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# Constraints on vertebrate range size predict extinction risk

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## Abstract

**Aim:** The only factor in the fossil record that consistently buffers against extinction risk is large geographical range. We ask whether extant vertebrate species with the smallest geographical range for their body size have a higher extinction risk, and thus whether the lower bound of the modern range–body size relationship could serve as an effective conservation prioritization tool.

**Location:** Global in scope.

**Time period:** Modern.

**Major taxa studied:** Six classes of vertebrates.

**Methods:** We compiled a database of geographical range, body size and extinction risk for six vertebrate classes ( $n = 26,076$ ). We characterized the shape of the relationship between geographical range and body size for each class, using 90% and 10% quantile regression to describe the upper and lower bounds, respectively. We then evaluated the degree of extinction vulnerability of species at the lower bound of the regression using generalized linear mixed models. All analyses accounted for phylogenetic dependence between related species.

**Results:** The relationships between species ranges and body sizes were generally positive at both the upper and the lower bounds, and segmented (nonlinear) relationships were common. Despite this variability, species near the lower boundary of the relationship were more often in higher extinction risk categories, and this remained true when the role of range size in the International Union for Conservation of Nature Red Listing criteria was accounted for.

**Main conclusions:** Variability in the upper and lower bounds of the range–body size relationship suggests that some classes of vertebrates exhibit combinations of ranges and body sizes that might not reflect historical patterns. Nonetheless, the range–body size relationship remains a reliable and useful predictor of extinction risk, more so than range size does alone. The range–body size relationship could therefore be used to track the trajectories of species towards or away from an extinction threshold and allow the tracking of how different human activities alter the range–body size relationship.

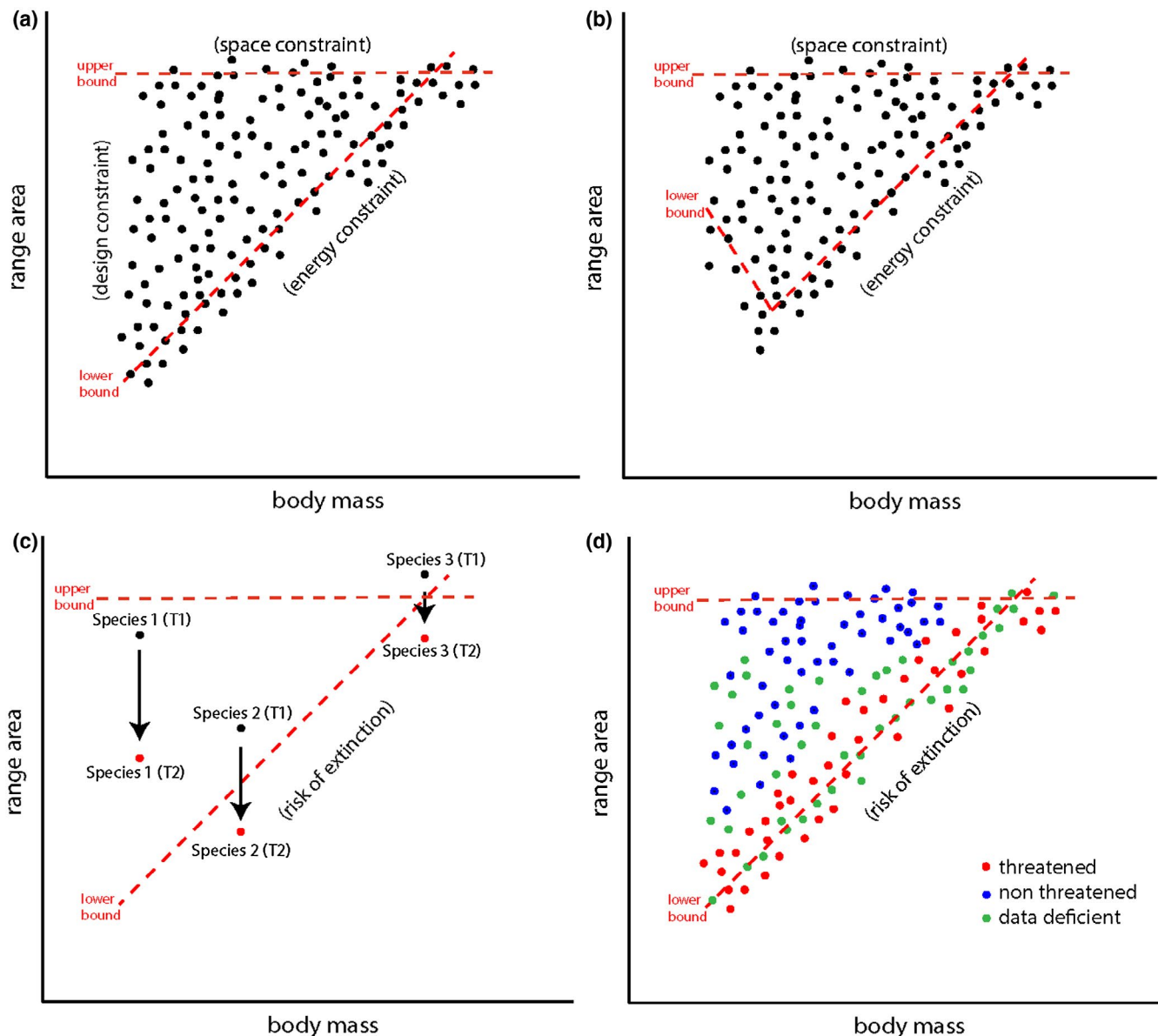
## KEYWORDS

biodiversity, body mass, extinction, range size, vertebrates

## 1 | INTRODUCTION

Variation in species traits, such as life history, may render some more prone to extinction than others (González-Suárez & Revilla, 2013). Wide geographical range, for instance, has been shown consistently to buffer against extinction risk in the fossil record (Payne & Finnegan, 2007). Nowadays, species with the smallest geographical range in addition to those with the largest (Ripple et al., 2019) and smallest body sizes (Kopf, Shaw, & Humphries, 2017) appear most vulnerable to decline, particularly among vertebrates (Ripple et al.,

2017). Relationships between geographical range, body size and extinction risk have received considerable attention and form the basis of seminal macroecological theory (Brown & Maurer, 1987). In particular, plots of geographical range versus body size at the scale of global or continental assemblages are expected to form a general triangular pattern defined by the upper and lower limits of the range–body size trait space (Figure 1a; Brown & Maurer, 1987). A common explanation for this pattern is that larger species require more energy to survive, placing a hard lower boundary on the range size required to support minimum viable populations (Brown & Maurer,



**FIGURE 1** Conceptual models of the relationship between geographical range size (range area), vertebrate body size (mass) and extinction risk at the scale of global or continental assemblages (modified after Brown & Maurer, 1987). (a) The predicted weak relationship at the upper bound (90% quantile regression), a strong positive relationship at the lower bound (10% quantile regression) and convergence when both variables are at their maxima. (b) The relationship uncovered by Agosta and Bernardo (2013), who found a breakpoint in the lower boundary for mammals. (c) This shows how the location of a species within the geographical range size to body size trait space can change over time (T1 and T2) as geographical range size declines and body size remains constant, with T2 being closer or below the extinction threshold at the lower bound. (d) Shows the prediction that threatened species listed under the International Union for Conservation of Nature Red List should be located closer to the lower bound of the geographical range size to body size trait space [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

1987). For large species to persist, they typically occupy larger areas than smaller species. The availability of habitat thus places a hard upper boundary on the range–body size trait space, set by the maximum range size a species can achieve given its energetic constraints. These constraints theoretically lead to large portions of trait space that are unoccupied by larger species, because species with a high energetic demand and small range sizes may be more vulnerable to extinction (Brown & Maurer, 1987).

