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Investing in Evolutionary History**: implementing a phylogenetic approach for mammal conservation**

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Abstract

Under the impact of human activity, global extinction rates have risen a thousand times higher than fossil record rates. 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 has been used to prioritize species according to their degree of unique evolutionary history (Evolutionary Distinctiveness) weighted by conservation urgency (Global Endangerment - EDGE). 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.

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 maximising Phylogenetic Diversity (PD) should be one of the main goals of priority-setting for conservation (3-6). This is due 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: 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).

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.

Figure 1 approximately here

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.

Review of PD-based approaches for species conservation
The concept of utilizing evolutionary history in conservation prioritization has been around for at least two decades (4-5). These first approaches developed metrics concerning Taxonomic Distinctiveness (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 Taxonomic Distinctiveness or 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, ESS-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 descendant 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 evolutionary distinctiveness 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 (GE) based on the quantitative and objective framework provided by the 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 descendant 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 Evolutionary Distinctiveness score (HED) is used to generate a HEDGE score. There has been criticism of EDGE and EL approaches due 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 non-linear (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 ref 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 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 Data Deficient 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.

Methods
EDGE scores
We collated mammal conservation status data from the IUCN Red List (48-49), and included genuine change in status from (50). We used a composite 'supertree' phylogeny (51-53) to calculate ED scores for mammals, following the procedure reported in (28). Briefly, we divided the total phylogenetic diversity of each clade amongst 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 3rd edition of 'Mammal Species of World' (MSW3; 54), whereas the original list of Isaac et al.(28) used the 2nd 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, 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 alternate 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 >2 descendents) 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 (>20) of descendents, 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 (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 1,000 resolved trees using BEAST [v1.6.1] (60) to analyze 5 independent runs of ~2,000,000 iterations and a sampling interval of 1,000. We assessed the burnin, convergence and mixing manually for each run using Tracer v1.5 (61) and produced the final distribution by combining all independent runs and subsampling to every 9,000 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 we suspected might be EDGE priorities. 'Surrogate' ED scores for these species were crudely estimated as the likely time of divergence, based either on molecular or geological data (see supplementary materials table S1, refs S2 and S4). Finally, IUCN categories were matched for 5123 species, of which 692 are Data Deficient, 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 due to reassessment of the conservation status of the species (i.e. updated Red List status, which may or may not be due 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.

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, geographic and morphological species traits: body mass (grams), gestation length (days), home range size (km^2), litter size, geographic range size (km^2), 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 (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. Due 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 ? = 0.05 (63-64). All analyses were conducted in R version 2.12.1 (65).

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; Figure 2) and changes in Red List status (Figure 3). The taxonomy of the majority of species remains unchanged (~70%; Table 2). Of the changes to species taxonomic status, approximately 20% have been split, 5% are new species descriptions, and about 2.5% have been either lumped or represent non-nested taxonomic changes. The relatively minor impact of these taxonomic 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).

Figure 2 approximately here

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 ranks). 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 8 of the 2,503 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 (CR, EN, VU) and non-threatened categories (NT, LC), 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.

Figures 3 & 4 approximately here

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 supplementary materials Table S2 and S3). The greatest support across orders was for geographic range (eight orders showed significant correlation), followed by bodymass and gestation length (Table 4). Tests on the component parts of species EDGE score revealed that the relationship with geographic range is driven by the GE component (i.e. correlates of extinction risk), whereas morphological and reproductive traits (bodymass, gestation length and litter size) showed strong correlation with ED score (Tables S2 and S3).

Discussion
It is important that approaches to conservation priority-setting are able to satisfy two conditions: they must capture biodiversity, a complex and multifaceted 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.

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 due to non-genuine impacts on status, i.e. changing taxonomy, new information, and reassessment of the quality of existing data used for assessments in 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 Data Deficient 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, ref 38) but this has yet to be implemented.

We also find evidence across numerous mammalian orders to support findings previously identified in smaller-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 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; ref 66). 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 chose 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 (67). Other recent studies, while not formally quantifying evolutionary distinctiveness, have also adopted EDGE's conceptual framework to make conservation recommendations on the basis of relative ages of different clades (e.g. 68) or taxonomic distinctiveness (69-70), or at least to acknowledge evolutionary distinctiveness as a key component of conservation prioritization (e.g. 71). 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 (72), 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% 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.

