

Priorities for conserving the world's terrestrial mammals based on over-the-horizon extinction risk

Running title: Future extinction risk in mammals

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Summary

Three major axes of global change put the world's mammal biodiversity at risk: climate change, human population growth and land-use change¹⁻¹². In some parts of the world the full effects of these threats on species will only be felt in decades to come, yet conservation emphasizes species currently threatened with extinction, by threats that have already occurred. There have been calls for conservation to become more proactive by anticipating and protecting species that may not yet be threatened, but have a high chance of becoming threatened in the future^{3,6,8,10,12-14}. We refer to this as "over-the-horizon" extinction risk, and we identify such species among the world's nonmarine mammals by considering not only the severity of increase in threats faced by each species, but also the way each species' biology confers sensitivity or robustness to threats. We define four future risk factors based on species' biology and projected exposure to severe change in climate, human population and land use. We regard species with two or more of these risk factors as especially vulnerable to future extinction risk^{10,15-19}. Our models predict that by 2100 up to 1057 (20%) of nonmarine mammal species will have combinations of two or more future risk factors. These species will be particularly concentrated in two future risk hotspots in Sub-Saharan Africa and southern/eastern Australia. Proactively targeting species with over-the-horizon extinction risk could help to future-proof global conservation planning, and prevent a new wave of mammal species becoming threatened with extinction by the end of this century.

Keywords:

Biodiversity; Climate Change; Extinction; IUCN Red List; Land-use change; Protected Areas

Results

Number and distribution of species with multiple future risk factors

Forecasting future extinction risk is not simply a matter of projecting threatening processes to future times. Species are not equally sensitive to any given threat, because extinction risk is determined by the way species' life-history and ecological traits mediate their responses to external pressures^{15,16,18,20,21}. To avoid underestimating extinction risk for some species and overestimating risk for others, it is therefore critical to incorporate biology into assessments of species future risk. We use phylogenetically and spatially explicit generalized least-squares (GLS) models to show that 14-32% of the variance in species current threat status (within each of six biogeographic realms) is explained by mean adult body mass and geographic range size alone (Data S1). From the fitted values of the GLS models we derive "latent" extinction risk: the difference between current and modelled threat status¹³. Among currently unthreatened species, those with larger body size, smaller range size, or both, tend to have high latent risk, which may indicate greater potential for threat status to increase if there is an increase in their exposure to threatening processes.

To quantify over-the-horizon extinction risk for mammal species, we define, *a priori*, four future risk factors. One is based on high latent risk (which is a single, invariable value for each species), and the other three are based on the severity of projected change in climate, human population density, and land use, to the year 2100 (which varies among projection scenarios). For each mammal species we modelled the area of climatic suitability (hereafter climatic range) at 20-year intervals to 2100 by fitting 16 species distribution models, bracketing a wide range of assumptions about global circulation models, emissions scenarios and species' ability to disperse to track shifting climates. Additive or synergistic effects of multiple threats may confer elevated risk of extinction^{15-17,19}: for example, a species that loses much of its distribution under climate change will be at even greater risk if its remaining distribution is in an area of severe change in land use or human population. We therefore define high future extinction risk as species with combinations of two or more risk factors: either predicted exposure to two or more external threats, or exposure to at least one external threat together with high latent extinction risk.

Globally, the number of terrestrial mammal species that our models predict will have at least one of the four future risk factors by 2100 ranges from 2099 (40%) under a middle of the road emissions scenario (SSP2-4.5) with broad species dispersal, to 3040 (58%) under a fossil-fuelled development scenario (SSP5-8.5) with no dispersal. Fewer species are predicted to have combinations of two or

more future risk factors (496-1057; 9.5-20%), three or more risk factors (93-299; 1.8-5.7%), or all four risk factors (19-60; 0.4-1.1%), by 2100 (Data S2Q). This suggests that the overlap between sets of species with different future risk factors is comparatively low.

There is substantial geographic variation in the number of species per 100x100km grid cell predicted to have combinations of two or more future risk factors. Most strikingly, the numbers are higher in the Afrotropic realm than elsewhere in the world (Figure 1A). The proportion of species per grid cell with two or more future risk factors is highest in southern and eastern Australia (Figure 1B). The basis of these geographic patterns is seen in the pairwise combinations of risk factors among species. For example, of the 619 Afrotropical species with any of the future risk factors under the scenario depicted in Figure 1, 189 (31%) are predicted to be exposed to both rapid climatic range contraction and rapid increases in land-use modification. The equivalent figure for Australasia is 16%, and <10% in all other realms (Figure 1A). With one exception (the combination of high latent risk + rapid climatic range contraction in Australasia), the percentages for all other pairwise combinations of future risk factors are also higher for Afrotropical species than for species in other realms (Figure 1A).

When we examine absolute numbers and proportions of species with each future risk factor separately (Methods S1), we see geographic patterns that reflect the different intensities of threat types in different parts of the world ^{7,10,12,14,22}. For example, in the high Arctic a high proportion of mammal species are predicted to suffer severe climatic range collapse, but to be little affected by rapid increases in human population density or land-use modification. In contrast, in sub-Saharan Africa each one of the four risk factors affects a large number of species. In southern and eastern Australia, high proportions of species have high latent risk, are exposed to severe climatic range contraction and to severe increase in land-use modification, but few species are exposed to severe increase in human population density (Methods S1). These patterns of overlap in risk factors lead to strong geographic heterogeneity in the numbers and proportions of species exposed to at least one, two, three, and four risk factors (Figure 1, Methods S2). Sub-Saharan Africa emerges as the primary region in which species with up to four future risk factors are concentrated, while southern and eastern Australia shows a concentration of species with up to three future risk factors. The geographic patterns described above are robust to modelling decisions, with most combinations of Global Circulation Model, SSP, and species dispersal model revealing sub-Saharan Africa and southern/eastern Australia as global hotspots of over-the-horizon extinction risk (Methods S1, S2).

Shifting species distributions and future risk factors

By modelling the dynamic spatial interactions between projected climate-driven species range shifts, human population growth and land-use change, we identify species expected to become exposed to threats to a greater degree than would be predicted from changes in any one of these threats alone. Climate change is expected to cause species distributions to contract away from some areas, to encroach onto new areas, or to remain static. The relative amounts of projected change in human population density and land-use modification within areas of contraction, stasis, and encroachment, determines the degree to which a species will be exposed to these two threats by the end of this century. Figure 2 shows projected human population density and land-use modification in species' areas of encroachment (areas projected to be added to a species' distribution) relative to areas of contraction (areas projected to be lost from a species' current distribution). Species in the lower right corner of each of these plots will expand into areas of high human population density or highly modified land use, and contract away from areas of lower human population density or less highly modified land use. The Afrotropic realm has the highest proportion of species expected to expand into areas of severe increase in both threats; in Figure 2, this is indicated by the relative number of points below the diagonal lines and the relative height of the red bars. In contrast, the pattern is generally the opposite in other parts of the world, with most species predicted to show more contraction away from areas of higher human population growth and land-use change than encroachment onto new areas with greater future risk (ie the green bars are higher than the red ones). This shows that Africa is a hotspot of over-the-horizon extinction risk not simply because of the independent effects of projected climatic range contraction, human population growth, and land-use change, but by the expected spatial interactions among these three risk factors over the coming decades.

Protected area representation and future risk factors

Protected areas are one of the most effective and widely used tools for conservation and a key means of achieving global biodiversity goals²³⁻²⁵. Planning for the strategic expansion of the protected area network often involves setting *a priori* targets for the adequate representation of species within protected areas. Representation adequacy targets typically specify a level of representation proportional to range size, by seeking complete representation (100%) for narrow-

ranged endemic species and a minimum level of representation (e.g. 10%) for species with broad distributions^{24,25}. We examine the degree to which mammal species we identify as having high future risk are protected within reserves, comparing targets based on range size only with targets that are multiplied by the number of risk factors for each species.

