

Climate and topography explain range sizes of terrestrial vertebrates

Yiming Li^{1*†}, Xianping Li^{1,2†}, Brody Sandel^{3,4}, David Blank⁵, Zetian Liu^{1,2}, Xuan Liu¹ and Shaofei Yan^{1,2}

Identifying the factors that influence range sizes of species provides important insight into the distribution of biodiversity¹, and is crucial for predicting shifts in species ranges in response to climate change^{2–4}. Current climate (for example, climate variability and climate extremes)^{5,6}, long-term climate change⁴, evolutionary age², topographic heterogeneity, land area^{3,7} and species traits such as physiological thermal limits⁸, dispersal ability⁹, annual fecundity and body size^{3,10} have been shown to influence range size. Yet, few studies have examined the generality of each of these factors among different taxa, or have simultaneously evaluated the strength of relationships between range size and these factors at a global scale. We quantify contributions of these factors to range sizes of terrestrial vertebrates (mammals, birds and reptiles) at a global scale. We found that large-ranged species experience greater monthly extremes of maximum or minimum temperature within their ranges, or occur in areas with higher long-term climate velocity and lower topographic heterogeneity or lower precipitation seasonality. Flight ability, body mass and continent width are important only for particular taxa. Our results highlight the importance of climate and topographic context in driving range size variation. The results suggest that small-range species may be vulnerable to climate change and should be the focus of conservation efforts.

Terrestrial vertebrates are ideal for studying factors that influence range size variation owing to good records of their geographic distributions compared with many other taxa³. Further, data on physiological thermal limits for the vertebrates (for example, mammals, birds and reptiles) have been well documented^{11–13}, providing a good opportunity to test the role of physiological thermal limits in shaping range sizes of these taxa.

We created a database on the geographical range sizes of 522 terrestrial vertebrate species (283 mammals, 131 birds and 108 reptiles) and their potential determinants using an equal-area grid at a relatively fine resolution (approximately 30' × 30' at the Equator; Methods). We used this database to compare differences in range size among mammals, birds and reptiles or among biogeographic realms. The range sizes of these species varied from 1 to 5,586 grid cells, with a median of 133 grid cells. The distribution of range sizes was highly skewed to the right, with 122 species occupying ≤50 grid cells (Supplementary Fig. 1 and Supplementary Table 1). Range sizes differed among classes (Kruskal–Wallis test, $\chi^2 = 46.805$, $d.f. = 2$, $P < 0.001$, two-tailed), with the largest median range size observed in birds (Fig. 1a), followed by mammals and reptiles. Ranges of birds were significantly larger than those of mammals and reptiles (both $P < 0.001$). Range size also differed

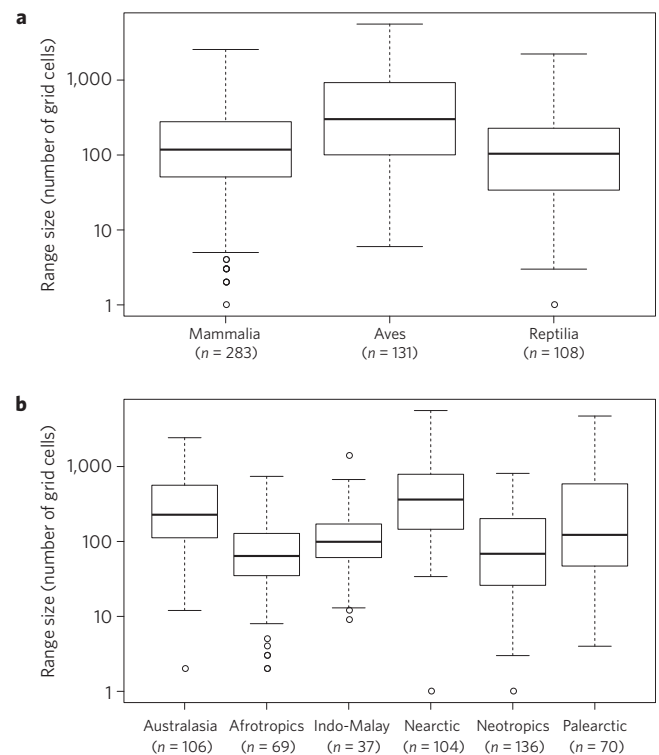


Figure 1 | Boxplots of range sizes for the terrestrial vertebrates in fine resolution. a, Among taxa. **b**, Among biogeographic realms. The black line inside the box indicates the median. The bottom and top borders of the box represent the first and third quartiles. The vertical dotted lines represent upper and lower limits.

among biogeographic realms ($\chi^2 = 111.158$, $d.f. = 5$, $P < 0.001$). The largest median range size was found in the Nearctic (Fig. 1b), followed by Australasia, Palearctic, Indo-Malay, Neotropics and Afrotropics.