Since the initial interest in the range–body size relationship (Brown & Maurer, 1987), follow-up assessments have primarily focused at regional spatial scales (see review by Gaston & Blackburn, 2000). Global-scale assessments have focused on birds and terrestrial mammals. Boyer and Jetz (2012), for instance, found evidence of a positive lower bound in the relationship between range and body size for birds and terrestrial mammals, suggesting a robust scaling relationship between range and body size for these vertebrates. Agosta and Bernardo (2013), however, found a breakpoint in the relationship in the lower boundary for terrestrial mammals, whereby the lower bound for range size decreases with body size for the smallest mammals, but increases for larger mammals (Figure 1b). This suggested that the relationship between range and body size is more complex than generally appreciated. More recently, Smith, Elliott Smith, Lyons, Payne, and Villaseñor (2019) found that the overall shape of the range–body size relationship for mammals has changed over time as a result of human-driven extinctions and the subsequent body size downgrading of vertebrates since the late Quaternary. This indicates that contemporary data might not reflect historical macroecological patterns based on the fossil record (Smith et al., 2019).

Variation in the shape of the relationship between range and body size has important implications for understanding whether species close to the lower boundary of the range–body size relationship are more likely to be threatened with extinction, as predicted (Figure 1c; Brown & Maurer, 1987; Gaston & Blackburn, 1996). This prediction has not been assessed globally beyond birds and mammals (Boyer & Jetz, 2012), despite such information being a potentially powerful predictive tool for conservation decision making and interventions. The International Union for Conservation of Nature (IUCN) Red List (IUCN, 2018) Categories and Criteria is the most widely used metric to assess extinction risk. Under criterion B (small range area and decline), a species qualifies as being threatened when its range size is restricted ( $<20,000 \text{ km}^2$ ) and other risk factors are identified (Mace et al., 2008). However, unlike population size and decline rates, the range size that represents a critical threshold linked to extinction risk has remained elusive, plagued by methodological difficulties and biological complexities (Keith, 1998; Mace et al., 2008).

To address these important theoretical and applied knowledge gaps, we assessed the relationship between range and body size across six classes of vertebrates (amphibians, birds, bony fish, cartilaginous fish, mammals and reptiles) globally. For each class, we first characterized the shape of the range–body size relationship by assessing the shape and slope of the upper and lower bounds of the datasets. We then explored whether species listed as threatened under the IUCN Red List (status Vulnerable, Endangered or Critically

Endangered) fall closer to the lower bound of the range–body size relationship. Our expectation, based on theory (Brown & Maurer, 1987; Gaston & Blackburn, 1996) and empirical studies (Agosta & Bernardo, 2013; Boyer & Jetz, 2012), was that species listed as threatened would fall closer towards the lower bound of the range–body size relationship in comparison to those listed as non-threatened (status Least Concern or Near Threatened) (Figure 1d). In our analysis, we used a global dataset of coarsened geographical range maps, which results in range size estimates that are more in line with extent of occurrence (EOO) than area of occupancy (AOO). This helps to mitigate potential biases resulting from variability in the level of detail in the source maps and sensitivity to the choice of resolution and method of measurement (which can impact AOO estimates heavily; see Gaston & Fuller, 2009). Moreover, it facilitates making connections with theoretical work related to historical ranges (i.e., ranges in the absence of strong anthropogenic effects) because EOO provides an estimate of the current maximum range area/extent, irrespective of unoccupied holes. Conversely, AOO was assumed to be more sensitive to anthropogenic pressures because it does not include unoccupied holes. Given that a range size of  $<20,000 \text{ km}^2$  is used to list some species as threatened (criterion B, small range area and decline; IUCN, 2018), we repeated the extinction risk analysis after removing all species with a range size  $\leq 20,000 \text{ km}^2$ . This was undertaken to assess potential circularity and to determine whether range and body size can be used reliably to predict extinction risk. We also assessed whether range size alone is a better predictor of extinction risk than using the range–body size relationship. We use the results to describe modern patterns of the range–body size relationship, and specifically, whether the modern range–body size relationship has value for complementing existing approaches aimed at assessing and classifying extinction risk for the Earth's vertebrates.

## 2 | METHODS

### 2.1 | Body size, extinction risk and other data

Body sizes (mass) for six vertebrate classes (amphibians, birds, bony fish, cartilaginous fish, mammals and reptiles) were obtained from Ripple et al. (2019). This included body sizes for 47,013 vertebrate species; however, we focused on the 26,132 species with known ranges. Of these, 26,076 (99.8%) are contained within the taxonomic classes we considered: amphibians (1,557), birds (9,119), bony fish (ray-finned fish; 8,445), cartilaginous fish (896), mammals (4,521) and reptiles (1,538). Species extinction risk data were derived from the IUCN Red List (IUCN, 2018). When not assessed (NA), data deficient (DD), extinct in the wild (EW) and extinct (EX) species were excluded, the total number of species was 23,611 (amphibians, 1,393; birds, 9,094; bony fish, 6,998; cartilaginous fish, 566; mammals, 4,068; and reptiles, 1,492). Additionally, for the portions of our analysis not involving extinction risk, we included species classified as DD (but not EW/EX species owing to a lack of range maps). Species ranges originally came from the IUCN Red List (IUCN, 2018) and BirdLife (BirdLife International, 2018) range maps and were based on regions

where each species was classified as “native” and either “extant” or “probably extant” (IUCN, 2018). To deal with inconsistencies in the range maps (some maps had more fine-scale detail than others), we coarsened the range maps using a 100-km resolution grid (i.e. 100 km x 100 km, so 10,000 km<sup>2</sup> cell area) in Behrmann cylindrical equal area projection (Hurlbert & Jetz, 2007). We treated a species as present in a grid cell if any part of its polygon range overlapped the cell. To avoid conflating body mass with taxonomic class, we conducted all analyses at the class level, considering only the following major taxonomic classes: amphibians (Amphibia), birds (Aves), bony fish (Actinopterygii), cartilaginous fish (Chondrichthyes), mammals (Mammalia) and reptiles (Squamata only). In order to use phylogenetic comparative methods, we restricted our analysis further to species that are included in class-specific phylogenetic trees, resulting in a total of 1,446 amphibians (Jetz & Pyron, 2018), 7,313 birds (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Jetz et al., 2014), 8,195 bony fish (Rabosky et al., 2018), 836 cartilaginous fish (Stein et al., 2018), 3,523 mammals (Faurby et al., 2018a, 2018b) and 1,391 squamate reptiles (Tonini, Beard, Ferreira, Jetz, & Pyron, 2016). For each class, we used the first 100 phylogenetic tree estimates provided from these sources.