When targets are determined by simple scaling with current range sizes, current representation meets or exceeds targets for 49-65% of the species with two or more future risk factors. However, such targets assume that extinction risk is determined primarily by range size and do not account for the potential for future declines based on the four future risk factors. Under targets that incorporate both range size and future risk, we find that the percentage of species meeting or exceeding these targets falls to 33-52%. When future risk is incorporated into representation targets, the proportion of species failing to meet targets, and in particular, the proportion of species falling substantially short of their target, varies among realms. In the Afrotropic realm, comparatively few species have a target shortfall of more than 50%, but much higher proportions of species in the Nearctic, Australasian and Indo-Malay realms have shortfalls of more than 50% (Figure 3).

Discussion

Species listed as Threatened under the IUCN Red List²⁶ are prioritized for conservation action because this is widely understood to be an effective short-term strategy for mitigating biodiversity loss. However, there are two key reasons why an emphasis on currently threatened species may not be an optimal longer-term strategy. First, programs to recover populations of species on the brink of extinction and restore them to viability are likely to be less successful or cost-effective than preventing populations from declining in the first place: i.e., prevention is better than cure²⁷⁻³¹. Second, the changing intensity and extent of threatening processes through time means that many of the threatened species of the future may be ones that are not currently threatened, and not considered a high priority for conservation. A more proactive approach to conservation planning requires a means of forecasting changing threats, and identifying emerging threatened species, over the coming decades^{3,6,8,10,12-14}.

A key finding of our study is the striking geographic pattern of species richness of mammals exposed to multiple future threats, in particular the appearance of sub-Saharan Africa and southern/eastern Australia as hotspots of over-the-horizon extinction risk. Tropical regions, including tropical South

America, southern Asia and sub-Saharan Africa have previously been identified as regions of potential threat to large mammals from future human population growth and economic development¹⁰. However, what sets sub-Saharan Africa apart from other tropical regions is the expected rate of economic growth yet to come: in the next four decades sub-Saharan Africa is forecast to account for over half of the global increase in human population (3.2 billion people), and over half of the global expansion of area under cropland (430 million ha)¹⁰. Much of this growth will occur in Africa's savanna, tropical grassland and montane grassland biomes that harbour some of the world's most diverse large-mammal assemblages. Furthermore, this region will be one of the world's most severely impacted by climate change: across central and southern Africa, median projected temperature increase from global warming by 2100 is around 1.5 times the global average³². It is this congruence of expected future threats – climate change, human population growth, and land-use change – together with a high diversity of large-bodied mammal species that are inherently more sensitive to many threats¹⁵, that causes sub-Saharan Africa to emerge as a major global hotspot of future extinction risk in our models.

Of the mammal species without any future risk factors, 49-60% (across the 16 projection scenarios) are currently listed as not threatened, but these proportions increase progressively for species with more future risk factors (Figure 4). This may be cause for concern because the prevailing conservation paradigm strongly (and understandably) prioritizes threatened over non-threatened species for conservation action³³. Conservation interventions are demonstrably effective at preventing species declines^{34,35}, but species not listed as threatened may be overlooked for conservation action until it is too late^{3,13}. In the past many species have moved rapidly from Least Concern status to Threatened; indeed, the history of conservation is replete with examples of previously abundant and widespread species that have suffered catastrophic declines³⁶. Our study offers an objective, informed basis for anticipating such cases.

One of the most effective ways to secure biodiversity is through addition of land to the world's protected area network, but it is widely acknowledged that this must be done strategically in order to meet protection targets efficiently²³⁻²⁵. Global protected area coverage has increased rapidly in recent years and this is expected to continue under the Post-2020 Global Biodiversity Framework target to increase coverage from 16% to 30% by 2030³⁷. This offers an opportunity to broaden the goals of the world's protected area system from an emphasis on threatened and endemic species, to include species considered to be at high future risk of extinction. The results of our over-the-horizon models reinforce the central role that Africa is likely to play in a more proactive approach to global planning for mammal conservation.

However, the expansion of protected areas has attracted some controversy. It has been argued that declared protected areas represent an imposition of Western ideas of “wilderness” that do not translate well to many parts of the world and may lead to poor outcomes for Indigenous people³⁸. This controversy has been especially acute in Africa, so although the current reserve system in the Afrotropic realm protects species with over-the-horizon risk better than many other realms (Figure 3), it will be a challenge to expand the network in a way which achieves biodiversity protection outcomes while respecting or enhancing Indigenous rights. Australia’s Indigenous Protected Areas (IPAs) are a good example of a system that seems to achieve this successfully. IPAs are areas under Indigenous ownership that are declared part of Australia’s National Reserve System by voluntary agreement with Traditional Owners and managed by ranger groups formed from local communities. IPAs play a critical role in Australian biodiversity conservation, representing around half of the area of the National Reserve System. This scheme is perhaps a good model for the integration of Indigenous and other forms of community-led conservation practice with a broader conservation scheme, that achieves positive environmental and social outcomes at the local level but also contributes to global biodiversity protection goals.

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Author contributions

MC designed the study, carried out the GLM and protected area coverage analyses, prepared the figures and wrote the Introduction, Results, Discussion and part of the Methods; AS compiled datasets, designed and carried out the SDM and future projections analyses, and wrote part of the Methods; RD designed and carried out the encroachment & contraction analyses; all authors helped to revise the manuscript.

Declaration of interests

The authors declare no competing interests.

Figure 1. Concentrations of terrestrial mammal species with multiple future risk factors. (A) number and (B) proportion of terrestrial mammal species per grid cell predicted to have two or more future risk factors by 2100, under a SSP5-8.5 emissions scenario, MIROC6 global circulation model and body-sized linked dispersal. (C) Realm boundaries. NA: Nearctic; NT: Neotropic; PA: Palearctic; AF: Afrotropic; IM: Indo-Malay; AU: Australasia. The 3x3 grids for each realm show (for those species with one or more future risk factors) the percentage of the species with each pairwise combination of risk factors. Colour scale of percentage classes at bottom left. LR: latent risk; CR: climatic range; HPD: human population density; LM: land-use modification. For each realm one example of a species with multiple future risk factors is pictured, with a line indicating the centroid of its current distribution. From top centre, these species, with their risk factors in brackets, are: Granada Hare *Lepus granatensis* (LR, CR, LM); Javan Warty Pig *Sus verrucosus* (CR, HPD, LM); Red-legged Pademelon *Thylagale stigmatica* (LR, CR, HPD); Grey-cheeked Mangabey *Lophocebus albigena* (LR, CR, HPD, LM); Chacoan Titi Monkey *Callicebus pallascens* (LR, LU); Townsend's Chipmunk *Neotamias townsendii* (LR, CR, HPD).