We then performed multimodel inference based on information theory¹⁴ to quantify the relative importance of predictors for range sizes of the terrestrial vertebrates. We began with a full model based on phylogenetic generalized least-squares (PGLS) regression with log-transformed range size as the response variable. The predictor variables were mean seasonality of temperature and precipitation (intra-year temperature and precipitation variability), maximum temperature (max-temperature), minimum temperature

¹Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, China. ²University of Chinese Academy of Sciences, 19 Yuquan Road, Shijingshan, Beijing 100049, China. ³Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Aarhus 8000 C, Denmark. ⁴Center for Massive Data Algorithmics (MADALGO), Aarhus University, Aarhus 8000 C, Denmark. ⁵Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, No. 818, South Beijing Road, Urumqi 830011, China. [†]These authors contributed equally to this work. *e-mail: liym@ioz.ac.cn

Table 1 | Results of model averaging for the effects of current climates, long-term climate velocity, species traits and geographic factors on range sizes of mammals, birds and reptiles at a global scale.

Variables	Mammals				Birds				Reptiles			
	β	95% CI		W_{ip}	β	95% CI		W_{ip}	β	95% CI		W_{ip}
Temperature seasonality	0.0000	0.0000	0.0001	0.47	0.0000	0.0000	0.0001	0.55	0.0000	0.0000	0.0001	0.35
Precipitation seasonality	-0.0056	-0.0075	-0.0037	1.00	-0.0071	-0.0106	-0.0035	1.00	-0.0091	-0.0133	-0.0049	1.00
Minimum temperature	-0.0079	-0.0133	-0.0026	0.92	-0.0138	-0.0221	-0.0055	0.97	-0.0092	-0.0171	-0.0013	0.81
Minimum temperature (exp.)	-0.0052	-0.0078	-0.0026	1.00	0.0059	0.0022	0.0097	0.97	0.0043	-0.0004	0.0089	0.63
Maximum temperature	0.0159	0.0039	0.0280	0.90	0.0396	0.0224	0.0568	1.00	0.0375	0.0214	0.0536	1.00
Maximum temperature (exp.)	-0.0025	-0.0156	0.0105	0.27	-0.0110	-0.0300	0.0080	0.38	0.0078	-0.0218	0.0375	0.26
Minimum precipitation	-0.7340	-1.0734	-0.3945	1.00	-0.4734	-1.0849	0.1381	0.53	-0.8412	-1.3121	-0.3702	1.00
Minimum precipitation (exp.)	-3.4226	-5.2816	-1.5637	1.00	-21.8794	-30.6142	-13.1446	1.00	-3.3804	-5.8494	-0.9115	0.93
Maximum precipitation	0.3542	0.1891	0.5192	1.00	0.3191	0.0154	0.6229	0.77	0.2867	-0.0223	0.5957	0.67
Maximum precipitation (exp.)	1.3087	0.9843	1.6331	1.00	0.8981	0.3649	1.4312	0.99	0.9822	0.4236	1.5408	0.98
Range of thermal limits	-0.0020	-0.0087	0.0047	0.29	0.0073	-0.0022	0.0169	0.51	0.0033	-0.0109	0.0174	0.25
Climate change velocity	0.3418	0.2285	0.4550	1.00	0.4688	0.2745	0.6630	1.00	0.4511	0.2381	0.6641	1.00
Body mass	0.0079	-0.0367	0.0524	0.27	-0.0159	-0.1078	0.0760	0.25	-0.0597	-0.1504	0.0310	0.43
Clutch/litter size	0.0673	-0.0965	0.2312	0.33	-0.0257	-0.2492	0.1979	0.24	0.0406	-0.1665	0.2477	0.23
Flight ability	0.0502	-0.0067	0.1072	0.61	-0.0039	-0.1846	0.1767	0.23	-	-	-	-
Continental width	0.1606	-0.0008	0.3221	0.71	-0.0809	-0.3470	0.1853	0.28	0.1421	-0.1759	0.4602	0.31

Long-term climate velocity, body mass, clutch/litter size, continental width and flight ability were log₁₀-transformed. β : model-averaged regression coefficients; 95% CI: the 95% confidence intervals of regression coefficients β ; W_{ip} : relative variable importance, the sum of W_i across all models including that variable. W_{ip} with high value and β whose 95% confidence intervals do not encompass zero are shown in bold; exp.: expected values of the climate extremes.