## 2.2 | Modelling range versus body size

For each taxonomic class, we constructed scatter plots of range versus body size, colouring points according to the threatened status of species. For each model, we used the logarithm of range as the response and the logarithm of body size as the predictor variable. Since species are not evenly distributed with respect to (log<sub>10</sub>) body size, it can be difficult to assess visually how the distribution of range size varies as a function of body size. To deal with this and to provide robust inference on how these variables are related, we used quantile regression (Cade & Noon, 2003). Quantile regression involves modeling a quantile of the distribution of the response variable as a function of one or more covariates. We considered it the most appropriate tool to characterize the shape of the relationship between geographical range and body size because it has been hypothesized that the body size of a species places a lower bound or constraint on potential range size, and habitat availability places an upper constraint on potential range size (Agosta & Bernardo, 2013; Agosta, Bernardo, Ceballos, & Steele, 2013; Brown & Maurer, 1987). We fitted quantile regression models for the 90% and 10% quantiles to describe the upper and lower bounds, respectively.

To account for phylogenetic dependence between related species, we included a residual auto-covariate derived from phylogenetic tree distance as a predictor (Bardos, Guillera-Aroita, & Wintle, 2015; Crase, Liedloff, & Wintle, 2012). This was constructed by first fitting each quantile regression model without the phylogenetic residual auto-covariate and then calculating the auto-covariate using the inverse distance squared weighted mean of the non-phylogenetic model residuals for the other species within the class. For our phylogenetic distance measure, we used the unshared branch length within the scaled phylogenetic tree (e.g., species that have only the

root node in common are assigned distance one) or, equivalently, one minus the phylogenetic correlation matrix. Letting  $d_{ij}$  be the  $(i, j)$  element of the distance matrix and  $r_j$  be the  $j^{\text{th}}$  residual from the corresponding non-phylogenetic model, the  $i^{\text{th}}$  value of the auto-covariate  $a_i$  is given by:

$$a_i = \sum_{j \neq i} \frac{1}{d_{ij}^2} r_j / \sum_{j \neq i} \frac{1}{d_{ij}^2}$$

In the residual auto-covariate approach, we first modelled the response directly with the main predictors. There may be residual autocorrelation, with closely related species tending to have high (or low) residuals, which we can reduce by including a predictor derived from (phylogenetically) nearby residuals. Constructing the auto-covariate using residuals rather than the response directly helps to reduce bias in regression coefficients (Crise et al., 2012). As evidence of the effectiveness of this procedure, we report  $\lambda$ , the phylogeny scaling parameter, which ranges from zero (independence) to one (Brownian motion) associated with both the phylogenetic and non-phylogenetic quantile regression model residuals (Pagel, 1999). We estimated  $\lambda$  by fitting intercept-only phylogenetic generalized least squares models to the model residuals. Given that quantile regression residuals do not necessarily exhibit a normal distribution with constant mean,  $\lambda$  provides only a rough measure of the phylogenetic signal. Treating the sampled phylogenetic trees that we obtained as multiple imputation samples (e.g., attempts to reconstruct the true, unknown, phylogenetic tree), we fitted each model using 100 different trees and then pooled the results using Rubin's rules (Nakagawa & De Villemereuil, 2019). We verified that all parameters achieved a relative efficiency of  $\geq 99\%$ , indicating that the inclusion of additional trees would not substantially alter our results (Nakagawa & De Villemereuil, 2019). All analyses were performed using R (R Development Core Team, 2009). Quantile regressions were fitted using the “rq” function in the “quantreg” R package (Koenker, 2018), and phylogenetic signal was estimated using “phylolm” in the “phylolm” R package (Tung Ho & Ané, 2014), with 20 bootstrap resamples per tree used to calculate the standard errors of the estimates of  $\lambda$ . All  $p$ -values were false discovery rate adjusted (across models) to control the expected proportion of incorrect null hypothesis rejections (Benjamini & Hochberg, 1995). To estimate the quantile regression lower bounds as functions of body mass alone, we set the auto-covariate to its average value. Thus, the boundaries that we show are for species with average values of the residual auto-covariate.

For each class and quantile, we then fitted segmented models with respect to body mass. This allows for the possibility of segmented relationships, such as those shown at the lower boundary for mammals (Agosta & Bernardo, 2013). For each segmented model, the location of the breakpoint was estimated using maximum likelihood. Standard errors of the breakpoint and other model parameters were calculated using 100 nonparametric bootstrap resamples per tree. Nonparametric bootstrapping was used because the residual phylogenetic signal was weak, and it allows for uncertainty in the location of the breakpoint to be accounted for when estimating the other parameters. We obtained estimates and standard errors

for differences in slopes on either side of the breakpoint using the bootstrap samples, and when the 95% confidence intervals (CIs) for these differences did not overlap zero, we reported the segmented model results rather than the linear model results.

To explore how our results varied with ecosystem type, we also fitted models for each class and ecosystem combination that had  $\geq 50$  observations. For those with  $\geq 500$  observations, we selected between segmented and linear models, and for those with fewer observations, we used only linear models, because segmented models were difficult to fit. Ecosystem type data come from the IUCN Red List and, for each species, are one or more of: freshwater, marine and terrestrial.

## 2.3 | Modelling extinction risk

We used  $\log_{10}$  relative area, which we defined as the logarithm of the ratio of a species' actual range area to its range area predicted using the 10% quantile regression, to predict Red List threatened status (binary).  $\log_{10}$  relative area is equivalent to the vertical distance between a species' data point on the (logarithmic scale) scatter plot and its 10% quantile lower bound. For each class, these models were fitted as phylogenetic generalized linear mixed models using the "phylglm" function in the "phylolm" R package (Tung Ho & Ané, 2014). For this part, we omitted species with unknown population trends. As with the quantile regression models, we fitted models for each class using 100 different phylogenetic tree estimates and pooled parameters using Rubin's rules for multiple imputation, verifying that  $\geq 99\%$  relative efficiency was achieved for all parameters. For each tree, we calculated pseudo- $R^2$  based on comparing the log-likelihood of the full (actual) and reduced (intercept only) models using the "R2.lik" function in the "rr2" R package (Ives, 2019; Ives & Li, 2018). We also calculated the area under the receiver operating characteristic curve (AUC) using the "auc" function in the "pROC" R package (Robin et al., 2011) and the Akaike information criterion (AIC). For each model and metric ( $R^2$ , AUC and AIC), we then averaged the 100 values (one per phylogenetic tree) together. To provide context, we repeated the logistic phylogenetic regression procedure using  $\log_{10}$  range size alone as the predictor. We then repeated this analysis after removing all species with range size  $\leq 20,000$  km<sup>2</sup> (the cut-off for a species potentially being listed as Vulnerable under the IUCN criteria).

