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Global priorities for conserving the evolutionary history of sharks, rays, and chimaeras

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Abstract

In an era of accelerated biodiversity loss and limited conservation resources, systematic prioritization of species and places is essential. In terrestrial vertebrates, Evolutionary Distinctness (ED) has been used to identify species and locations that embody the greatest share of evolutionary history. We estimate ED for a large marine vertebrate radiation on a dated taxon-complete tree for all 1,192 chondrichthyan fishes (sharks, rays, and chimaeras) by augmenting a new 610-species molecular phylogeny using taxonomic constraints. Chondrichthyans are by far the most evolutionarily distinct of all major radiations of jawed vertebrates—the average species embodies 26 million years of unique evolutionary history. With this metric, we identify 21 countries with the highest richness, endemism, and ED of threatened species as targets for conservation prioritization. On average, threatened chondrichthyans are more evolutionarily distinct – further motivating improved conservation, fisheries management, and trade regulation to avoid significant pruning of the chondrichthyan tree of life.

The global extinction crisis is a wicked problem – it is generally accepted that prioritization is necessary due to limited resources and an expanding list of threatened species to save[1–4]. Various prioritization goals and frameworks exist, nevertheless one clear goal of biological conservation is to maximally preserve the Tree of Life[5,6]. A key priority is identifying evolutionarily isolated species with few close relatives that consequently embody a greater share of unique evolutionary history[7]. With rapid developments in phylogenetic inference for major taxonomic groups, we now have the tools for ranking species based on evolutionary isolation.

Evolutionary isolation is a useful metric for placing the current biodiversity crisis in a historical context and for identifying priority species and places in combination with other prioritization criteria. Every year, the chondrichthyan tree accumulates ~1,200 years of unique evolutionary history, yet the modern extinction of a single species would prune tens-to-hundreds of millions of years of evolutionary history. Furthermore, identifying locations of high evolutionary isolation can potentially capture areas of unique forms, functions, and genomes[8]. The International Union for the Conservation of Nature's (IUCN) Red List Assessments[9] provide species-specific threat statuses and geographic distribution maps that can be combined with taxon-complete phylogenies to identify the most imperiled species and places that embody significant amounts of unique evolutionary history. This combined prioritization framework is the focus of one international conservation endeavor (EDGE: www.edgeofexistence.org) and has been applied, almost exclusively, to terrestrial vertebrate lineages including mammals[10], amphibians[11], birds[8], and, most recently, squamates[12]. Applying this EDGE approach to a marine vertebrate lineage will address a key question – what is the taxonomic and geographic distribution of evolutionary distinctness in the oceans.

Here, we apply this EDGE approach to the sharks, rays, and chimaeras (Class Chondrichthyes), one of only two extant divisions of jawed vertebrates and one of the three classes of fishes. Chondrichthyans fill a range of ecological roles, most notably functioning as apex and mesopredators in the upper trophic levels of oceanic, nearshore, and freshwater foodwebs[13,14]; helping to shape and control food web structure[15,16]. Chondrichthyans provide an important perspective to interpreting functional and life history evolution as the sister group to all other extant jawed vertebrates (Gnathostomes). For example, they mark the appearance of the

vertebrate brain archetype[17] and many species give birth to live young nourished through a placenta or other forms of maternal investment[18]. Importantly, chondrichthyans are among the most imperiled marine organisms[19], with up to a quarter facing an elevated risk of extinction[20].

First, we rank all 1,192 shark, ray, and chimaera species by their evolutionary isolation, measured as Evolutionary Distinctness (ED)[10,21] using recently developed methods for combining time-calibrated molecular phylogenies with taxonomic information to produce distributions of robust taxon-complete trees[22,23] (Fig. 1). Second, we then combine ED with imperiled status (species threatened or predicted to be threatened)[20], life history and ecological traits, and geographic distributions. We ask the following five questions: (1) Which are the most evolutionary distinct lineages of all the major vertebrate radiations? (2) Which are the most imperiled evolutionary distinct species, the extinction of which would lead to disproportionate losses of chondrichthyan evolutionary history? (3) Is evolutionary distinctness and extinction risk driven more by species' life history and ecological traits or their underlying evolutionary phylogenetic relationships? (4) Where are the global locations that harbour the greatest evolutionary distinctness? Finally, (5) where are the places that harbour the trifecta of greatest species richness, greatest endemism, and greatest richness of the most evolutionarily distinct species?

Results

Evolutionary Distinctness across major vertebrate radiations

The total evolutionary history (the sum of all branch lengths and sum of all ED scores) encompassed in the chondrichthyan tree is 36,840 MY (Million Years; 5th and 95th centiles: 21,812 - 60,108, Fig. 1). Evolutionary isolation, as measured by ED, is log-normally distributed with the median chondrichthyan embodying 26 MY of ED (Fig. 2a; 5th & 95th centiles: 13 – 64 MY). Indeed, among the major radiations of living vertebrates, and with the exception of two living fossil lineages (the coelacanths and the lungfishes), only the jawless hagfishes and lampreys (Agnatha) embody more evolutionary history per species than the average chondrichthyan. An average shark, ray, or chimaera is likely to represent more than twice the evolutionary history of an average amphibian (10.1 MY) or squamate reptile (11.1 MY), three

times the history of an average mammal (8 MY), and four times the history of the average bird species (6.2 MY; Fig. 2a).

The taxonomic distribution of ED across Chondrichthyans

There is surprisingly consistent average ED among the four main super-ordinal lineages within Chondrichthyes, despite their widely differing species richness (chimaeras, Holocephali median ED = 40 MY; sharks, Squalomorphii 36 MY, Galeomorphii 33 MY; and rays, Batoidea 28 MY; Fig. 2b), while averages across orders vary considerably (Fig. 2b). In particular, two radiations comprise numerous, relatively low ED species: skates (Rajiformes, 293 species, median ED = 17 MY); and ground sharks (Carcharhiniformes, 281 species, median ED = 24 MY). Conversely, two depauperate lineages contain high ED species: mackerel sharks (Lamniformes, 15 species, median ED = 64 MY); and cow sharks (Hexanchiformes, 7 species, median ED = 79 MY; Fig. 2b).

Two orders are characterized by both a high median ED and a high percentage of threatened species, making them of potentially high conservation concern: mackerel sharks (Lamniformes) and guitarfishes, wedgefishes, and sawfishes (Rhinopristiformes). Mackerel sharks comprise 15 species of mainly large pelagic sharks, 10 of which are threatened due to longline fisheries targeting tuna and billfishes. The extinction of a single species within this group could result in a median loss of 64 MY of evolutionary history (as measured by ED). Guitarfishes, wedgefishes, and sawfishes comprise 59 species of moderate-to-large coastal benthopelagic species, 29 of which are threatened due to their retention in near-shore trawl and gillnet fisheries. An extinction within this group could result in a median loss of 37 MY of evolutionary history.

High and low ED lineages are distributed throughout the 14 chondrichthyan orders (Fig. 3a). The lowest ED species are found within the skate genus *Bathyraja* (three species with median ED = 7.4 MY) while the single most evolutionarily distinct species is the Striped Panray (*Zanobatus schoenleinii*; median ED = 188 MY; Fig. 3b). The 120 species in the top 10% ED are drawn from 13 out of 14 orders – only the angel sharks (Squatiniformes) are not represented – and 45 of 60 families. Together, these top 10% ED species embody 8,581 MY, or 23%, of total evolutionary distinctness.

The 20 most evolutionarily distinct species include some unique ecomorphological specializations that would be lost with their extinction. The top three ED species are rays: Striped Panray, Coffin Ray (*Hypnos monopterygius*), and Sixgill Stingray (*Hexatrygon bickelli*; Fig. 3b, b). The top three sharks are all members of the species-poor and high-ED order of mackerel sharks (Lamniformes): Goblin Shark (*Mitsukurina owstoni*; ranked 4th overall), Sandtiger Shark (*Carcharias taurus*; 8th) and Bigeye Thresher (*Alopias superciliosus*; 9th; Fig. 3b). It is important to highlight that three of the top 20 ED are Data Deficient: the Striped Panray, Broadnose Sevengill Shark (*Notorynchus cepedianus*), and Viper Dogfish (*Trigonognathus kabeyi*; Fig. 3b). The top 20 most evolutionarily distinct and threatened species includes all five sawfishes in the family Pristidae – three species are Critically Endangered and two are Endangered making them one of the most threatened family of marine fishes[20]. There are eight threatened high ED sharks, including: Fossil Shark (*Hemipristis elongata*; 19th), Broadnose Sevengill Shark (*Notorynchus cepedianus*; 11th), Colclough's Shark (*Brachaelurus colcloughi*; 16th), Horn Shark (*Heterodontus francisci*; 38th), and White Shark (*Carcharodon carcharias*; 42th). The remaining seven imperiled high ED rays include: Sharkray (*Rhina ancyclostoma*; 10th), two guitarfishes (*Zapteryx* spp.), two eagle rays (*Aetobatus* spp.), as well as two fanrays (*Platyrhina* spp.; Fig. 3c). An additional three species in the top 20 ED and threatened are Data Deficient: Banded Guitarfish (*Zapteryx exasperata*), Hyuga Fanray (*Platyrhina hyugaensis*), and Horn Shark (Fig. 3c). We also flag some recently radiated, low ED, endemic skates and freshwater sharks that are highly threatened (Supplementary Data).

Traits, extinction risk, and the likely loss of evolutionary history

A key conservation concern is whether extinction risk covaries with evolutionary distinctness; if so then overfishing – the main threat to marine biodiversity[24,25] – may result in a disproportionate loss of evolutionary history. The most widely accepted system for estimating extinction risk is the IUCN Red List[26,27]. Here, we defined imperiled species as those 179 chondrichthyans categorized by the IUCN Red List as Critically Endangered, Endangered, or Vulnerable, plus the 63 Data Deficient species predicted to be threatened based on correlates of IUCN threat status[20]. Of the 1,192 species considered here, we rank the 242 imperiled species by median ED. The Lamniformes (mackerel sharks) and Rhinopristiformes (guitarfishes, wedgefishes, and

sawfishes) dominate the top 20 imperiled species list (Fig. 3c). Taken together, these 242 imperiled species embody 8,875 MY (24%) of the total ED of the group. On average, imperiled chondrichthyans embody significantly more ED—7 to 8 million years more—than non-threatened chondrichthyans (phylogenetic ANOVA, all species: $t = 4.73$, d.f. = 359, $p < 0.0001$; sharks only: $t = 3.22$, d.f. = 136, $p < 0.01$; rays only: $t = 6.42$, d.f. = 236, $p < 0.0001$). This pattern contrasts with the lack of covariation between threat status and ED in mammals[28], birds[8], and squamates[12]. This suggests that overfishing is endangering not just a disproportionate number of species in this group, but also a disproportionate fraction of evolutionary history.