(min-temperature), maximum precipitation (max-precipitation) and minimum precipitation (min-precipitation) (that is, monthly extremes of temperature and precipitation at any single grid cell within their range), mean long-term climate velocity (since the Last Glacial Maximum), range of physiological thermal limits, flight ability, body mass, clutch/litter size and continent width. For mammals and birds, upper and lower thermal limits were defined using critical minimum temperatures and critical maximum temperatures^{12,13}, which are thermal neutral boundaries at which the resting metabolic rate is constant at the minimum. For reptiles, upper and lower thermal limits were measured with lower and upper critical temperatures¹¹. Large ranges will, on average, experience wider climate extremes than small ranges because of a simple sampling effect. To avoid this problem, we simulated the expected climate extremes of random ranges for each species (Methods). Inclusion of both observed and expected extremes in the model can control for the sampling effect on parameter estimates of observed extremes. As climate change velocity was highly correlated with topographic heterogeneity⁴, and the velocity explained more variation in range size than topographic heterogeneity in all situations (Methods), we present results using climate change velocity. Results using topographic heterogeneity were similar and can be found in Supplementary Tables 2–13, with topographic heterogeneity having importance values comparable to the velocity but being negatively related to range size.

The model averaging showed that max- and min-temperatures, long-term climate velocity and precipitation seasonality commonly had very high relative importance (0.81–1.00) for range sizes

in mammals, birds and reptiles (Table 1). Model-averaged 95% confidence intervals of parameter estimates (β) for these variables also did not include zero. Max-precipitation was important for both mammals and birds, and min-precipitation for mammals and reptiles (Table 1). The predictors above were also contained in highly supported models ($\Delta AICc \leq 2$; Supplementary Tables 14–16). Range sizes increased ($\beta > 0$) with max-temperature and long-term climate velocity but decreased ($\beta < 0$) with min-temperature and precipitation seasonality for all taxa. Range size also increased with max-precipitation for mammals and birds, but decreased with min-precipitation for mammals and reptiles. Other variables, such as temperature seasonality, range of physiological thermal limits, clutch/litter size, body mass and continent width had very low values of relative importance, with 95% confidence intervals of β encompassing zero for all taxa (Table 1). When the range of physiological thermal limits was replaced with upper and lower thermal limits, results were similar, with continent width becoming important for mammals (Supplementary Tables 17–19).

As species ranges were imperfectly known, and these imperfections become less noticeable as the resolution of an analysis decreases, we repeated the multimodel inference at a coarser resolution (approximately 1° × 1° at the Equator) to evaluate the generality of the relative importance of each predictor at different resolutions. The main results were similar, but flight ability and continent width were also important predictors for mammals, and max-precipitation and body mass for reptiles (Supplementary Tables 20–25).

We compared our results with PGLS null models that included climate variables and continent width from random ranges across