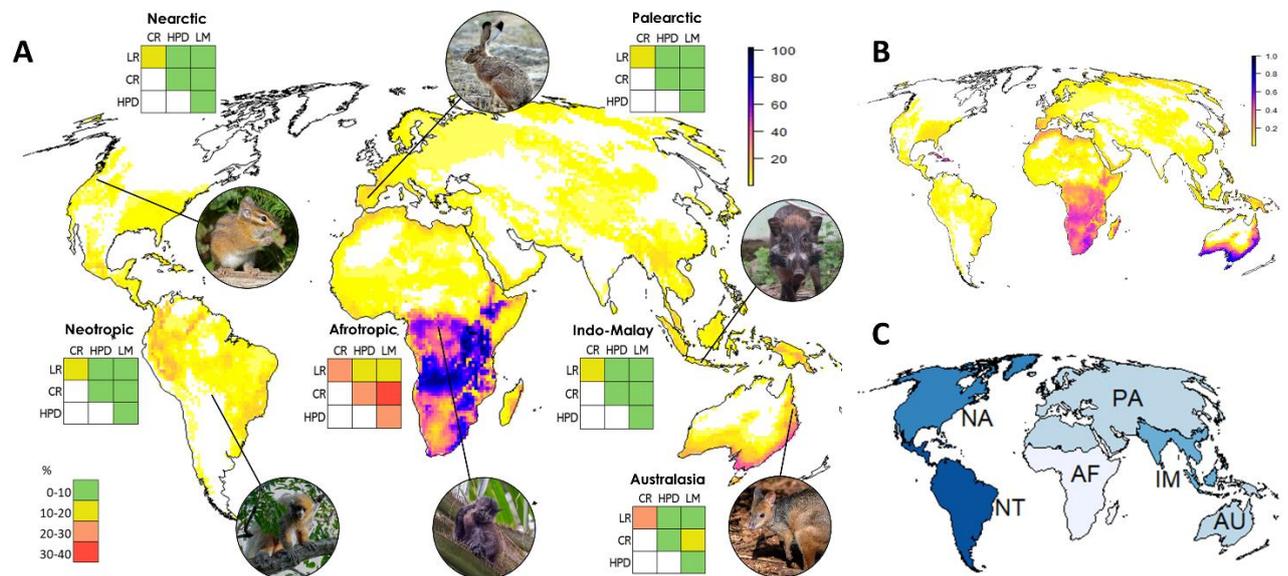


Figure 2. Human population growth and land-use change in areas of encroachment and contraction of species ranges.

Plots show the percentage of species projected areas of range encroachment (x-axis) and contraction (y-axis) in which human population density exceeds 100 people/km² (left column), and in which modified land use exceeds 50% (right column). Species below the diagonal line on each plot will encroach on areas of more rapid increase in these two threats; those above the line will contract away from areas of more rapid increase. The coloured bars beside each plot summarize the information in the plots, showing the relative number of species below the line (red), above the line (green), and on the line (yellow). Projections are for the year 2100 under a SSP5-8.5 emissions scenario, MIROC6 global circulation model and body-sized linked dispersal.

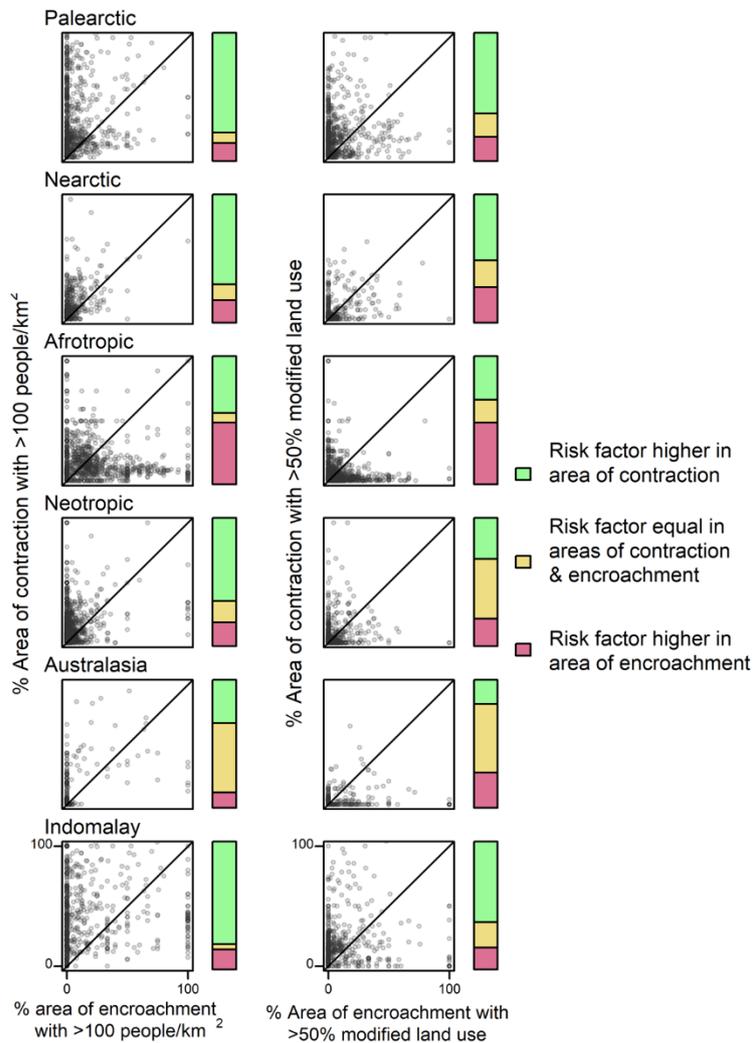


Figure 3. Adequacy of current representation within protected areas for species with two or more future risk factors.

The x-axis shows the proportion of a species' current distribution represented within protected areas minus the representation adequacy target for the species. Negative values (yellow-red) indicate a shortfall, positive values (greens) indicate the target is met or exceeded. Targets are defined based on current range size only (left column), and on range size together with the number of future risk factors (right column). Future risk is determined for the year 2100 under a SSP5-8.5 emissions scenario, MIROC6 global circulation model and body-sized linked dispersal.

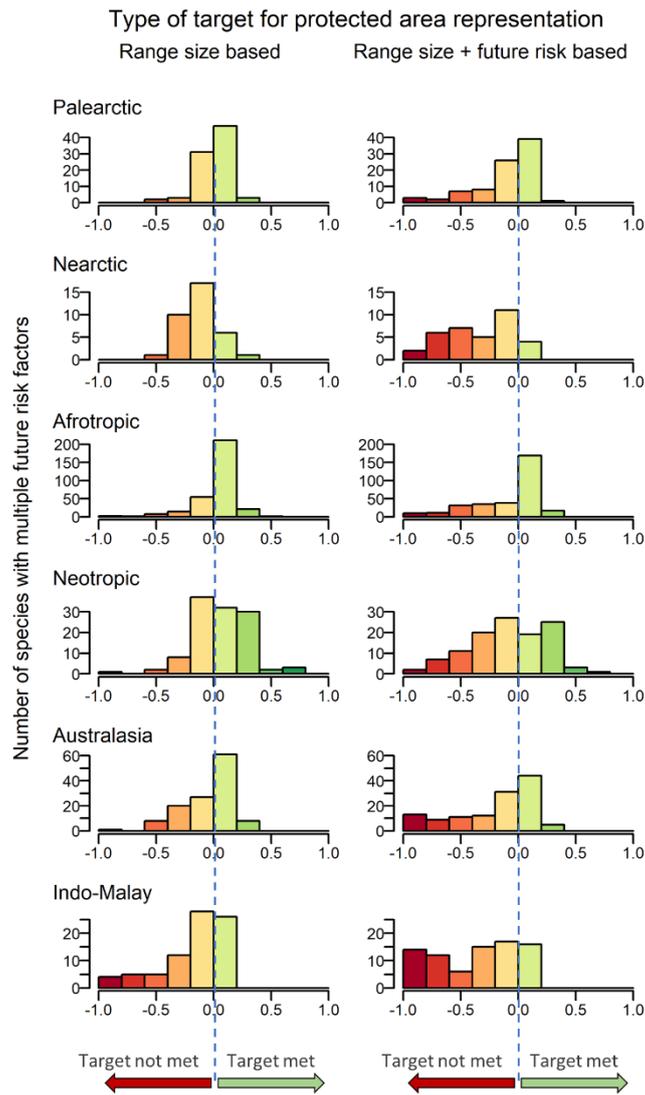
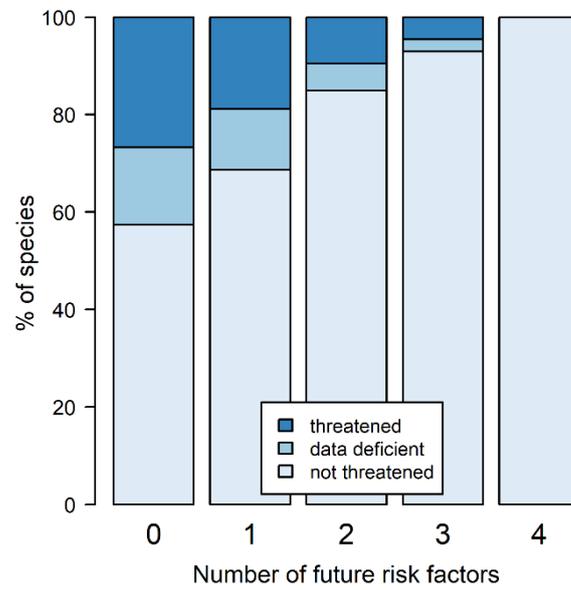


Figure 4. Over-representation of currently unthreatened species with multiple future risk factors. Bars show the proportions of species with 0-4 coincident future risk factors that are currently threatened, unthreatened or data deficient.



