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RESEARCH ARTICLE

Environmental correlates of body size influence range size and extinction risk: A global study in rodents

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Abstract

Aim: Species-level traits, such as body and range sizes, are important correlates of extinction risk. However, both are often related and are driven by environmental factors. Here, we elucidated links between environmental factors, body size, range size and susceptibility to extinction, across the whole order of rodents.

Location: Global.

Time period: Current.

Major taxa studied: Rodents (order Rodentia).

Methods: We compiled an unprecedentedly large database of rodent morphology, phylogeny, range size, conservation status, global climate and normalized difference vegetation index (NDVI), comprising >86% of all described species. Using phylogenetic regressions, we initially explored the environmental factors driving body size. Next, we modelled the relationship between body size and range size. From this relationship, we computed and mapped (at the assemblage level) an index of relative range size, corresponding to the deviation from the expected range size of each species, given its body size. Finally, we tested whether relative range was correlated with the risk of extinction of the species derived from an assessment by the International Union for Conservation of Nature.

Results: We found that, contrary to the expectations of Bergmann's rule, the body size of rodents was mostly influenced by variation in NDVI (rather than latitude/temperature). Body size, in turn, imposed a constraint on species range size, as evidenced by a triangular relationship that was segmented at the lower bound. The relative species range size derived from this relationship highlighted four geographical regions where rodents with small relative range were concentrated globally. We demonstrated that lower relative range size was associated with increased risk of extinction.

Main conclusions: Species that, given their body size, are distributed across ranges that are smaller than expected have elevated extinction risk. Therefore, investigating the relationships between environmental drivers, body size and range size might help to detect species that could become threatened in the near future.

1 | INTRODUCTION

Given the global decrease in biodiversity, now more than ever, there is a need to identify and focus conservation efforts proactively on species that are susceptible to extinction. One way to identify such susceptible species is by use of a "comparative extinction risk analysis" whereby those at risk are identified from intrinsic and extrinsic traits (see Murray et al., 2014). Several species-level traits have been associated with increasing extinction risk in vertebrates. Perhaps the most important among the intrinsic factors is a large body size and among the extrinsic factors is perhaps a small range size (Böhm et al., 2016; Cardillo et al., 2006; Lucas et al., 2019; Owens & Bennett, 2000; Tingley et al., 2013), and undoubtedly, these factors are correlated. Range size and body size have also evolved in relationship to environmental conditions, which means that some ecological factors have probably shaped intrinsic and extrinsic species traits linked to their present-day extinction risk over long-term evolutionary processes.

Range size is an interesting species trait to study from both evolutionary and conservation perspectives (Gaston, 1998). Some argue that a smaller range size has among the strongest effects on extinction risk (Böhm et al., 2016; Davidson et al., 2009; Purvis et al., 2000); therefore, understanding the origins of range size variation has important practical implications for conservation. The range size of a species can generally be described as a function of its dispersal ability (Gaston, 2003; but see Lester et al., 2007) and its niche breadth (i.e., the range of resources the species can use or its environmental tolerance; Slatyer et al., 2013). Moreover, range area is expected to covary with species-level traits that influence species dispersal ability, creating a complex interaction between ecological factors, species intrinsic traits and range size.

Several hypotheses have been proposed to explain variation in range size. One such hypothesis is Rapoport's rule, which posits that the ranges tend to be smaller at lower latitudes (and vice versa) (Stevens, 1989). It is mostly explained as a consequence of higher latitudes being associated with greater seasonal variability, which, in turn, are occupied by species with a greater tolerance for variable climates, allowing them to occupy a larger range size (Böhm et al., 2017; Stevens, 1989). An expected consequence is to find more small-ranged species in the tropics, where this trait would exacerbate extinction risk in these species-rich areas (Ceballos & Ehrlich, 2006). Although this rule has been found to apply in various vertebrates (e.g., Arita et al., 2005; Blanchet et al., 2013; Böhm et al., 2017; Whitton et al., 2012), support for it is far from being universal, and whether it constitutes a true rule has been debated (Gaston et al., 1998).

Variation in range size has also been explained in terms of body size (Blackburn & Gaston, 1996). Under this hypothesis, there is a

lower limit to species range size set by body size (i.e., larger species need larger areas because of energetic constraints; Newsome et al., 2020). The association between body size and range size differs among taxa (Böhm et al., 2017). In mammals, the relationship is triangular (Blackburn & Gaston, 1996; Davidson et al., 2009), where the lower bound of range area is constrained by body size because of energetic constraints, while the upper boundary is simply a consequence of habitat availability (Newsome et al., 2020). Additionally, range size is often associated with body size because animals with larger bodies can withstand broader thermal differences across a large, climatically variable range (and vice versa) (Böhm et al., 2017).

Range size is not the only commonly studied correlate of body size. Bergmann's rule is a well-known explanation of body size variation, which postulates that larger body sizes are associated with higher latitudes, which have lower temperatures (Mayr, 1956). This is generally attributed to an evolutionary adaptation for thermoregulation (Meiri, 2011). Therefore, Bergmann's rule has often been extended beyond a simple latitudinal gradient to a relationship between body size and temperature, and is thus commonly studied by exploring the association between species body mass or size and climatic variables (Alhajeri & Steppan, 2016; Meiri, 2011). The positive relationship between body size and temperature is thus explained because small-sized species are better at heat dissipation, whereas larger species are more efficient in terms of heat retention (Mayr, 1956), which, incidentally, makes the latter less susceptible to climatic variation and thus able to occupy large range areas. As a consequence, it might have unexpected conservation implications, with environmental drivers of body size influencing the extinction risk of species by imposing a constraint on range size. Given that larger species tend to be found at higher latitudes and lower temperatures, they, in turn, might have a larger range size, and therefore be less prone to extinction. Conversely, species adapted to warmer environments would generally be smaller, have smaller range size, and thus face higher extinction risk (see Newsome et al., 2020).