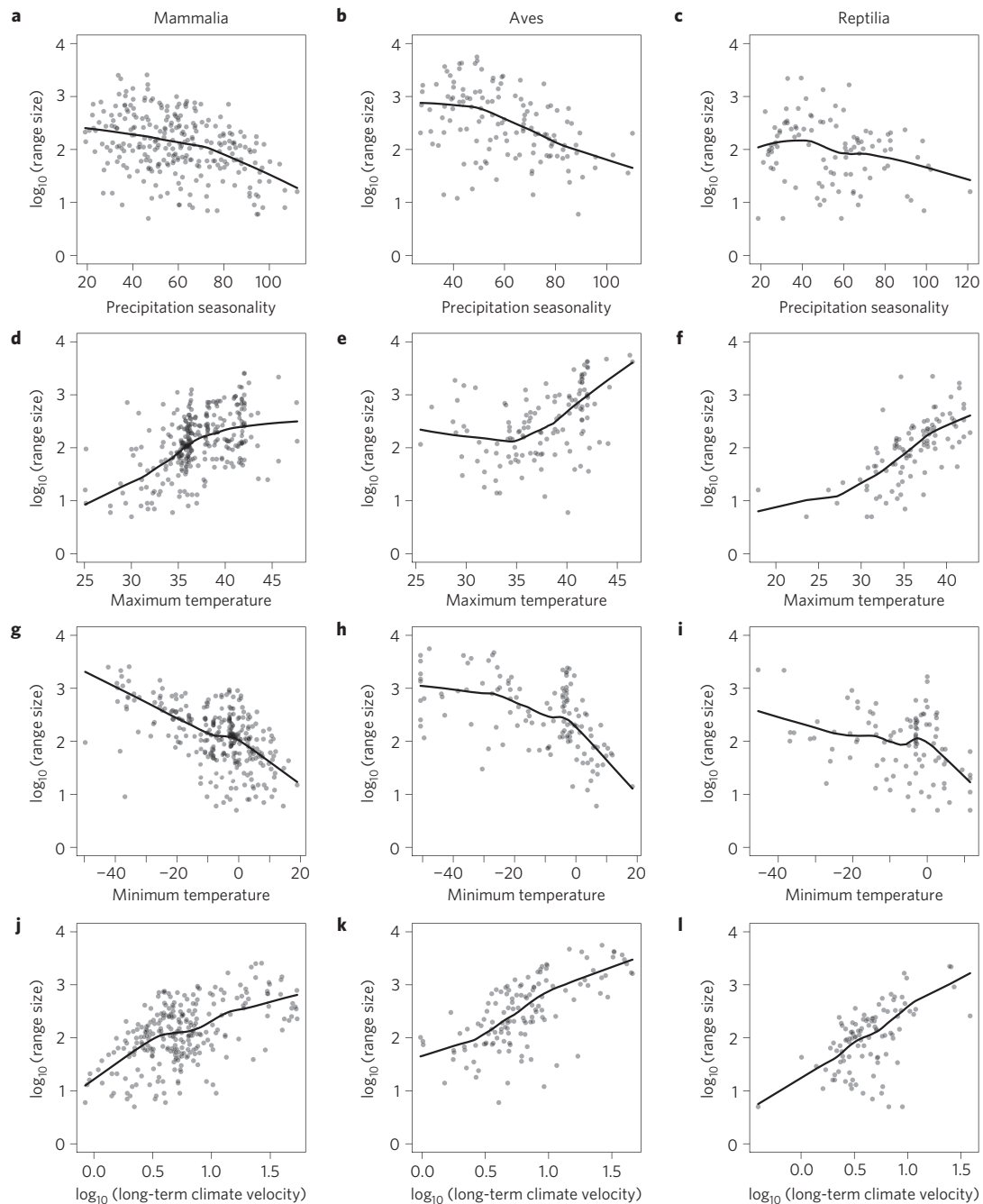


Figure 2 | Scatter plots between log-transformed range size and four predictors for each taxon in fine resolution. a–c, Precipitation seasonality. **d–f,** Maximum temperature. **g–i,** Minimum temperature. **j–l,** Log-transformed long-term climate velocity. The black line demonstrates the general tendency fitting with a LOWESS smoother that used locally weighted polynomial regression (implemented in R using the lowess function in the stats package with a smoother span of 2/3).

each species (Methods) to test whether our results are statistical artefacts¹⁵. The relationship (r^2) between range size and each of the important observed predictors was stronger than those of null models (Supplementary Tables 26 and 27). Furthermore, the relationship between range size and important observed predictors together for each taxon was stronger than expected by chance (Supplementary Tables 28 and 29), indicating that these relationships were robust. Figure 2 shows the relationships between range size and important observed predictors for mammals, birds and reptiles.

Our study provides evidence for effects of current climate, long-term climate velocity and topographic heterogeneity on the range

size of terrestrial vertebrates at a global scale. A species' range size increases as it experiences greater monthly extremes of maximum and minimum temperatures at any location within its range or if it occurs in areas with higher long-term climate velocity and lower topographic heterogeneity or lower precipitation seasonality. Some expected climate extremes (for example, expected maximum precipitation) are also important for range size (Table 1), suggesting that a sampling effect indeed exists in the climate extremes.