STAR Methods

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Marcel Cardillo (marcel.cardillo@anu.edu.au)

Materials availability

This study did not generate new unique materials.

Data and code availability

- All original data used in this study are publicly available from online repositories. Sources for all datasets are listed in the Key Resources Table.
- All original code will be deposited at Zenodo and be publicly available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

All data used in this study were obtained from publicly available online sources. Original data sources are listed in the Key Resources Table. Processed and derived data used in analyses can be reproduced using the custom R code provided, and are available in Data S2.

METHOD DETAILS

Data compilation and processing

Mammal phylogeny, spatial distributions, traits, and threat status

We collated spatial, phylogenetic, and trait data for terrestrial mammals from a variety of sources. Trait data were obtained from ³⁹ for six traits (body mass, litter size, diel activity, diet, volancy, and habitat breadth) for 5,232 mammal species. The Cooke *et al.* database [39] is itself a compilation of data from ⁴⁰, ⁴¹ and ⁴². Phylogenetic data were a set of 100 phylogenies selected randomly from a posterior set of 10,000 supertrees of 5,911 mammal species ⁴³. Spatial data on 5323 species distributions (extent of occurrence polygons) were from ²⁶.

We harmonized taxon names in each dataset to the IUCN nomenclature for downstream analyses. Where possible we matched synonyms or misspelled names between datasets to reduce the number of mismatched species. First, we found recognized synonyms from the ITIS database using the *synonyms* functions in the taxize R package⁴⁴. We then examined the remaining mismatched species manually to determine if they were (1) a synonym not found using taxize, (2) a subspecies of a recognized species in another database, or (3) genuinely missing in another database. We found 38 species in the IUCN list were subspecies of a species in the phylogeny, 77 species were a synonym, 11 species were misspelled, and 24 were missing. In the trait database, 103 species from the IUCN list were missing, three were misspelled, 124 were synonyms and 30 were subspecies. In this way we were able to match 5312 species between the IUCN and phylogeny, and 5221 species between the IUCN and trait data, for a total dataset of 5209 species found in all three datasets.

Spatial data: recent and projected climate, human population density and land use

Current climates were represented by recent (1970-2000) climate data from Worldclim⁴⁵ at a resolution of 10 arc minutes (approximately 18.5km at the equator) and resampled to a 100x100km equal-area grid in a Mollweide projection using bilinear interpolation. Future climate projections were obtained at 10 arc minutes from Worldclim across five 20-year intervals (2021-2040, 2041-2060, 2061-2080, 2081-2100). We used projections from the CMIP6 generation of climate models under two global circulation models (GCMs; CNRM-ESM2 and MIROC6) and two Shared Socioeconomic Pathways (SSPs; SSP2 and SSP5). SSPs model alternative trajectories for demographic, climatic, land-use, and economic change based on potential response scenarios for mitigating climate change. SSP2 reflects a 'middle-of-the-road' scenario in which human population growth is moderate and some progress is made towards sustainable development goals. SSP5

assumes continued growth in exploitation of fossil fuels to drive rapid increase in economic and social development. The global warming projections associated with these two scenarios are SSP2-4.5 and SSP5-8.5, respectively. Projections of Human population density (HPD) were from ⁴⁶ and projections of land-use change (LU) at 10-year intervals from 2010-2100, under the same two SSPs, were from ⁴⁷.

Species distribution modelling

Presence points, background selection, and pseudo-absence points

We used Maxent ⁴⁸ to fit species distribution models (SDMs). Maxent is a presence-only method for estimating distribution models by finding the probability distribution that maximizes entropy, given constraints. We use Maxent because it is the most widely-used software for SDM analyses, and hence probably the best understood, but also because the ENMeval package [62] makes the process of finding the best-performing combination of analytical choices and parameter estimates for Maxent models far more robust (see below). All spatial analyses were done using a Mollweide equal-area projection of species ranges and environmental variables at a resolution of 100x100km grid cells, the finest resolution at which IUCN polygons are considered to be accurate representations of species distributions ⁴⁹. We estimated SDMs separately for each mammal species, but given the large number of species and their geographic and ecological diversity, we developed a pipeline that would work for all species with a degree of automated fine-tuning, rather than applying a unique rule-set to each species.

We sampled pseudo-presence points from within species' extant, resident ranges (excluding introductions and vagrancies) as represented by IUCN spatial polygons. We sampled presence points regularly across species polygons by taking all 100x100km grid cells whose centroid fell within the polygonal range of the species. This meant that each species was sampled at the same spatial density.

The background area should reflect the geographic area in which a species could plausibly exist within the contemporary or recent historical dispersal distance of each species. The background area should not be so small as to contain insufficient environmental variation to discriminate the environmental conditions of a species range, but should also not be so large as to contain environments that differ too greatly from the species current distribution ^{50,51}. To balance these trade-offs, we used broad eco-climatic biomes ⁵² within the biogeographic realm each species is found in to select background points. We buffered these background regions to ensure they were

entirely within the feasible dispersal capacity of non-volant mammal species within 20 years. Following⁵³ we used a buffer of 3000km from the range boundary of each species. We sampled a maximum of 10,000 pseudo-absence points from within this background region, a number shown to be suitable when working across diverse taxa and regions⁵⁴. However, given that most background regions contained fewer than 10,000 unique 100x100km grid cells, the actual number of background points was often less than this and varied between species.

Environmental predictors

To accurately model species distributions we should select the variables that are most likely to limit distributions, while minimizing superfluous or redundant variables⁵⁵. While Maxent is capable of dealing with intercorrelated variables, to reduce complexity and increase biological interoperability, there have been recent calls for selecting biologically and ecologically relevant predictors *a priori*⁵⁶. Studies that model distributions of many species and/or species across higher taxonomic groups typically select a small subset of predictor variables that may capture general aspects of species' physiology or ecological niches, such as temperature, rainfall, and environmental energy^{53,57}. In this study we followed⁵⁸ and selected four variables from Worldclim that capture annual variation and extremes in temperature and precipitation; temperature seasonality (bio04), precipitation seasonality (bio15), mean temperature of the warmest quarter (bio10), and precipitation of the wettest quarter (bio16). These four variables are weakly intercorrelated and therefore reflect relatively independent axes of environmental variation.

Model evaluation

Maxent feature classes and regularization parameters determine the complexity of response curves between environmental variables and the probability of a species presence. Complex models are permitted when the number of pseudo-presence points is high, however complex models are not necessarily a better description of species response curves, and evaluating models of varying complexity is encouraged⁵⁹⁻⁶². We fitted 30 different models of varying complexity for each species using five regularization parameters (0.1, 0.5, 1, 2, and 4), covering a range commonly used^{58,63,64}, and six feature class combinations using either single feature classes (linear(L), quadratic (Q), hinge (H)) or multiple feature classes (product (P) and LQ, LQ, and QH). Goodness-of-fit was assessed using a spatially explicit cross-validation method which partitions presence points into four bins based on latitude and longitude; three of these bins are used to train the model while the fourth is

used to validate the model. This ‘block’ method assesses the performance of the models when translocated in space (or time), which is desirable for forward projection onto future climate scenarios.