The diversity of mammals has been particularly threatened by human activity (Andermann et al., 2020; Barnosky et al., 2011). High extinction risk in mammals is associated with a large body size and a small range size (Cardillo et al., 2006, 2008), two factors that are correlated (Newsome et al., 2020). Thus, at least in theory, small-bodied mammals should be less vulnerable to extinction. However, this does not appear to be the case, because rodents, which are among the smallest mammal species, still face high extinction risk [*c.* 14.5% are classified at least as "vulnerable" in the International Union for Conservation of Nature (IUCN) red list], especially in some regions (Kennerley et al., 2021). The full extent of extinction risk in rodents might be underestimated, given that there has been less conservation assessment of rodents than of larger mammals (Verde Arregoitia, 2016). Understanding the role that range size plays in the

extinction risk of rodents can help to predict which species might become threatened, especially if the relationship between range size and body size, in addition to the environmental drivers of the latter, are also clarified.

Here, we use a recently compiled, unprecedentedly large dataset of morphological measurements of rodents (Alhajeri, Fourcade, et al., 2020), in addition to publicly available data on environmental factors, phylogeny, range size and extinction risk, to disentangle the complex relationships between environmental correlates of body size, range size and extinction risk in rodents. Previous evidence showed that although ecogeographical patterns, such as Bergmann's rule, generally hold for vertebrates, they might not necessarily do so in rodents, whose size seems to covary more with precipitation-related climatic factors (Alhajeri & Fourcade, 2019; Alhajeri & Steppan, 2016), in accordance with the "resource availability hypothesis" (see Alhajeri, Porto, & Maestri, 2020). Therefore, we initially tested Bergmann's rule (correlating body size with latitude and temperature) and the resource availability hypothesis (correlating body size with precipitation and vegetation productivity) to determine the drivers of body size variation in this taxon. Next, we modelled the relationship between the body size of rodents and their range area. Finally, we identified species with smaller ranges than expected relative to their size (i.e., species that deviate from the lower bound) and linked this to their extinction risk. This is the first global phylogenetic comparative study on extinction risk of rodents to be carried out based on such a large sample size and at large taxonomic and spatial scales. Our results have the potential to help in identification of threatened rodent species based on their traits, allowing the implementation of early preventative conservation efforts.

2 | METHODS

2.1 | Species data

This study relies largely on a considerable, recently compiled morphological dataset, originally used to investigate the relationship between appendage length and climate (i.e., Allen's rule; Alhajeri, Fourcade, et al., 2020). In that dataset, head-and-body length was collected from 285 different sources, including museum databases and the literature, forming a total of 81,880 measurements of 2212 rodent species. From this dataset, we extracted the mean and standard deviation of the head-and-body length of each species. According to Burgin et al. (2018), there are a total of 2552 described rodent species, which means that our dataset covered >86% of all described species. Although the dataset compiled by Alhajeri, Fourcade, et al. (2020) also contains measurements of body mass, we used head-and-body length as a proxy for body size here because the former was available for only 1191 species and because the two variables were highly correlated. The date of collection was not always available, but the specimens examined span at least the 19th and 20th centuries.

We obtained species range maps from the International Union for Conservation of Nature (IUCN, 2017) for all 2212 species. These data are distributed in the form of shapefiles (available at: www. iucnredlist.org/resources/spatial-data-download) depicting the known global distribution of each species as assessed by the IUCN. Such distributional data are mostly produced by expert knowledge, supplemented by empirical records and habitat filtering. As such, they might fail to account for fine-scale variation in species presence and absence (Herkt et al., 2017) but provide a nearly comprehensive assessment that would otherwise be difficult to gather at such a large spatial and taxonomic scale (Schipper et al., 2008). In particular, we expect them to be accurate enough to rank species properly by their range area (see e.g., Alhajeri, Fourcade, et al., 2020; Newsome et al., 2020; Rodrigues et al., 2006), and they have been shown to be as effective as true occurrence data in estimating basic climatic conditions experienced by each species (Alhajeri & Fourcade, 2019). Here, we extracted species range size as the total area covered by all polygons where each species is present currently, using the "letsR" package (Vilela & Villalobos, 2015) for the software R v.4.0.2 (R Core Team, 2020). The full description of the database and collection methods, including morphology and species range, is available in the paper by Alhajeri, Fourcade, et al. (2020). From the IUCN maps, we also extracted the mean and standard deviation of the latitudinal coordinates of each species range.

In addition, we used the IUCN database to obtain the conservation status of each species and the criteria that led to this status (IUCN, 2017), which was used to characterize extinction risk and filter species (see section 2.5). The IUCN reports conservation status using a scale of seven categories from "least concern" to "extinct"; this ranks species on whether they are threatened with extinction according to a series of criteria related to population trends and the size of the remaining natural range (Rodrigues et al., 2006). Among the 2212 rodent species that we analysed, 351 were classified as "data deficient", which means that their conservation status was evaluated, but insufficient information was available for a reliable conclusion regarding their extinction risk. These species were thus not used in the analyses involving extinction risk but were retained in all other steps. In total, 83% of the remaining species (1548) are not immediately threatened (categories "least concern" and "near threatened"), while 17% (311) are at risk of extinction (categories "vulnerable", "endangered" and "critically endangered"), and another two species are already extinct. The conservation status of species was accessed with the R package "rredlist" (Chamberlain, 2020).