There is no consensus on the generality of physiological thermal limits in shaping the distribution of species among taxa^{8,16–18}. Consistent weak evidence for effects of physiological thermal limits in this study may be due to two reasons. First, many

mammals, birds and reptiles have thermoregulation behaviours of using (or building) shade or burrows (for example, thermal refuges) in heterogeneous habitats to avoid uncomfortably warm or cool conditions^{18,19}. Some mammals and birds can elude the times of daily overheating or cold exposure or seasonally harmful temperatures using physiological responses such as daily torpor or hibernation¹⁹, and most of the reptiles can rely on hibernation to avoid seasonally adverse temperatures¹⁸. These behaviours or physiological responses may enable the vertebrates to occupy broader climate niches than their physiological tolerances would suggest, and are likely to reduce the role of physiological thermal limits in limiting range size^{18–20}. For example, terrestrial ectotherms generally live at higher latitudes than would be predicted by their cold tolerance alone and overfill their potential ranges at the poleward boundary because of such behaviours or physiological responses²⁰. Second, biotic interactions (for example, competition and predation pressures) can limit the expansion of terrestrial vertebrates in their full potential ranges. For instance, ectothermic vertebrates are generally underfilling their potential low-latitude range that their upper thermal limits would suggest, owing to the more complicated biotic interactions towards the Equator²⁰.

Factors such as temperature and precipitation extremes have rarely been incorporated in range size studies^{6,15,21}. After controlling for the sampling effect in observed climate extremes, we detected effects of the temperature extremes on range sizes of terrestrial vertebrates. The observed temperature extremes may reflect species' thermoregulatory behaviours (such as using thermal refuges in heterogeneous habitats)¹⁸ or physiological responses (such as daily torpor or hibernation)¹⁶ or both to avoid adverse temperatures. The species with better such abilities are more likely to occupy a larger range size. An increase in precipitation seasonality may limit food availability and increase resource bottlenecks²², and therefore can reduce range size. Weak evidence for the effect of temperature seasonality may be due to the fact that the role of temperature seasonality on range sizes is largely restricted to the regional scales but has rarely been observed at a global scale²¹.

Climate change since the Last Glacial Maximum has been found to affect the distributions of small-ranged amphibians, mammals and birds⁴. Contrary to previous studies that showed no relationship between such climate change and range sizes of amphibians²¹, we detected effects of the velocity on range sizes for mammals, birds and reptiles, consistent with a recent study that revealed velocity as an important predictor of range sizes for plants²³. Therefore, effects of long-term climate velocity on range size may be more general, applying to both vertebrates and plants. Climate velocity is a complex variable deriving from the temporal and spatial gradient in temperature (Methods), and contains a part of the effect of topographic heterogeneity. Disentangling the effect of topographic heterogeneity from climate velocity is difficult. When included in models, topographic heterogeneity consistently was an important predictor in all situations (Supplementary Tables 2–13), suggesting that it had an effect on range size. Topographically heterogeneous areas may impose constraints on dispersal, resulting in smaller range size^{3,7}.

We found effects of flight ability, body mass and continent width on range size only for some taxa under some conditions, and the relative importance of these variables was generally lower (Table 1 and Supplementary Tables 14–25). A positive effect of flight ability on range sizes of mammals suggests that dispersal ability facilitates large range sizes^{9,10,24}. Weak evidence for an effect of flight ability on range sizes of birds may be because a large proportion of migrant birds with better dispersal ability have been excluded from the bird data set owing to high variation in upper and lower thermal limits measured for these birds¹³. As a result, the variations in flight ability in the data set are very small (Supplementary Table 1), reducing the explanatory power of flight ability. Effects of body

size or continent width on range size may be different depending on the taxa or continents studied^{7,10,23,24}. No effect of clutch/litter size on range size for the vertebrates is in contrast to a study that showed a positive relationship between clutch size and range size for birds¹⁰.

Larger range sizes for birds than for mammals or reptiles might be partly because birds experience lower minimum temperature than mammals or experience higher maximum temperature, and occur in areas with higher long-term climate velocity than reptiles (Supplementary Tables 30 and 31). However, differences in range sizes across all biogeographic realms (Fig. 1b) must be interpreted with caution, as sample sizes for each taxon in some realms were low.

