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Research

Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation

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Under the impact of human activity, global extinction rates have risen a thousand times higher than shown in the fossil record. The resources available for conservation are insufficient to prevent the loss of much of the world's threatened biodiversity during this crisis. Conservation planners have been forced to prioritize their protective activities, in the context of great uncertainty. This has become known as 'the agony of choice'. A range of methods have been proposed for prioritizing species for conservation attention; one of the most strongly supported is prioritizing those species that maximize phylogenetic distinctiveness (PD). We evaluate how a composite measure of extinction risk and phylogenetic isolation (EDGE) has been used to prioritize species according to their degree of unique evolutionary history (evolutionary distinctiveness, ED) weighted by conservation urgency (global endangerment, GE). We review PD-based approaches and provide an updated list of EDGE mammals using the 2010 IUCN Red List. We evaluate how robust this method is to changes in phylogenetic uncertainty, knowledge of taxonomy and extinction risk, and examine how mammalian species that rank highly in EDGE score are representative of the collective from which they are drawn.

Keywords: charismatic species; comparative methods; conservation prioritization; decline; phylogenetically distinct; phylogeny

1. INTRODUCTION

In the current era of unprecedented global change, where the rate of biodiversity loss continues unabated [1,2], decision-making about the focus of conservation investment has become a central part of both academic research and conservation action. It has been strongly argued that maximizing phylogenetic diversity should be one of the main goals of priority-setting for conservation [3–6]. This is owing to the fact that species represent different amounts of evolutionary history, reflecting different rates of divergence across any given phylogenetic tree. As such, limited conservation resources should be focused on those species that represent the greatest amounts of unique evolutionary history, whose loss would be felt most keenly.

There are two main arguments for choosing prioritization techniques that aim to conserve the maximum possible amount of evolutionary history. The first is a pragmatic perspective: phylogenetic distinctiveness (PD) is a compound metric of all forms of genotypic, phenotypic ('feature' or 'character' diversity) and functional diversity, both measurable and unmeasurable [7], so maximizing PD thereby provides biological systems with the most options to respond to a changing world, both at species level and community level. Moreover, PD could be used as a measure of ecosystem function, as phylogenies may reflect integrated phenotypic differences among taxa and so be a more encapsulating measure than sets of singular, discretely measured traits [8,9]. Prioritizing conservation by evolutionary history has been demonstrated to be an effective approach for capturing the range of morphological and ecological diversity that has evolved in a given phylogenetic group, reflecting the positive correlation between amount of evolutionary change and amount of time elapsed [10,11]. The second is from more of an ethical perspective, whereby maximizing the conservation of PD best preserves the immense history of the Earth [12].

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One contribution of 14 to a Theme Issue 'Global strategies for the conservation of mammals'.

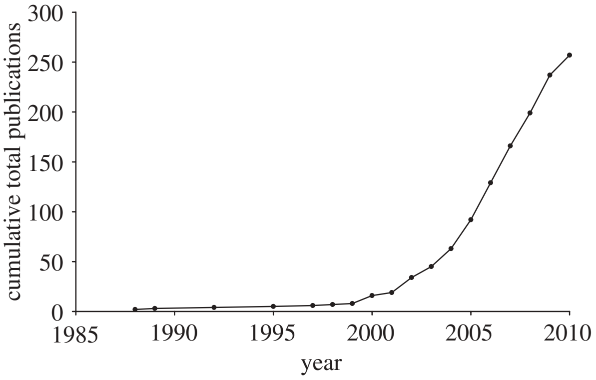

Figure 1. Cumulative total number of publications containing the search term 'supertree*' from the ISI Web of Knowledge database.

Evolution, in terms of both evolutionary history and evolutionary potential, is increasingly being recognized as the 'missing component' for conservation prioritization and planning (e.g. [13,14]). Now, more than at any other time, tools to both measure and incorporate evolutionary history into conservation priority-setting and planning are available. The expanding number of phylogenetic trees plotting the relationships among species (figure 1; [15]) and ever-increasing amount of information for conservation decision-making (e.g. species conservation status; [16]) are creating a wealth of knowledge that can be applied to address the current biodiversity crisis.

Prioritizing conservation efforts on the basis of evolutionary history are of further importance because phylogenetic comparisons have revealed that the current human-caused loss of species is taxonomically selective rather than random, that extinction risk is clustered, and that mammals, birds, plants and other taxa with few close relatives are particularly likely to be at risk [17–19]. Evolutionarily distinctive species are known to have already experienced greater levels of extinction both during the recent historical era [20] and during recent millennia [21], leading to increasing imbalance in the mammalian phylogeny over the course of the Holocene Epoch. This pattern is associated in mammals and birds with the elevated level of extinctions of island species, including many ancient species-poor mammal lineages (e.g. Bibymalagasia, Solenodontidae, Thylacinidae; [22]).

The correlation between PD and species richness can be quite close, although there is substantial variation in this relationship [23,24]. However, PD is not often effectively captured by straightforward taxon-based conservation policies [25], because variance among grid cells in species richness is far greater than the variance in species' PD. Gains in taxon richness and PD can also be decoupled, particularly when the underlying phylogeny is unbalanced and species are not randomly distributed on the landscape [26]. Therefore, in general terms, conservation approaches that maximize species richness, such as endemic species hotspots [27], may not always protect PD, particularly at sub-global scales. This has led to the development of conservation programmes that aim to objectively assign PD values to species so that decisions can be made as to the most urgent focus of conservation action. In this study, we briefly review PD-based approaches to conservation priority-setting before examining how one measure, EDGE [28], has been implemented in mammals. We evaluate how robust this method is to changes in knowledge of taxonomy and extinction risk, examine how mammalian species that rank highly in EDGE score are representative of the collective from which they are drawn, assess the barriers to using PD, and report a set of conservation recommendations for new taxa.