We then selected the best fitting model using the following procedure: First we selected models with the lowest Akaike Information Criterion corrected for small sample sizes (AICc). Where multiple models shared the lowest AICc we used the AUC_{Test} metric, which is the area under the curve (AUC) of the receiver operating characteristic plot evaluated on the test data withheld during cross-validation⁶². If multiple models also had the same average test AUC_{Test} , we used AUC_{diff} which is the difference between the AUC calculated on the test and training data during cross validation. If these too were the same, we selected the model with the fewest parameters. Finally, if these were also equal among models, we broke the tie between competing models by selecting a model at random. All maxent model fitting and evaluation was performed using the R package ENMeval⁶². Some species ($n=325$) have very narrow distributions and too few occurrence records to fit species distribution models reliably. For future projections of human population density and land-use change for these species (see below), we used IUCN polygons rather than modelled climatic ranges, and assumed the boundaries of their ranges remain unchanged through time.

Overall, the models performed well as judged by AUC_{test} values (although see Lobo et al.⁶⁵ for a warning against the use of AUC alone to assess model performance). Among species for which SDM models could be fitted, median AUC_{test} value was 0.902, 94% of species had $AUC_{test} \geq 0.7$, the value often considered to indicate a “fair” model⁶⁶, and 84% had $AUC_{test} \geq 0.8$, the value considered to indicate a “good” model. Omitting species with poor model performance ($AUC_{test} < 0.7$) from the downstream analyses used to generate Figure 1 made no discernable difference to the results, so for all downstream analyses we used all species for which an SDM could be fitted.

Species distribution models: future projections of climatic ranges

We predicted probability of climate suitability under future climate change scenarios using the best model for each species for current climate data (2020) and for climate data projected to the years 2040, 2060, 2080 and 2100, under the two different SSPs and two GCMs. We converted climate suitability to predicted presence and absence using a 10% omission rate threshold, rejecting the lowest 10% of predicted values⁶⁷.

Many species are likely to neither occupy the full range of suitable climatic conditions in the future due to dispersal limitations, nor to remain completely static, with some middle ground being more likely. It is certain that different species vary greatly in their ability to disperse to track changing climatic conditions, but direct data on dispersal ability is very limited, and in choosing dispersal models to apply across all mammal species, we are required to make many simplifying assumptions. To bracket a range of possibilities and compare their influence on the projections, we modelled four alternative scenarios for species ability to disperse from suitable areas between one timestep and the next:

- (1) High dispersal (HD): species are able to disperse from one timestep to the next into all suitable areas within the background range (3000km buffer within biomes, see above).
- (2) Limited dispersal (LD): species are able to disperse from one timestep to the next within a maximum 100km dispersal radius (one grid cell).
- (3) Body size-linked dispersal (BSLD): species dispersal ability scales positively with mean adult body mass according to the function: dispersal distance = body mass(g)^{0.16} – 1. The exponent value of 0.16 was determined by trial and error to produce a distribution of dispersal distances with a median value ~1 grid cell, similar to that of the LD model.
- (4) No dispersal (ND): species ability to disperse from one timestep to the next is less than the grid resolution of 100x100km.

Under all the above dispersal scenarios we disallowed any overwater dispersal, so that all species are constrained to remain on the land masses (islands or continents) on which they are currently found. While many species can cross water barriers, given the short time frames of our models we felt that it was more realistic to apply this restriction across all species, than to allow unrestricted overwater dispersal, or attempt to apply different constraints for different species.

Overall, for each of the 5209 species we produced 16 alternative range projections (2 SSPs x 2 GCMs x 4 dispersal models) at each of four future times (2040, 2060, 2080, 2100). We refer to these as “climatic ranges”, and we consider these projections to represent the area of suitable climate that could plausibly be occupied by a species.

Comparative models and latent extinction risk

Body size has been identified as one of the strongest and most consistent biological predictors of extinction risk in mammals^{15,16,20,68}. To quantify species’ inherent sensitivity, we therefore modelled the association between threat status and mean adult body mass using generalized least-squares

(GLS) models that account for covariation with geographic range size (area of IUCN polygon distributions), and both spatial and phylogenetic non-independence in the data. Other biological traits have been shown to be associated with threat status in mammals^{16,20}, but body mass and range size typically have by far the greatest explanatory power and the most complete data coverage across species. Missing data meant that adding other biological variables as predictors reduced the species coverage considerably, for relatively little gain in explanatory power, so we fitted models including only body size, range size, and the interaction and quadratic terms. The GLS models were run separately for species within biogeographic realms, both for computational efficiency and because each realm harbours a largely distinct mammal fauna with a unique combination of threats. The mammal species dataset was divided into six biogeographic realms (Nearctic, Neotropical, Palearctic, Afrotropical, Indo-Malay, Australasia) and species assigned to the realms in which they currently occur. Species whose distributions cross realm boundaries were assigned to multiple realms, but for these species their global geographic range size was used as the predictor in the models.

Both predictor variables were log-transformed, standardized to units of standard deviation, and centred to mean = 0. The response variable was a pseudo-numeric coding of the Red List categories: Least Concern = 0, Near Threatened = 1, Vulnerable = 2, Endangered = 3, Critically Endangered = 4, Extinct in the Wild/Extinct = 5. For the very few species (n=8) with a value of 5, the geographic range size used in GLS models was that from the IUCN, based on the known or presumed recent distribution. Species classified as Data Deficient (DD) have not been assigned to a threat category and could not be included in the models. Following common practice, species listed as threatened (Vulnerable, Endangered or Critically Endangered) under Red List criterion B (which includes a threshold range size criterion) were omitted from model fitting, because of the potential circularity of including range size both as part of the predictor and part of the response variable^{20,69}. In practice, however, removal of criterion B threatened species made little difference to the parameter estimates. The majority of criterion B threatened species have data on body size and range size that allowed a fitted value of threat status to be calculated from the models.

It is widely accepted that comparative analyses in which the data are hierarchically structured according to phylogeny should account for possible non-independence by incorporating a phylogenetic covariance structure, and this is standard practice for models of extinction risk. While it is also well known that many of the spatial variables involved in extinction risk analyses are spatially autocorrelated, rendering the data spatially non-independent, until fairly recently there have been no methods to account simultaneously for phylogenetic and spatial covariances in comparative analyses. We do this using a modified form of a model first described by Bromham *et al.*⁷⁰, with

phylogenetic covariances derived from the sample of mammal phylogenies, and spatial covariances from great-circle distances among the centroids of species current distributions. A description and code for these spatio-phylogenetic GLS models is available online ⁷¹. To assess the additional variance in parameter estimates added by sampling phylogenies from the posterior distribution, we repeated models using 25 randomly-chosen phylogenies. Because the extra variance was very small, we use models based on one phylogeny only for all downstream analyses. For each model, we calculated a coefficient of determination using R^2_{lik} , a pseudo- R^2 measure which is formulated explicitly for models with a covariance structure ⁷².

Latent extinction risk ¹³ was calculated for the 4311 species for which we had both a Red List category and a fitted value from the GLS models. Latent risk is the difference between the fitted value and the species current threat status coded on the pseudo-numeric scale. In part, this difference is due to the imperfect fit of the model, but because the response variable (threat status) can change through time under influence of the predictors and external threatening processes, we can also interpret latent risk as proportional to the potential for future increase in a species' threat status ¹³. A species with a high latent risk value is currently less threatened than the GLS models would predict from its body size and geographic range size, and this may be (for example) because it inhabits a region in which habitats have remained relatively little-disturbed. The implication is that if the level of impact increases in the future, a species with high latent risk (due to a large body size, small range size, or both) is likely to be more susceptible to decline than one with a low latent risk. As an example, a species with one of the highest latent risk values of 3.03, the Obi Cuscus (*Phalanger rothschildii*), is relatively large (~1.4kg) and confined to a small distribution (<2500km²) in eastern Indonesia, where its rainforest habitat, although potentially threatened by logging, is still largely intact ²⁶.

