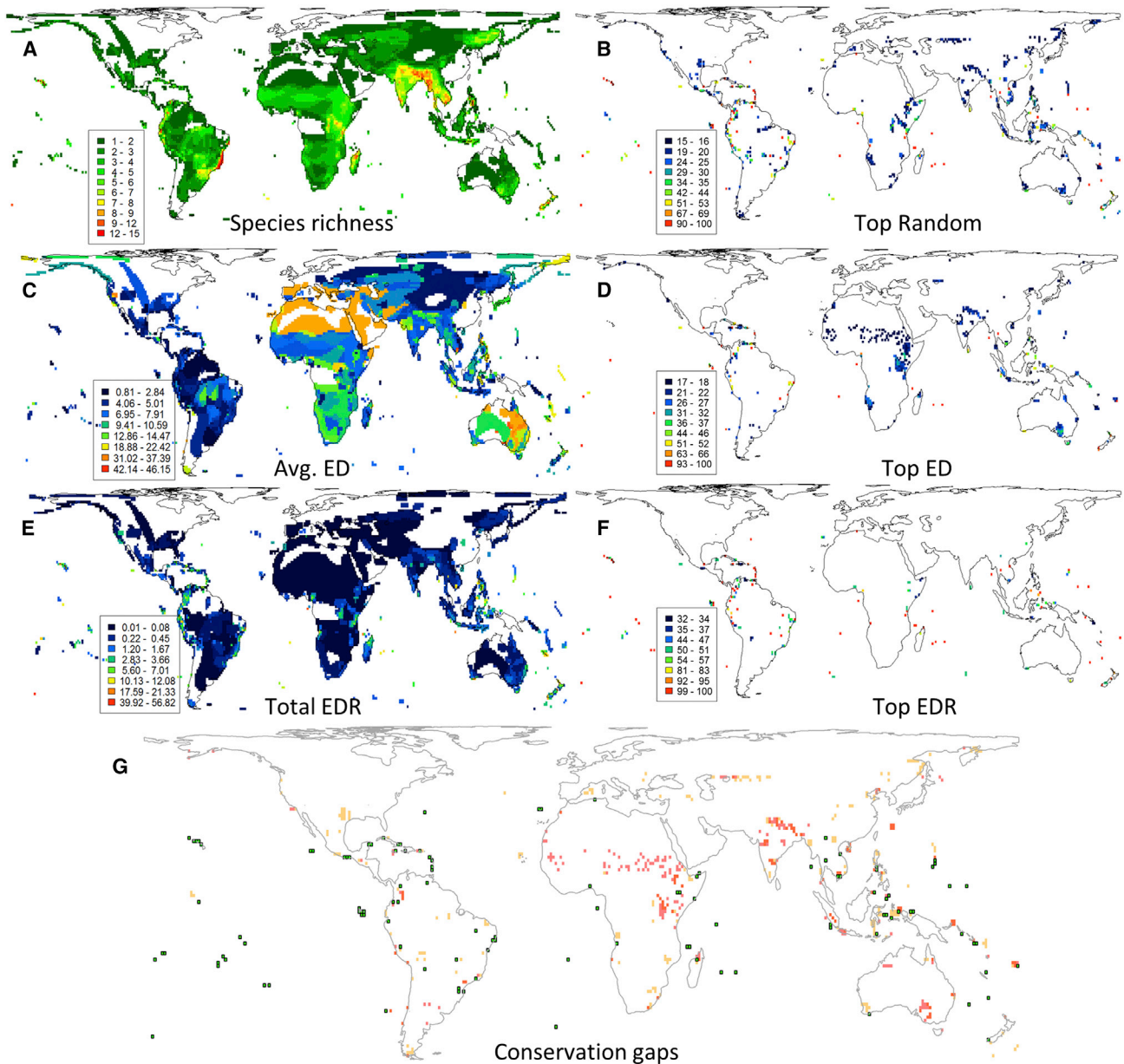
Figure 6. Richness and Distinctness of Imperiled Species and Priority Areas for Conservation

(A, C, and E) Richness (A), average ED (C), and total EDR (E) (both weighted by range size) for all 575 Imperiled species.

(B, D, and F) The geographic consequences of different prioritization scenarios for saving at least 60% of the PD of these species (see Figure 5 for details). Maps show the percent median selection frequency (based on 100 runs for each of ten trees) for the top minimum cells required for each scenario (i.e., 670, 480, and 180 cells, for random, ED, and EDR, respectively; see Figure 5). A score of 100 indicates that a cell is selected under all runs and is thus irreplaceable for the given objective.