(a) *Review of phylogenetic diversity-based approaches for species conservation*

The concept of using evolutionary history in conservation prioritization has been around for at least two decades [4,5]. These first approaches developed metrics concerning taxonomic distinctiveness (TD; relative to other species; [5]) and PD (sum of phylogenetic branch length of species in a given region; [4]). Many derivations have subsequently been developed from these approaches (see [12]), but these essentially all fall under one of these two categories.

Evolutionary history consists of two distinct components, the branching pattern of a phylogenetic tree and the length of its branches, and early attempts to integrate PD into conservation priority-setting were typically restricted to using information on branching pattern alone (i.e. they represented scores of TD; see [29]). However, the increasing availability of temporally calibrated branch lengths for phylogenies of large taxonomic groups has made it possible to calculate PD using both components [15]. This in turn has led to the development of a family of related measures of PD-based priority-setting approaches, which differ in their use of scoring methods for distributing among species the shared component of evolutionary history represented by deep phylogenetic branches, and in different methods for calculating and incorporating the extinction risk of different species across the phylogeny.

In addition to the original concept of PD [4], the two most widely followed scoring methods in the recent literature are equal splits (ES; [30,31]) and evolutionary distinctiveness (ED; [28]), also known as fair proportion (and which is very close to another, evolutionarily stable strategy game inspired measure, the Shapley index; [32], see [33] for wider review). ES hierarchically partitions branch lengths by the number of descendent edges, such that for a given branch, a descendent species receives credit equal to 0.5 to a power equal to the number of splits between the branch and the species. ED instead partitions branches by the total number of species descending from them, regardless of nested tree structure, such that the contribution of a given ancestral branch to the ED score is 1/number of descendants of that branch. Further modifications to the ED approach have been proposed, allowing it to also include abundance information to generate a metric of abundance-weighted ED that can be used to prioritize populations, species, habitats and biogeographical regions [12]. These alternative methods for scoring evolutionary history are then combined with a measure of threat to provide prioritization indices to inform conservation, as first carried out by Weitzman [34] and Avise [35]. The EDGE approach combines ED scores directly with a ranked measure of extinction risk (global endangerment; GE) based on the quantitative and objective framework provided by the International Union for Conservation of Nature (IUCN) Red List, to generate EDGE scores [28]. ES scores were similarly combined with a probability of extinction score (Pe) to generate a species-specific expected loss of evolutionary history (EL) metric [31]. EDGE is, in effect, a special case of EL in which each increase in the Red List category represents a doubling of extinction risk, an arbitrary approach that avoids the resultant list being dominated by species of only the highest threat category.

EDGE and EL scores assigned to species are independent of the conservation status of other taxa. However, other approaches for combining extinction risk also take the conservation status of related species into account. This is based on the consideration that some future 'sets' of species are more likely to persist than others as a result of interspecific variation in extinction risk; at-risk species with close relatives that are also threatened with extinction should represent higher conservation priorities, because such species are predicted to represent a higher amount of unique evolutionary history in the future [36]. The corollary of this is that systems like EDGE might overestimate the importance of species with safe relatives. For example, extinction of a 1 Myr-old species lineage would result in the loss of one million years of evolution, but the future extinction of its currently threatened sister species results in the loss of another one million years of evolution as well as the deeper branch connecting the now-extinct species pair to the rest of the phylogeny. The probability of losing an internal branch in a phylogeny is, therefore, related to the number of descendent species and is the product of their probabilities of extinction, which is not accounted for by the EDGE or EL approaches.

In order to account for this issue, the basic PD approach [4] was modified by Witting & Loeschcke [6], Witting *et al.* [37] and Faith [36] to provide a measure of the expected or probabilistic PD for a given species that will result from different extinction scenarios affecting other species of varying relatedness. A similar method has also been developed by Steel *et al.* [38], where a heightened ED score (HED) is used to generate a HEDGE score. There has been criticism of EDGE and EL approaches owing to their dependency on a static apportioning of credit for branches and their failure to incorporate extinction probabilities of related species [36]. In particular, Faith argued that PD-based conservation initiatives should instead adopt probabilistic PD to properly take complementarity into account [36]. However, in reality this modification is unlikely to make much of a difference in conservation prioritization, because it has been demonstrated that most species derive the majority of their ED from terminal branches [28], and comparisons of HED and ED scores show very strong correlations (e.g. 0.94 for prosimians; [38]).

A second debate has also addressed appropriate methods for quantifying conservation status. IUCN Red List categories are ranks representing probabilities of extinction [39,40]. However, extinction risk ranks need to be assigned numerical values (an 'urgency score') when they are combined with other criteria, such as when integrated with phylogenetic trees to develop EDGE-style priority rankings. This raises the question, does movement between ranks represent a constant change in probability or is it nonlinear [41]? The EDGE approach treats IUCN Red List categories as equivalent intervals of risk [28,41,42]; however, alternative approaches can also be adopted, for example, by using empirical estimates from population viability analyses [43] for data-rich taxa. The greatest variation between PD-based priority rankings is caused by assuming latent risk (the 'pessimistic' approach of Mooers *et al.* [43]), which gives higher weight to PD because all taxa are considered to be at some risk of extinction, and includes species that are less threatened (see [44,45]). Some authors have also included Data Deficient (DD) species in PD-based prioritization approaches, for example, by arbitrarily (though probably conservatively) estimating their extinction risk as being between the Least Concern and Near Threatened categories [45]. While this may be a legitimate assumption with birds [46], evidence suggests that the probable status of DD species in many taxonomic groups might be more likely to be threatened [47]; at the very least, some unknown proportion of DD species are threatened, so treating DD species as a single value is not informative.