When investigating interspecific variation in species traits, it is essential to consider that species are not independent of each other, because they are all phylogenetically related. Therefore, in all analyses described below, we adopted statistical approaches that accounted for the phylogenetic relatedness of the species. For this purpose, we obtained a sample of 100 trees (because there are uncertainties in phylogenetic placements and node ages) from the phylogenetic trees estimated by Upham et al. (2019), which are currently the most up-to-date source for these data. We used both "DNA-only" trees, which are those that contain only the species

for which DNA data were available, and "completed" trees, where species missing DNA data were imputed. Some species in our morphological database were missing from the phylogenetic dataset; therefore, ultimately, analyses were based on 2170 species when using the completed trees and 1466 species when using the DNA-only trees. Additional information regarding phylogenetic trees and the way in which we handled taxonomic matching between morphological and phylogenetic databases can be found in the papers by Upham et al. (2019) and Alhajeri, Fourcade, et al. (2020).

2.2 | Environmental variables

We obtained climatic variables from the WorldClim project (v.2), which compiles mean temperature and precipitation from a set of weather stations, from the years 1970 to 2000, to interpolate global raster maps of climate (Fick & Hijmans, 2017). Specifically, we downloaded all 19 bioclimatic rasters at a resolution of 2.5 arc-min (from https://www.worldclim.org/), which are biologically meaningful climate variables derived from monthly temperature and rainfall. Instead of considering all bioclimatic variables and testing which is correlated best with body size, we reduced our set of predictors using a varimax-rotated principal components analysis (PCA), as implemented in the "psych" R package (Revelle, 2020). The resulting principal components 1 and 2 represent >70% of the total climatic variation and are strongly related to temperature and precipitation variables, respectively (Supporting Information Table S1; Figure S1). This allowed us to summarize global climatic variation into two predictors that are based on the climatic aspects that are most relevant to the species examined. Given that there might be discrepancies between the dates of morphological measurements and climate data, we tested whether climate variables from different time periods would lead to the same results. For this, we created the same climate variables using monthly precipitation, minimum and maximum temperature for the periods 1901–1905 and 2001–2005 (i.e., two climate datasets separated by one century), downloaded from the CHELSAcruts database (Karger et al., 2017; Karger & Zimmermann, 2018).

In addition, we used the normalized difference vegetation index (NDVI), which is a remote sensing-derived index of vegetation productivity, as a proxy of global variation in resource availability. As a source of NDVI data, we compiled all bimonthly rasters from the Global Inventory Modelling and Mapping Studies (GIMMS) NDVI3g database, for the period 1990–2009. The GIMMS project is a long-term NDVI time series derived from several Advanced Very-High-Resolution Radiometer (AVHRR) sensors (Zeng et al., 2013). Here, we accessed the GIMMS NDVI data using the "gimms" R package (Detsch, 2020) and calculated an average global NDVI at 5 arc-min resolution using the mean values over the aforementioned period.

To account for intraspecific variability in the environmental conditions experienced by species within their distribution, we extracted, for each species, the mean and standard deviation of both climate variables (PCA axes) and NDVI across their entire range.

2.3 | Correlates of body size

We first tested the association between head-and-body length and several environmental variables to disentangle the role of the latter in shaping the evolution of body size. Following the hypothesis of Bergmann's rule (Mayr, 1956), whereby relatively larger species are expected to be found closer to the poles, we initially tested whether there was a geographical gradient in body length by regressing head-and-body length with latitude. Given that this hypothesis is usually defined in a context of thermoregulation, we also estimated the relationship between head-and-body length and the first axis of our varimax-rotated PCA of bioclimatic variables (Supporting Information Figure S1), which is highly correlated with temperature variables (Supporting Information Table S1). There are additional hypotheses regarding the drivers of body size in rodents, namely that precipitation and resource availability might play a role in explaining geographical variation in body size (Alhajeri, Porto, & Maestri, 2020; Alhajeri & Steppan, 2016). Therefore, we also estimated the association between head-and-body length and the second axis of the varimax-rotated PCA of bioclimatic variables (associated with precipitation variables; see Supporting Information Table S1; Figure S1) and NDVI, respectively.

We followed here the approach developed by Alhajeri, Fourcade, et al. (2020). Analyses were carried out as phylogenetic linear regressions to correct for relatedness among species, which were computed using the "phylolm" R package (Ho & Ané, 2014) with a Pagel's λ phylogenetic model of trait evolution (Pagel, 1999). To account for phylogenetic uncertainty, all analyses were repeated for each of the 100 phylogenetic trees, for both the DNA-only and the completed trees. Given that intraspecific phenotypic variability can also be a source of bias in cross-species analyses (Silvestro et al., 2015), we also repeated each analysis 100 times, each time sampling: (1) an arbitrary value of head-and-body length from a truncated normal distribution (ensuring that sampled values were positive) with the mean and standard deviation obtained from the observed values from our database of morphological measurements, and (2) an arbitrary value of latitude, climate (temperature or precipitation) or NDVI, following a normal distribution with the mean and standard deviation of the observed values within the species range. For each of the DNA-only and the completed sets of trees, we report the mean estimate of the slope between head-and-body length and latitude, climate or NDVI, with 95% confidence intervals (CIs) based on the distribution of these values across the 100 trees and the 100 sampled values (i.e., 10,000 phylogenetic regressions per variable), in addition to the proportion of positive or negative coefficients that were significant at the α = .05 level. Values of head-and-body length were ln-transformed before analyses, and explanatory variables were scaled and centred such that effects sizes could be compared. We also compared the coefficients of the regression between body size and temperature (PCA axis 1) or precipitation (PCA axis 2), estimated using climate from 1901–1905 or from 2001–2005, in order to determine whether the time period of climate data influenced our results.