Defining future risk factors

Because the focus of our study is on proactive conservation, ie. taking action to prevent species declines before they occur, we wished to identify those mammal species that may be at elevated risk of extinction by the end of this century, even if they are not currently listed as threatened ("over-the-horizon" extinction risk). A species' current threat status is the result of the way its biology (particularly body size) mediates the effect of external threatening processes (e.g. habitat loss, hunting, or invasive species) on the size of its population or distribution ^{16,18,20,73}. We therefore based

future risk factors both on the species inherent sensitivity to threats (biological attributes statistically associated with high threat status), and proxies for the major external threats faced by species. The future risk factors were defined using cutoff values (in a similar way to the Red List categories themselves), as follows:

- (1) Latent risk ≥ 1 . Biological predictors in the comparative models explained 14-32% of the variance in threat status (Data S1), so we cannot regard latent risk as a precise quantitative measure of the potential for threat status to increase. Instead, we chose a relatively large threshold value of latent risk to define species with a high potential for increased threat status (latent risk values range from -3.64 to 3.34; median is 0.19; a value of one is at the 90th percentile). A value of one is equivalent to the difference between two adjacent Red List categories, on our pseudo-numeric scale.
- (2) Reduction in area of climatic range by 2100 to $\leq 50\%$ of current climatic range. Absolute size of geographic range is a strong predictor of species' current threat status, and rate of decline in range size forms part of criterion A for the evaluation of species as threatened under the Red List. However, because modelled climatic range is only a broad reflection of a species' extent of occurrence, we chose a large proportional decrease in climatic range (halving of current area) as a conservative criterion for defining species at elevated future risk.
- (3) Doubling of the proportion of species climatic range shared with ≥ 100 people/km² by 2100. Human population density is a proxy for many of the direct threats to mammal populations, including hunting, overharvesting, habitat loss or modification, and density of invasive species^{3,6,74}. Previous studies suggest that the amount of area with relatively few people that a species has access to is more important than the mean human population density across the species' range^{3,20}. Moreover, there is evidence for "critical human densities" at which population extinction risk is elevated; in carnivores, these critical densities range widely from <10 to over 1800 people/km²⁷⁴. There is unlikely to be any single value for critical density that best captures threats from human population density for all mammal species; 100 people/km² provides a statistically tractable distribution of values at the global scale. Because the proportion is calculated for each species' modelled climatic distribution, the value is dependent on the dynamic spatial interaction between projected human population growth and climate-driven range expansions and contractions.
- (4) Doubling of the proportion of species climatic ranges in which land cover is $\geq 50\%$ human-modified. Modified land cover was defined as those areas classified as "cropland_other", "cropland_bioenergy", or "built_up", in the 7-class classification scheme of the global land-use database⁴⁷. Again, the figure of 50% modified was chosen as a compromise value across the large

number of mammal species that certainly vary widely in their ability to thrive in anthropogenic landscapes. As for human population density, the value is calculated on species' modelled climatic range, so is dependent on dynamic interactions between projected land-use change and climate-driven range changes.

Protected area representation adequacy targets and global gap analysis

We assume that mammal species identified as having multiple future risk factors, as defined above, are at elevated risk of extinction in the medium to long term (up to the end of this century), and therefore should be afforded priority for protection. To establish targets for the adequate representation of these species current distributions within the global protected area network, we first followed previous studies^{24,25} in setting representation adequacy targets based solely on size of distribution, with a target of 100% for species with distributions <1000km², 10% for species with distributions >250000km², and a log-linear scaling of targets with range size in between. We then adjusted these targets to account for future risk factors, by multiplying the target by the number of risk factors for each species. This adjustment produces representation targets that increase progressively for species with two or more risk factors, reflecting our belief that these are the species most likely to become threatened in the future, justifying a higher proportion of their distributions being protected within reserves. For these two alternative sets of targets, we calculated each species' current overlap with protected areas and the amount by which this fell short or exceeded the species-specific target. Protected area spatial data were from the World Database on Protected Areas⁷⁵.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data analyses, including phylogenetically and spatially-explicit general linear models were performed using custom scripts in R (available online, see Data and code availability). Details of statistical analyses including sample sizes are given in Method details.

Supplemental Information titles and legends

Data S1. Threat status model summaries for 25 phylogenies, related to STAR Methods.

Each row of each table shows the phylogeny number, pseudo-R² value (Rsqlik), the proportion of variance in threat status attributed to spatial autocorrelation, the proportion of variance in threat status attributed to phylogenetic autocorrelation, followed by the slope estimate, standard error of the estimate, t-value and p-value, for the intercept and model predictor variables, respectively. All values are rounded to three decimal places, so values of zero represent <0.001. Values are shown for six biogeographic realms: (A) Palearctic, (B) Nearctic, (C) Afrotropic, (D) Neotropic, (E) Australasia, (F) Indo-Malay

Data S2. Future risk factors for mammal species for the year 2100, related to STAR Methods and Figure 1.

For each species, columns indicate current IUCN threat status coded on a 0-5 pseudo-numeric scale, presence or absence within each biogeographic realm, whether the species has each of four future risk factors, and the total number of risk factors. Values are shown for 16 projection scenario combinations of Shared Socioeconomic Pathway (SSP2, SSP5), Global Circulation Model (GCM, MIROC), and species dispersal model (BSLD, LD, ND, HD): (A) SSP2+CNRM+BSLD (B) SSP2+CNRM+LD (C) SSP2+CNRM+ND (D) SSP2+CNRM+HD (E) SSP2+MIROC+BSLD (F) SSP2+MIROC+LD (G) SSP2+MIROC+ND (H) SSP2+MIROC+HD (I) SSP5+CNRM+BSLD (J) SSP5+CNRM+LD (K) SSP5+CNRM+ND (L) SSP5+CNRM+HD (M) SSP5+MIROC+BSLD (N) SSP5+MIROC+LD (O) SSP5+MIROC+ND (P) SSP5+MIROC+HD. (Q) Summary data showing numbers of species with different numbers of future risk factors. Values are shown for each of the above scenarios, for each of four time periods: t2 (2020-2040), t3 (2040-2060), t4 (2060-2080), t5 (2080-2100).

Methods S1. Concentrations of terrestrial mammal species with each future risk factor under 16 climate change scenarios, related to STAR Methods and Figure 1.

Numbers (left) and proportions (right) of species per grid cell with each risk factors, derived from projections of climatic ranges, human population density, and land use change to 2100 under a unique combination of Global Circulation Model, Shared Socioeconomic Pathway, and species dispersal model. The code at the top of each figure indicates the time period (t5 = 2080-2100),

Shared Socioeconomic Pathway (SSP2, SSP5), Global Circulation Model (CNRM, MIROC), and dispersal model (HD, LD, BSLD, ND). (A) SSP2+CNRM+BSLD (B) SSP2+CNRM+LD (C) SSP2+CNRM+ND (D) SSP2+CNRM+HD (E) SSP2+MIROC+BSLD (F) SSP2+MIROC+LD (G) SSP2+MIROC+ND (H) SSP2+MIROC+HD (I) SSP5+CNRM+BSLD (J) SSP5+CNRM+LD (K) SSP5+CNRM+ND (L) SSP5+CNRM+HD (M) SSP5+MIROC+BSLD (N) SSP5+MIROC+LD (O) SSP5+MIROC+ND (P) SSP5+MIROC+HD.

Methods S2. Concentrations of terrestrial mammal species with different numbers of future risk factors under 16 climate change scenarios, related to STAR Methods and Figure 1.