Although correlative, our comprehensive analyses may yield the practical recommendation that conservation efforts be focused on small-range species. Positive relationships between range sizes and greater temperature extremes for the vertebrates indicate that species with a narrow thermal niche (for example, low temperature extremes) have a small range size. These species may be vulnerable owing to the narrow niche that limits their responses to climate change. Precipitation seasonality is expected to increase at higher latitudes in the Northern Hemisphere under climate change²². As range size is negatively correlated with precipitation seasonality, an increase in precipitation variability would decrease the range size of species in these regions, especially for small-range species. Therefore, conservation efforts should be focused on small-range species that experience lower temperature extremes or occur in regions with increased precipitation variability under climate change.

Methods

Methods and any associated references are available in the [online version of the paper](#).

Received 9 March 2015; accepted 9 November 2015;
published online 21 December 2015

References

1. Jetz, W. & Rahbek, C. Geographic range size and determinants of avian species richness. *Science* **297**, 1548–1551 (2002).
2. Gaston, K. J. Geographic range limits: achieving synthesis. *Proc. R. Soc. B* **276**, 1395–1406 (2009).
3. Brown, J. H., Stevens, G. C. & Kaufman, D. M. The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.* **27**, 597–623 (1996).
4. Sandel, B. *et al.* The influence of late quaternary climate-change velocity on species endemism. *Science* **334**, 660–664 (2011).
5. Janzen, D. H. Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249 (1967).
6. Pither, J. Climate tolerance and interspecific variation in geographic range size. *Proc. R. Soc. Lond. B* **270**, 475–481 (2003).
7. Hawkins, B. A. & Felizola Diniz-Filho, J. A. Beyond Rapoport's rule: evaluating range size patterns of New World birds in a two-dimensional framework. *Glob. Ecol. Biogeograph.* **15**, 461–469 (2006).
8. Calosi, P., Bilton, D. T., Spicer, J. I., Votier, S. C. & Atfield, A. What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). *J. Anim. Ecol.* **79**, 194–204 (2010).
9. Lester, S. E., Ruttenberg, B. I., Gaines, S. D. & Kinlan, B. P. The relationship between dispersal ability and geographic range size. *Ecol. Lett.* **10**, 745–758 (2007).
10. Laube, I. *et al.* Towards a more mechanistic understanding of traits and range sizes. *Glob. Ecol. Biogeograph.* **22**, 233–241 (2013).
11. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* **278**, 1823–1830 (2011).
12. Araújo, M. B. *et al.* Heat freezes niche evolution. *Ecol. Lett.* **16**, 1206–1219 (2013).
13. Khaliq, I., Hof, C., Prinzing, R., Böhning-Gaese, K. & Pfenninger, M. Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc. R. Soc. B* **281**, 20141097 (2014).

14. Burnham, K. P. & Anderson, D. R. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach* (Springer, 2002).
15. Morin, X. & Lechowicz, M. J. Niche breadth and range area in North American trees. *Ecography* **36**, 300–312 (2013).
16. Bozinovic, F., Calosi, P. & Spicer, J. I. Physiological correlates of geographic range in animals. *Annu. Rev. Ecol. Syst.* **42**, 155–179 (2011).
17. Arribas, P. *et al.* Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *J. Biogeogr.* **39**, 984–994 (2012).
18. Sunday, J. M. *et al.* Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl Acad. Sci. USA* **111**, 5610–5615 (2014).
19. Kronfeld-Schor, N. & Dayan, T. Thermal ecology, environments, communities, and global change: energy intake and expenditure in endotherms. *Annu. Rev. Ecol. Syst.* **44**, 461–480 (2013).
20. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nature Clim. Change* **2**, 686–690 (2012).
21. Whitton, F. J. S., Purvis, A. & Orme, C. D. L. Olalla-Tarraga MA. Understanding global patterns in amphibian geographic range size: does Rapoport rule? *Glob. Ecol. Biogeogr.* **21**, 179–190 (2012).
22. Bonebrake, T. C. & Mastrandrea, M. D. Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proc. Natl Acad. Sci. USA* **107**, 12581–12586 (2010).
23. Morueta-Holme, N. *et al.* Habitat area and climate stability determine geographical variation in plant species range sizes. *Ecol. Lett.* **16**, 1446–1454 (2013).
24. Luiz, O. J. *et al.* Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proc. Natl Acad. Sci. USA* **110**, 16498–16502 (2013).