## 3 | RESULTS

### 3.1 | Range versus body size

The shape of the range–body size relationship was characterized by a positive relationship for at least part of the 90% quantile (i.e., at least one side of a breakpoint) for all taxonomic groups (Figure 2; Supporting Information Table S1). We found support for segmented relationships for all taxonomic groups except amphibians and reptiles (Figure 2; Supporting Information Table S1), but this varied in different ecosystem types (Supporting Information Figure S1). Segmented relationships were found for the 90% quantile, with threshold models

being more parsimonious than linear models for bony fish, cartilaginous fish and mammals (Supporting Information Table S1).

Three of the six taxonomic groups (amphibians, cartilaginous fish and reptiles) had linear relationships for the 10% quantile, and three (amphibians, birds and reptiles) had linear relationships for the 90% quantile (Figure 2). The only negative slope estimates were for small birds (10% quantile) and small mammals (10 and 90% quantiles), with only the negative terms for mammals being statistically significant ( $p < .05$ ; Supporting Information Table S1). With the exceptions of amphibians (10% quantile), small birds (10%), small cartilaginous fish (90%) and small mammals (10% and 90%), all other terms were positive, with strong statistical significance ( $p < .001$ ), and ranged from estimated increases in range size per doubling in body mass of 7.7% [95% CI: (3.6%, 12%)] for reptiles (90% quantile) to 179.2% (58.0%, 393.5%) for larger cartilaginous fish (90% quantile) (Figure 2; Supporting Information Table S1). Estimated breakpoints for segmented models ranged from 0.040 kg for bony fish (90% quantile) to 57.54 kg for cartilaginous fish (90% quantile) (Supporting Information Table S1). With the exception of the 10% quantile model for amphibians, the residual phylogenetic signal was weak, ranging from 0.091 (amphibians, 10% quantile) to 0.343 (bony fish, 10% quantile), especially compared with the corresponding non-phylogenetic model residual signal estimates (Supporting Information Table S1).

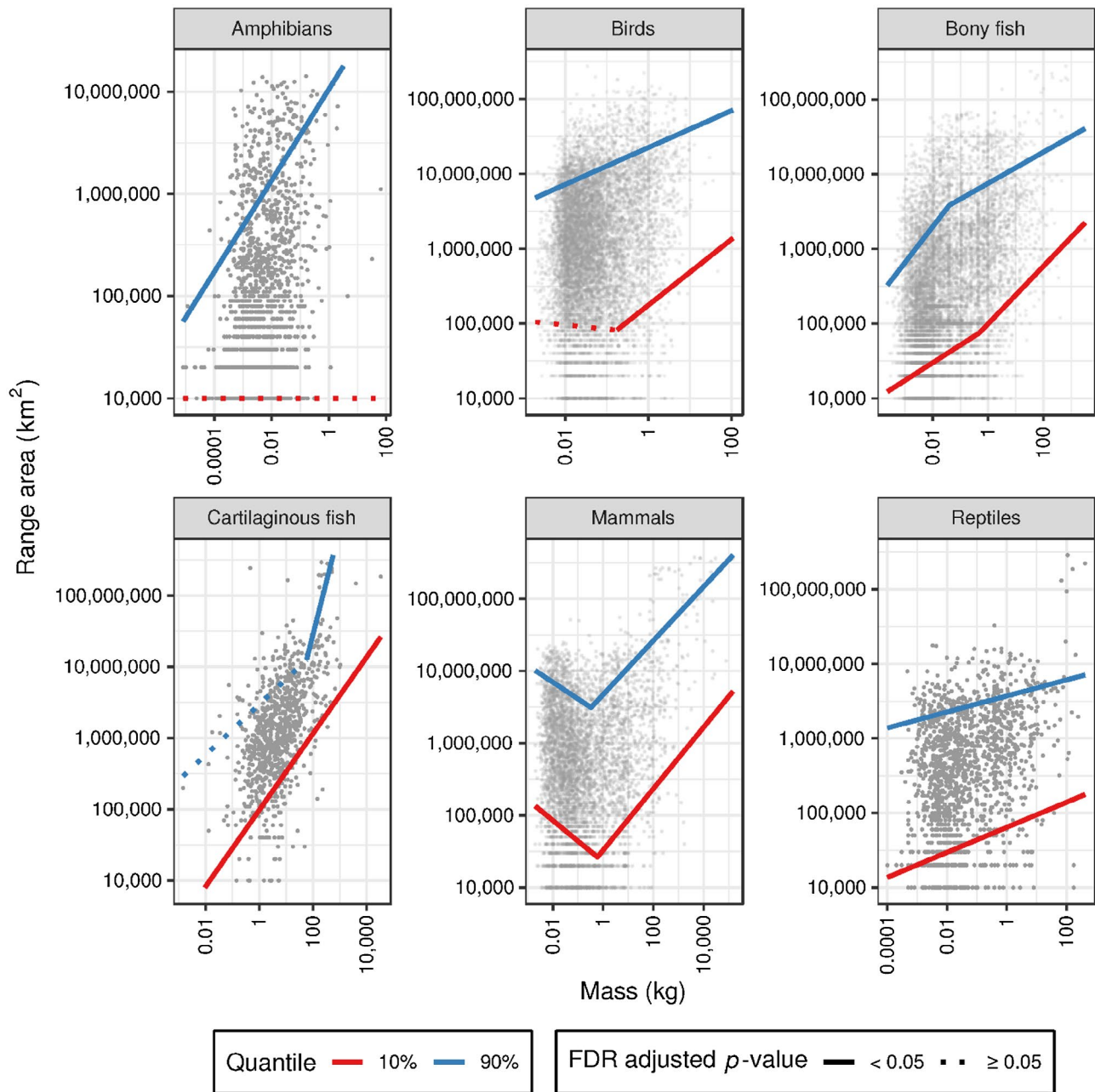
### 3.2 | Extinction risk

We found that species range size relative to the 10% quantile regression lower bound (i.e., "relative range area") is an excellent predictor of extinction risk for all classes except cartilaginous fish (Figures 1c, 3 and 4; Supporting Information Table S2). With the exception of cartilaginous fish, relationships between these variables for each class were estimated to be strongly negative, with model pseudo- $R^2$  values ranging from 0.35 for birds to 0.66 for amphibians (Figure 4; Supporting Information Table S2). This general pattern holds even when excluding species with range size  $\leq 20,000$  km<sup>2</sup> (pseudo- $R^2$  excluding cartilaginous fish, 0.28–0.51; Figure 5; Supporting Information Tables S3 and S4; Figure S2). In addition, our comparative assessment of extinction risk using range size alone as a predictor suggests that relative range size is generally better than range size alone, although the differences in explanatory power might not be large, as indicated by the similar  $R^2$  and AUC values (Supporting Information Tables S2 and S4; Figure S3). A total of 1,133 non-threatened species fall below the 10% quantile regression (Supporting Information Table S5). The majority are birds ( $n = 565$ ) and bony fish (296), and 1,006 of these species weigh  $< 1$  kg.