2. METHODS

(a) *EDGE scores*

We collated mammal conservation status data from the IUCN Red List [48,49], and included genuine change in status from Hoffmann *et al.* [50]. We used a composite 'supertree' phylogeny [51–53] to calculate ED scores for mammals, following the procedure reported in Isaac *et al.* [28]. Briefly, we divided the total phylogenetic diversity of each clade among its members by applying a value to each branch equal to its length divided by the number of descendent species. The ED of a species is simply the sum of these values for all branches from which the species is descended, to the root of the phylogeny. The new mammal EDGE list presented here is constructed using an updated mammal taxonomy and the most recent Red List assessments, but also differs in several other ways, detailed below.

The new list uses the third edition of *Mammal Species of the World* (MSW3; [54]), whereas the original list of Isaac *et al.* [28] used the second edition taxonomy (MSW2; [55]). A phylogenetic tree in the MSW3 taxonomy was provided by Fritz *et al.* [53], who converted it from the MSW2 format tree of Bininda-Emonds *et al.* [51]. MSW3 contains 5416 species, when compared with 4629 species in MSW2. Only 291 of the additional species have been newly described since MSW2, so taxonomic changes (splitting and lumping) have accounted for a net gain of nearly 500 species (i.e. more than 10% growth). Such instability in taxonomic status presents wide-scale technical and philosophical challenges for research applications that use species lists, especially in evolutionary and conservation biology [56–58].

However, phylogenetic metrics such as EDGE are somewhat less sensitive to taxonomic change than alternative biodiversity measures such as counts of endemic or threatened species [28].

Species values of ED were calculated as the geometric mean of scores under the three sets of branch lengths. The algorithm for calculating ED scores [28] was applied with a modification to the way in which scores were corrected for polytomies (nodes with more than two descendants) and uncertainty in the estimated divergence times. Polytomies in supertrees result from poor or conflicting data rather than a true representation of the speciation process, so the distinctiveness of branches subtending them is overestimated, thus leading to biased ED scores. Isaac *et al.* [28] used a statistical fit to simulated data in order to correct the ED scores of nodes descended from polytomies. Their correction factor decreased to zero for nodes with large numbers (more than 20) of descendants, which leads to an underestimate of the ED score of many species in poorly resolved areas of the phylogeny (in this study, mainly bats and rodents). To deal with uncertainty in the branch length estimates, Isaac *et al.* [28] reported the geometric mean ED scores based on three sets of node ages (best, upper and lower) from Bininda-Emonds *et al.* [51].

For the new list, we calculated ED scores for each of 1000 supertrees, each of which was resolved using Bayesian methods described in Kuhn *et al.* [59]. These fully resolved supertrees represent the pseudo-posterior distribution of the underlying mammalian phylogeny. We modified the PolytomyResolver R script [59] in order to incorporate uncertainty in the estimates of individual node ages by placing a normally distributed prior constraint onto each resolved node of the starting tree [53]. These priors each had a mean equal to the best age estimate reported in Fritz *et al.* [53], and a standard deviation of (best−worst estimate)/1.96, where the worst estimate is defined as the estimate (upper or lower) that was furthest from the best. We created 1000 resolved trees using BEAST (v. 1.6.1) [60] to analyse five independent runs of approximately 2 000 000 iterations and a sampling interval of 1000. We assessed the burnin, convergence and mixing manually for each run using Tracer v. 1.5 [61] and produced the final distribution by combining all independent runs and subsampling to every 9000 iterations.

The MSW3 format phylogeny [53] contains 5020 species, i.e. 396 valid names were missing. Of these, 75 are known to be extinct [22]. We estimated ED scores for 250 of the extant missing species as the mean ED of congeneric species, such that only 71 extant species still lacked ED scores. We also estimated ED for two recently described species, *Laonastes aenigmamus* and *Pseudoryx nghetinhensis*, which were likely to represent EDGE priorities on the basis of their high taxonomic distinctiveness. 'Surrogate' ED scores for these species were crudely estimated as the likely time of divergence based on available molecular data (see electronic supplementary material, table S1, references S2 and S4). Finally, IUCN categories were matched for 5123 species, of which 692 are DD, producing a list of 4431 EDGE scores.

Changes in EDGE score between [28] and the results reported in this study are due to a number of reasons that are not mutually exclusive. EDGE score may change owing to reassessment of the conservation status of the species (i.e. updated Red List status, which may or may not be owing to a genuine change in species status; [42]), or a change in taxonomic status between MSW2 and MSW3. The latter is further complicated by new species discoveries and by the splitting and lumping of existing species, resulting in a changed phylogeny for both a given species and any sister taxa it may have. We tracked changes in taxonomy and Red List status between the old and new EDGE lists, recording changes in taxonomic status as new species described, species split, species lumped, or non-nested [56], in which there is no simple relationship between the species taxonomy in MSW2 and MSW3.

(b) *Trait analysis*

We followed the method of Redding *et al.* [10] to evaluate how mammal species that rank highly in EDGE score are representative of the collective from which they are drawn. We used six mammalian trait measures drawn from Jones *et al.* [62] of reproductive, behavioural, geographical and morphological species traits: body mass (grams), gestation length (days), home range size (square kilometres), litter size, geographical range size (square kilometres) and latitudinal midpoint of range (decimal degrees). Each trait was log10 transformed to lessen the effect of outliers and equalize variance. For each species value, we calculated absolute mean distance from the median value of the trait for the order; the greater the distance from the median value, the more unusual that species is in a given trait for its order.