Numbers (left) and proportions (right) of species per grid cell with one, two, three and four of the risk factors, derived from projections of climatic ranges, human population density, and land use change to 2100 under a unique combination of Global Circulation Model, Shared Socioeconomic Pathway, and species dispersal model. The code at the top of each figure indicates the time period (t5 = 2080-2100), Shared Socioeconomic Pathway (SSP2, SSP5), Global Circulation Model (CNRM, MIROC), and dispersal model (HD, LD, BSLD, ND). (A) SSP2+CNRM+BSLD (B) SSP2+CNRM+LD (C) SSP2+CNRM+ND (D) SSP2+CNRM+HD (E) SSP2+MIROC+BSLD (F) SSP2+MIROC+LD (G) SSP2+MIROC+ND (H) SSP2+MIROC+HD (I) SSP5+CNRM+BSLD (J) SSP5+CNRM+LD (K) SSP5+CNRM+ND (L) SSP5+CNRM+HD (M) SSP5+MIROC+BSLD (N) SSP5+MIROC+LD (O) SSP5+MIROC+ND (P) SSP5+MIROC+HD.

References

1. Andermann, T., Faurby, S., Turvey, S.T., Antonelli, A., and Silvestro, D. (2020). The past and future human impact on mammalian diversity. *Science Advances* 6, eabb2313. doi:10.1126/sciadv.abb2313.
2. Bowler, D.E., Bjorkman, A.D., Dornelas, M., Myers-Smith, I.H., Navarro, L.M., Niamir, A., Supp, S.R., Waldo, C., Winter, M., Vellend, M., et al. (2020). Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People and Nature* 2, 380-394. <https://doi.org/10.1002/pan3.10071>.
3. Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J., and Mace, G.M. (2004). Human Population Density and Extinction Risk in the World's Carnivores. *PLOS Biology* 2, e197. 10.1371/journal.pbio.0020197.
4. Etard, A., Pigot, A.L., and Newbold, T. (2022). Intensive human land uses negatively affect vertebrate functional diversity. *Ecology Letters* 25, 330-343. <https://doi.org/10.1111/ele.13926>.
5. IPBES (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. <https://doi.org/10.5281/zenodo.3831673>.
6. McKee, J.K., Sciulli, P.W., Fooce, C.D., and Waite, T.A. (2004). Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* 115, 161-164. [https://doi.org/10.1016/S0006-3207\(03\)00099-5](https://doi.org/10.1016/S0006-3207(03)00099-5).
7. Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., et al. (2015). Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45-50. 10.1038/nature14324.
8. Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., et al. (2015). Assessing species vulnerability to climate change. *Nature Climate Change* 5, 215-224. 10.1038/nclimate2448.
9. Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J., et al. (2008). The Status of the World's Land and Marine Mammals: Diversity, Threat, and Knowledge. *Science* 322, 225-230. doi:10.1126/science.1165115.
10. Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., and Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature* 546, 73-81. 10.1038/nature22900.
11. Urban, M.C. (2015). Accelerating extinction risk from climate change. *Science* 348, 571-573. 10.1126/science.aaa4984.
12. Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S.H.M., Joppa, L., Alkemade, R., Di Marco, M., Santini, L., Hoffmann, M., et al. (2016). Projecting Global Biodiversity Indicators under Future Development Scenarios. *Conservation Letters* 9, 5-13. <https://doi.org/10.1111/conl.12159>.
13. Cardillo, M., Mace, G.M., Gittleman, J.L., and Purvis, A. (2006). Latent extinction risk and the future battlegrounds of mammal conservation. *Proc Natl Acad Sci USA* 103, 4157-4161.
14. Visconti, P., Pressey, R.L., Giorgini, D., Maiorano, L., Bakkenes, M., Boitani, L., Alkemade, R., Falcucci, A., Chiozza, F., and Rondinini, C. (2011). Future hotspots of terrestrial mammal loss. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366, 2693-2702. doi:10.1098/rstb.2011.0105.
15. Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., and Purvis, A. (2005). Multiple Causes of High Extinction Risk in Large Mammal Species. *Science* 309, 1239-1241.

16. Davidson, A.D., Hamilton, M.J., Boyer, A.G., Brown, J.H., and Ceballos, G. (2009). Multiple ecological pathways to extinction in mammals. *Proceedings of the National Academy of Sciences* *106*, 10702-10705. doi:10.1073/pnas.0901956106.
17. Mantyka-pringle, C.S., Martin, T.G., and Rhodes, J.R. (2012). Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology* *18*, 1239-1252. <https://doi.org/10.1111/j.1365-2486.2011.02593.x>.
18. Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Şekercioğlu, Ç.H., Alkemade, R., Booth, H., and Purves, D.W. (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings of the Royal Society B: Biological Sciences* *280*, 20122131. doi:10.1098/rspb.2012.2131.
19. Williams, J.J., Freeman, R., Spooner, F., and Newbold, T. (2022). Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Global Change Biology* *28*, 797-815. <https://doi.org/10.1111/gcb.15978>.
20. Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J., and Purvis, A. (2008). The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B: Biological Sciences* *275*, 1441-1448. doi:10.1098/rspb.2008.0179.
21. Fritz, S.A., Bininda-Emonds, O.R.P., and Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters* *12*, 538-549. <https://doi.org/10.1111/j.1461-0248.2009.01307.x>.
22. Harfoot, M.B.J., Johnston, A., Balmford, A., Burgess, N.D., Butchart, S.H.M., Dias, M.P., Hazin, C., Hilton-Taylor, C., Hoffmann, M., Isaac, N.J.B., et al. (2021). Using the IUCN Red List to map threats to terrestrial vertebrates at global scale. *Nature Ecology & Evolution* *5*, 1510-1519. 10.1038/s41559-021-01542-9.
23. Allan, J.R., Possingham, H.P., Atkinson, S.C., Waldron, A., Marco, M.D., Butchart, S.H.M., Adams, V.M., Kissling, W.D., Worsdell, T., Sandbrook, C., et al. (2022). The minimum land area requiring conservation attention to safeguard biodiversity. *Science* *376*, 1094-1101. doi:10.1126/science.abl9127.
24. Rodrigues, A.S., Akcakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D., Da Fonseca, G.A., and Gaston, K.J. (2004). Global gap analysis: priority regions for expanding the global protected-area network. *BioScience* *54*, 1092-1100.
25. Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T., Butchart, S.H.M., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., et al. (2014). Targeting Global Protected Area Expansion for Imperiled Biodiversity. *PLOS Biology* *12*, e1001891. 10.1371/journal.pbio.1001891.
26. IUCN. (2021). The IUCN Red List of Threatened Species. Version 2021-3.
27. Wilson, H.B., Joseph, L.N., Moore, A.L., and Possingham, H.P. (2011). When should we save the most endangered species? *Ecology Letters* *14*, 886-890. <https://doi.org/10.1111/j.1461-0248.2011.01652.x>.
28. Layton, C., Coleman, M.A., Marzinelli, E.M., Steinberg, P.D., Swearer, S.E., Vergés, A., Wernberg, T., and Johnson, C.R. (2020). Kelp Forest Restoration in Australia. *Frontiers in Marine Science* *7*. 10.3389/fmars.2020.00074.
29. Possingham, H.P., Bode, M., and Klein, C.J. (2015). Optimal Conservation Outcomes Require Both Restoration and Protection. *PLOS Biology* *13*, e1002052. 10.1371/journal.pbio.1002052.
30. Hamer, R.P., Robinson, N., Brewster, R., Barlow, M., Morrigan, G., Morgan, H., Mifsud, A., and Kutt, A.S. (2022). Not waiting for the death knell. A pilot study to examine supplementation and survivorship in a declining population of Tasmanian eastern quoll (*Dasyurus viverrinus*). *Research Square*. 10.21203/rs.3.rs-1292781/v1.