Electronic supplementary materials

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Tables

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 (72).

Rank	Species	Order	Family	Status	ED	EDGE
1=	Zaglossus attenboroughi	Monotremata	Tachyglossidae	CR	55.21737845	6.801814656
1=	Zaglossus bartoni	Monotremata	Tachyglossidae	CR	55.21737845	6.801814656
1=	Zaglossus bruijnii	Monotremata	Tachyglossidae	CR	55.21737845	6.801814656
4	Mystacina robusta	Chiroptera	Mystacinidae	CR	54.10322232	6.781796918
5	Lipotes vexillifer	Cetacea	Lipotidae	CR	38.67180179	6.453229375
6	**Burramys parvus**	Diprotodontia	Burramyidae	CR	32.75582928	6.291741844
7=	Solenodon cubanus	Soricomorpha	Solenodontidae	EN	61.69215212	6.217677816
7=	Solenodon **paradoxus**	Soricomorpha	Solenodontidae	EN	61.69215212	6.217677816
9	Dicerorhinus sumatrensis	Perissodactyla	Rhinocerotidae	CR	29.44751148	6.188592988
10	Bunolagus monticularis	Lagomorpha	Leporidae	CR	27.88392179	6.135873823
11	Diceros bicornis	Perissodactyla	Rhinocerotidae	CR	26.63195412	6.091561583
12	Lasiorhinus krefftii	Diprotodontia	Vombatidae	CR	25.98457399	6.067854091
13	**Camelus** ferus	Artiodactyla	Camelidae	CR	25.29566761	6.041992918
14	Rhinoceros sondaicus	Perissodactyla	Rhinocerotidae	CR	24.64177112	6.016811428
15	Laonastes aenigmamus	Rodentia	Diatomyidae	EN	44.3	5.892748574
16	Bradypus pygmaeus	Pilosa	Bradypodidae	CR	20.88097152	5.858206101
17	Elephas maximus	Proboscidea	Elephantidae	EN	39.76418423	5.7872454
18	Octodon pacificus	Rodentia	Octodontidae	CR	18.43970169	5.739906176
19	Ailuropoda melanoleuca	Carnivora	Ursidae	EN	36.77014331	5.710960473
20	Tapirus indicus	Perissodactyla	Tapiridae	EN	36.03587836	5.69132867
21	Abrocoma boliviensis	Rodentia	Abrocomidae	CR	17.4621309	5.688310378
22=	Monachus monachus	Carnivora	Phocidae	CR	16.79398976	5.651449469
22=	Monachus schauinslandi	Carnivora	Phocidae	CR	16.79398976	5.651449469
24	Ailurops melanotis	Diprotodontia	Phalangeridae	CR	16.6544188	5.64357483