Following Redding *et al.* [10], we used Pearson correlations to test for a relationship between EDGE score (and its components, ED and GE) and absolute distance from the median value for each trait. Owing to the repeated tests, we used a correction factor to account for false discoveries and the possibility of elevated type I errors. This procedure accounts for the number of false-positive hypotheses that would be accepted with raw p-values, given a predefined significance value of $\alpha = 0.05$ [63,64]. All analyses were conducted in R v. 2.12.1 [65].

3. RESULTS

Our new analysis of EDGE scores has generated a new priority list of mammals requiring urgent conservation attention on the basis of a combination of high ED and high threat status (table 1). Our data show that there has been some change in the ranks of species between EDGE lists, but that the overall priority set appears robust to these changes. These rank changes can be attributed to both changes in taxonomy (table 2 and figure 2) and changes in Red List status (figure 3). The taxonomy of the majority of species remains unchanged (approx. 70%; table 2). Of the changes to species taxonomic status, approximately 20 per cent have been split, 5 per cent are new species descriptions, and about 2.5 per cent have been either lumped or represent non-nested taxonomic changes. The relatively minor impact of these taxonomic

Table 1. Top 100 mammal EDGE scores, representing the highest priority mammal species requiring urgent conservation attention on the basis of a combination of high ED and high threat status. Conservation attention was assessed following the methods used by Sitas *et al.* [66]. CR, Critically Endangered; EN, Endangered VU, Vulnerable.

rank	species	order	family	status	ED	EDGE	conservation attention
1=	*Zaglossus attenboroughi*	Monotremata	Tachyglossidae	CR	55.21737845	6.801814656	none
1=	*Zaglossus bartoni*	Monotremata	Tachyglossidae	CR	55.21737845	6.801814656	limited
1=	*Zaglossus bruijnii*	Monotremata	Tachyglossidae	CR	55.21737845	6.801814656	none
4	*Mystacina robusta*	Chiroptera	Mystacinidae	CR	54.10322232	6.781796918	none
5	*Lipotes vexillifer*	Cetacea	Lipotidae	CR	38.67180179	6.453229375	none
6	*Burramys parvus*	Diprotodontia	Burramyidae	CR	32.75582928	6.291741844	active
7=	*Solenodon cubanus*	Soricomorpha	Solenodontidae	EN	61.69215212	6.217677816	none
7=	*Solenodon paradoxus*	Soricomorpha	Solenodontidae	EN	61.69215212	6.217677816	limited
9	*Dicerorhinus sumatrensis*	Perissodactyla	Rhinocerotidae	CR	29.44751148	6.188592988	active
10	*Bunolagus monticularis*	Lagomorpha	Leporidae	CR	27.88392179	6.135873823	active
11	*Diceros bicornis*	Perissodactyla	Rhinocerotidae	CR	26.63195412	6.091561583	active
12	*Lasiorhinus krefftii*	Diprotodontia	Vombatidae	CR	25.98457399	6.067854091	active
13	*Camelus ferus*	Artiodactyla	Camelidae	CR	25.29566761	6.041992918	limited
14	*Rhinoceros sondaicus*	Perissodactyla	Rhinocerotidae	CR	24.64177112	6.016811428	active
15	*Laonastes aenigmamus*	Rodentia	Diatomyidae	EN	44.3	5.892748574	none
16	*Bradypus pygmaeus*	Pilosa	Bradypodidae	CR	20.88097152	5.858206101	none
17	*Elephas maximus*	Proboscidea	Elephantidae	EN	39.76418423	5.7872454	active
18	*Octodon pacificus*	Rodentia	Octodontidae	CR	18.43970169	5.739906176	none
19	*Ailuropoda melanoleuca*	Carnivora	Ursidae	EN	36.77014331	5.710960473	active
20	*Tapirus indicus*	Perissodactyla	Tapiridae	EN	36.03587836	5.69132867	active
21	*Abrocoma boliviensis*	Rodentia	Abrocomidae	CR	17.4621309	5.688310378	none
22=	*Monachus monachus*	Carnivora	Phocidae	CR	16.79398976	5.651449469	active
22=	*Monachus schauinslandi*	Carnivora	Phocidae	CR	16.79398976	5.651449469	active
24	*Ailurops melanotis*	Diprotodontia	Phalangeridae	CR	16.65441885	5.643574834	none
25	*Natalus jamaicensis*	Chiroptera	Natalidae	CR	16.59446732	5.640173218	none
26	*Coleura seychellensis*	Chiroptera	Emballonuridae	CR	16.5694351	5.638749473	limited
27	*Natalus primus*	Chiroptera	Natalidae	CR	16.40073806	5.629101345	none
28	*Choeropsis liberiensis*	Artiodactyla	Hippopotamidae	EN	33.17906211	5.611054779	limited
29	*Indri indri*	Primates	Indridae	EN	33.00886339	5.60606272	active
30	*Galagoides rondoensis*	Primates	Galagidae	CR	15.61252133	5.58274543	none
31	*Myrmecobius fasciatus*	Dasyuromorphia	Myrmecobiidae	EN	32.0385503	5.577116612	active
32	*Pharotis imogene*	Chiroptera	Vespertilionidae	CR	15.302246	5.563891612	none
33	*Aproteles bulmerae*	Chiroptera	Pteropodidae	CR	15.29611383	5.563515386	none
34	*Phalanger matanim*	Diprotodontia	Phalangeridae	CR	15.26573074	5.561649208	none
35	*Potorous gilbertii*	Diprotodontia	Potoroidae	CR	15.14476359	5.554184483	active
36	*Marmosops handleyi*	Didelphimorphia	Didelphidae	CR	14.89316215	5.538477686	none
37	*Varecia variegata*	Primates	Lemuridae	CR	14.71875348	5.527443211	active
38	*Amorphochilus schnablii*	Chiroptera	Furipteridae	EN	30.2569337	5.521682772	none
39	*Tapirus bairdii*	Perissodactyla	Tapiridae	EN	30.00565773	5.513611237	active
40	*Romerolagus diazi*	Lagomorpha	Leporidae	EN	29.85224334	5.508651007	none
41	*Prolemur simus*	Primates	Lemuridae	CR	14.3982973	5.506845661	active
42	*Pentalagus furnessi*	Lagomorpha	Leporidae	EN	29.4589476	5.495821338	limited
43	*Beatragus hunteri*	Artiodactyla	Bovidae	CR	14.12584734	5.488993747	limited
44	*Pseudoryx nghetinhensis*	Artiodactyla	Bovidae	CR	13.68	5.459074745	limited
45	*Pongo abelii*	Primates	Hominidae	CR	13.66284712	5.45790561	active
46	*Rhynchocyon chrysopygus*	Macroscelidea	Macroscelididae	EN	28.12701704	5.451107706	limited
47	*Hapalemur alaotrensis*	Primates	Lemuridae	CR	13.49001975	5.446048842	active
48	*Tokudaia muenninki*	Rodentia	Muridae	CR	13.48531689	5.44572423	none
49	*Gymnobelideus leadbeateri*	Diprotodontia	Petauridae	EN	27.62231266	5.433628118	active