We also find that life history and ecological traits associated with threat risk are correlated with evolutionary distinctness, but these interrelationships vary between sharks and rays. Previous work has revealed that chondrichthyans with larger body size, shallow depth distributions – and hence greater exposure to fisheries – and greater Extent of Occurrence (EOO)[20,29,30] are more likely to be threatened. Across all chondrichthyans, greater Evolutionary Distinctness was found in species with: larger body size (Generalized Linear Model [GLM] $\beta = 0.07 \pm 0.02$ SE), shallower depth ($\beta = -0.09 \pm 0.01$), and larger geographic range size (EOO; $\beta = 0.05 \pm 0.01$; Fig. 4a-c; Akaike Information Criterion [AIC] = -265). These life history and ecological traits and ED show strong phylogenetic patterning (Supplementary Methods) such that phylogenetically corrected models have considerably lower AIC scores (Phylogenetic Generalized Least Squares [pGLS] average model AIC = -1800 for resolved 1192 species trees; AIC = -840 for molecular 610 species trees).

These ED-trait relationships differ between the major lineages. Within sharks, only larger maximum body size ($\beta = 0.13 \pm 0.03$) and larger EOO ($\beta = 0.03 \pm 0.01$) were related to higher ED (Fig. 4d,f; AIC = -270). These relationships are partially driven by the large-bodied, oceanic-pelagic, high ED mackerel sharks (Lamniformes), and removing them from the analysis reduced the strength of the relationships for body size-range size traits (body size: $\beta = 0.10 \pm 0.05$; EOO: $\beta = 0.02 \pm 0.02$). Within rays, there was only marginally greater ED with larger maximum body size ($\beta = 0.07 \pm 0.04$) but greater ED at shallower depths ($\beta = -0.2 \pm 0.02$; Fig. 4g,h; AIC = -121). Here, the greater ED in shallow waters appears to be driven by the radiation

of low ED skates (Rajiformes) in deeper waters. Large-bodied wide-ranging sharks (especially mackerel sharks) and large-bodied shallow water rays (particularly guitarfishes, wedgefishes, and sawfishes) should be of primary conservation concern due to their combination of high ED and high threat.

Spatial patterns in richness, endemicity, and evolutionary distinctness

We identify spatial conservation priorities, focusing on those locations with the greatest number of species that contribute disproportionately to total ED, rather than cumulative or average ED. Conservation targets based on ED presented here extend previous work that considered hotspots of shark ecomorphotypes[31], threatened tunas and billfishes[32], chondrichthyan richness[20], and threatened endemic chondrichthyans[33]. The intrinsic value of diversity is captured in a compelling manner through the number of ED species, which is more relevant to conservation practitioners than composite indices[34]. We identify conservation priority hotspots for all species and for the subset of only threatened species using the degree of congruence of three different biodiversity metrics: (i) species richness, (ii) endemicity, and (iii) richness of high ED species.

The most species-rich locations tend to have greater numbers of high ED species (Fig. 5a, c), but not necessarily the most endemics (Fig. 5b). While we cannot discern between causes (recent extinction or low relative speciation), our finding supports emerging evidence that hotspots of marine species richness arise, in part, from the accumulation of relictual species (remnants of formerly large clades)[8] and the overlap of wide-ranging species[35] rather than resulting from high levels of local speciation alone.

The locations of greatest species richness and high ED species richness are patchily distributed, but mostly congruent, in tropical and subtropical coastal waters centered on (1) Australia and the Indo-West Pacific Biodiversity Triangle, (2) Japan, China, Taiwan Province of China, (3) SW Indian Ocean, and (4) western Africa (Fig. 5a, d). This high richness-high ED pattern diverges in the Americas—while there is high species richness in the SW Atlantic, Gulf of Mexico, and Gulf of California, there are almost no coastal high ED species in the Americas. These places, however, have a number of wide-ranging, oceanic-pelagic high ED species, notably Basking Shark (*Cetorhinus maximus*) and Bigeye Thresher. This mirrors a major terrestrial biogeographic

pattern in which the "Old World" harbors relictual species and the "New World" is colonized by relatively recently evolved radiations of low ED species[8]. The highly diverse, low ED radiation of endemic freshwater stingrays in South America is a clear example of recent radiation into novel habitat (Fig. 5a-c). An analysis of the congruence of these hotspots of species richness, endemism, and richness of high ED species (herein "triple hotspots") shows the global importance of seven countries: Australia, China, Taiwan Province of China, Japan, South Africa, and Mozambique (Fig. 6a). These countries have previously been identified as critical and potentially viable targets for expansion of no-take Marine Protected Areas and improved shark fisheries management[33] and the concentration of high ED species in these countries' jurisdictions provides further motivation for conservation action. While such maps aid geopolitical funding allocations and actions, local planning and conservation effort is required in a large number of countries (48) with coastal waters harboring single-metric hotspots (Fig. 6b). For example, while the Americas are neither richness nor high ED hotspots, they include hotspots of endemicity, particularly of the low ED recent radiation of freshwater stingrays (Fig. 6b).

With important distinctions, the priority locations for threatened species are a narrower subset of these global biogeographic patterns. In addition to three major hotspots of species richness and ED, we identify the SW Atlantic Ocean as a key priority for threatened species (Fig. 5d-f). The importance of the SW Atlantic Ocean is most apparent from an analysis of the congruence of high species richness, high endemism, and high ED of threatened species (priority triple hotspots; Fig. 6c). We find 21 countries, within five regions, which harbor congruent priority triple hotspots, from west to east: (a) SW Atlantic Ocean (Uruguay and Brazil), (b) western Africa (Benin, Nigeria, Cameroon, Equatorial Guinea, Senegal, The Gambia, Guinea Bissau and Gabon), (c) SW Indian Ocean (South Africa and Mozambique), (d) NW Pacific (China, Taiwan Province of China, Japan, and to a lesser extent Philippines, Thailand, Malaysia, Singapore and Indonesia), and (e) SW Pacific Ocean (Australia; Fig. 6c). Similarly, we find 44 countries harboring single-metric threatened hotspots (Fig. 6d). While coastal species richness hotspots are largely congruent across 13 taxonomic groups[36] at large-scales, this may not be the case at finer scales for widely differing taxa[37] and additional analyses should be conducted to pinpoint conservation targets for other taxa. Nevertheless, chondrichthyans may be considered an exemplar for revealing major marine biogeographic and conservation priority patterns because

they are (1) one of the seven major vertebrate radiations, (2) globally distributed, (3) threatened from overfishing - the main threatening pressure in the ocean, (4) have complete, peer-reviewed geographic range maps, and (5) now have a complete phylogeny.

Conserving the future of the ocean's evolutionary past

We reveal the large amount of evolutionary history embodied in one of the oldest vertebrate radiations, as well as the distribution of this evolutionary history across species and geographic space. Conservatively, the combination of high ED and elevated threat status suggests that two orders – mackerel sharks (Lamniformes) and guitarfishes, wedgefishes, and sawfishes (Rhinopristiformes) – should be prioritized for targeted conservation and fisheries management. Following our strategic large-scale overview, we suggest local conservation planning is necessary due to the divergent ecologies of these groups and the locally varying fisheries pressure. Most mackerel sharks are threatened by pelagic longline fisheries targeting species for their meat (i.e., Shortfin and Longfin Mako Sharks [*Isurus oxyrinchus* and *I. paucus*] and the Porbeagle Shark [*Lamna nasus*]) and their fins — some of which are traded in high volumes[38,39]. Notwithstanding the successful protection and recovery of some species, such as the White Shark in a handful of countries[40,41], Lamniformes are wide-ranging oceanic pelagic predators distributed throughout tropical and temperate ocean basins that require fisheries management catch limits and, in some cases, regulation of international meat and fin trade[42]. In contrast, the guitarfishes, wedgefishes, and sawfishes are retained as valuable secondary catch in coastal subsistence and artisanal gill net fisheries as well as industrial shrimp trawls in tropical nations. While the meat and liver oil is usually consumed locally, the fins of the larger guitarfishes and sawfishes are among the most revered and highly prized in the Asian soupfin trade[39,43]. All sawfishes are Endangered or Critically Endangered, and have received an increasing amount of scientific and conservation attention in the past decade[44,45]. However, many species of the related guitarfishes and wedgefishes are Data Deficient and in urgent need of status assessment and management consideration[46]. Their coastal habitats and smaller geographic ranges mean that conservation planning and fisheries management at the regional and national level is a priority.

We are in an era of rapidly expanding marine protections, but these tend to encompass low value residual places that contribute little to conserving threatened, high-value species[33]. Our spatial

analysis of global chondrichthyan ED combined with other measures reveals five priority triple hotspots of threatened biodiversity spanning 21 countries in: (a) SW Atlantic Ocean, (b) western Africa, (c) SW Indian Ocean, (d) NW Pacific Ocean, and (e) SW Pacific Ocean. This is a significant step toward narrowing the scope of the vast chondrichthyan conservation challenge which far exceeds that of many terrestrial species[30]. Previous work has only considered hotspots of species richness and endemism of sharks alone—i.e., without rays or chimaeras—and recovered an impractically large and geographically diffuse array of 4,103 priority grid cells (14.2% of all cells considered)[31]. By comparison, our analysis recovers more coherent hotspots in fewer countries. We focus on places with the greatest accumulation of ED as we believe this to be an easy-to-communicate measure of evolutionary value and conservation concern rather than area-weighted ratios[8,47]. The combination of threatened richness-endemic-evolutionary distinct hotspots can serve as a focus for global strategic conservation efforts, and reveals a number of priority areas of more interest to national and regional conservation efforts. Future work could focus on downscaling these global analyses considering species-specific ecologies and national conservation likelihood in order to tailor conservation and fisheries management in these target regions[33].

Priority countries will likely have different management needs based on the varying local status of chondrichthyan species in their jurisdictions[30]. The global scale of IUCN assessments belies regional and local variation in status due to variation in fishing pressure and strength of management[48]. MPAs are but one widely lauded tool for protecting chondrichthyans, but broad scale conservation and sustainable fisheries management have great potential when effectively enforced[40,42,49]. For example, Australia, Canada, New Zealand, and USA already have enforced fisheries and conservation management in place for many chondrichthyan species[42,50]. By comparison the Indo-West Pacific Biodiversity Triangle, SW Indian Ocean, western Africa, SW Atlantic Ocean, and China, and Taiwan Province of China need considerable scientific and management capacity building and aid relief and reorganization to enable conservation action and fisheries management[30,33]. These regions encompass some of the largest shark and ray fishing and fin trading nations that have experienced recent declines in catches, indicative of overfishing and under-management[19,20].