In addition to examining effect sizes, we identified the main driver of head-and-body length variation across species by comparing models computed with different sets of variables according to their corrected Akaike information criterion (AICc; Burnham & Anderson, 2002). For each replicate of sampled values and phylogenetic tree, we performed six phylogenetic regressions: four univariate models with each of the four variables we aimed to test (latitude, temperature, precipitation and NDVI) as single explanatory variables, one model that incorporated both temperature and precipitation variables to test whether climate as a whole could be the best predictor of body size, and one null model (intercept-only model that served as a reference to test whether our selected predictors had an effect on body size variation). We then extracted the AICc weight of each model and summarized this value across the 10,000 replicates.

2.4 | Modelling body size constraints on range size

Following Agosta and Bernardo (2013) and Newsome et al. (2020), we described the association between range size and body size (head-and-body length) as a triangular log–log relationship, where a breakpoint in the lower bound is expected to occur at mid-values of body size. For this purpose, we fitted quantile regressions for the 95 and 5% quantiles to estimate the upper and lower bounds of the relationship. Specifically, the lower quantile was fitted with a segmented regression to allow for a change in the slope, and the location of the breakpoint was estimated using the maximum-likelihood approach implemented in the "segmented" R package (Muggeo, 2008). Quantile regressions were computed with the "quantreg" R package (Koenker, 2021).

Phylogenetic interdependence between the species was accounted for, following the approach of Newsome et al. (2020). First, (segmented) quantile regressions were fitted without incorporating phylogenetic information. Second, we calculated a phylogenetic residual auto-covariate using the inverse distance squared weighted mean of the residuals, where phylogenetic distances were defined as one minus the phylogenetic correlation matrix between the species. Finally, we refitted the (segmented) quantile regressions with the phylogenetic residual auto-covariate included as an additional predictor to adjust for phylogenetic relatedness. To verify that this procedure effectively reduced the phylogenetic signal in model residuals, we report Pagel's λ derived from an intercept-only phylogenetic regression (computed with the "phylolm" R package) fitted to the residuals of the (segmented) quantile regressions, before and after incorporating the phylogenetic residual auto-covariate.

Although theoretical hypotheses and empirical observations in mammals (Newsome et al., 2020) pointed to a triangular relationship, we tested, in addition to quantile regressions, whether a simple linear relationship could exist between range size and head-and-body length. Therefore, we also ran phylogenetic regressions using the "phylolm" R package, with the same procedure as used for the analyses of the environmental correlates of body size. The whole approach (i.e., quantile regression for the upper quantile, segmented

quantile regression for the lower quantile, and linear phylogenetic regression) was repeated 20,000 times, because we sampled 100 values of head-and-body length, and we used 100 random samples of DNA-only and completed phylogenetic trees. We report the mean estimates and 95% CIs of all parameters (slopes, breakpoints, etc.) from the distribution of these values across the replicates. We also report the proportion of positive or negative coefficients that were significant at the $\alpha = .05$ level.

2.5 | Extinction risk and range size

To describe how the constraints that body size imposes on range size influence, in turn, the extinction risk of the species, we first defined relative range size as the ln-transformed ratio of the observed range area for the species divided by its theoretical minimum range area given its body size, as predicted by the lower bound of the quantile regression described in the previous section (see Newsome et al., 2020). For illustrative purposes, we plotted the variation in mean estimated relative range size of species across the phylogenetic tree of rodents, computing ancestral values using the re-rooting maximum-likelihood method of the "phytools" R package (Revell, 2012). In addition, we mapped the global variation in relative range size across assemblages of rodents, defined as 2° equal-area grid cells where species were considered present if their distribution overlapped any surface of it. Using the relative range size we had estimated for each species, we counted, in each grid cell, the number of species with a small relative range (defined as 5.62, corresponding to the mean minus one standard deviation of estimated values), which we divided by the total number of rodent species in each grid cell.

We chose to model extinction risk as a continuous variable; for this, we converted IUCN conservation status to values ranging between zero and one, representing increasing risk of species extinction. Since there are six possible conservation status, extinction risk was coded as follows: "least concern" = 0, "near threatened" = .2, "vulnerable" = .4, "endangered" = .6, "critically endangered" = .8 and "extinct" = 1. We modelled the relationship between extinction risk of species and their relative range size using phylogenetic regressions computed with the "phylolm" R package, after logit transformation of extinction risk to model a logistic relationship. To account for phylogenetic uncertainties and intraspecific body size variation, phylogenetic regressions were repeated for 20,000 values of relative range size that correspond to each replicate of the quantile regressions that modelled body size constraints on range size, using the corresponding phylogenetic tree that served to compute the phylogenetic residual auto-covariate. Given that IUCN conservation assessments are based, in part, on species range size, we carried out this analysis for those species whose conservation status was not decided based on criterion B (small range size) (Le Breton et al., 2019), therefore excluding 257 species. For comparison, we also report results for the whole set of rodent species used in this study. Again, we report the mean estimate and the 95% CIs from the distribution of regression coefficients across replicates and report

the proportion of positive or negative coefficients that were significant at the α = .05 level.

Given that IUCN conservation categories are essentially an ordinal variable, we acknowledge that our continuous interpretation of extinction risk is imperfect. This approach was taken here in order to keep a consistent framework consisting of 20,000 repetitions of phylogenetic regressions fitted with the "phylolm" R package (which does not include ordinal regressions). For comparison, we also fitted a Bayesian phylogenetic ordinal model using the "brms" R package (Bürkner, 2017). Owing to computation time, we would have been unable to fit 20,000 such models. Therefore, we present in the Supporting Information (Figure S4) only one ordinal model fitted to one sample of phylogenetic tree and morphology.