					5	4
25	Natalus jamaicensis	Chiroptera	Natalidae	CR	16.5944673 2	5.64017321 8
26	Coleura seychellensis	Chiroptera	Emballonurida *e*	CR	16.5694351	5.63874947 3
27	Natalus primus	Chiroptera	Natalidae	CR	16.4007380 6	5.62910134 5
28	Choeropsis liberiensis	Artiodactyla	Hippopotamida *e*	EN	33.1790621 **1**	5.61105477 9
29	Indri indri	Primates	Indridae	EN	33.0088633 9	5.60606272
30	Galagoides rondoensis	Primates	Galagidae	CR	15.6125213 3	5.58274543
31	Myrmecobius fasciatus	Dasyuromorphia	Myrmecobiidae	EN	32.0385503	5.57711661 2
32	Pharotis imogene	Chiroptera	Vespertilioni dae	CR	15.302246	5.56389161 2
33	Aproteles bulmerae	Chiroptera	Pteropodidae	CR	15.2961138 3	5.56351538 6
34	Phalanger matanim	Diprotodontia	Phalangeridae	CR	15.2657307 4	5.56164920 8
35	Potorous gilbertii	Diprotodontia	Potoroidae	CR	15.1447635 9	5.55418448 3
36	Marmosops handleyi	Didelphimorphia	Didelphidae	CR	14.8931621 5	5.53847768 6
37	Varecia variegata	Primates	Lemuridae	CR	14.7187534 8	5.52744321 **1**
38	Amorphochilus schnablii	Chiroptera	Furipteridae	EN	30.2569337	5.52168277 2
39	Tapirus bairdii	Perissodactyla	Tapiridae	EN	30.0056577 3	5.51361123 7
40	Romerolagus diazi	Lagomorpha	Leporidae	EN	29.8522433 4	5.50865100 7
41	Prolemur simus	Primates	Lemuridae	CR	14.3982973	5.50684566 **1**
42	Pentalagus furnessi	Lagomorpha	Leporidae	EN	29.4589476	5.49582133 8
43	Beatragus hunteri	Artiodactyla	Bovidae	CR	14.1258473 4	5.48899374 7
44	Pseudoryx nghetinhensis	Artiodactyla	Bovidae	CR	13.68	5.45907474 5
45	Pongo abelii	Primates	Hominidae	CR	13.6628471 2	5.45790561
46	Rhynchocyon chrysopygus	Macroscelidea	Macroscelidid ae	EN	28.1270170 4	5.45110770 6
47	Hapalemur alaotrensis	Primates	Lemuridae	CR	13.4900197 5	5.44604884 2
48	Tokudaia muenninki	Rodentia	Muridae	CR	13.4853168 9	5.44572423
49	Gymnobelideus leadbeateri	Diprotodontia	Petauridae	EN	27.6223126 6	5.43362811 8
50	Dugong dugon	Sirenia	Dugongidae	**VU**	56.0771148 6	5.43069760 7
51	Neohylomys hainanensis	Erinaceomorpha	Erinaceidae	EN	27.3633418 2	5.42453907 2
52	Podogymnura	Erinaceomorpha	Erinaceidae	EN	27.2272720	5.41973014

	aureospinula				4	6
53=	Chinchilla chinchilla	Rodentia	Chinchillidae	CR	12.9791909 9	5.41015858 8
53=	Chinchilla lanigera	Rodentia	Chinchillidae	CR	12.9791909 9	5.41015858 8
55	Spilocuscus rufoniger	Diprotodontia	Phalangeridae	CR	12.7830528 6	5.39602850 6
56	Mystacina tuberculata	Chiroptera	Mystacinidae	VU	54.1032223 2	5.39550255 7
57	Sminthopsis aitkeni	Dasyuromorphia	Dasyuridae	CR	12.6916508 4	5.38937494 2
58	Lepilemur septentrionalis	Primates	Lepilemuridae	CR	12.6566784 9	5.38681739 **1**
59	Micropotamogale lamottei	Afrosoricida	Tenrecidae	EN	26.2043168 2	5.38281720 9
60	Platanista gangetica	Cetacea	Platanistidae	EN	26.1912258 2	5.38233588 3
61	Bradypus torquatus	Pilosa	Bradypodidae	EN	25.3386649 7	5.35047955 2
62	Hipposideros lamottei	Chiroptera	Hipposiderida *e*	CR	11.8752596	5.32789633 2
63	Phocoena sinus	Cetacea	Phocoenidae	CR	11.8267157 5	5.32411888 6
64	Oreonax flavicauda	Primates	Atelidae	CR	11.6137951 3	5.30737978 9
65	Propithecus perrieri	Primates	Indridae	CR	11.5914411 5	5.30560603 2
66	Loris tardigradus	Primates	Lorisidae	EN	23.6740826 8	5.28519495
67	Cavia intermedia	Rodentia	Caviidae	CR	11.2545912 4	5.27848938 4
68	Gorilla gorilla	Primates	Hominidae	CR	11.2191434 4	5.27559257 9
69	Trichechus inunguis	Sirenia	Trichechidae	VU	47.2479680 6	5.26264807 5
70	Nilopegamys plumbeus	Rodentia	Muridae	CR	11.0253090 3	5.25960223 7
71	Catagonus wagneri	Artiodactyla	Tayassuidae	EN	22.6655559 7	5.24346219 8
72	Neamblysomus gunningi	Afrosoricida	Chrysochlorid ae	EN	22.3538677 9	5.23020415 6
73	Balaenoptera physalus	Cetacea	Balaenopterid ae	EN	22.2468741 1	5.22561221 8
74	Tapirus pinchaque	Perissodactyla	Tapiridae	EN	22.1451727 5	5.22122778
75	Balaenoptera musculus	Cetacea	Balaenopterid ae	EN	22.0606205 2	5.21756796 5
76	Dendromus kahuziensis	Rodentia	Nesomyidae	CR	10.4727276 7	5.21256143 4
77	Chrysospalax trevelyani	Afrosoricida	Chrysochlorid ae	EN	21.9086252 7	5.21095503 **1**
78	Leporillus apicalis	Rodentia	Muridae	CR	10.0214324 **1**	5.1724305
79	Hypogeomys antimena	Rodentia	Nesomyidae	EN	20.8661309 2	5.16438044 8
80	Tylomys bullaris	Rodentia	Cricetidae	CR	9.89451726	5.16084838