31. Possingham, H.P., Andelman, S.J., Burgman, M.A., Medellín, R.A., Master, L.L., and Keith, D.A. (2002). Limits to the use of threatened species lists. *Trends in Ecology & Evolution* 17, 503-507. [https://doi.org/10.1016/S0169-5347\(02\)02614-9](https://doi.org/10.1016/S0169-5347(02)02614-9).
32. Eriksen, S., O'Brien, K., and Rosentrater, L. (2008). *Climate Change in Eastern and Southern Africa: Impacts, Vulnerability and Adaptation*. University of Oslo.
33. Convention on Biological Diversity (2011). *Strategic Plan for Biodiversity 2011-2020*. www.cbd.int/decision/cop/?id=12268.
34. Bolam, F.C., Mair, L., Angelico, M., Brooks, T.M., Burgman, M., Hermes, C., Hoffmann, M., Martin, R.W., McGowan, P.J.K., Rodrigues, A.S.L., et al. (2021). How many bird and mammal extinctions has recent conservation action prevented? *Conservation Letters* 14, e12762. <https://doi.org/10.1111/conl.12762>.
35. Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., et al. (2010). The Impact of Conservation on the Status of the World's Vertebrates. *Science* 330, 1503-1509. doi:10.1126/science.1194442.
36. Leung, B., Hargreaves, A.L., Greenberg, D.A., McGill, B., Dornelas, M., and Freeman, R. (2020). Clustered versus catastrophic global vertebrate declines. *Nature* 588, 267-271. 10.1038/s41586-020-2920-6.
37. Convention on Biological Diversity (2022). *Open-ended Working Group on the Post-2020 Global Biodiversity Framework. Draft Report of Third Meeting*.
38. Brockington, D., and Wilkie, D. (2015). Protected areas and poverty. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370, 20140271. doi:10.1098/rstb.2014.0271.
39. Cooke, R.S.C., Bates, A.E., and Eigenbrod, F. (2019). Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology and Biogeography* 28, 484-495. <https://doi.org/10.1111/geb.12869>.
40. Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., and Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95, 2027-2027. <https://doi.org/10.1890/13-1917.1>.
41. Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P., and Rondinini, C. (2013). Generation length for mammals. *Nature Conservation* 5. 10.3897/natureconservation.5.5734.
42. Myhrvold, N.P., Baldrige, E., Chan, B., Sivam, D., Freeman, D.L., and Ernest, S.K.M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* 96, 3109-3109. <https://doi.org/10.1890/15-0846R.1>.
43. Upham, N.S., Esselstyn, J.A., and Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology* 17, e3000494. 10.1371/journal.pbio.3000494.
44. S, C., E, S., Z, F., Z, A., C, B., K, R., I, B., J, B., J, O.D., J, O., et al. (2013). taxize: Taxonomic information from around the web.
45. Fick, S.E., and Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302-4315. <https://doi.org/10.1002/joc.5086>.
46. Gao, J. (2017). Downscaling Global Spatial Population Projections from 1/8-degree to 1-km Grid Cells.
47. Fujimori, S., Hasegawa, T., Ito, A., Takahashi, K., and Masui, T. (2018). Gridded emissions and land-use data for 2005–2100 under diverse socioeconomic and climate mitigation scenarios. *Scientific Data* 5, 180210. 10.1038/sdata.2018.210.
48. Phillips, S.J., Dudík, M., and Schapire, R.E. (2004). A maximum entropy approach to species distribution modeling. *Proceedings of the twenty-first international conference on Machine learning*. Association for Computing Machinery.

49. Hurlbert, A.H., and Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences* 104, 13384-13389. doi:10.1073/pnas.0704469104.
50. Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., and Villalobos, F. (2011). The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling* 222, 1810-1819. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>.
51. Thuiller, W., Brotons, L., Araújo, M.B., and Lavorel, S. (2004). Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27, 165-172. <https://doi.org/10.1111/j.0906-7590.2004.03673.x>.
52. Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., et al. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51, 933-938. 10.1641/0006-3568(2001)051[0933:Teotwa]2.0.Co;2.
53. Thuiller, W., Guéguen, M., Renaud, J., Karger, D.N., and Zimmermann, N.E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications* 10, 1446. 10.1038/s41467-019-09519-w.
54. Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., and Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19, 181-197. <https://doi.org/10.1890/07-2153.1>.
55. Fourcade, Y., Besnard, A.G., and Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography* 27, 245-256. <https://doi.org/10.1111/geb.12684>.
56. Austin, M.P., and Van Niel, K.P. (2011). Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38, 1-8. <https://doi.org/10.1111/j.1365-2699.2010.02416.x>.
57. Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., and Araujo, M.B. (2011). Consequences of climate change on the tree of life in Europe. *Nature* 470, 531-534. 10.1038/nature09705.
58. Jarvie, S., and Svenning, J.-C. (2018). Using species distribution modelling to determine opportunities for trophic rewilding under future scenarios of climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373, 20170446. doi:10.1098/rstb.2017.0446.
59. Anderson, R.P., and Gonzalez, I. (2011). Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecological Modelling* 222, 2796-2811. <https://doi.org/10.1016/j.ecolmodel.2011.04.011>.
60. Merow, C., Smith, M.J., Edwards Jr, T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, W., Wüest, R.O., Zimmermann, N.E., and Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography* 37, 1267-1281. <https://doi.org/10.1111/ecog.00845>.
61. Merow, C., Smith, M.J., and Silander Jr, J.A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36, 1058-1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>.
62. Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., and Anderson, R.P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution* 5, 1198-1205. <https://doi.org/10.1111/2041-210X.12261>.
63. Owens, H.L., Lewis, D.S., Dupuis, J.R., Clamens, A.-L., Sperling, F.A.H., Kawahara, A.Y., Guralnick, R.P., and Condamine, F.L. (2017). The latitudinal diversity gradient in New World

swallowtail butterflies is caused by contrasting patterns of out-of- and into-the-tropics dispersal. *Global Ecology and Biogeography* 26, 1447-1458.

<https://doi.org/10.1111/geb.12672>.

64. Ralston, J., DeLuca, W.V., Feldman, R.E., and King, D.I. (2016). Realized climate niche breadth varies with population trend and distribution in North American birds. *Global Ecology and Biogeography* 25, 1173-1180. <https://doi.org/10.1111/geb.12490>.
65. Lobo, J.M., Jimenez-Valverde, A., and Real, R. (2008). AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17, 145-151.
66. Araujo, M.B., Pearson, R.G., Thuiller, W., and Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology* 11, 1504-1513.
67. Nenzén, H.K., and Araújo, M.B. (2011). Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* 222, 3346-3354. <https://doi.org/10.1016/j.ecolmodel.2011.07.011>.
68. Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., and McCauley, D.J. (2017). Extinction risk is most acute for the world’s largest and smallest vertebrates. *Proceedings of the National Academy of Sciences* 114, 10678-10683. [10.1073/pnas.1702078114](https://doi.org/10.1073/pnas.1702078114).
69. Purvis, A., Gittleman, J.L., Cowlishaw, G., and Mace, G.M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267, 1947-1952. doi:10.1098/rspb.2000.1234.
70. Freckleton, R.P., and Jetz, W. (2009). Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B: Biological Sciences* 276, 21-30. doi:10.1098/rspb.2008.0905.
71. Bromham, L., Dinnage, R., Skirgård, H., Ritchie, A., Cardillo, M., Meakins, F., Greenhill, S., and Hua, X. (2022). Global predictors of language endangerment and the future of linguistic diversity. *Nature Ecology & Evolution* 6, 163-173. [10.1038/s41559-021-01604-y](https://doi.org/10.1038/s41559-021-01604-y).
72. Ives, A.R. (2018). *R*²s for Correlated Data: Phylogenetic Models, LMMs, and GLMMs. *Systematic Biology* 68, 234-251. [10.1093/sysbio/syy060](https://doi.org/10.1093/sysbio/syy060).
73. Fisher, D.O., Blomberg, S.P., and Owens, I.P.F. (2003). Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270, 1801-1808. doi:10.1098/rspb.2003.2447.
74. Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3, 165-173. [10.1111/j.1469-1795.2000.tb00241.x](https://doi.org/10.1111/j.1469-1795.2000.tb00241.x).
75. UNEP-WCMC, and IUCN (2022). Protected Planet: The World Database on Protected Areas (WDPA)/OECM Database.