The 242 species of imperiled chondrichthyans have, on average, higher ED than non-threatened species. The traits underpinning greater extinction risk (large body size, shallow depth, and large EOO) are associated with greater evolutionary distinctness; in contrast to the main patterns seen on land in birds, mammals, and squamate reptiles[8,10,12]. Efficient, effective, and enforceable species and spatial management strategies should be adopted to ensure that overfishing – the main threatening process in the coastal seas and oceans – does not prune significant amounts of evolutionary history from the tree of chondrichthyan life.

Methods

Taxon set and taxonomic data

The class Chondrichthyes is composed of two subclasses, the Holocephali (chimaeras) and the Elasmobranchii (sharks and rays), and includes 14 orders, 60 families, 198 genera and 1192 species (Supplementary table 1). Systematic relationships within Chondrichthyes, as with other taxa, are in flux[51–54], so we used the most recent combination of taxonomy and phylogeny to identify our taxon set (Chondrichthyan Tree of Life; http://sharksrays.org/; downloaded October 15, 2015). Due to the inherent prolonged time required for analyses of this nature, taxonomic revisions often occur prior to completion and publication[55–59]. To aid readers in navigating recent changes that we could not incorporate into the analysis, we provide annotations to our master taxonomy highlight recent taxonomic revisions (Supplementary Table 1, column G) and include recently described species that have not been assessed and could not be included in this study (Supplementary Table 6). The subclass Holocephali includes one superorder (Holocephalimorpha) containing one order of Chimaeriformes (chimaeras); three families, six genera, and 49 species. The subclass Elasmobranchii includes three superorders: Batoidea, Galeomorphii, and Squalomorphii[60]. The superorder Batoidea includes four orders Myliobatiformes (stingrays), Rajiformes (skates), Rhinopristiformes (guitarfishes, wedgefishes, and sawfishes), and Torpediniformes (electric and thornback rays); 23 families, 86 genera, and 639 species. The sharks comprise two superorders: Galeomorphii and Squalomorphii. The superorder Galeomorphii includes four orders: Carcharhiniformes (ground sharks), Heterodontiformes (bullhead sharks), Lamniformes (mackerel sharks), and Orectolobiformes (carpet sharks); 23 families, 75 genera and 347 species. The superorder Squalomorphii includes five orders Hexanchiformes (cow sharks), Pristiophoriformes (saw sharks), Echinorhiniformes

(bramble sharks), Squaliformes (dogfish sharks), and Squatiniformes (angel sharks); 11 families, 31 genera, and 157 species. The taxonomic hierarchy described above comprises the taxonomic data that we used to place and constrain those taxa without DNA sequence data (see Supplementary Table 1 and "Taxon-complete Analyses" subsection below).

DNA data matrix

We assembled a DNA data supermatrix from pre-existing GenBank and Barcode of Life Data System records (downloaded on or before September 15, 2014) as well as 54 novel sequences generated for this study. Data from GenBank can present particular challenges, outlined in Naylor *et al*. 2012[51], thus all sequence and species validity was checked prior to analysis. Of particular concern with GenBank sequence data is the potential for misidentified specimens leading to erroneous placement. As a check for this an initial set of trees were generated using RAxML[61] and topology was hand checked to verify reasonable placement of species included in our matrix. The matrix is composed of a novel set of 15 coding and non-coding regions as follows: 2 non-protein-coding mitochondrial loci (12S and 16S rDNA, 2,037 bp), 11 protein-coding mitochondrial loci (CO1, CO2, CO3, Cyt *b*, ND1, ND2, ND3, ND4, ND4L, ND5, and ND6; 10,341 bp), and 2 nuclear protein-coding loci (RAG1, 2,538 bp; SCFD2, 582 bp; Supplementary table 2). The novel sequence data generated for this study include 8 CO1, 1 Cyt *b*, 1 ND2, 1 ND4, and 42 RAG1 sequences. The supermatrix included representatives from all 14 orders, 59/60 families (98%), 173/198 genera (88%), and 642 species (645 originally, of which three were subsequently synonymized with valid names and removed) out of 1192 species (54%). At its maximum extent, the DNA data matrix comprises 15,498 bp; however, the alignment is sparse and taxonomic coverage averages 30% across loci (mitochondrial loci: 13–81%; nuclear loci 12–27%; Supplementary Table 2).

We used MAFFT v.7.221[62–64] to conduct local alignments for each locus. Nuclear and mitochondrial protein-coding sequences are straightforward to align, but mitochondrial non-protein-coding sequences are subject to high frequencies of insertions and deletions (indels). Therefore, we aligned the indel-rich mitochondrial 12S and 16S non-protein coding sequences in two stages: first, we aligned the sequences by taxonomic order, and second, we combined the resulting order-specific alignments and realigned the entire set together. We removed start and

stop codons from aligned protein-coding sequences prior to testing nucleotide substitution models. We used JMODELTEST 2.0[65,66]and AIC criterion to identify the best-fit nucleotide substitution model for each locus. Three closely related best-fit models were identified: GTR + Γ (nuclear RAG1), GTR + Γ + I (mitochondrial 12S, 16S, CO1, CO2, Cyt *b*, ND1, ND2, ND3, ND4, ND4L, ND5 and ND6) and SYM + Γ + I (mitochondrial CO3 and nuclear SCFD2). Invariant site models, such as GTR + Γ + I and SYM + Γ + I, have been criticized because the proportion of invariant sites and the gamma shape parameter cannot be optimized independently. As a consequence, it is impossible to obtain reliable estimates for these parameters simultaneously[67]. The SYM model is a constrained, nested version of the GTR model.

We used RAXML[61] to infer individual gene trees and species trees based on partitioned, concatenated analyses. RAXML uses a computationally efficient version of GTR (GTRCAT) that accommodates rate heterogeneity and GTRCAT is a good fit for our small set of best-fit models. In the final step, the GTRCAT model optimizes parameters and calculates likelihood under GTR + Γ[61]. We conducted 1,000 bootstrap replicates in each analysis and inspected the resulting topologies for consistency and bootstrap support before proceeding with partitioned, concatenated analyses. We used a pragmatic and iterative approach to partitioning, which was informed by constraints on a small, sparse dataset and trade-offs associated with variation in nucleotide substitution rate and process. Nuclear sequences typically evolve slowly relative to mitochondrial sequences, and the two nuclear protein-coding sequences (RAG1 and SCFD2) were assigned to separate partitions. Although the mitochondrion is inherited as a single locus, its protein-coding and nonprotein-coding sequences exhibit different nucleotide substitution rates and indel frequencies. As a consequence, mitochondrial nonprotein-coding and protein-coding loci were assigned to two separate partitions. Mitochondrial protein-coding sequences are subject to codon-position-specific rate variation. One consequence of this rate variation is that the faster evolving mitochondrial 3rd codon position nucleotides (M3CPN) can become saturated over long periods of evolutionary time, and there is precedence for excluding M3CPN from phylogenetic reconstructions for ancient clades[68,69]. As part of our iterative approach to partitioning, we first conducted RAXML analyses with 1,000 bootstrap replicates and then used ROGUENAROK (http://rnr.h-its.org/)[70] to identify rogue taxa that erode bootstrap support. In ROGUENAROK analyses we specified the parameters as follows: Threshold: 50% majority rule consensus,

Optimize: support, and Max Drop Set: 3. Additionally, we employed a raw-improvement-score threshold (0.5), which corresponds to a relatively large improvement of overall support, to identify and exclude rogue taxa[70].

When we excluded the M3CPN, RAxML analyses generated trees with low-overall bootstrap support, and two iterations of rogue identification yielded 60 rogue taxa (9.3%). Despite concerns over saturation, we tried including the M3CPN in a standard, uniform block alignment. This resulted in a substantial increase in overall bootstrap support, and two iterations of rogue identification yielded just 22 rogue taxa (3.4%). However, bootstrap support remained low at relatively deep nodes (among orders and among families within orders) within the superorder Batoidea. Batoidea comprises 4 orders and 23 families: Myliobatiformes (10 families), Rajiformes (3 families), Rhinopristiformes (5 families), and Torpediniformes (5 families). As a consequence, the impact of low bootstrap support on topology is large. In an attempt to reduce the potential negative impacts of saturation and generate increased bootstrap support for the deeper nodes within Batoidea, we implemented a novel, staggered-by-order alignment approach for the M3CPN. Instead of using a single uniform block alignment, we extracted all of the M3CPN and placed them in a separate partition. This resulted in two partitions for the mitochondrial protein-coding loci, one with first- and second-codon position nucleotides and another with third-codon position nucleotides. The partition containing first- and second-codon position nucleotides remained as a standard uniform block alignment. For the partition containing the 3rd codon position nucleotides, we staggered the alignment by taxonomic order. The consequence of this novel partitioning/alignment approach is that the M3CPN sequence data can only speak to affinities within, but not between, orders. This approach resulted in increased bootstrap support within Batoidea without loss of support in other parts of the phylogeny. Two iterations of rogue identification yielded 21 rogue taxa (3.3%). Importantly, 11 taxa, including the worst offenders in both analyses including M3CPN, were included in the shared subset of rogue taxa. Using the staggered-by-order approach for the M3CPN alignment and two iterations of rogue identification, we identified and excluded 21 rogue taxa from 15 genera: *Bathyraja* (n=2), *Carcharhinus* (2), *Centrophorus*, *Dipturus* (2), *Discopyge*, *Isogomphodon*, *Leptocharias*, *Mustelus*, *Narke* (2), *Orectolobus*, *Potamotrygon* (3), *Raja*, *Spiniraja*, *Squalus,* and *Squatina* (Supplementary Table 1). There were still many nodes with bootstrap support < 70% and these

were collapsed prior to incorporating unresolved taxa, when the identified rogue taxa were also reintroduced. This means that there was likely very little effect of rogue selection on overall topology. While the novel staggered-by-order approach employed here with the M3CPN partition appears promising, it warrants further study.