(*Continued.*)

Table 1. (*Continued.*)

rank	species	order	family	status	ED	EDGE	conservation attention
50	*Dugong dugon*	Sirenia	Dugongidae	VU	56.07711486	5.430697607	active
51	*Neohylomys hainanensis*	Erinaceomorpha	Erinaceidae	EN	27.36334182	5.424539072	none
52	*Podogymnura aureospinula*	Erinaceomorpha	Erinaceidae	EN	27.22727204	5.419730146	none
53=	*Chinchilla chinchilla*	Rodentia	Chinchillidae	CR	12.97919099	5.410158588	none
53=	*Chinchilla lanigera*	Rodentia	Chinchillidae	CR	12.97919099	5.410158588	none
55	*Spilocuscus rufoniger*	Diprotodontia	Phalangeridae	CR	12.78305286	5.396028506	none
56	*Mystacina tuberculata*	Chiroptera	Mystacinidae	VU	54.10322232	5.395502557	active
57	*Sminthopsis aitkeni*	Dasyuromorphia	Dasyuridae	CR	12.69165084	5.389374942	active
58	*Lepilemur septentrionalis*	Primates	Lepilemuridae	CR	12.65667849	5.386817391	limited
59	*Micropotamogale lamottei*	Afrosoricida	Tenrecidae	EN	26.20431682	5.382817209	none
60	*Platanista gangetica*	Cetacea	Platanistidae	EN	26.19122582	5.382335883	limited
61	*Bradypus torquatus*	Pilosa	Bradypodidae	EN	25.33866497	5.350479552	limited
62	*Hipposideros lamottei*	Chiroptera	Hipposideridae	CR	11.8752596	5.327896332	none
63	*Phocoena sinus*	Cetacea	Phocoenidae	CR	11.82671575	5.324118886	limited
64	*Oreonax flavicauda*	Primates	Atelidae	CR	11.61379513	5.307379789	limited
65	*Propithecus perrieri*	Primates	Indridae	CR	11.59144115	5.305606032	limited
66	*Loris tardigradus*	Primates	Lorisidae	EN	23.67408268	5.28519495	limited
67	*Cavia intermedia*	Rodentia	Caviidae	CR	11.25459124	5.278489384	none
68	*Gorilla gorilla*	Primates	Hominidae	CR	11.21914344	5.275592579	active
69	*Trichechus inunguis*	Sirenia	Trichechidae	VU	47.24796806	5.262648075	limited
70	*Nilopegamys plumbeus*	Rodentia	Muridae	CR	11.02530903	5.259602237	none
71	*Catagonus wagneri*	Artiodactyla	Tayassuidae	EN	22.66555597	5.243462198	active
72	*Neamblysomus gunningi*	Afrosoricida	Chrysochloridae	EN	22.35386779	5.230204156	none
73	*Balaenoptera physalus*	Cetacea	Balaenopteridae	EN	22.24687411	5.225612218	active
74	*Tapirus pinchaque*	Perissodactyla	Tapiridae	EN	22.14517275	5.22122778	limited
75	*Balaenoptera musculus*	Cetacea	Balaenopteridae	EN	22.06062052	5.217567965	active
76	*Dendromus kahuziensis*	Rodentia	Nesomyidae	CR	10.47272767	5.212561434	none
77	*Chrysospalax trevelyani*	Afrosoricida	Chrysochloridae	EN	21.90862527	5.210955031	none
78	*Leporillus apicalis*	Rodentia	Muridae	CR	10.02143241	5.1724305	none
79	*Hypogeomys antimena*	Rodentia	Nesomyidae	EN	20.86613092	5.164380448	active
80	*Tylomys bullaris*	Rodentia	Cricetidae	CR	9.894517263	5.160848382	none
81	*Callicebus barbarabrownae*	Primates	Pitheciidae	CR	9.869378529	5.158538249	none
82=	*Sorex sclateri*	Soricomorpha	Soricidae	CR	9.853968549	5.1571195	none
82=	*Sorex stizodon*	Soricomorpha	Soricidae	CR	9.853968549	5.1571195	none
84	*Tylomys tumbalensis*	Rodentia	Cricetidae	CR	9.789790788	5.151189112	none
85	*Bettongia penicillata*	Diprotodontia	Potoroidae	CR	9.741552342	5.146708339	active
86	*Cryptotis nelsoni*	Soricomorpha	Soricidae	CR	9.73005188	5.145637114	none
87	*Mesocapromys sanfelipensis*	Rodentia	Capromyidae	CR	9.715985838	5.144325352	none
88	*Mesocapromys nanus*	Rodentia	Capromyidae	CR	9.707420414	5.14352572	none
89	*Manis pentadactyla*	Pholidota	Manidae	EN	20.35572093	5.140761205	limited
90	*Manis javanica*	Pholidota	Manidae	EN	20.30695965	5.138475305	limited
91	*Brachyteles hypoxanthus*	Primates	Atelidae	CR	9.65114119	5.138255763	limited
92=	*Trichechus manatus*	Sirenia	Trichechidae	VU	41.57146606	5.137478579	active
92=	*Trichechus senegalensis*	Sirenia	Trichechidae	VU	41.57146606	5.137478579	active
94	*Potorous longipes*	Diprotodontia	Potoroidae	EN	20.22170929	5.134466223	active
95	*Cremnomys elvira*	Rodentia	Muridae	CR	9.532109427	5.127017354	none
96	*Millardia kondana*	Rodentia	Muridae	CR	9.299543578	5.104688304	none