## 4 | DISCUSSION

We found that the contemporary range–body size relationship is typically positive at both the upper and lower bounds, and segmented relationships are common (Figure 2). Despite this variability, and with the exception of cartilaginous fish, species near the

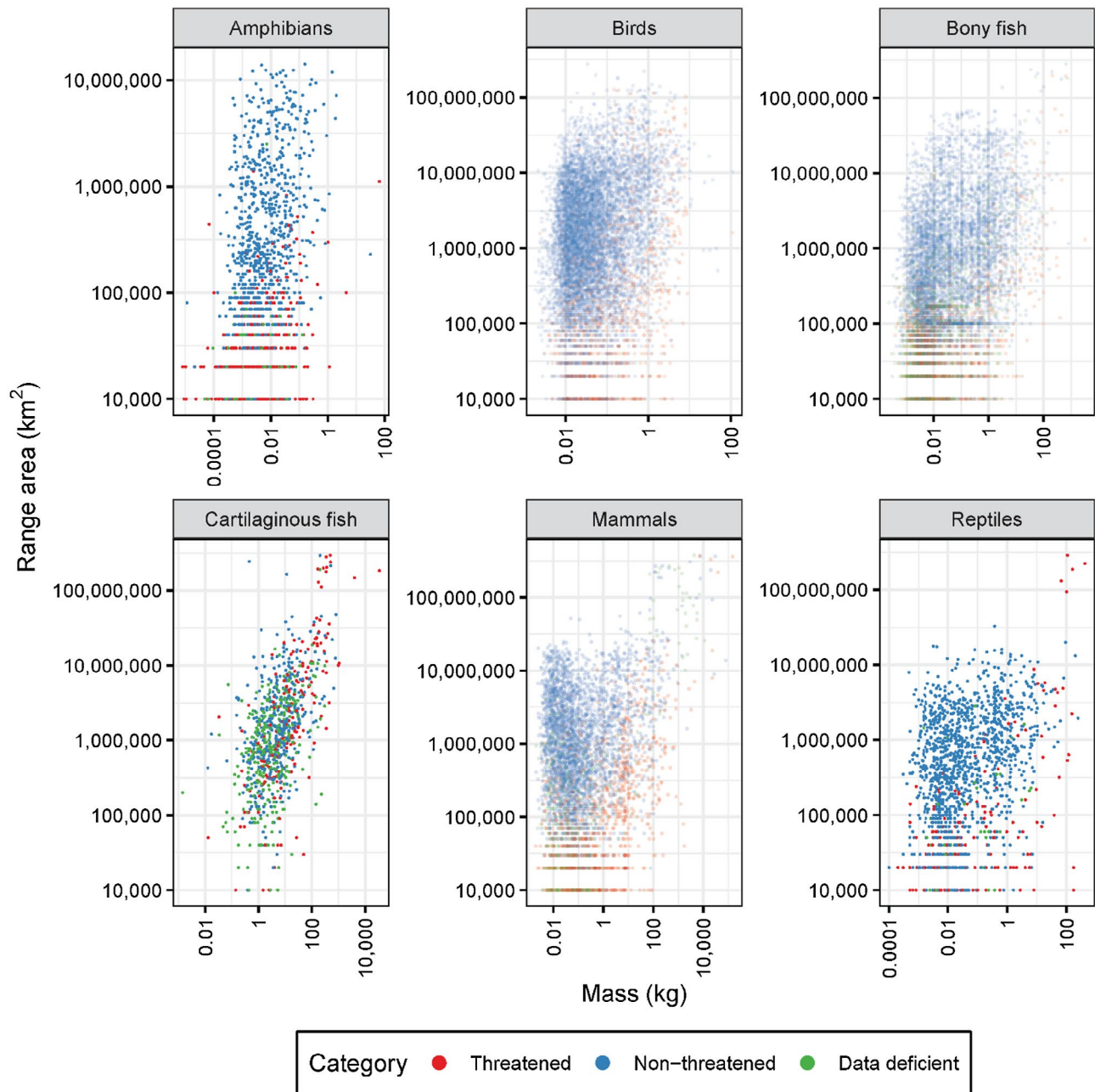




**FIGURE 2** Quantile regression fitted lines for the 10% (red) and 90% (blue) quantiles (Supporting Information Table S1). Models shown are segmented, except when the slopes on either side of the breakpoint were not significantly different from each other, in which case we used linear models instead. A residual auto-covariate based on phylogenetic tree distance was included to account for potential dependence (Supporting Information Table S1). Points indicate the observations in our dataset (i.e., each point corresponds to a different species) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

lower boundary of the range–body size relationship are increasingly in higher extinction risk categories, and this general pattern holds true after accounting for the role of range size in IUCN Red Listing criteria. This suggests that species extinction risk increases for species with smaller ranges for their body size, and that plots of range size versus body size at the scale of global or continental assemblages might be a useful tool for predicting extinction risk, hence informing conservation actions. Positive relationships at the upper boundaries of the range–body size relationship also suggest that small body size constrains the access to and exploitation of habitats

across large geographical areas, and that this applies to narrowly and broadly distributed species alike. This unoccupied or thinly occupied trait space above the upper boundary is potentially set by dispersal limitation preventing some smaller species from maintaining large ranges. However, differences between modes of dispersal (e.g., flight, swimming or walking) and environment (marine, terrestrial and freshwater; Supporting Information Figure S1) influence energetic constraints and efficiency of movement, potentially affecting the range–body size relationship. Clarification of the factors that influence the upper constraints on range size, across different habitat