Temporal Calibration

Ideally, calibration fossils should be subjected to a formal phylogenetic analysis or exhibit diagnostic apomorphies[71]; unfortunately, relatively few fossils assigned to Chondrichthyes meet these criteria[72]. There are three exceptions: (1) *Chondrenchelys problematicus*, which has affinities with stem Holocephalii (Chimaeriformes)[73], (2) *Tingitanius tenuimandibulus*, which has affinities with stem Platyrhinidae (thornback rays)[74], and (3) *Protospinax annectans*, which has affinities with the stem of the superorder Squalomorphii, a clade including Hexanchiformes, Pristiophoriformes, Squaliformes, and Squatiniformes[75]. We identified 7 additional calibration fossils that are distributed across the Chondrichthyan phylogeny; several of these are represented by substantial articulated remains (Supplementary Table 3). *Chondrenchelys problematicus* is the only formally-vetted calibration fossil and, importantly, it provides a hard minimum bound for the chondrichthyan root node (333.56 MY)[72]. The root node of Chondrichthyes is further characterized by a soft maximum bound of 422.4 MY (see Benton et al., 2015 for justification). Following Ho and Phillips[76], we used these hard minimum and soft maximum bounds to specify a lognormal calibration density and selected a mean that bounded 95% of the probability density within the 88.84 MY interval between the hard minimum and soft maximum bounds and a standard deviation that split the probability density evenly across the midpoint (377.98 MY) of this interval. While the ages of the 9 other calibration fossils provide hard minimum bounds for their calibrated nodes, there is not sufficient information to generate a calibration density for any of them.

We used *treePL* 1.0 in Ubuntu 14.04[77], which implements a flexible rate-smoothing algorithm, to assign a timeline of diversification to the phylogeny. Given the rate-smoothing behavior of *treePL* and the reported low substitution rate in chimaeras[78], we expect the actual crown Chimaeriformes to be older, and the Elasmobranchii crown age to be younger, than those reported here. Given uncertainty in the precise phylogenetic affinities of at least 7 of the 9

additional fossils, we chose to conduct two sets of dating analyses, one that included *C. problematicus* only, and another that included all 10 calibration fossils (Supplementary Table 3). For both of these calibration scenarios we generated a random sample of 500 root-node ages from the lognormal calibration density that we constructed for the root node (together measuring the root age we report), and then conducted separate *treePL* analyses using each of the 500 root-node ages. Our *treePL* analyses proceeded in two stages. In the first, we performed cross validation analyses ("cv" and "randomcv" commands) and tested performance of the available optimization routines ("prime" command). In the second, we incorporated control options ("thorough" command) to ensure that the preferred optimization routine converged. The 500 resulting *treePL*-dated topologies for each of the two calibration scenarios were subsequently used in the taxon complete analyses described below. Importantly, the topology recovered from our RAXML analyses of the concatenated data matrix, remained fixed across all of these *treePL* analyses; only the timeline of diversification changed between the two calibration scenarios and across the 500 root-node ages. The *treePL* output was converted into a single 500-tree Newick file, processed with TreeAnnotator 1.7.5 [79] using the default settings (no burnin; posterior probability limit 0.0; maximum clade credibility tree; median node heights).

Taxon-complete trees

We added taxa without DNA sequence data to each of the 500 *treePL*-dated, molecular trees ("stage 1" trees) and then used a taxon-addition and polytomy-resolver algorithm (modified from Kuhn et al. 2011; details below) to generate a large distribution of fully resolved, taxon-complete candidate phylogenies. We used two taxonomic sources: the Chondrichthyan Tree of Life (http://sharksrays.org) and the International Union for the Conservation of Nature Red List (http://www.redlist.org). Our distribution of taxon-complete trees includes three types of species[80]. Type 1 species have genetic data and are represented in the stage 1 trees. Type 2 species have no genetic data (or were identified as rogue taxa), but have at least one congener represented in the stage 1 trees. Type 3 species have no genetic data (or were identified as rogue taxa), and have no congeners in the stage 1 trees. Type 2 and Type 3 species were allowed to populate particular clades using taxonomic information and the topology (via node identities) of the stage 1 trees. We outline the rules we used to include taxa without any sequence data below.

Type 1 species were anchored relative to one another as resolved in the stage 1 trees, and we used 70% bootstrap-support (BS) as a threshold to topologically constrain inferred nodes during taxon addition. There were four scenarios in which the stage 1 trees needed to be modified to enforce genus, family, or order monophyly (Supplementary Table 4).

- First, there were nine genera with relatively weak support (BS < 70%; range: 7-68%) for genus monophyly within a highly supported clade (BS ≥ 70%; Supplementary Table 4). For these nine genera instances we pruned ten type 1 taxa from the stage 1 trees, reducing its size from 620 to 610 sp. We reincorporated these ten pruned taxa subsequently as type 2 species by constraining them to their named clades.
- Second, there were four families (Anacanthobatidae, Hemigaliidae, Somniosidae, and Triakidae) where there was weak support (BS < 70%; range: 33-62%) for family non-monophyly. In these four instances we collapsed the weakly supported nodes and subsequently reconstituted clades to enforce family monophyly[80] (Supplementary Table 4).
- Third, there were 24 mixed-genus and/or mixed-family clades with strong evidence (BS ≥ 70%) against monophyly for at least one genus or family. These "mixed clades" took on a variety of forms, from simple paraphyly to complex interdigitation of sub-genera or sub-families. We enforced genus monophyly for any genus or family *within* these mixed clades, unless there was strong evidence (BS ≥ 70%) against monophyly.
- Finally, for consistency between taxa with and without genetic data, we assumed that all genera, families, and orders were monophyletic unless there was strong evidence (BS ≥ 70%) against monophyly in the stage 1 trees. This rule affected one subgenus (*Galeus* minor clade), nine genera (*Atlantoraja*, *Centrophorus*, *Chiloscyllium*, *Halaelurus*, *Mobula*, *Rajella*, *Rhinobatos*, *Sphyrna* and *Squalus*), one mixed-genus clade (*Dentiraja*, *Dipturus*, *Spiniraja* together with *Zearaja*), one family (Pristidae) and one order (Orectolobiformes) in our stage 1 trees – each of these had only weak evidence (BS < 70%; range 32-69%) for monophyly.

After using these rules to modify the stage 1 trees, we imposed topological constraints on the placement of the remaining type 2 and type 3 species, including the 21 rogue taxa. Each type 2 species was restricted to its genus or its mixed-genus clade. There were four genera (*Dasyatis*,

Galeus, *Himantura,* and *Triakis*) with strong evidence (BS ≥ 70%) against monophyly in the stage 1 trees that also required the addition of type 2 species. For these four genera, type 2 congeners were added to the largest candidate sub-clade for the genus. Each type 3 species was restricted to its named genus, and the entire genus was constrained in its placement among other genera according to higher-level (supergenus, family or order) taxonomic information (Supplementary Table 1). Twenty-three of the 198 recognized genera were not represented in the stage 1 trees, and these 23 genera were restricted to 6 of the 14 orders and 18 of the 60 families (Supplementary Table 1). There were 9 type 3 species not assigned to a family on http://sharksrays.org/. In these instances, we referred to the IUCN http://iucn.org/ for the original family-level designation (Supplementary Table 1).

The 500 dated taxon-complete trees were then each resolved using Polytomy Resolver[22], modified to allow for the partial constraints enumerated above. The Polytomy Resolver algorithm uses a customized R-script to generate an input file for BEAST 1.x, based on the original dated phylogeny, and the taxonomy additions outlined above. The generated input file leverages BEAST's ability for "prior only sampling", combined with a series of hierarchical topology constraints—both time-based and monophyly-based—that define the original tree topology and allowable taxon additions, to sample taxon-complete trees across tree-space. For both fossil calibration scenarios mean Growth Rate (birth – death) was unconstrained, while we set uniform flat priors for relative Death Rate (death/birth; one fossil calibration: 0.4 – 0.85; ten fossil calibration: 0.25 – 0.75). Each taxon infilling scenario was run in BEAST 1.7.5[79] for 3 million generations including a 1 million generation burn-in. Samples were drawn every 100,000 generations to avoid temporal autocorrelation between draws, and the resulting 20 trees from each of 500 scenarios were collated into a pseudo-posterior distribution of 10,000 fully resolved trees. Trees are available for download via www.sharktree.org.

Evolutionary Distinctness

Evolutionary isolation metrics rank species by the amount of ancestry shared with relatives. We used the evolutionary distinctness (ED) measure first presented by Redding (2003), which sums the lengths of the branches on the path from a species to the root, with each branch inversely weighted by the number of species that it subtends: species with longer branches on the path

leading to the root of the tree, and with fewer relatives that share these branches have higher evolutionary distinctness scores. As intuited by Hartmann (2013)[81], and shown formally by Fuchs and Jin (2015)[82], evolutionary distinctness is formally equivalent to the Shapley index[83] on rooted trees[84]. Importantly, the sum of the ED values across all tips equals the total evolutionary history of the tree. Given this, for Fig. 2, we calculated the expected ED per species for each major vertebrate lineage using species richness and crown age and the method of moments estimator of diversification rate[85]. When calculating the expected total tree length of a birth death tree from theorem 4 of Mooers et al. 2012[86], setting extinction rate = 0.75*speciation rate produced the best global fit to the true average ED scores for birds, mammals, amphibians, squamate reptiles, and chondrichthyans. Input data and references can be found in Supplementary Table 5. When measured on the same scale (e.g. millions of years for time-calibrated trees), ED scores are broadly comparable across large taxonomic groups[87]. ED is also the metric currently used by the Zoological Society of London to rank species for its Edge of Existence program (www.EdgeofExistence.org).

Extinction Risk Assessment and Estimation

We used the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria[26] to assign relative extinction risk. The IUCN Shark Specialist Group categorized 604 of 1192 taxonomically valid species into one of five categories: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC). In addition, there was 588 species that were either categorized as Data Deficient (n = 477) or recognized on http://sharksrays.org/ that are Not Evaluated by the IUCN Shark Specialist Group (n=111). We categorized these species as threatened or otherwise based on a Generalized Linear Model with binomial link and three traits: body size (cm, total length), upper depth limit (m), and depth range (m). These models have good predictive power (area under the curve = 0.77). To test for relationships among candidate covariates of threat and ED we compared our three traits (body size, depth, and Extent Of Occurrence (as a measure of range size: EOO)) across all chondrichthyan species and subsets of Elasmobranchii (sharks and rays) using a General Linear Modeling framework. Prior to testing all traits and median estimates of species specific ED were $\log_{10}$ transformed. Prediction intervals were generated across the full range of each trait holding the others to their median value. Tests of covariation were repeated using Phylogenetic

Generalized Least Squares (pGLS) to account for non-independence of species using `caper` version 0.5.2[88]. To account for uncertainty in the topology, pGLS analyses were performed on 100 trees randomly sampled from the posterior tree distribution. Means values of parameter estimates, standard errors, AIC, and λ are reported in the supplementary results.