					3	2
81	Callicebus **barbarabrownae**	Primates	Pitheciidae	CR	9.869378529	5.158538249
82=	Sorex sclateri	Soricomorpha	Soricidae	CR	9.853968549	5.1571195
82=	Sorex stizodon	Soricomorpha	Soricidae	CR	9.853968549	5.1571195
84	Tylomys tumbalensis	Rodentia	Cricetidae	CR	9.789790788	5.151189112
85	Bettongia penicillata	Diprotodontia	Potoroidae	CR	9.741552342	5.146708339
86	Cryptotis nelsoni	Soricomorpha	Soricidae	CR	9.730051884	5.145637114
87	Mesocapromys sanfelipensis	Rodentia	Capromyidae	CR	9.715985838	5.144325352
88	Mesocapromys **nanus**	Rodentia	Capromyidae	CR	9.707420414	5.143525724
89	Manis pentadactyla	Pholidota	Manidae	EN	20.35572093	5.140761205
90	Manis javanica	Pholidota	Manidae	EN	20.30695965	5.138475305
91	Brachyteles hypoxanthus	Primates	Atelidae	CR	9.65114119	5.138255763
92=	Trichechus manatus	Sirenia	Trichechidae	**VU**	41.57146606	5.137478579
92=	Trichechus senegalensis	Sirenia	Trichechidae	**VU**	41.57146606	5.137478579
94	Potorous longipes	Diprotodontia	Potoroidae	EN	20.22170929	5.134466223
95	Cremnomys elvira	Rodentia	Muridae	CR	9.532109427	5.127017354
96	Millardia kondana	Rodentia	Muridae	CR	9.299543578	5.104688304
97	Crateromys australis	Rodentia	Muridae	CR	9.257893072	5.100636187
98	Viverra civettina	Carnivora	Viverridae	CR	9.189373539	5.09393409
99	Habromys chinanteco	Rodentia	Cricetidae	CR	9.169551079	5.091986799
100	Amblysomus marleyi	Afrosoricida	Chrysochlorid**ae**	EN	19.23849603	5.087028077

Table 2. Change in taxonomic status of mammal species 1993-2005.

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	

(Numbers refer to species in the new (3rd) edition of Mammal Species of the World (55) and expressed relative to species status in the 2nd edition (54)).

Table 3. Pearson correlations of EDGE scores against distance of species-specific traits from the median value for each trait for **II** mammalian orders. *?* denotes correlation coefficient, ** p<O.OS, **p<O.Ol, ***p<O.OOI,* all adjusted as per (64).