Acknowledgements

We thank S. Meiri and F. Xu for providing data on life-history traits of some species and K. Bartoń for the suggestion about multimodel inference with package *MuMIn* in R. Funding was provided by the National Science Foundation of China (31530088 and 31200416) and the Ministry of Science and Technology of China (2013FY110300).

Author contributions

Y.L. and X.Li designed the study; X.Li, D.B., Z.L., X.Liu and S.Y. collected the data; Y.L., B.S. and X.Li developed the method for controlling for sampling effect in climate extremes; X.Li, Y.L. and B.S. analysed the data; Y.L., X.Li and B.S. wrote the manuscript.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to Y.L.

Competing financial interests

The authors declare no competing financial interests.

Methods

Species and range sizes. We compiled data on thermal limits and native geographic distributions for terrestrial vertebrates. We excluded island endemics and those species that are found in association with human residence, and that lack data on morphological characters. In total, our data set included 522 species with information on both upper and lower thermal limits and on native distributions (Supplementary Tables 32 and 33). We obtained occurrence records for these species from various databases and literature (Supplementary Table 33). Especially for the species distributed in China and adjacent territories (which may be underestimated in the databases above), we reviewed the relevant literature to collect more records. For those records that had only text descriptions of sampling sites, we inferred geographic coordinates of their locations using Google Maps (<http://maps.google.com>). We removed duplicated records for each species, excluded points outside their native ranges according to International Union for Conservation of Nature (IUCN) range maps (<http://www.iucn.org>) and checked against the species distribution maps from IUCN. For birds, we excluded the locations occupied during non-breeding or migration seasons using the birds' distribution maps²⁵. In total, we compiled 3,326,946 localities with an average of 6,374 localities per species (ranged from 1–389,661 localities; Supplementary Table 33).

All of the distribution data and the spatial variables mentioned afterwards were projected onto a Behrmann equal-area cylindrical projection and converted to grid cells at a fine resolution (approximately $30' \times 30'$ at the Equator). We considered a species occurring anywhere within a grid cell to be present in that cell. We calculated the range sizes for each species as the number of occupied grid cells. Cells for which land comprised <50% of the area were excluded from range size estimation⁷. The native realm of a species was assigned to one of the realms: Afrotropics, Australasia, Indo-Malay, Nearctic, Neotropics, Oceania and Palearctic²⁶, on the basis of the midpoint of its latitudinal and longitudinal range (Supplementary Table 32).

Predictor variables. On the basis of hypotheses from previous studies, we developed a set of expectations regarding the relationships of species range sizes with potential predictor variables (Supplementary Table 34).

Current climate. Six variables were used to describe variations and extremes that a species experiences. Temperature or precipitation seasonality was calculated as the average value of the temperature or precipitation seasonality across all grid cells within a species' range⁶. Seasonality in precipitation was measured as the coefficient of variation of intra-year monthly precipitation values^{4,21,23,27}. The coefficient of variation can be used to characterize only positive data on a ratio scale²⁸, and could not be applied for quantifying temperature seasonality because monthly temperatures are often negative (that is, below zero °C). We measured temperature seasonality as the standard deviation (s.d.) of intra-year monthly temperatures, which is widely used in macroecological and biogeographic research^{4,21,23,27}. Climate extremes refer to the lowest (or the largest) value of minimum (or maximum) temperature of the coldest month (the warmest month) at any single grid cell encompassed by a species range (that is, maximum and minimum temperature), and the lowest (or largest) value of precipitation of the driest month (or the wettest month) at any single grid cell encompassed by a species range (that is, minimum and maximum precipitation)⁶. The original data on these factors were downloaded from WorldClim (1950–2000) (<http://www.worldclim.org>) with a resolution of 10 arc-minutes²⁹, and then were aggregated to the present resolution after projection.

Long-term climate velocity. We measured long-term climate changes using climate change velocity, an index that integrates macroclimate shifts with local topoclimate gradients^{4,30}. We obtained the mean annual temperature (MAT) at the Last Glacial Maximum in 2.5 arc-minutes from WorldClim in two models: CCSM and MIROC. The current MAT was also obtained from WorldClim at the same resolution. We calculated the climate change velocity using the method adopted in ref. 4. We determined the temporal gradient by taking the difference between the current MAT and the MAT of the Last Glacial Maximum. The spatial gradient was based on the current MAT by considering the four nearest neighbours. The velocity was calculated by dividing the temporal gradient by the spatial gradient and aggregated to the present resolution.