3 | RESULTS

3.1 | Correlates of body size

Contrary to the expectations of Bergmann's rule, we found no evidence that the head-and-body length of rodents was associated with latitude [$\beta_{\text{completed trees}}$ = 0.008 (95% CI: −0.002 to 0.018); $\beta_{\text{DNA-only trees}}$ = 0.005 (95% CI: −0.005 to 0.016)]. There was also no clear effect of temperature variation, either alone or in association with precipitation, although we observed a tendency for shorter head-and-body length in warmer temperatures when analysing species with DNA information only [$\beta_{\text{completed trees}}$ = −0.004 (95% CI: −0.015 to 0.006); $\beta_{\text{DNA-only trees}}$ = −0.011 (95% CI: −0.021 to −0.001); Figure 1]. However, there was generally a positive relationship between head-and-body length and precipitation,

albeit mostly apparent, again, for species with DNA-based phylogenetic information [$\beta_{\text{completed trees}}$ = 0.014 (95% CI: 0.001–0.025); $\beta_{\text{DNA-only trees}}$ = 0.019 (95% CI: −0.007 to 0.031)]. Our analyses showed that the main environmental variable influencing the body size of rodents was NDVI, which was positively associated with the head-and-body length of species, as evidenced by positive and significant regression coefficients in most replicates [$\beta_{\text{completed trees}}$ = 0.015 (95% CI: 0.006–0.024); $\beta_{\text{DNA-only trees}}$ = 0.021 (95% CI: 0.011–0.032)] and a greater support for this variable in multi-model comparisons (lowest AICc in 59 and 63% of models, respectively; Figure 1). In any case, the relationship remained weak, with a mean adjusted R^2 < .01 (Supporting Information Table S2). Using climate data from contrasted time periods did not seem to change the results (Supporting Information Figure S2), which indicates that the possible mismatch between the dates of morphological measurements, climate variables and NDVI is unlikely to affect our conclusions.

3.2 | Body size constraints on range size

There was no linear relationship between range size and head-and-body length (all linear phylogenetic regressions led to non-significant coefficients; see Supporting Information Table S3). The upper quantile of range size showed a slightly positive relationship with head-and-body length [$\beta_{\text{completed trees}}$ = 0.225 (95% CI: 0.156–0.290); $\beta_{\text{DNA-only trees}}$ = 0.306 (95% CI: 0.162–0.417)], which was, however, non-significant for most replicates. We did, however, find support for a segmented relationship between the lower quantile of range size and head-and-body length (Figure 2). Before a breakpoint located around 19–35 cm, there was a slightly negative slope, with
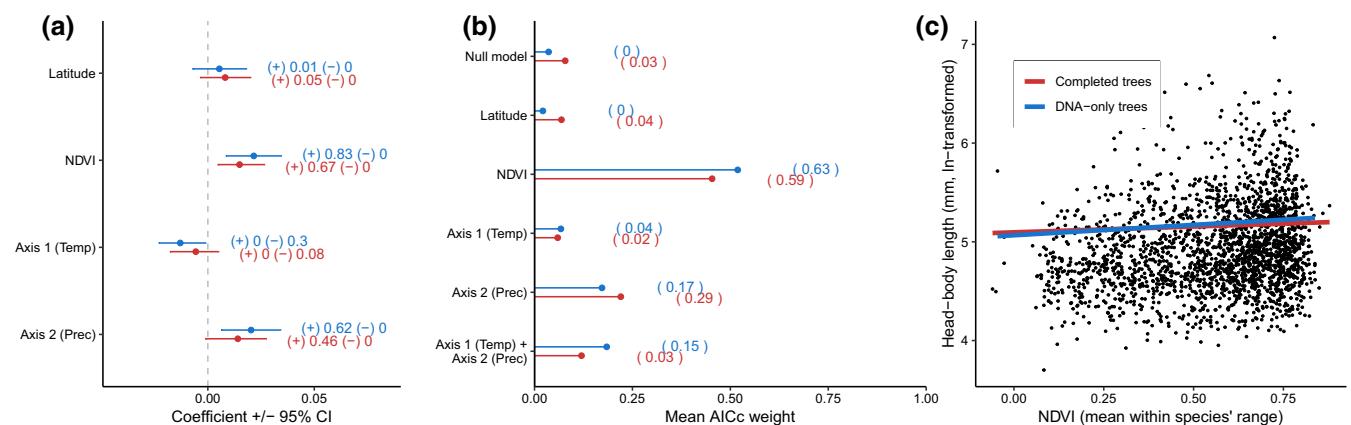

FIGURE 1 Environmental correlates of the body size of rodents. (a) Regression coefficients of phylogenetic models linking body size (ln-transformed) and one of the following variables: Absolute latitude, normalized difference vegetation index (NDVI), first axis of the varimax-rotated principal components analysis (PCA) on climate [correlated with temperature (Temp) variables] or second axis of the varimax-rotated PCA on climate [correlated with precipitation (Prec) variables]. Results are presented as the mean (±95% confidence intervals) coefficient estimates from 10,000 phylogenetic regressions (100 trees × 100 samples of body size) and as the proportion of replicates that provide significantly positive (+) and negative (−) coefficients. (b) Support for each univariate model, in addition to a null model (intercept only) and a climate model (temperature + precipitation), estimated by corrected Akaike information criterion (AICc) weight. Results are the mean weight across all samples of phylogenetic trees and body sizes. Numbers within parentheses indicate the proportion of samples for which the model had the lowest AICc. (c) Scatterplot and regression lines of the mean estimated relationship between body length and NDVI. In all plots, results are shown for all species with imputed phylogenetic trees (red) and for species with DNA information only (blue).