	IAfrosoricida		!Artiodactyla		**Carnivora**	IChiroptera
!Trait	ldf		I?		ldf	I?
	df	1?	df			
lbody mass	la.27	1a.ss	la.a9			
Geographic range	*a.*73	*a.*a9	*a.*73			
!gestation length	1a.l8	la.4a	1a.1a			
!home range	1a.11	Ia	Ia			
!latitudinal	la.a9	Ia	la.a9			
oi						
llitter size	la.a9	la.27	Ia			

Figures

FionrP 1

Figure !.Cumulative total number of publications containing the search term 'supertree*' from the lSI Web of Knowledge database.
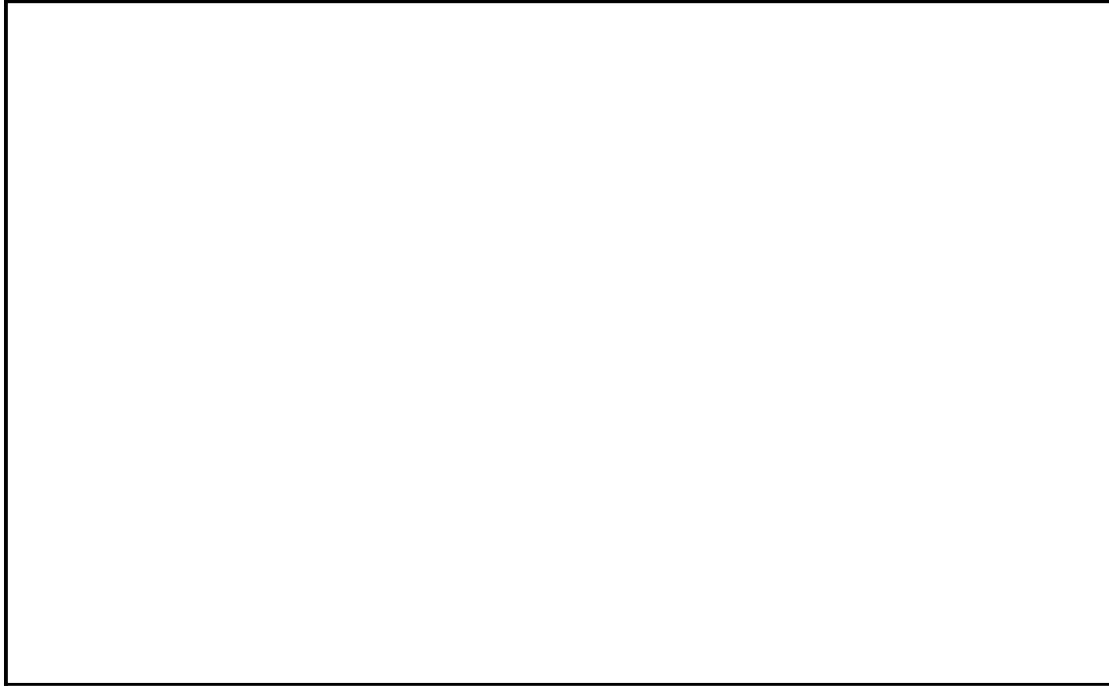
Fimm- ?.