(*Continued.*)

Table 1. (*Continued.*)

rank	species	order	family	status	ED	EDGE	conservation attention
97	*Crateromys australis*	Rodentia	Muridae	CR	9.257893072	5.100636187	none
98	*Viverra civettina*	Carnivora	Viverridae	CR	9.189373539	5.09393409	none
99	*Habromys chinanteco*	Rodentia	Cricetidae	CR	9.169551079	5.09198679	none
100	*Amblysomus marleyi*	Afrosoricida	Chrysochloridae	EN	19.23849603	5.087028077	none

Table 2. Change in taxonomic status of mammal species 1993–2005. Numbers refer to species in the new (third) edition of *Mammal Species of the World* [55] and expressed relative to species status in the second edition [54].

taxonomic status	no. of species	proportion of species
new species described	291	0.054
split	1099	0.203
lumped	142	0.026
non-nested	128	0.024
unchanged	3756	0.693
total	5416	

changes on ED score is apparent from figure 2, which shows a strong correlation between ED scores derived from MSW2 [55] and those derived from MSW3 [54].

Although there is an overall strong correlation between the ED scores reported in this study and previous estimates (figure 2), several anomalies do exist. For example, *Ochotona nubrica* has a large increase in ED score between the MSW2 (and 3) and the current estimate, resulting in an EDGE rank of 739 (a climb of 106 in the ranking). This difference in ED scores results from an error in the node age estimates of the original supertree, where the upper and lower age estimates appear to be reversed. This type of node age estimate issue is only relevant to eight of the 2503 nodes of the supertree, and does not dramatically alter ED scores for species other than *O. nubrica*.

Variation in Red List ranking has a much greater impact on the composite measure making up the EDGE score (figures 3 and 4). This variation reveals two clear patterns. Firstly, there is considerable movement of species between threatened categories (Critically Endangered, Endangered, Vulnerable) and non-threatened categories (Near Threatened, Least Concern), which probably reflects the gathering of new data and/or reassessments of the quality of old data on species threat status. Secondly, movement within the threatened categories is usually only by one category, and changes are rare for species that were already listed as threatened. It should be noted that of these changes, only 195 represent a change in Red List status brought about by a genuine deterioration or improvement in the status of the species [50], rather than a change in knowledge about the species (1246 species); and only 71 of these represent 'EDGE species', i.e. threatened species with above-average ED score.

In the EDGE species trait analysis, we evaluated how species that rank highly in EDGE score are representative of the collective from which they are drawn. Overall there was strong support for the positive correlation of mammal trait oddness and high EDGE score (table 3). This was also true of the component parts of the EDGE score, ED and GE (see electronic supplementary material, tables S2 and S3). The greatest support across orders was for geographical range (eight orders showed significant correlation), followed by body mass and gestation length (table 4). Tests on the component parts of species EDGE score revealed that the relationship with geographical range is driven by the GE component (i.e. correlates of extinction risk), whereas morphological and reproductive traits (body mass, gestation length and litter size) showed strong correlation with ED score (electronic supplementary material, tables S2 and S3).

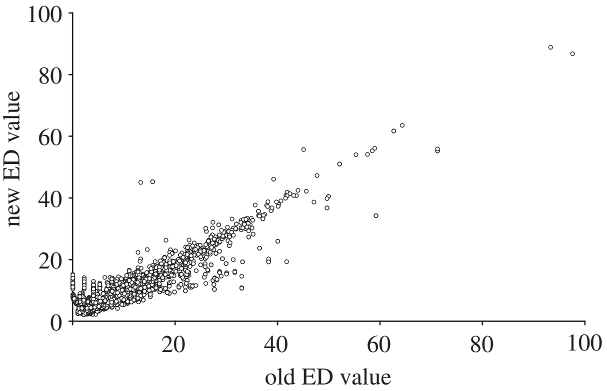

Figure 2. Comparison of ED values between EDGE lists. Old ED status is the value for each species as reported in Isaac *et al.* [28]; new ED status is the value for each species calculated in this study.