mixed support depending on the replicate [$\beta_{completed\ trees}$ = −0.867 (95% CI: −1.420 to −0.305); $\beta_{DNA-only\ trees}$ = −2.400 (95% CI: −3.430 to −1.460); Supporting Information Table S3]. After the breakpoint (i.e., for larger species), we observed a clear positive slope [$\beta_{completed\ trees}$ = 4.850 (95% CI: 1.640–9.080); $\beta_{DNA-only\ trees}$ = 3.200 (95% CI: 1.110–8.970); Figure 2; Supporting Information Table S3], which was congruent with the lower bound of the expected triangular relationship between range size and body length (Brown & Maurer, 1987). Phylogenetic signal, as measured by Pagel's λ, was
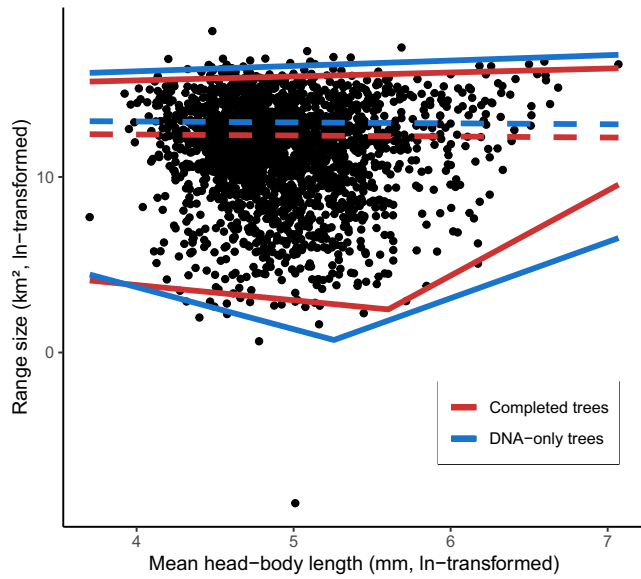

FIGURE 2 Relationship between the range size of rodents and their head-and-body length, estimated with a simple linear phylogenetic regression (dashed lines) or with a phylogenetically corrected quantile regression for the 5th (segmented regression) and 95th quantiles (continuous lines). Regression lines correspond to the mean estimates across multiple samples of trees and body size and are shown for all species with completed phylogenetic trees (red) and for the subset of species that have DNA information (blue).
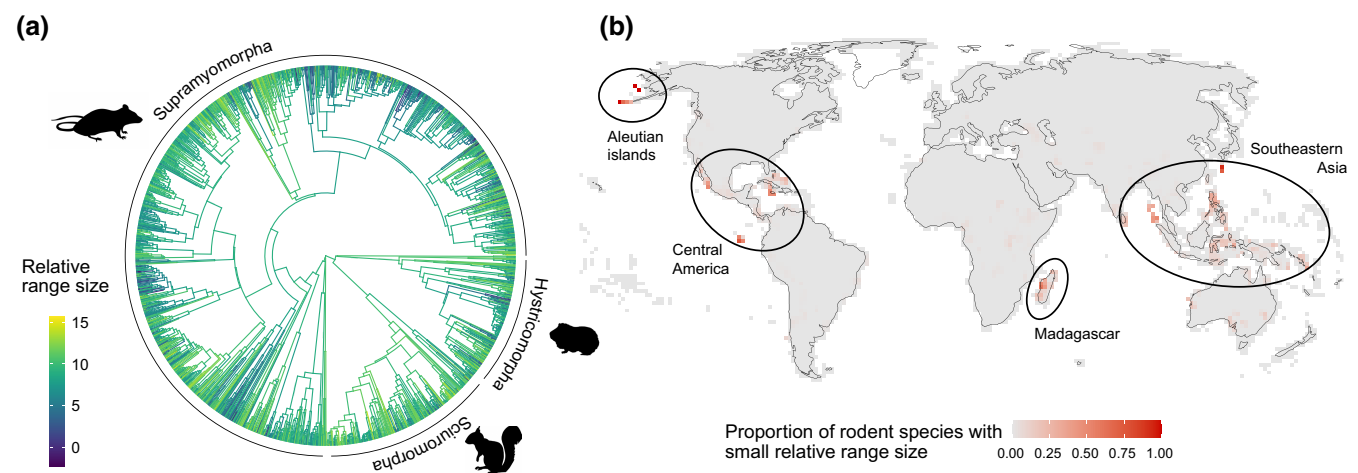
reduced in the models incorporating the phylogenetic residual autocovariate, showing that the approach effectively decreased phylogenetic autocorrelation (Supporting Information Table S3).

3.3 | Extinction risk and range size

We classified a total of 342 rodent species as having a small relative range according to our criterion (Supporting Information Table S4). Most assemblages of rodents did not contain any of these species; 260 grid cells were occupied by only one species with small relative range, 64 by two species, and 47 by more than two species, up to 11. Four main regions included a significant proportion of species with low relative range size, up to 100% (Figure 3): Central America (including the Caribbean), Madagascar, south-eastern Asia and the Aleutian islands, which harbours few rodent species, but a large proportion of those have a small relative range size.

It was clear visually that the most threatened species were those with a smaller relative range (Figure 4a,b). For example, species classified as "least concern" had a mean relative range size of 9.87 (SD = 2.12), whereas the relative range size of "critically endangered" species was 5.64 on average (SD = 2.58). Data-deficient species, which could not, by definition, be included in the statistical models linking extinction risk and relative range size, had a mean relative range size of 6.30 (SD = 2.81). Phylogenetic logistic regressions confirmed that extinction risk was negatively related to the relative range size of species, both when all species included in the completed trees were analysed [$\beta_{completed\ trees}$ = −0.155 (95% CI: −0.159 to −0.151); adjusted R^2 = 0.13] or only those in DNA-only trees [$\beta_{completed\ trees}$ = −0.133 (95% CI: −0.141 to −0.127); adjusted R^2 = 0.11; Figure 4c]. Unsurprisingly, the relationship was stronger when all species were combined, including those classified according to their range size (Supporting Information Figure S3; Table S5).