Spatial Analysis

We used the EOO maps from the IUCN Red List available on December 2015[27]. Geographic distributions (EOO) were not available for 111 species; hence only 1081 of the 1192 species were included in the spatial analysis. A key advantage of our approach is the use of the IUCN EOO maps, which are compiled and peer-reviewed by experts. The final maps are created using a minimum convex polygon around all location records accounting for the distribution of scientific collection and survey effort. Using point locality data, such as location records from the Global Biodiversity Information Facility (GBIF: http://data.gbif.org), are known to have spatial and species bias, i.e. towards higher GDP countries and commercially valuable species, and contain omission errors (a species is not present, when in fact it is)[89]. Although EOO maps are known to create commission errors (a species is mapped to be present in an area when in fact it is not), commission rather than omission errors are preferred [89,90].

We created a global hexagonal grid of 23,322 km^2 cells[91,92] . We define threatened species as those species in the IUCN Red List categories: Critically Endangered, Endangered, or Vulnerable, but we also included those 50 species with both an EOO map and predicted to be threatened. Together we refer to this combination of threatened and that are predicted to be threatened species as the imperiled species set. We define a species as endemic based on the median EOO range size (419,932 km^2; n = 541)[93,94]. We used this definition previously, but the value of the median used here differs slightly (595,749 km^2, n = 504) due to addition of species to the IUCN database and the inclusion of freshwater species[19]. We defined top 25% ED as those species within the highest quartile of mean ED scores and present the number of species per cell within the upper quartile ED.

To determine hotspots, we used R version 3.2.4[95] with packages `plyr` version 1.8.3[96], `sp` version 1.2-2[97], and Arc GIS version 10.3[98]. Smoothing was completed for visual clarity

purposes only. Hotspots, however, were not smoothed in order to preserve the accuracy of the locations. Hotspot cells were assigned to countries based on whether the cell, regardless of how much, overlapped with a country's Exclusive Economic Zone[99]. Regional analyses will need to be completed to more accurately assign hotspot responsibility to these countries.

Data Availability: The authors declare that all data supporting the findings of this study are available within the paper and it's Supplementary Information Files. Additionally, phylogenetic trees generated during this study are accessible via (www.sharktree.org).

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Author contributions

NKD and AOM conceived and led the project, RWS, CGM, JBJ, TSK, NCA, NKD and AOM designed the project. NCA, RWS, CGM, JBJ, GJS, LNKD acquired or provided data. RWS, TSK, JBJ, LNKD contributed essential code and analyses. RWS, CGM, LNKD, NKD and AOM drafted and revised the paper. RWS designed and led the phylogenetic work, CGM supported the phylogenetic work and led the subsequent statistical analyses; LNKD led the spatial analyses.

Competing Interests: The authors declare no competing financial interests.

Figure Legends

Figure 1. A representative taxon-complete tree with phylogenetic distribution of molecular data coverage. Clades are shaded according to molecular data coverage within each order, and those species with molecular data are indicated by outer ticks. Red dots highlight nodes defining orders with the paraphyletic order Rhinopristiformes delimited by two highly supported nodes.

Figure 2. Expected and observed evolutionary distinctness (ED) across (**a**) major vertebrate radiations and (**b**) chondrichthyan orders. For vertebrate radiations, large circles represent expected average ED while small circles represent the mean ED observed from taxon complete phylogenies. Between chondrichthyan orders boxplots denote median (solid line) and 25th and 75th centiles (box edge), and 5th and 95th centiles (whiskers). The color of silhouettes denotes the percentage of threatened species within each group.

Figure 3. Distribution of evolutionary distinctness (ED) across (**a**) a representative taxon-complete tree of all chondrichthyans highlighting (**b**) the top 20 species overall and (**c**) the top 20 threatened species as bar charts. On the phylogenetic tree branch color represents the ED (in millions of years) of lineages based on the color-ramp legend, where blue is low ED and red is high ED. Numbers indicate the species highlighted with red denoting threatened species. Boxplot colors of the top 20 overall and top 20 threatened species represent threat status, with the green to red colors depicting assessed species, and the blue shades indicating imperiled species (Data Deficient species that were predicted to be threated based on life history and ecological correlates). The order of species is denoted in parentheses (Rhi, Rhinopristiformes; Tor, Torpediniformes; Myl, Myliobatiformes; Lam, Lamniformes; Hex, Hexanchiformes; Car, Carcharhiniformes; Pri, Pristiophoriformes; Ore, Orectolobiformes; Squ, Squaliformes; and Het, Heterodontiformes).

Figure 4. Relationship between median evolutionary distinctness (ED) and traits associated with elevated threat status across (**a-c**) all chondrichthyans, (**d-f**) sharks only, and (**g-i**) rays only. Mean predictions (solid lines) and prediction interval (shaded area) of ED calculated across the range of a single trait holding other traits to their median value.

Figure 5. Species richness, endemism and evolutionary distinctness patterns for all chondrichthyan species (**a,b,c**) and for threatened chondrichthyan species only (**d,e,f**). Hottest hotspots are depicted in red.

Figure 6. Congruence, incongruence, and location of the overlapping hotspots of three conservation metrics (richness, endemicity, and upper quartile ED; **a,c**) and of hotspots based on a single metric (**b,d**; colors indicate relevant metric). Countries shaded dark grey have jurisdiction over these hotspots.

Supplementary File Legends

Supplementary Table 1 – Master Taxonomy The master taxonomy of 1,192 species used for this study with information on data type and recent taxonomic revisions.

Supplementary Table 2 – Accession Table The accession table for sequence information used to construct the 610 species molecular tree, including updated taxonomic information.

Supplementary Table 3 – Fossil Calibrations Fossil calibration information including clades, ages, and source references used for temporal calibration of stage 1 and stage 2 trees.

Supplementary Table 4 – Mixed Clades and Tree Modification Information on the taxonomic constraints used for polytomy resolution when there was strong evidence against monophyly in one genus or family, and the manual enforcement of monophyly when weakly supported along with the rules implemented and rationale.

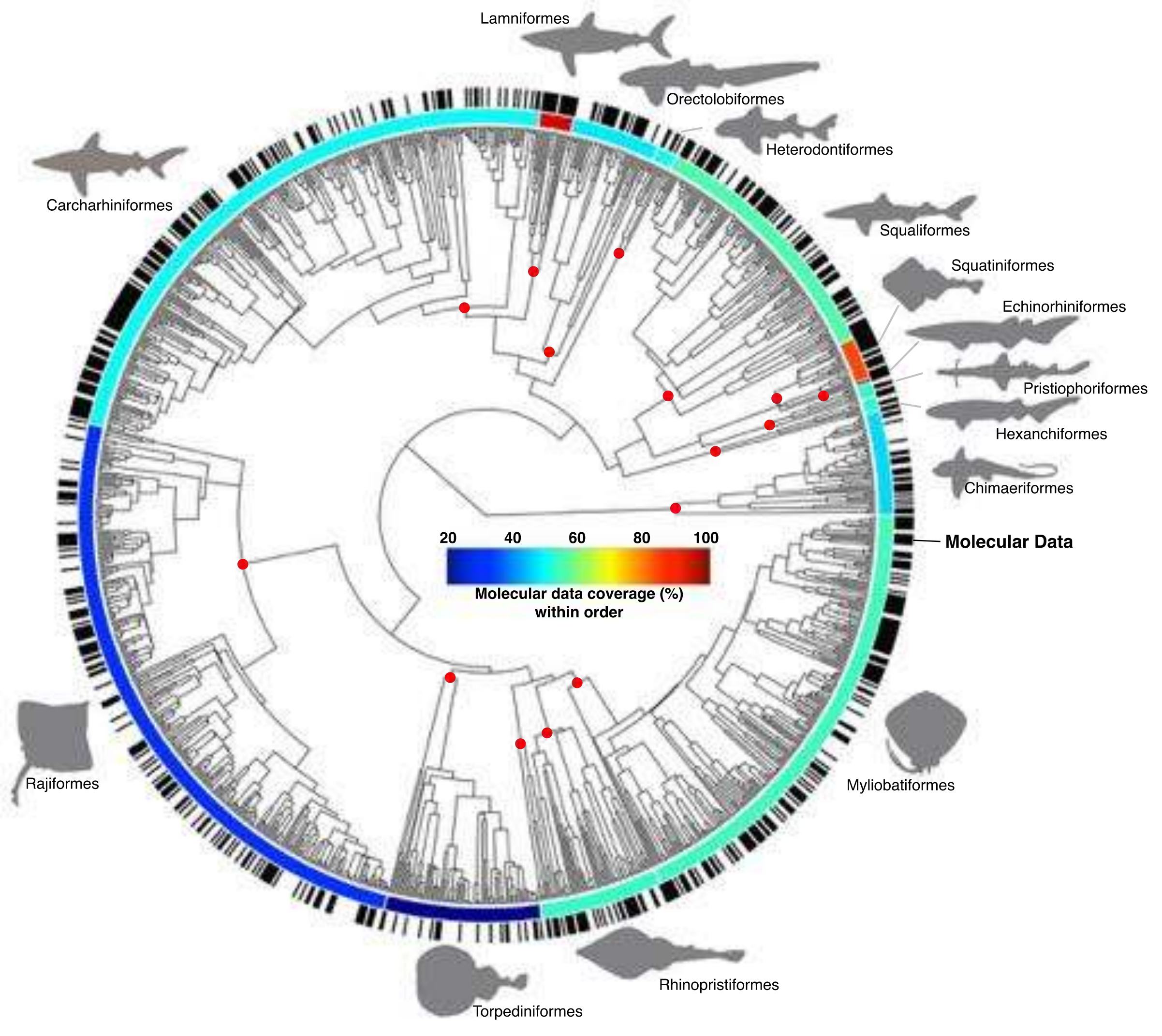
Supplementary Table 5 – Vertebrate Comparisons Information on the species richness (SR) and crown age (CA) of nine major vertebrate lineages used to generate predicted mean ED for comparison. Observed ED, when available, was included for comparison with predicted ED. Includes source information.