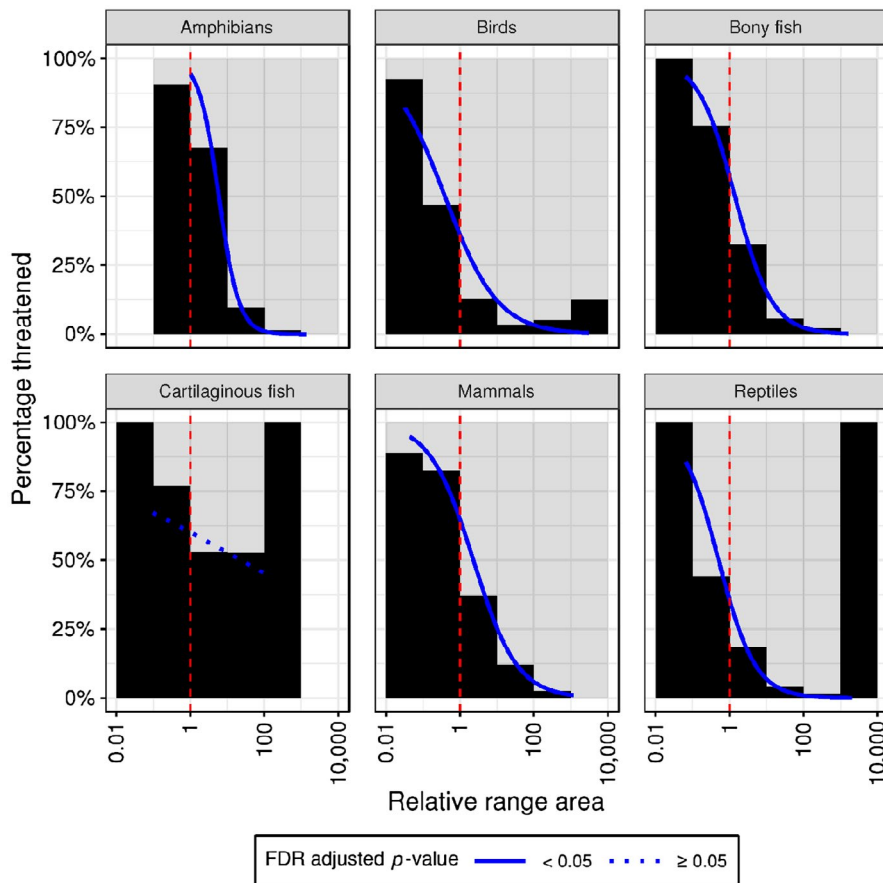


**FIGURE 3** Scatter plots of geographical range size (range area) versus body mass for each of the taxonomic classes in our analysis. Species are grouped into Threatened (International Union for Conservation of Nature Red List categories Vulnerable, Endangered and Critically Endangered), Non-threatened (categories Least Concern and Near Threatened) and Data Deficient (category Data Deficient). Range maps were coarsened using a 100 km x 100 km grid to ensure consistency across species [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

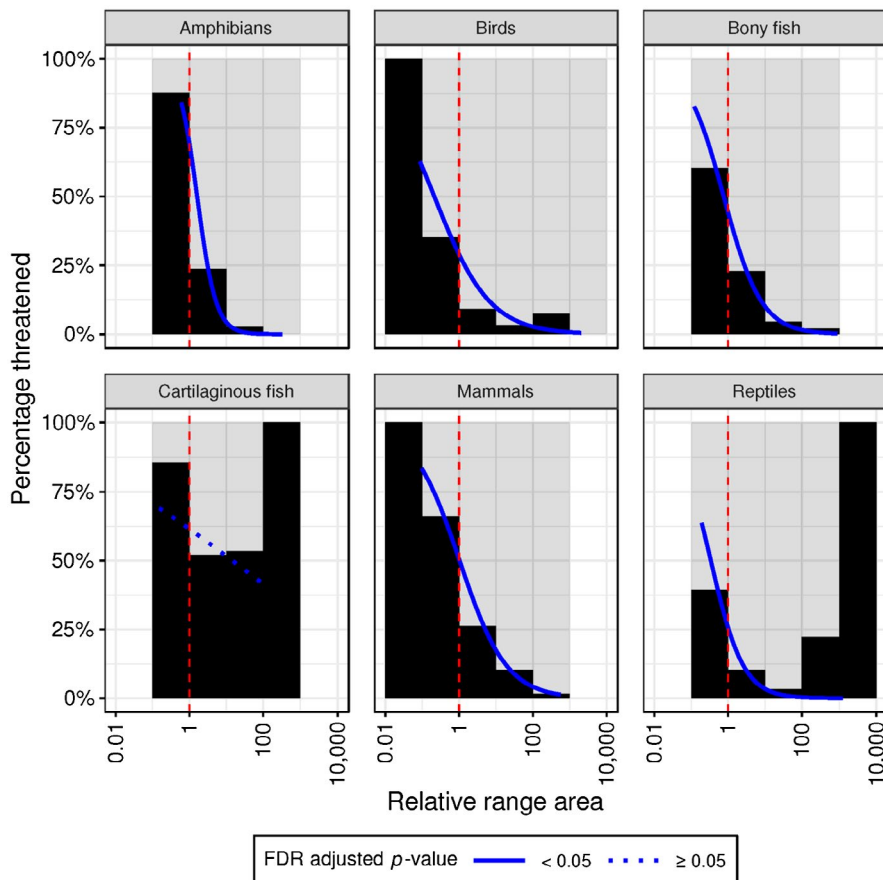
types, is thus an important knowledge gap that requires further examination.

We observed a segmented (nonlinear), negative relationship before the lower boundary breakpoint and a positive relationship after it for mammals (Figure 2). Agosta and Bernardo (2013) documented a similar breakpoint around the modal mammal body mass of 40 g. They attributed it to a trade-off between resource acquisition and conversion of resources into offspring, such that smaller and larger species require larger ranges to maintain viable populations. This

trade-off should be minimized at an optimal body size whereby the greatest amount of food resources can be most efficiently converted into offspring. According to Brown, Marquet, and Taper (1993), the body size at which this trade-off is optimized is 80–250 g. The breakpoint we observed at the lower bound is well above this hypothesized optimal body size, estimated at 597 g (95% CI: 217 g, 1,639 g) for mammals (Supporting Information Table S1). However, Brown et al. (1993) considered only terrestrial North American mammals, whereas we considered marine and terrestrial mammals at a global



**FIGURE 4** Relative range area versus percentage of species threatened for each of the classes in our analysis. Relative area is the range area of a species divided by the 10% quantile regression lower bound for that species, where the quantile regression models are based on using body mass to predict current range size (Figure 2; Supporting Information Table S1). Equivalently, the logarithm of the relative area is the vertical distance to the 10% quantile lower bound (Figure 2). The red vertical dashed lines correspond to range area equal to the 10% lower bound. Negative relationships in the histograms show that species with larger relative range areas tend to be less threatened. Blue lines are fitted probabilities based on phylogenetic logistic regression models [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 5** Relative range area versus percentage of species threatened for each of the classes in our analysis. Only species with range area of > 20,000 km<sup>2</sup> are considered here. Relative area is the range area of a species divided by the 10% quantile regression lower bound for that species, where the quantile regression models are based on using body mass to predict current range size (Supporting Information Figure S2; Table S4). Equivalently, the logarithm of the relative area is the vertical distance to the 10% quantile lower bound (Supporting Information Figure S2). The red vertical dashed lines correspond to range area equal to the 10% lower bound. Negative relationships in the histograms show that species with larger relative range areas tend to be less threatened. Blue lines are fitted probabilities based on phylogenetic logistic regression models [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



scale, which might explain the differences. In any case, we also observed a weak relationship (with negative point estimate) before the lower boundary (10% quantile) breakpoint and a positive relationship after it for birds (Figure 2). This suggests that the finding and conclusion by Agosta and Bernardo (2013) for mammals potentially extends to other taxonomic guilds. However, we note that our approach differed from that of Agosta and Bernardo (2013), who assessed relationships between range and body size either side of the mammal modal body mass of 40 g. We also included marine and terrestrial mammals together, although we found similar results when considering only terrestrial mammals (Supporting Information Figure S1).