The ordinal regression we fitted under a Bayesian framework showed that species with a large relative range had a higher

FIGURE 3 (a) One of the 100 completed phylogenetic trees used in phylogenetic regressions, with branch colours corresponding to the maximum likelihood estimates of the ancestral states for relative range size. (b) Map showing the proportion of rodent species with small relative range (<mean − 1SD) in 2° grid cells, with ellipses highlighting the regions that concentrate most of these species.
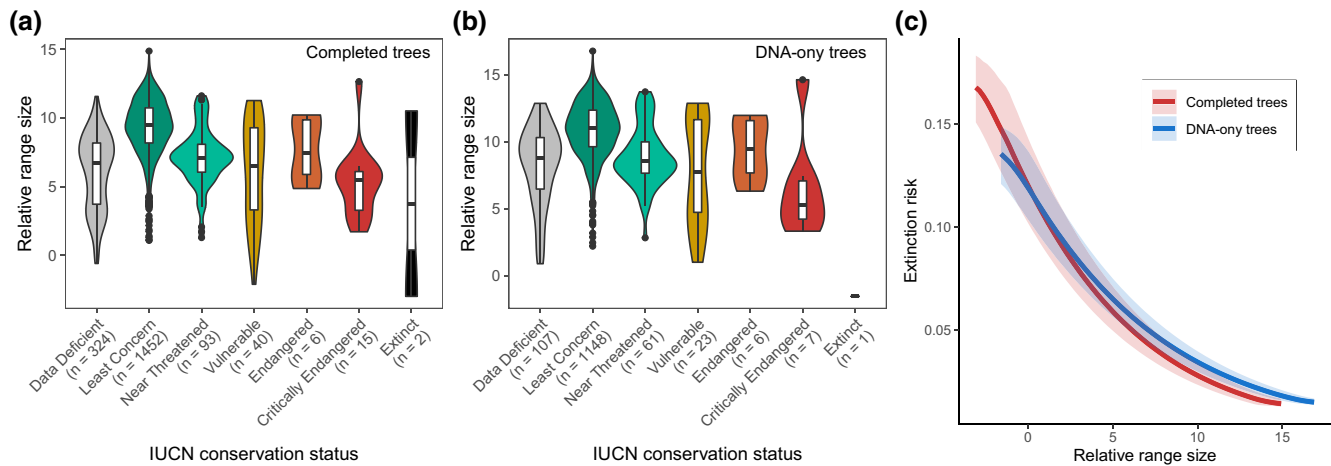
FIGURE 4 Effect of range size on the extinction risk of rodents. (a,b) Violin plots showing relative range size of species [ratio between the observed range area and the lower bound of the triangular relationship between range size and body size, estimated in phylogenetic regressions using (a) completed or (b) DNA-only phylogenetic trees] in relationship to their conservation status according to the International Union for Conservation of Nature (IUCN). (c) Estimated relationship between the extinction risk of species (coded according to IUCN conservation status: 0 = least concern and 1 = extinct) and relative range size. We show here results after excluding all species whose conservation status was decided based on criterion B (small range size) to avoid circularity; the same results for all species are shown in the Supporting Information (Figure S3).

probability of being classified as "least concern". On the contrary, a small relative range was associated with a higher probability of belonging to the "near threatened" to "critically endangered" categories (Supporting Information Figure S4). This also confirmed our hypothesis that species with a smaller relative range tended to be more threatened.

4 | DISCUSSION

We did not find support for Bergmann's rule in rodents; however, it appeared that larger species tended to be associated with regions characterized by high precipitation. Although this result had been demonstrated before using a relatively smaller rodent dataset (Alhajeri & Steppan, 2016), in the present study we confirmed this outcome using much larger datasets and more rigorous statistical approaches. It is possible that this relationship reflects an effect of resource availability on the body size of species, whereby productive regions (i.e., those associated with high precipitation) are able to support larger species. We tested this hypothesis by exploring the relationship between species body sizes and NDVI, as a proxy for productivity, and found that there was indeed a clear positive relationship, with larger species generally being found in regions with higher NDVI. Yet, this relationship remained weak, as was found before in a smaller rodent dataset (Alhajeri, Porto, & Maestri, 2020). This demonstrates that resource availability might play a role in shaping the evolution of body size in rodents, but also that more work is needed to find the factors, or combination of factors, that fully explain the observed variation of body size across rodent species.

The body size of species, which is constrained, in part, by environmental factors, especially resources as we demonstrated, in

turn constrains the evolution of species range size. We found support for a log–log triangular relationship between body length and range area, as was hypothesized earlier (Brown & Maurer, 1987). The lower bound of this relationship is because a larger range size is necessary for acquiring the resources needed to sustain larger species. However, we identified that the lower bound of range size for rodents was associated with a segmented relationship with body size, which appears to be found at the scale of mammals in general (Agosta & Bernardo, 2013; Newsome et al., 2020). An explanation for this segmented relationship is that there is, in fact, an optimal body size (around the breakpoint) for which the trade-off between range size and body size is minimized. Another possibility for the negative relationship before the breakpoint could be that endemic species (i.e., those with a very narrow range) have already gone extinct because they are naturally more susceptible to any disturbance, human driven or otherwise.

The relationship we observed between range size and body size means that there is a lower limit to species range size for a given body size, below which resource acquisition might become too difficult for sustaining populations in the long term. Therefore, species closer to this boundary are potentially more susceptible to disturbance, and therefore might exhibit elevated extinction risk. The IUCN database of rodent species we used lists a couple of extinct species; one of them, the Bramble Cay melomys (*Melomys rubicola*), became extinct in 2015, most probably because of sea-level rise (Woinarski et al., 2017). It was a medium-sized species (*c.* 15 cm) that was found in a very restricted range (2 ha) on a tiny Australian island, making it the species with the smallest relative range in our database (see Supporting Information Table S4). This anecdotal evidence is congruent with a real link between extinction and our estimate of relative range size.