(G) Priority cells identified in (B), (D), and/or (F) with <10% of their land area currently under protection and thus of particular conservation relevance. Green indicates the potential 113 top EDR "conservation gap" cells, red indicates additional cells identified by ED-based prioritization, and orange indicates further cells that only a random (i.e., non-ED- or non-EDR-focused) selection among Imperiled species would prioritize.

(12,778 cells). Note that this resulted in the exclusion of oceanic foraging ranges of seabirds or stopover and wintering ranges of migrants—distributions that are often more dynamic and less well described but of course important in conservation decision making. For the phylogenetic trees, we partially revised our recently published complete avian phylogeny [19], which used a four-step pipeline to infer a pseudoposterior sample of complete trees necessary for estimating global evolutionary isolation. We created a new tree distribution using the same approach but, given the ongoing debate and uncertainty about avian fossil evidence and placement [61], used three alternative strategies for calibration: (1) exclusion of the

disputed fossil *Mopsitta tanta* as a calibration for crown Psittaciformes and replacement with *Avolatavis tenens* [62] as a calibration for stem Psittaciformes; (2) exclusion (without replacement) of both *M. tanta* and the stem Charadriiform *Morsoravis sedilis*; and (3) exclusion of *M. tanta*, *M. sedilis*, and *Vegavis iaai* and replacement of *Gansus yumenensis* with a calibration from bird-bearing deposits of the Niobrara Chalk Formation of Kansas as the soft constraint on the root of Neornithes [63]. All three strategies yield highly similar results, and we selected (1) for presentation in the main results. See the Supplemental Experimental Procedures for additional details and results.

Evolutionary Distinctness Metrics

The nomenclature for measures of how isolated a species is on a phylogenetic tree has not yet been standardized. We used the fair proportion metric [9, 64], which is the weighted sum of the branch lengths along the path from the root of an ultrametric tree to the tip, with weights determined as 1/number of tips sharing (ultimately subtending) that branch. Significantly, this metric contrasts with "node counting" or "mean root path" measures by fully taking all branch lengths (in the case of our study, from all trees in the posterior distribution) into account. The metric is referred to as "evolutionary distinctness" by Isaac et al. [16], and we abbreviate the metric as ED here for consistency and continuity with the original notion of "taxonomic distinctness" [6], noting that the more general terms "evolutionary distinctiveness" and "evolutionary isolation" as well as more specific measures such as "species originality" [65] and "equal splits" [64] are also to be found in the literature (see e.g. [66] for an overview and yet another set of names). The fair proportion metric has a formal definition [67], is weighted by a species' unique evolutionary information (the length of the branch connecting it to the tree, or its "age"; [9]) and its sum across all species in a tree equals the tree's total "phylogenetic diversity" (PD; [10]). We used the fast algorithms developed in [68] to calculate sets of species values over a pseudoposterior distribution of 10,000 trees and used the quantiles from this distribution for further analysis. We developed a new species metric that relates a species' ED to the area (e.g., number of grid cells) to which its breeding range is restricted, which we call "evolutionary distinctness rarity" (EDR): EDR = ED / species geographic range size. Range size was estimated in spatial resolution of 110×110 km grid cells for all species to ensure comparability among island species (who sometimes may be restricted to islands much smaller than a grid cell) and mainland species (for which this may also be the case but is not equally well captured) [69]. We then re-expressed EDR as million years (MY)/10,000 km^2. EDR thus apportions evolutionary distinctness evenly over a species' occupied regions (e.g., grid cells; note that such an apportionment could also be conducted across individuals by using species population sizes). For a species endemic to one grid cell, all ED is contained in that one cell, whereas for one occurring in 100 cells, each cell is assumed to be steward of 1/100 of the species' ED. EDR could be considered a measure of expected ED loss from extinctions based on purely geographic extent as an extinction risk correlate, with every doubling in range size translating into a halving of extinction probability. We assessed the phylogenetic distributions of Imperiled, top 10% ED, and top 10% EDR species using the metric D [70]. D estimates the strength of phylogenetic signal in a binary trait and simulates data under a Brownian motion threshold model to allow statistical tests of departure from phylogenetic clustering and randomness. $D = 1$ implies that the trait is distributed randomly on the phylogeny whereas $D = 0$ implies phylogenetic signal consistent with Brownian motion. D may exceed 1, indicating phylogenetic overdispersion, or may be negative, indicating extreme phylogenetic clustering (e.g., if all species in a subclade share the same trait). We fitted D for each binary variable to 100 trees and conducted 1,000 permutations per tree. We report the mean and standard deviation of D among trees and the frequency of rejection for phylogenetic clustering and randomness.