Relationships between traits and range sizes of cartilaginous and bony fishes have not previously been compared globally, although range contractions are widespread (Worm & Tittensor, 2011). Below c. 100 kg body mass, cartilaginous and bony fishes had similar ranges (Figure 2), but at >100 kg, cartilaginous fishes had larger ranges than bony fishes (Figure 2). In our dataset, most bony fishes were freshwater species that evolved primarily in spatially confined river basins, whereas most cartilaginous fishes were of marine origin, with fewer geographical barriers to limit potential maximum range or body size. As such, it is not surprising that at >100 kg, the upper and lower boundary relationships for bony fishes were smaller in magnitude when compared with cartilaginous fishes. Conversely, the steep positive relationships and abundance of bony fish species <0.01 kg support hypotheses suggesting that small range size might be an important causal mechanism explaining the heightened extinction risk of small-bodied freshwater fishes (Kopf et al., 2017). Unusually, small ranges of some large bony fishes (e.g., sturgeon and salmon) may be sustained through anadromous life cycles, whereby adults access energy from the marine environment and use it for reproduction in freshwater. These marine energy subsidies allow these species to maintain large body sizes despite small freshwater ranges that are below the minimum boundary relationship. Many anadromous species (salmon and sturgeon) are threatened, but ecosystem energetics is only recently being invoked as an important issue limiting the conservation of freshwater fishes and river ecosystems (Naiman et al., 2012).

As noted above, our study confirms that vertebrates close to the lower boundary of the range–body size relationship are generally at greater risk of extinction, with negative relationships between percentage of species threatened and relative range area found for all classes except cartilaginous fish (Figures 3 and 4). Recent analyses show that range and body size are independently related to extinction risk (Ripple et al., 2017). Range size, in particular, has stood out as a good predictor of extinction risk for birds (Harris & Pimm, 2008; Manne, Brooks, & Pimm, 1999), some land mammals (Cardillo et al., 2004; Fritz, Bininda-Emonds, & Purvis, 2009; Purvis, Gittleman, Cowlishaw, & Mace, 2000) and squamate reptiles (Böhm et al., 2016). When we assessed range area alone as a predictor of extinction risk (Supporting Information Figure S3), we found that it was typically a poorer predictor than relative range area, based on a comparison of AIC,  $R^2$  and AUC values (Supporting Information Tables S2 and S4). This result supports Gaston and Blackburn (1996), who argued that

the range–body size plot might be more useful for assessing extinction risk than whether a given species is large or small or whether it is widespread or with a narrow distribution. They also argued that assessments of extinction risk using the range–body size plot may be meaningless if range was used to determine threat status at the outset. We attempted to overcome this issue by assessing extinction risk after excluding species with a range size  $\leq 20,000$  km<sup>2</sup> (the cut-off for a species potentially being listed as Vulnerable under the IUCN Red List criteria). We found that species range size relative to the 10% quantile regression lower bound (i.e., “relative range area”) is still a reliable predictor of extinction risk for all classes assessed, except cartilaginous fish (Figure 5; Supporting Information Table S4). This suggests the potential to use distance from the lower range–body size relationship as a complementary approach to assessing extinction risk for most taxonomic groups.

The IUCN Red List currently specifies that to be eligible as Vulnerable (lowest level of extinction risk necessary to be considered threatened), the extent of occurrence (equivalent to range size here) for a given species must be <20,000 km<sup>2</sup>. To overcome issues associated with species being incorrectly listed as threatened, they must also be severely fragmented and show either continuing declines or have extreme fluctuations in extent of occurrence, area of occupancy, number of locations or sub-populations or number of mature individuals. Aside from the 20,000 km<sup>2</sup> threshold being arbitrary, this approach relies on detailed population-level data for each species. As a consequence, the IUCN Red List has evaluated extinction risk for only <5% of the world's described species (IUCN, 2018), meaning that there is urgency in developing simple means by which extinction risk can be evaluated rapidly, including rules that can alert us to which species are most in need of urgent conservation intervention. The relationship between range and body size thus offers potential in this regard, especially for small-ranged species below the 20,000 km<sup>2</sup> threshold. In addition, our analysis uncovered that 1,133 non-threatened species fall below the lower bound (10% quantile regression; Supporting Information Table S5). If non-threatened species fall close to the lower bound or below it, it might indicate that they need further status assessments. Focusing on EOO (as assessed using coarsened IUCN range maps) is important in this regard, because AOO can be difficult to determine accurately for species that have not been studied intensively and might be rare or cryptic.

The range–body size relationship could also be used to track the trajectories of species towards extinction thresholds. If the range size of a given species declines over time owing to external pressures, the distance of a species to the lower bound of the range–body size relationship will decrease over time (Figure 1c). By plotting this trajectory, it might offer a crucial warning about species reaching points where they are increasingly threatened with extinction. This process ideally requires historical range sizes, which can differ dramatically from the current range sizes used in our analysis, to be plotted against body size to enable the original lower bound or extinction threshold to be defined. But where historic range size is unknown for a majority of species in a given class, this approach requires acceptance of the threshold being defined by today's estimates. Assuming

that there has been a retraction of range size of most species over time, the current lower bound identified herein is likely to sit lower than historically, which potentially underestimates extinction risk. However, given that our comparison of extinction risk using distance to the 10% quantile regression supports threatened species status under the IUCN Red List (Figure 3), this quantile is arguably an appropriate baseline for future assessments. It is also important to note that historical geographical ranges were likely to be less impacted by some anthropogenic pressures, with habitat fragmentation and loss in particular being a key driver of vertebrate extinctions (Ripple et al., 2017). The historic lower boundary of the range–body size relationship might therefore have been sharper or less variable and set by energetic constraints and longer-term macroevolutionary processes of speciation and extinction. Current variability in the lower boundary is potentially caused by species exhibiting combinations of ranges and body sizes that may be evolutionarily maladaptive and transient. Nowadays, human activity pulls species down the y axis by reducing range size (Figure 1c) but might also, through conservation efforts (e.g., species reintroductions and population supplementation), artificially maintain some species in regions of the range–body size trait space that would usually see them rapidly go extinct.

## DATA ACCESSIBILITY STATEMENT

All the data used in this paper come from publicly available sources, as outlined by Ripple et al. (2017, 2019).