More generally, we demonstrated here that species with smaller relative range size were associated with unfavourable conservation status, even when we excluded species classified according to criterion B (i.e., range size). There is a known tendency for a species to be more threatened if it is larger in size (Dirzo et al., 2014) and smaller in range (Cardillo et al., 2008). The combination of these two factors in a single species is expected to raise extinction risk even more than if they occur individually. Thus, from a conservation perspective, more attention must be paid to small-ranged species that are distributed across a smaller area (e.g., endemic species) than expected relative to their body size. Among the species that have a small relative range size, many are classified as "data deficient" (125 of 342; i.e., 36.5%), meaning that their conservation status could not be estimated adequately. Given that these species are typically distributed across a small region, it is not surprising that they have remained relatively unnoticed by the scientific community. Moreover, we observed that "data deficient" species have, on average, a relative range size equivalent to species classified as "vulnerable". Therefore, we argue that they should be given more attention, because it is likely that some of them are already (unknowingly) threatened or that they will become vulnerable in the near future.

Although the relationship between relative range and extinction risk was unambiguous, we could observe some notable exceptions (i.e., species with small relative range but favourable conservation status). Among the species with the smallest relative range, the Kalinga shrew-mouse (*Soricomys kalinga*) and the cloud rat *Batomys uragon* are endemic to the montane forests of the Philippines, where they are currently not considered under threat ("least concern") (Balete et al., 2006, 2015). The fact that they are confined to small areas of montane forests, where traditional cultural practices ensure the sustainable use of forest habitat, probably explains why they have managed to keep viable populations. However, we encourage conservationists to scrutinize all species that exhibit small ranges relative to their body size and to consider them as candidate targets for conservation efforts, because they might be particularly at risk of extinction even if their present trends do not appear alarming.

Overall, we identified four regions containing a significant proportion of rodent species with a small relative range, which include, in part, the known global hotspots of mammal diversity (Ceballos & Ehrlich, 2006). Three of them correspond to tropical forests, which is a type of habitat that is currently under threat (Myers, 1993). We expected to find narrower range sizes (Rapoport's rule; Stevens, 1989) and smaller body sizes (Bergmann's rule; Mayr, 1956) in the tropics. Interestingly, species that have a smaller than expected range size are also concentrated in the tropics. We can hypothesize that competitive interactions in these diversity hotspots lead to a further reduction of species range area, leading to smaller distributions than expected given their body size (Pianka, 1989). There is thus a combination of intrinsic (smaller than expected distribution area) and extrinsic (human-driven deforestation) factors that might endanger rodent biodiversity in these areas in several ways. It is noticeable that the main hotspot that we detected is located in the Philippines and Indonesia. We hypothesize that the geological history of the area,

made of isolated islands and mountains, promoted the diversification of many species with small ranges, leading to considerable levels of endemism (Heaney et al., 1998). The fourth region, the Aleutian islands, is a species-poor area but hosts a large proportion of species with a small relative range. It is a known region of endemism for mammals (Cook & MacDonald, 2001) and has been subjected to an invasion by rats (*Rattus norvegicus*) that threatens the local fauna (Kurle et al., 2008). It appears, based on our result, that it should be among the priority targets for conservation of rodents.

Given that the relative range size we report originates in the evolution of body size driven by environmental factors, changes in these factors might lead to a cascade of consequences and indirectly influence the extinction risk of species. For instance, following Bergmann's rule, climate warming should select for smaller individuals (Sheridan & Bickford, 2011) and thus push species further away from the lower boundary of a triangular relationship between body size and range size. In rodents, we demonstrated that this relationship is segmented and that resource availability is the main factor influencing body size. The effect of climate change on the relative range of species is therefore uncertain. It is clear, however, that short- (Wolf et al., 2009) and long-term (Renaud et al., 2005) variation in climatic conditions affect the morphology of rodents. It will be important, therefore, to monitor how climate change and direct human pressure, by modifying species range and selecting certain traits, lead to the displacement of species within the body size–range size space.

Despite the nearly comprehensive database on the morphological traits, distribution and conservation status of rodents that we used in the present study, one must keep in mind that we explored only a few factors as correlates of body size, range size and extinction risk and that most of the relationships we revealed were relatively weak. A large number of additional factors are certainly associated with extinction risk. In this regard, some traits frequently linked to higher extinction risk include habitat specialization (Clavel et al., 2011) or long generation time (Staerk et al., 2019). In addition, many aspects of human activity are clearly responsible for extinction of species in the wild, such as land conversion, invasive species or overexploitation (Harfoot et al., 2021). Therefore, although our study highlights some interesting links between macroecological patterns and conservation assessments, more research is needed to draw a complete picture of extinction risk in rodents and to determine whether our findings are generalizable to other taxa.

In conclusion, we showed that environmental variables, especially those related to resource availability, contribute to the evolution of body size in rodents. Body size, in turn, imposes a constraint on the minimal range size of species, because larger species need larger areas. In the context of today, when human activity acts as a strong disturbance to most species, this makes some species particularly at risk of extinction because, given their body size (the evolution of which has been shaped by environmental factors), they are distributed in narrow ranges. This shows that biogeographical history and evolutionary legacy are important to consider from a conservation perspective. Although the contribution of these processes

to current extinction risk remains weak, characterizing these complex relationships between environmental drivers, body size and range size could help us to detect species that might become threatened in the near future.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All analyses are based on publicly available data from the IUCN (range area and conservation status: https://www.iucnredlist.org/), WorldClim (climate data: https://worldclim.org/), museum databases and the literature (morphological data were compiled and made available by Alhajeri, Fourcade, et al., 2020).

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SUPPORTING INFORMATION

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