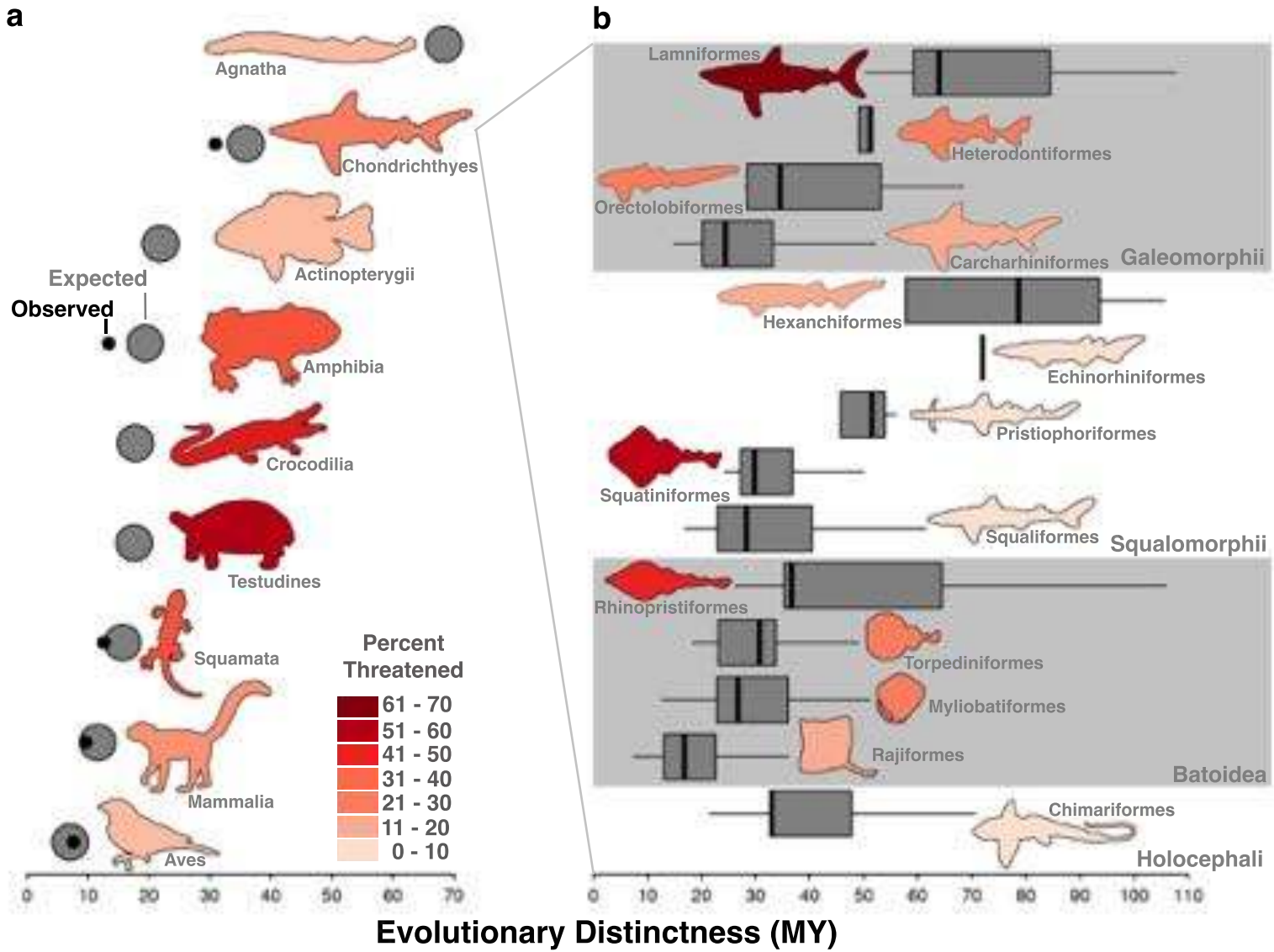
Supplementary Table 6 – Recently Described Species Taxonomic information of 90 recently described species (updated from[55–57,59,58]) that we were unable to include in this analysis.

Supplementary File 1 – Species Addition Script R script used to add species with taxonomic information onto the 610 species molecular tree to create starting trees for polytomy resolver.

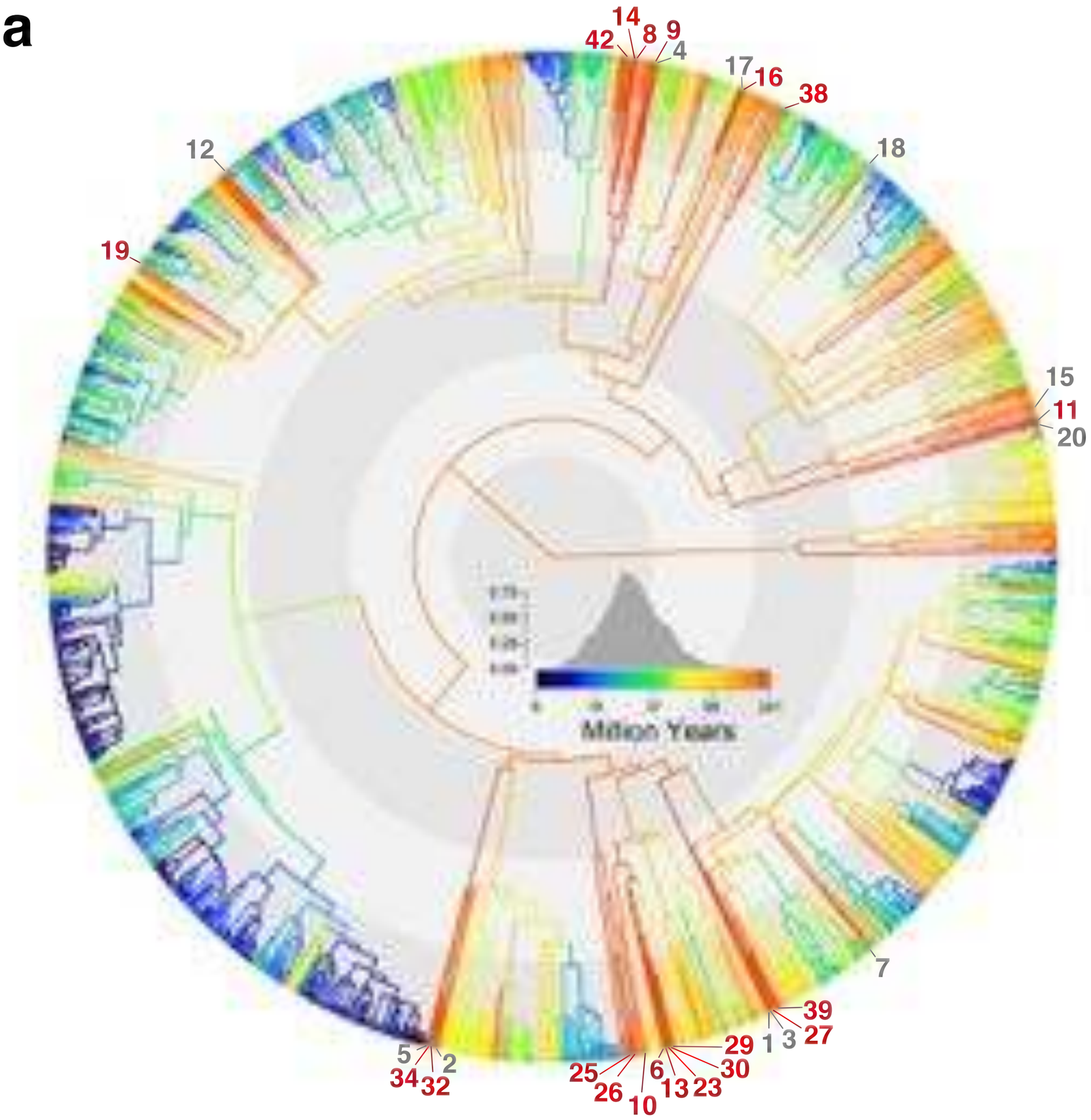
Supplementary File 2 – Polytomy Resolver Script R script used to automate the polytomy resolver for generating distributions of fully resolved trees.

Supplementary File 3 – XML Creator Script R script for generating XML input files prior to polytomy resolution.

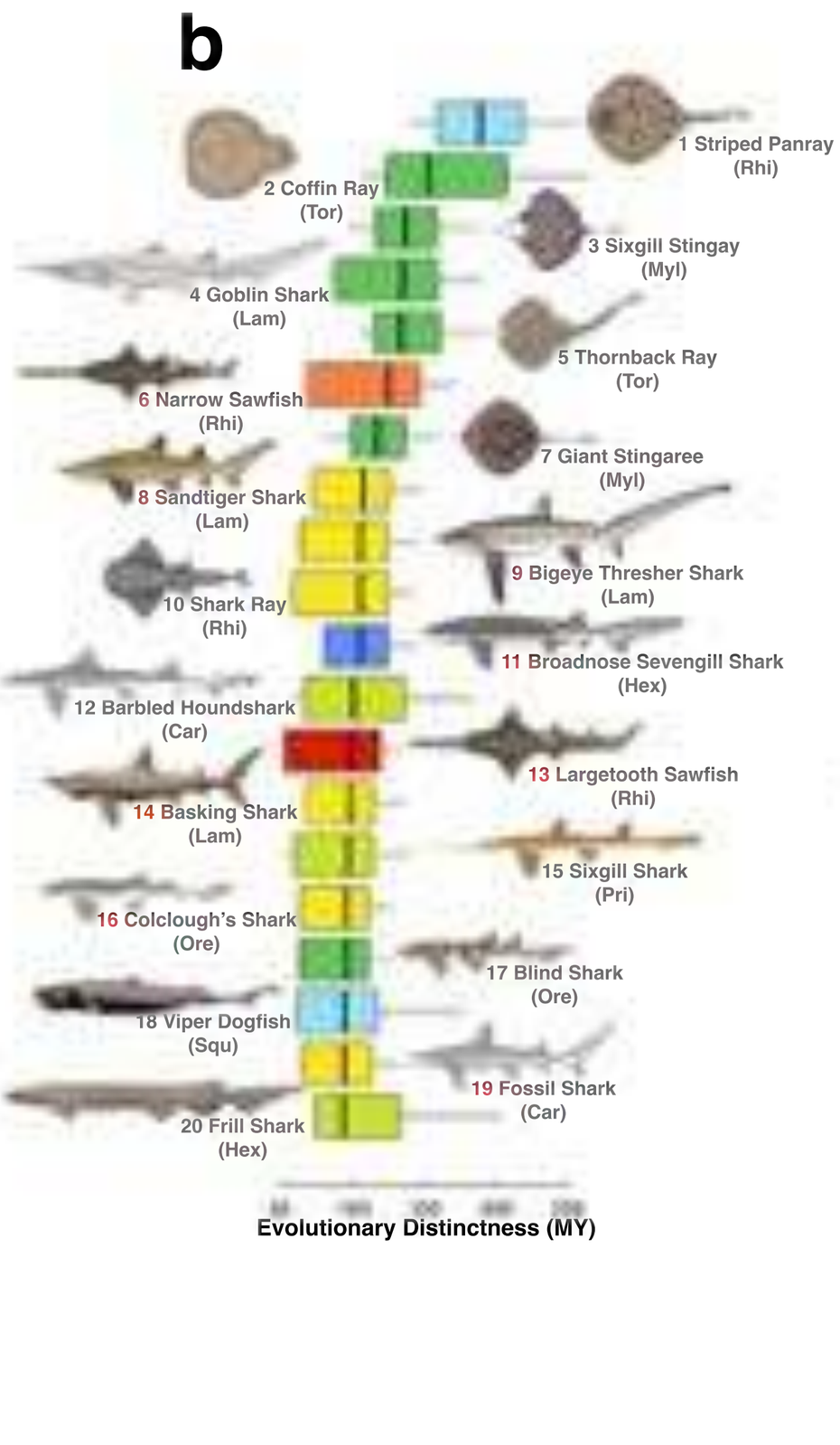

Lamniformes
Orectolobiformes
Heterodontiformes
Carcharhiniformes
Squaliformes
Squatiniformes
Echinorhiniformes
Pristiophoriformes
Hexanchiformes
Chimaeriformes
Molecular Data
20
40
60
80
100
Molecular data coverage (%)
within order
Rajiformes
Myliobatiformes
Rhinopristiformes
Torpediniformes