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## REFERENCES

- Agosta, S. J., & Bernardo, J. (2013). New macroecological insights into functional constraints on mammalian geographical range size. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20130140. <https://doi.org/10.1098/rspb.2013.0140>
- Agosta, S. J., Bernardo, J., Ceballos, G., & Steele, M. A. (2013). A macro-physiological analysis of energetic constraints on geographic range size in mammals. *PLoS ONE*, 8, e72731. <https://doi.org/10.1371/journal.pone.0072731>
- Bardos, D. C., Guillera-Aroita, G., & Wintle, B. A. (2015). Valid auto-models for spatially autocorrelated occupancy and abundance data. *Methods in Ecology and Evolution*, 6, 1137–1149. <https://doi.org/10.1111/2041-210X.12402>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- BirdLife International. (2018). *BirdLife international and handbook of the birds of the world. Bird species distribution maps of the world* (Version 2018.1). Retrieved from <http://datazone.birdlife.org/species/taxonomy>
- Böhm, M., Williams, R., Bramhall, H. R., McMillan, K. M., Davidson, A. D., Garcia, A., ... Collen, B. (2016). Correlates of extinction risk in squamate reptiles: The relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography*, 25, 391–405. <https://doi.org/10.1111/geb.12419>
- Boyer, A. G., & Jetz, W. (2012). *Conservation biology. Metabolic ecology: A scaling approach*. Oxford: John Wiley & Sons Ltd.
- Brown, J. H., & Maurer, B. A. (1987). Evolution of species assemblages: Effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *The American Naturalist*, 130, 1–17. <https://doi.org/10.1086/284694>
- Brown, J. H., Marquet, P. A., & Taper, M. L. (1993). Evolution of body size: Consequences of an energetic definition of fitness. *The American Naturalist*, 142, 573–584. <https://doi.org/10.1086/285558>
- Cade, B. S., & Noon, B. R. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 1, 412–420. [https://doi.org/10.1890/1540-9295\(2003\)001\[0412:AGITQR\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2)
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology*, 2, e197. <https://doi.org/10.1371/journal.pbio.0020197>
- Crase, B., Liedloff, A. C., & Wintle, B. A. (2012). A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography*, 35, 879–888. <https://doi.org/10.1111/j.1600-0587.2011.07138.x>
- Faurby, S., Davis, M., Pedersen, R. Ø., Schowaneck, S. D., Antonelli, A., & Svenning, J. (2018a). Data from: PHYLOCINE 1.2: The phylogenetic atlas of mammal macroecology. *Dryad Digital Repository*, 9. <https://doi.org/10.5061/dryad.bp26v20>
- Faurby, S., Davis, M., Pedersen, R. Ø., Schowaneck, S. D., Antonelli, A., & Svenning, J. (2018b). PHYLOCINE 1.2: The Phylogenetic atlas of mammal macroecology. *Ecology*, 99, 2626.
- Fritz, S. A., Bininda-Emonds, O. R. P., & 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>
- Gaston, K. J., & Blackburn, T. M. (1996). Conservation implications of geographic range size–body size relationships. *Conservation Biology*, 10, 638–646.
- Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and process in macroecology*. Oxford: Blackwell Publishing.
- Gaston, K. J., & Fuller, R. A. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology*, 46, 1–9. <https://doi.org/10.1111/j.1365-2664.2008.01596.x>
- González-Suárez, M., & Revilla, E. (2013). Variability in life-history and ecological traits is a buffer against extinction in mammals. *Ecology Letters*, 16, 242–251. <https://doi.org/10.1111/ele.12035>
- Harris, G., & Pimm, S. L. (2008). Range size and extinction risk in forest birds. *Conservation Biology*, 22, 163–171. <https://doi.org/10.1111/j.1523-1739.2007.00798.x>
- Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 13384–13389. <https://doi.org/10.1073/pnas.0704469104>
- IUCN. (2018). *The IUCN red list of threatened species* (Version 2018.1). Gland, Switzerland: International Union for Conservation of Nature and Natural Resources. <https://www.iucnredlist.org/>
- Ives, A. R. (2019).  $R^2$ s for correlated data: Phylogenetic models, LMMs, and GLMMs. *Systematic Biology*, 68, 234–251. <https://doi.org/10.1093/sysbio/syy060>
- Ives, A. R., & Li, D. (2018). rr2: An R package to calculate  $R^2$ s for regression models. *Journal of Open Source Software*, 30, 1028. <https://doi.org/10.21105/joss.01028>
- Jetz, W., & Pyron, R. A. (2018). The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology & Evolution*, 2, 850–858. <https://doi.org/10.1038/s41559-018-0515-5>
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444–448. <https://doi.org/10.1038/nature11631>

- Jetz, W., Thomas, G. H., Joy, J. B., Redding, D. W., Hartmann, K., & Mooers, A. O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, 24, 919–930. <https://doi.org/10.1016/j.cub.2014.03.011>
- Keith, D. A. (1998). An evaluation and modification of World Conservation Union Red List criteria for classification of extinction risk in vascular plants. *Conservation Biology*, 12, 1076–1090. <https://doi.org/10.1046/j.1523-1739.1998.97202.x>
- Koenker, R. (2018). *quantreg: Quantile regression* (R package version 5.05). Vienna, Austria: R Foundation for Statistical Computing.
- Kopf, R. K., Shaw, C., & Humphries, P. (2017). Trait-based prediction of extinction risk of small-bodied freshwater fishes. *Conservation Biology*, 31, 581–591. <https://doi.org/10.1111/cobi.12882>
- Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akcakaya, H. R., Leader-Williams, N., ... Stuart, S. N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, 22, 1424–1442. <https://doi.org/10.1111/j.1523-1739.2008.01044.x>
- Manne, L. L., Brooks, T. M., & Pimm, S. L. (1999). Relative risk of extinction of passerine birds on continents and islands. *Nature*, 399, 258–261. <https://doi.org/10.1038/20436>
- Naiman, R. J., Alldredge, J. R., Beauchamp, D. A., Bisson, P. A., Congleton, J., Henny, C. J., ... Wood, C. C. (2012). Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 21201–21207. <https://doi.org/10.1073/pnas.1213408109>
- Nakagawa, S., & De Villemereuil, P. (2019). A general method for simultaneously accounting for phylogenetic and species sampling uncertainty via Rubin's rules in comparative analysis. *Systematic Biology*, 68, 632–641. <https://doi.org/10.1093/sysbio/syy089>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Payne, J. L., & Finnegan, S. (2007). The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 10506–10511. <https://doi.org/10.1073/pnas.0701257104>
- Purvis, A., Gittleman, J. L., Cowlshaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*, 267, 1947–1952. <https://doi.org/10.1098/rspb.2000.1234>
- R Development Core Team. (2009). *R: A language and environment for statistical computing* (Version 2.92). Vienna, Austria: R Foundation for Statistical Computing.
- Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., ... Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392–395. <https://doi.org/10.1038/s41586-018-0273-1>
- Ripple, W. J., Wolf, C., Newsome, T. M., Betts, M. G., Ceballos, G., Courchamp, F., ... Worm, B. (2019). Are we eating the world's megafauna to extinction? *Conservation Letters*, e12627. <https://doi.org/10.1111/conl.12627>
- Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., & McCauley, D. J. (2017). Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 10678–10683. <https://doi.org/10.1073/pnas.1702078114>
- Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., & Müller, M. (2011). pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, 12, 77. <https://doi.org/10.1186/1471-2105-12-77>
- Smith, F. A., Elliott Smith, R. E., Lyons, S. K., Payne, J. L., & Villaseñor, A. (2019). The accelerating influence of humans on mammalian macroecological patterns over the late Quaternary. *Quaternary Science Reviews*, 211, 1–16. <https://doi.org/10.1016/j.quascirev.2019.02.031>
- Stein, R. W., Mull, C. G., Kuhn, T. S., Aschliman, N. C., Davidson, L. N. K., Joy, J. B., ... Mooers, A. O. (2018). Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nature Ecology & Evolution*, 2, 288–298. <https://doi.org/10.1038/s41559-017-0448-4>
- Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, 204, 23–31. <https://doi.org/10.1016/j.biocon.2016.03.039>
- Tung Ho, L. s., & Ané, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, 63, 397–408. <https://doi.org/10.1093/sysbio/syu005>
- Worm, B., & Tittensor, D. P. (2011). Range contraction in large pelagic predators. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 11942–11947. <https://doi.org/10.1073/pnas.1102353108>

## BIOSKETCH

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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