4. DISCUSSION

It is important that approaches to conservation priority-setting are able to satisfy two conditions: they must capture biodiversity, a complex and multi-faceted concept, and must be robust to uncertainty. As knowledge continues to develop about the relationships among species and the extinction risk that these species face, techniques such as the one presented here must allow for the prospect that lists of priority species may change. This is a necessary part of incorporating new knowledge to the best effect into prioritization initiatives. Nevertheless, the most appropriate approaches will often be those that are least subject to the vagaries of these inevitable changes in our knowledge of extinction risk and taxonomy. The EDGE method appears on the evidence presented here to represent a robust approach to incorporating evolutionary history into priority-setting in mammals.

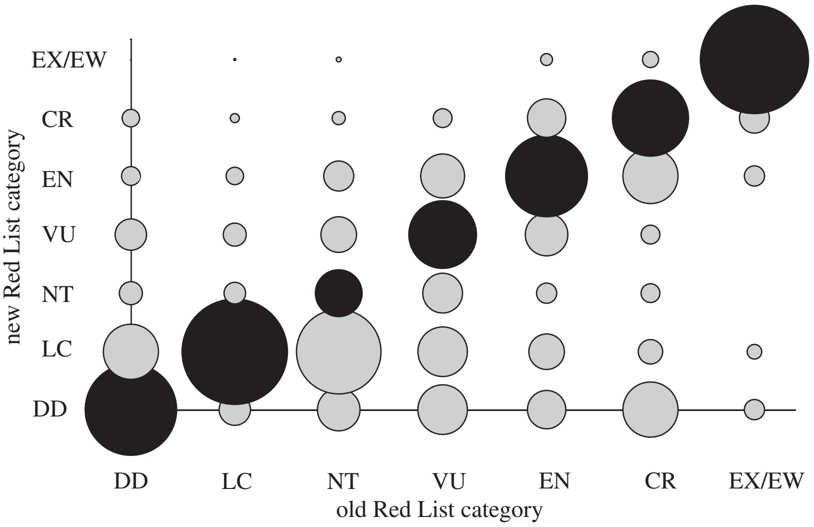

Figure 3. Comparison of Red List status between EDGE lists. Old Red List status is the categories of species reported in [28]; new Red List status is the category of species calculated in this study, following Schipper *et al.* [48]. Black shading indicates where no category change has taken place. Bubble size is scaled to the number of cases of a given category, as a proportion of the species that used to be in that category in the previous version of the Red List. $n = 4708$ mammal species for which direct comparison could be made. DD, Data Deficient, LC, Least Concern, NT, Near Threatened, VU, Vulnerable, EN, Endangered, CR, Critically Endangered, EX/EW, Extinct/Extinct in the Wild.

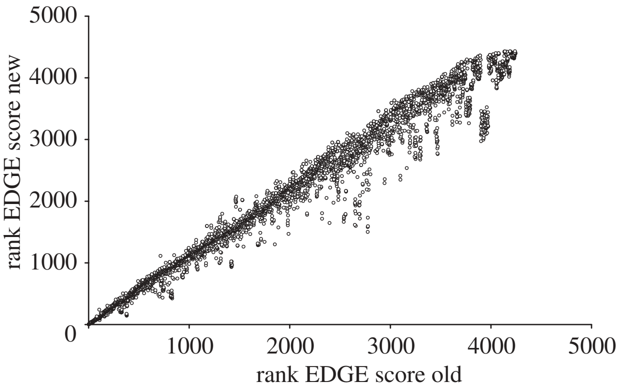

Figure 4. Comparison of EDGE ranks between EDGE lists. Rank EDGE score old is the value for each species as reported in Isaac *et al.* [28]; rank EDGE score new is the value for each species calculated in this study.

The majority of the changes in species ranks between this and the previous version of the EDGE list [28] are due to changes in Red List status. The 195 changes in mammal conservation status, which principally represent changes to more threatened categories of Red List status, are of serious concern; they are leading to a net deterioration in conservation status across the group and an erosion of biodiversity [50]. This study also reveals the number of reassessments of mammalian species extinction risk category owing to non-genuine impacts on status, i.e. changing taxonomy, new information and reassessment of the quality of existing data used for assessments in the light of new understanding. While such changes are potentially problematic for priority-setting schemes, such as EDGE, the expanding knowledge of species conservation status is undoubtedly a positive advance for conservation. Nevertheless, such changes are quite numerous, even in a well-studied group like mammals. These changes appear to be greatest for species in non-threatened or DD categories, whereas threatened species tend only to move a single category. The result of such patterns will be that large jumps in ranking will be experienced by species undergoing the greatest steps of change between threatened and non-threatened categories, and vice versa. The level to which this matters depends on the scale of conservation we wish to achieve. Lower down the ranking, even a small change in score can lead to a large change in rank. However, species actually classed as EDGE species reside towards the top of the ranking, where such changes are far smaller.

By avoiding priority lists that are dominated by highly threatened species, an approach that uses a roughly equal weighting of extinction risk and PD buffers high-ranking species from change, in cases such as mammals where the range of the two component scores is similar (roughly two orders of magnitude). The EDGE programme, which implements practical on-the-ground conservation actions for focal species from the top 100 list of EDGE species (table 1), makes use of this benefit. Although the EDGE programme is important for identifying species as foci for conservation at the global scale, the approach is not yet suitable for application to regional conservation planning (e.g. reserve design). As discussed above, this is because EDGE does not incorporate the principle of complementarity [36]. Modification of the EDGE algorithm is possible (a ‘HEDGE’ list, [38]) but this has yet to be implemented.