a
Agnatha
Chondrichthyes
Actinopterygii
Expected
Observed
Amphibia
Crocodilia
Testudines
Squamata
Mammalia
Aves
Percent Threatened
61 - 70
51 - 60
41 - 50
31 - 40
21 - 30
11 - 20
0 - 10
0 10 20 30 40 50 60 70
b
Lamniformes
Heterodontiformes
Orectolobiformes
Carcharhiniformes
Galeomorphii
Hexanchiformes
Echinorhiniformes
Pristiophoriformes
Squatiniformes
Squaliformes
Squalomorphii
Rhinopristiformes
Torpediniformes
Myliobatiformes
Rajiformes
Batoidea
Chimariformes
Holocephali
0 10 20 30 40 50 60 70 80 90 100 110
Evolutionary Distinctness (MY)

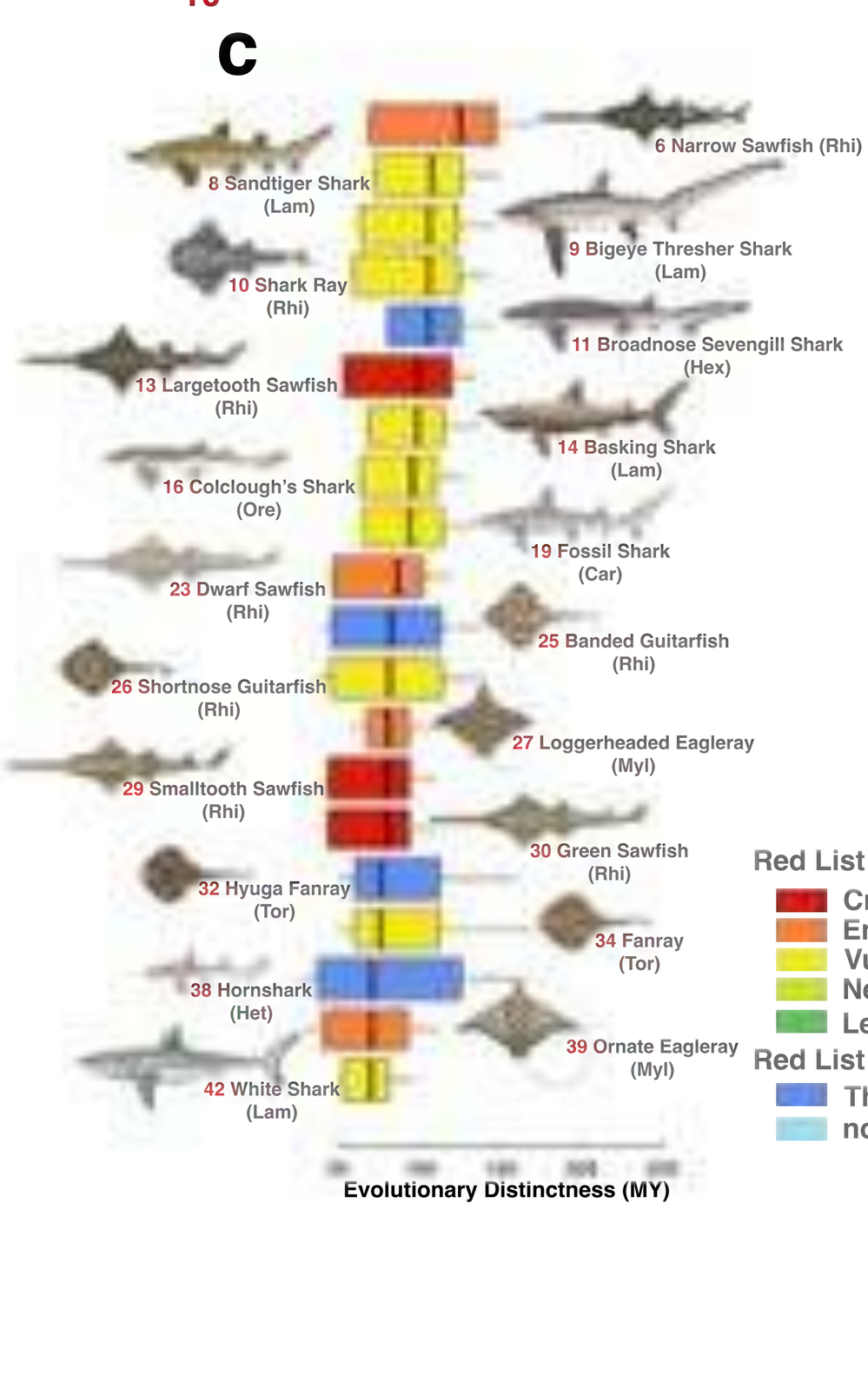
a

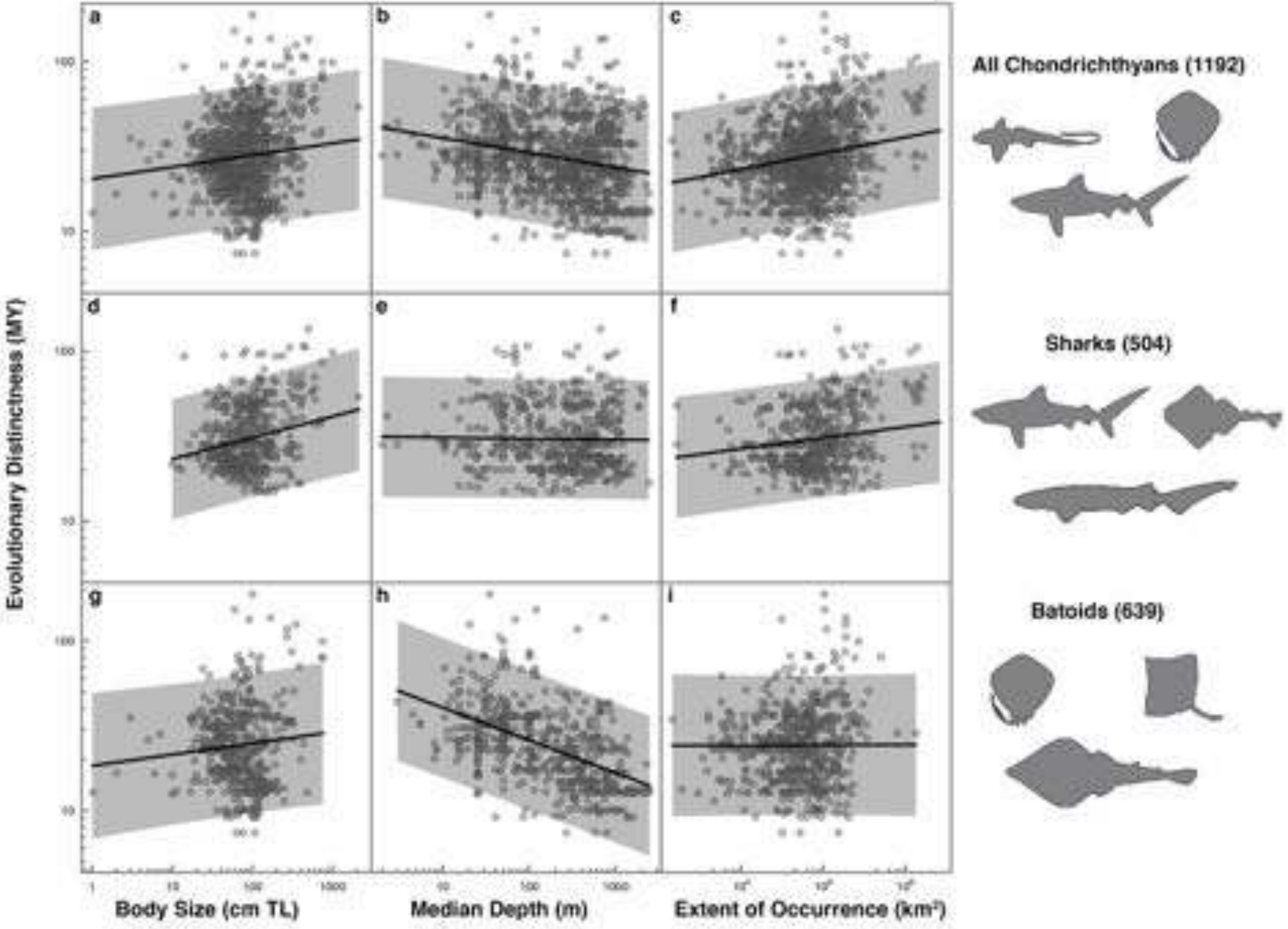

14
42
8
9
4
17
16
38
12
18
19
15
11
20
Million Years
7
39
1
3
27
29
5
2
34
32
25
26
10
6
13
23
30