Capturing Phylogenetic Diversity

Evolutionary isolation metrics were not designed to capture expected phylogenetic diversity [9, 53], that is, the sum of the branch lengths connecting species that persist into the future [10]. However, we can ask whether they do. Simulation results indicate that subtrees composed of high-ED species represent more PD than subtrees made of random species [9]. This suggests that preferentially conserving at-risk high-ED species might lead to more of the total tree being likely to persist than otherwise. We tested this important prediction directly. We first assumed that conservation efforts will be directed toward at-risk species and so identified as "Imperiled" the 575 species that the 2012 IUCN Red List designated as Endangered or Critically Endangered. We focused on this set of species for all further evaluations. We then asked how much PD would persist if the highest-ED, highest-EDR, or randomly selected species from this set persisted. Given that conservation action occurs over very short timescales, we ignored low levels of background extinction within the rest of the tree. We performed this assessment in the following way. We first ranked Imperiled species by ED or EDR and then cumulatively chose the top-ranked species in ten-species increments. At each increment, we calculated the additional PD that would be preserved on the avian tree of life if these species were conserved and all other Imperiled species were lost. To compare, we also calculated the PD that could be preserved if

the optimal ten, twenty, etc. species were chosen for conservation (using a simple greedy algorithm for maximum PD capture [71]) or if a set of ten additional species were chosen randomly from among the Imperiled species. We repeated this on ten trees chosen randomly from the posterior distribution.

Spatial Solutions

We used simulated annealing as implemented in Marxan [52, 72] and the 110×110 km equal-area grid cell global occurrence matrix of Imperiled species to estimate minimum area needs for the above prioritization strategies. For every ten-species increment and each of the four strategies, we performed 100 runs with 500,000 iterations, assuming equal "cost" of all grid cells. We set as a fixed target the conservation of at least 10% of grid cells occupied by a species, with a minimum of one. Each run of the algorithm produced an estimated "minimum set" of grid cells addressing this objective. For all increments, solutions were highly stable with limited variation in required grid cells among runs. We calculated the median value among 100 runs for each of the ten trees for visualization in Figure 4A. When prioritized by ED, EDR, or at random (in ten-species intervals; see above), $\sim$60% of the total possible PD gain is captured by 131, 261, and 351 species, respectively. We examined the specific spatial layout of Marxan-identified minimum conservation sets. Over 100 runs, simulated annealing provided a number of different solutions for meeting the same target, with their union covering many more grid cells than any single solution. The number of times a given cell was selected in all runs (i.e, its selection frequency among all ten runs and ten trees) provides a measure of its overall importance (or "irreplaceability") for meeting the target. We represent this selection frequency as a percentage score, with a value of 100 indicating that a grid cell is irreplaceable for a given objective. We map this score for the median number of cells among all 100 runs and ten trees identified by a given prioritization strategy.

We used the most recent (January 2014) version of the World Database on Protected Areas [73] to calculate the proportion of land in each 110×110 km grid cell under some form of protection. This was based on a spatial union of all terrestrial protected areas of all categories (I to VI). For 170,017 reserves, polygon information could be used directly. For the 15,847 reserves with only central coordinate and reserve size information, we used a circle centered on that point with an area of the reported size for intersection. For 7,011 reserves with only central location information, we assumed a 1 km^2 size. For this baseline evaluation, we designated a cell with <10% protected land as insufficient to safeguard a species occurring there. We note that whether such a proportion is indeed sufficient (or necessary) will depend on a number of factors, including but not limited to the existence of other conservation management activities, the effectiveness of reserves, other pressures on land (e.g., from land use or direct exploitation), and a species' within-cell distribution relation to protected areas. The spatial accuracy (or "minimum reliable grain") of global expert maps for birds does not currently allow an assessment at spatial resolutions finer than 100 km, below which ecologically and geographically nonrandom false presence rates impede inference [69, 74].

Supplemental Information

Supplemental Information includes three figures, three tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.03.011.

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