Figure 2.Comparison of ED values between EDGE lists. Old ED status is the value for each species as reported in (28); new ED status is the value for each species calculated in this study.
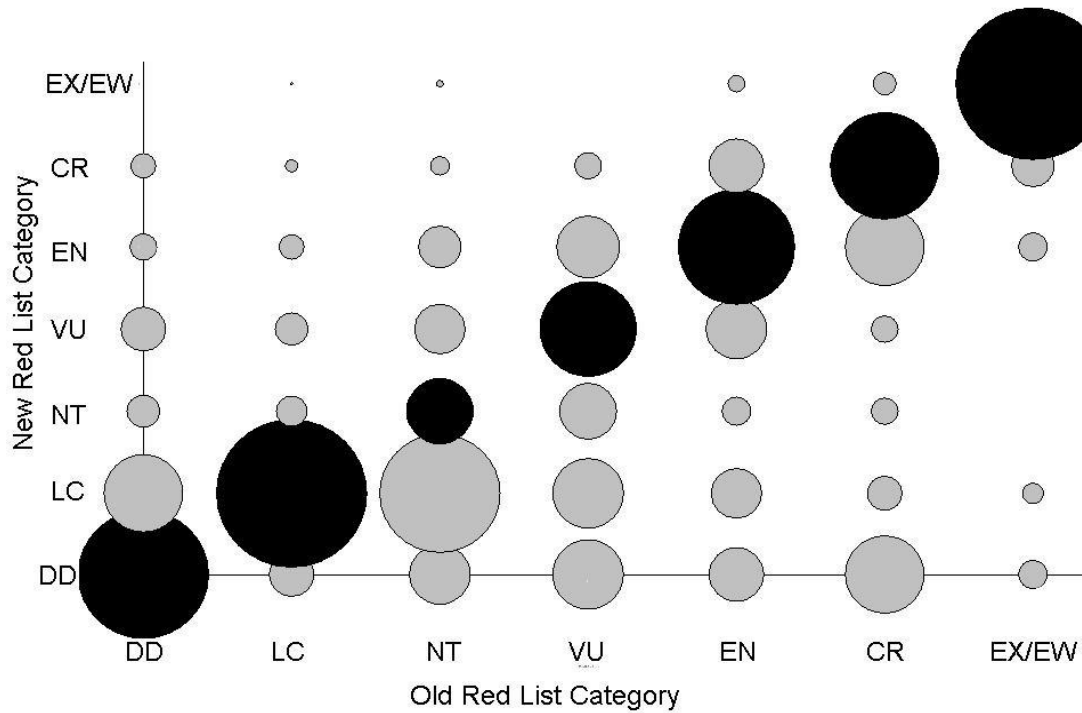
Figure 3.

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 (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.
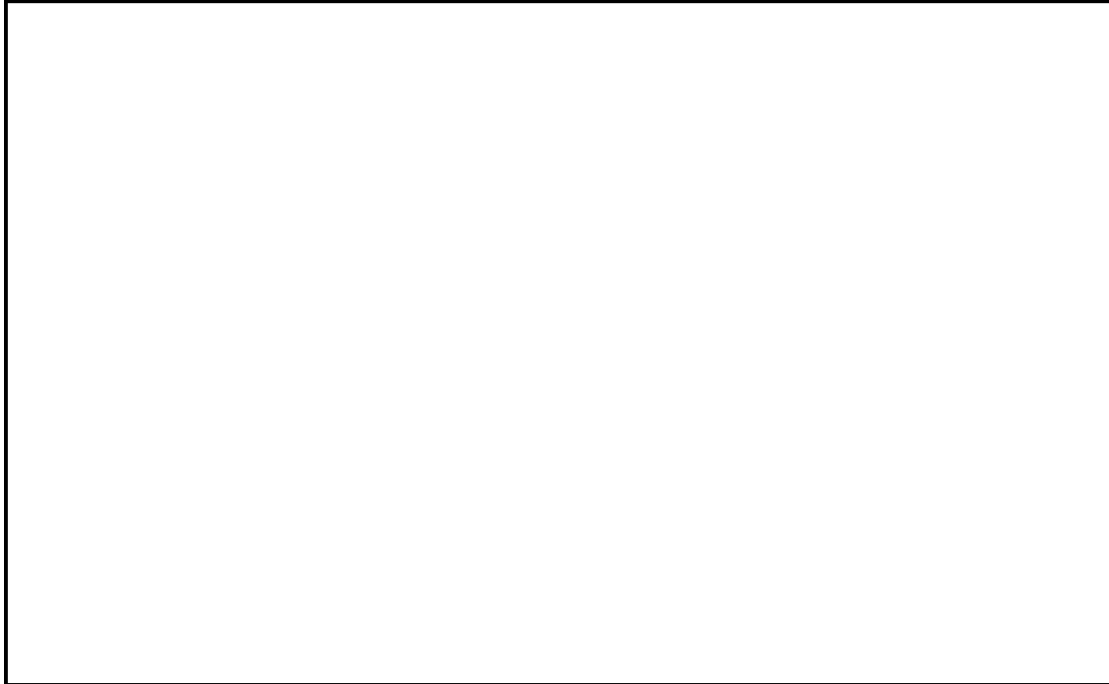
Figure 4.Comparison of EDGE ranks between EDGE lists. Rank EDGE old is the value for each species as reported in (28); rank EDGE new is the value for each species calculated in this study.