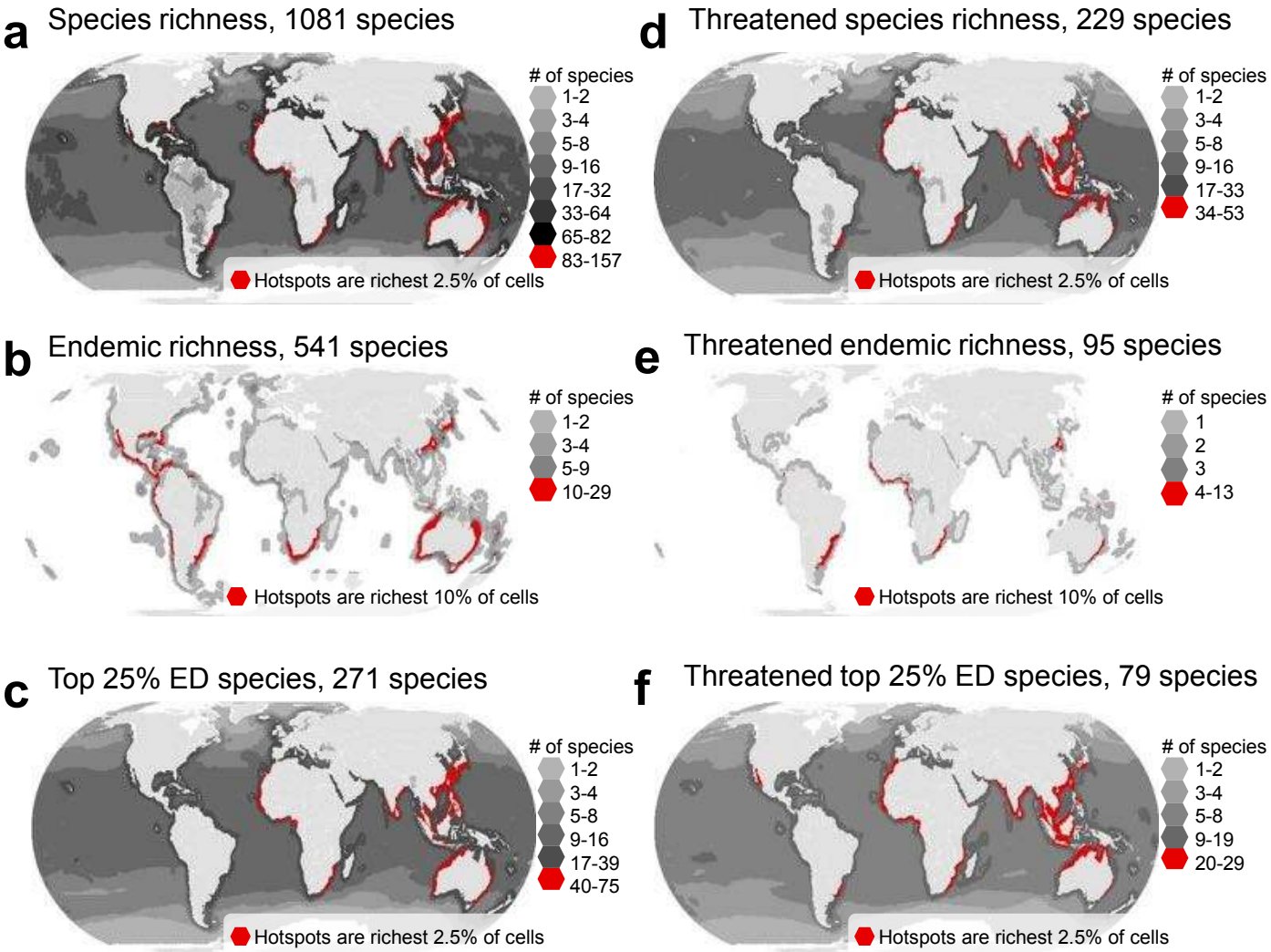
b

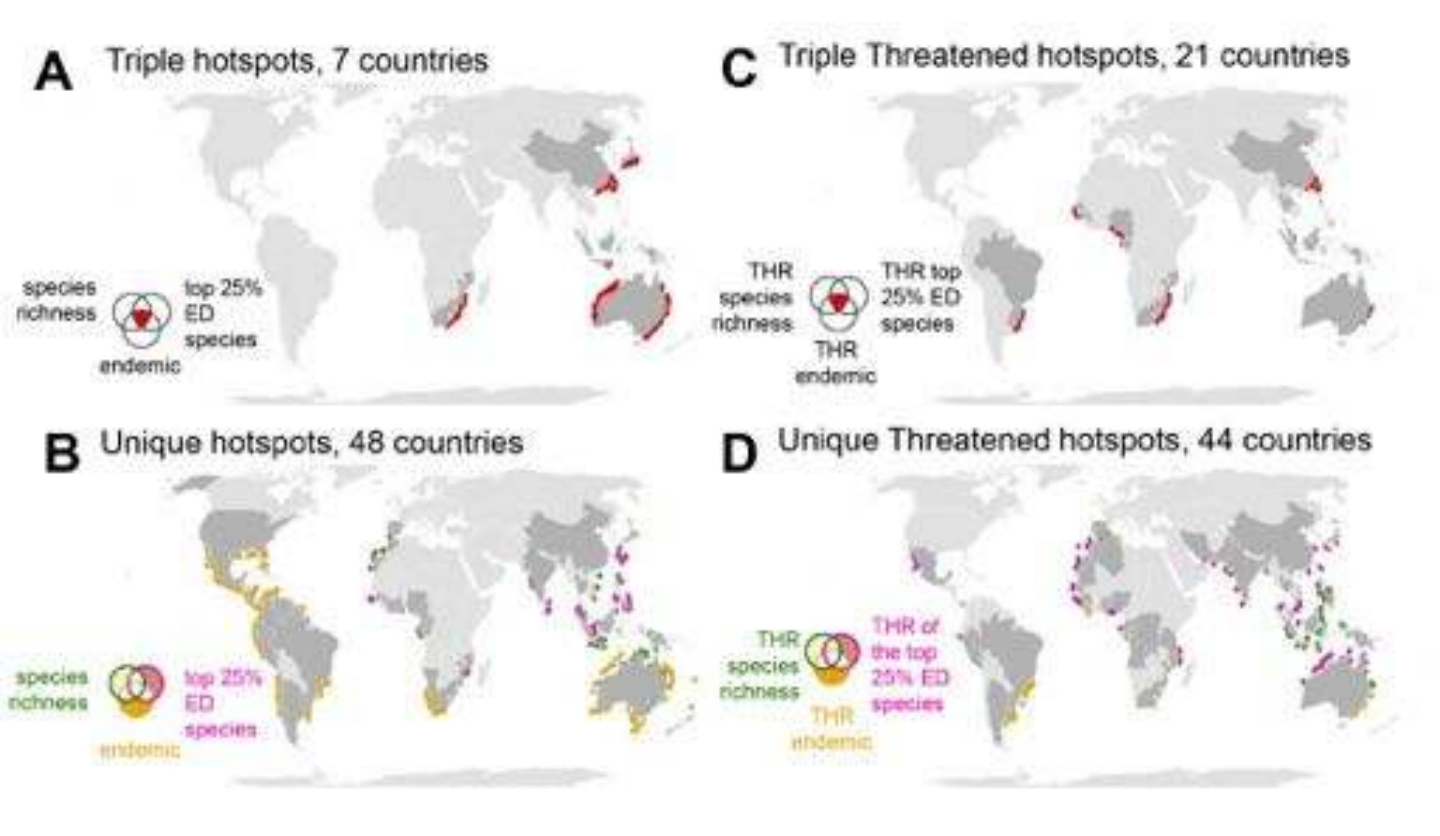

1 Striped Panray (Rhi)
2 Coffin Ray (Tor)
3 Sixgill Stingay (Myl)
4 Goblin Shark (Lam)
5 Thornback Ray (Tor)
6 Narrow Sawfish (Rhi)
7 Giant Stingaree (Myl)
8 Sandtiger Shark (Lam)
9 Bigeye Thresher Shark (Lam)
10 Shark Ray (Rhi)
11 Broadnose Sevengill Shark (Hex)
12 Barbled Houndshark (Car)
13 Largetooth Sawfish (Rhi)
14 Basking Shark (Lam)
15 Sixgill Shark (Pri)
16 Colclough's Shark (Ore)
17 Blind Shark (Ore)
18 Viper Dogfish (Squ)
19 Fossil Shark (Car)
20 Frill Shark (Hex)
Evolutionary Distinctness (MY)

c


6 Narrow Sawfish (Rhi)
8 Sandtiger Shark (Lam)
9 Bigeye Thresher Shark (Lam)
10 Shark Ray (Rhi)
11 Broadnose Sevengill Shark (Hex)
13 Largetooth Sawfish (Rhi)
14 Basking Shark (Lam)
16 Colclough's Shark (Ore)
19 Fossil Shark (Car)
23 Dwarf Sawfish (Rhi)
25 Banded Guitarfish (Rhi)
26 Shortnose Guitarfish (Rhi)
27 Loggerheaded Eagleray (Myl)
29 Smalltooth Sawfish (Rhi)
30 Green Sawfish (Rhi)
32 Hyuga Fanray (Tor)
34 Fanray (Tor)
38 Hornshark (Het)
39 Ornate Eagleray (Myl)
42 White Shark (Lam)
Evolutionary Distinctness (MY)
Red List Status (known)
Critically Endangered
Endangered
Vulnerable
Near Threatened
Least Concern
Red List Status (predicted)
Threatened
not-Threatened


a
b
c
d
e
f
g
h
i
Evolutionary Distinctness (MY)
100
10
1
10
100
1000
Body Size (cm TL)
Median Depth (m)
Extent of Occurrence (km²)
All Chondrichthyans (1192)
Sharks (504)
Batoids (639)


a
Species richness, 1081 species
# of species
1-2
3-4
5-8
9-16
17-32
33-64
65-82
83-157
Hotspots are richest 2.5% of cells
b
Endemic richness, 541 species
# of species
1-2
3-4
5-9
10-29
Hotspots are richest 10% of cells
c
Top 25% ED species, 271 species
# of species
1-2
3-4
5-8
9-16
17-39
40-75
Hotspots are richest 2.5% of cells
d
Threatened species richness, 229 species
# of species
1-2
3-4
5-8
9-16
17-33
34-53
Hotspots are richest 2.5% of cells
e
Threatened endemic richness, 95 species
# of species
1
2
3
4-13
Hotspots are richest 10% of cells
f
Threatened top 25% ED species, 79 species
# of species
1-2
3-4
5-8
9-19
20-29
Hotspots are richest 2.5% of cells


A
Triple hotspots, 7 countries
species richness
top 25% ED species
endemic
C
Triple Threatened hotspots, 21 countries
THR species richness
THR top 25% ED species
THR endemic
B
Unique hotspots, 48 countries
species richness
top 25% ED species
endemic
D
Unique Threatened hotspots, 44 countries
THR species richness
THR of the top 25% ED species
THR endemic