We also find evidence across numerous mammalian orders to support findings previously identified in small-scale studies [10,11] that species with high EDGE scores are biologically and/or ecologically atypical of the groups from which they are drawn [10]. However, correlations of trait values with ED or EDGE are not consistent across mammalian orders, providing further evidence that threatened and evolutionarily distinct species represent a truly unique set of taxa, comprising varied traits that contribute disproportionately to biodiversity. One common criticism of

Table 3. Pearson correlations of EDGE scores against distance of species-specific traits from the median value for each trait for 11 mammalian orders. ρ denotes correlation coefficient; all statistical values adjusted as per Benjamini & Yekutieli [64].

	Afrosoricida		Artiodactyla		Carnivora		Chiroptera		Dasyuromorphia		Didelphimorphia	
trait	d.f.	ρ	d.f.	ρ	d.f.	ρ	d.f.	ρ	d.f.	ρ	d.f.	ρ
body mass	35	0.012	175	0.007	218	0.153	615	0.158**	55	0.161	51	−0.088
gestation length	7	0.920*	150	0.18	154	0.141	148	0.078	33	0.036	6	−0.035
home range	—	—	60	−0.045	96	0.111	—	—	6	−0.565	8	0.393
litter size	20	0.035	154	0.207*	187	−0.061	429	−0.122*	45	0.167	24	0.382
geographical range	42	0.400*	185	0.338***	198	0.393***	841	0.406***	62	0.265	43	0.434
latitudinal midpoint	42	0.460**	185	−0.203*	198	−0.105	841	−0.022	62	0.007	43	0.101
	Diprotodontia		Lagomorpha		Primates		Rodentia		Soricomorpha			
body mass	110	0.082	58	0.039	236	0.129	1199	0.059*	164	0.401*		
gestation length	41	0.317	33	0.01	132	0.171	402	0.297***	37	0.198		
home range	29	−0.075	22	−0.281	141	0.099	225	0.057	24	−0.072		
litter size	102	0.072	54	0.316	184	−0.05	835	0.039	107	0.104		
geographical range	129	0.350***	80	0.409**	291	0.082	1565	0.361***	291	0.344***		
latitudinal midpoint	129	0.202	80	0.086	291	0.127	1565	−0.119***	291	−0.178**		

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 4. Proportion of mammal orders showing significant positive support for relationship between trait oddity and EDGE score, ED score and GE score.

trait	EDGE	ED	GE
body mass	0.27	0.55	0.09
geographical range	0.73	0.09	0.73
gestation length	0.18	0.40	0.10
home range	0.11	0	0
latitudinal midpoint	0.09	0	0.09
litter size	0.09	0.27	0

phylogeny-based conservation prioritization is that it may preferentially select relictual species that might be less likely to contribute to future evolutionary radiations. The only study to our knowledge that has explicitly evaluated this question [10] found no strong tendency for primate species with high EDGE scores to have ancestral characteristics, suggesting that such species instead possess both rare and derived characters. While such an analysis was beyond the scope of this study, it would be an obvious avenue for further research. Furthermore, while we followed Redding *et al.*'s [10] method to calculate biological oddness, this method probably works better for species traits with distributions that have a strong central tendency (e.g. life-history traits; [67]). One could potentially scale trait deviations by branch length to identify species that deviate more or less than expected under a Brownian null model of trait evolution. An alternative avenue for future research would be to restrict such correlations to a 'biologically interesting' subset, perhaps the upper quartile or even just the top 100. This is because the majority of species have extremely low ED and EDGE scores such that they contribute more 'noise' than 'signal' to any correlation.

EDGE-style approaches are increasingly being adopted to diagnose conservation priorities within an evolutionary framework. For example, Agnarsson *et al.* [45] used both EDGE and HEDGE approaches to assess conservation priorities for mammalian carnivore species. Although these authors recognized that priority rankings were strongly dependent on the particular chosen parameters, a consistent series of species were high-ranking in most analyses. Similar analyses have also used the EDGE approach to prioritize conservation of evolutionarily significant units within species [68]. Other recent studies, while not formally quantifying ED, have also adopted EDGE's conceptual framework to make conservation recommendations on the basis of relative ages of different clades (e.g. [69]) or TD [70,71], or at least to acknowledge ED as a key component of conservation prioritization (e.g. [72]). Other approaches have recently incorporated EDGE into other contexts, e.g. biogeographic/ecoregion analyses of conservation priorities or evolutionary history [12,44]. However, despite this growing body of literature citing evidence for the importance of evolutionary history and its incorporation into conservation priority-setting [13], species PD levels remain completely uncorrelated with levels of conservation attention [66], and many of the species identified as conservation priorities in these recent EDGE-style approaches have been acknowledged to be receiving little or no conservation attention [45]. Indeed, 64 per cent of the top 100 ranked species in our new EDGE mammal list (table 1) are currently receiving little or no conservation attention.

We have conducted our EDGE priority-setting approach on mammals because they are one of the best-studied groups, with near-complete data now available on both phylogenetic relationships and extinction risk for component species. Unfortunately, most higher = order taxonomic groups still lack sufficient phylogenetic data to permit calculation of ED scores, and also lack any formal IUCN Red List assessment (although see [73,74]). Given that large numbers of evolutionarily distinct species are inadequately served by existing conservation strategies, the priority must be to fast-track the necessary Red Listing [75] and phylogeny-building exercises to ensure that an imminent loss of large quantities of our global evolutionary heritage does not occur.

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