Species traits. We used the range of upper and lower thermal limits as a substitution of physiological thermal limits. We obtained the upper and lower critical temperatures for reptiles from ref. 11, and the thermal neutral zone boundaries for mammals and birds from refs 12, 13 (Supplementary Table 32). In addition, we intensively reviewed the studies that measured physiological thermal limits with the same standard for Chinese native species, and an additional 16 reptiles, 22 birds and 4 mammals were obtained (Supplementary Table 32). When the thermal limits for several subspecies of a species were available, the mean values of the subspecies were used. We did not include the plasticity of upper and lower thermal limits in our study as data on these variables are not available for most species¹¹. For each species, we obtained data on body mass, clutch/litter size and wingspan from

online databases or published literature (Supplementary Table 35). We used flight ability based on wingspan as a measurement of dispersal ability. As the wingspan is in scale with body mass, for birds and bats, the wingspans were calibrated with body mass (Wingspan³/Mass) for controlling the scale effect³¹. The flight abilities were set to zero for the mammals and reptiles without wings.

Geographic factors. We used continental width as the measurement of continent extent⁷. The continent width for a species was calculated as the average length of horizontal lines between coastlines at the midpoint of all grid cells in the species' range⁷. Topographic heterogeneity was measured using altitudinal range^{1,32}. We calculated the range of elevation values found within each grid cell, based on the WorldClim 1 km DEM. For each species, we calculated the topographic heterogeneity within that species' range as the average of these elevational ranges, giving, for each species, a measure of whether that species occurs primarily in flat or mountainous areas.

Our measure of within-range topographic heterogeneity is very much like our measure of within-range temperature seasonality. With temperature seasonality, we take the within-cell standard deviation (across time) and average it across all range cells. With topographic heterogeneity, we take the within-cell range (across space) and average it across all range cells. Thus, they are conceptually similar, but altitudinal range instead of the standard deviation of altitude is the most commonly used for measuring topographic heterogeneity^{1,32}, although the two measures are highly correlated (Pearson's correlation tests, $r > 0.97$, $P < 0.001$ for each taxa).

Statistical analysis. *Phylogenetic generalized least-squares regression models.* Range sizes, long-term climate velocity, body mass, clutch/litter size, topographic heterogeneity, continental width and flight ability were log₁₀-transformed to improve linearity. There were weak correlations ($r < 0.7$ for most pairs of predictors) among predictor variables (Supplementary Table 36). We tested our hypotheses by using long-term climate velocity or topographic heterogeneity separately because they are highly correlated. Long-term climate velocity is derived from the temporal and spatial gradient in temperature, and is a more complicated variable, containing part of the effect of topographic heterogeneity. Therefore, long-term climate velocity is likely to be linked to both climatic stability and dispersal barriers between similar environments⁴. Topographic heterogeneity mainly affects macroclimate³³, and the effects of topographic heterogeneity are possibly submerged into effects of some climate factors. Topographic heterogeneity is correlated with current climate variables (Supplementary Table 36). Velocity individually explained more variance in range size than topographic heterogeneity in all situations. For example, velocity explained 29.05%, 44.22% and 33.24% of the variance (r^2) in range size for mammals, birds and reptiles in fine resolution, separately, whereas heterogeneity explained only 2.38%, 12.14% and 16.90% of the variance in the same circumstances (Supplementary Tables 2–4 and Supplementary Tables 14–16). Therefore, we provided the results using long-term climate velocity in the main manuscript, and attached the results containing topographic heterogeneity as Supplementary Tables 2–13.

To account for phylogenetic non-independence, we used phylogenetic generalized least-squares regression models (PGLS) with log-transformed range size as the response variable and all possible combinations of potential determinants of range size as predictors. We used the parameter lambda (Pagel's lambda) to reflect the phylogenetic covariance between response and explanatory variables, with zero indicating no phylogenetic signal, and one suggesting a strong phylogenetic effect that follows Brownian motion perfectly³⁴. Phylogenetic information for mammals was obtained from ref. 35, and for birds we used the supertree provided in ref. 36 based on the Hackett tree. As there is no completed phylogenetic tree for reptiles, we built the tree on the basis of various literature (Supplementary Fig. 2).

Residual spatial autocorrelation in regression models can lead to error in parameter estimates and biased P values. However, we found no evidence of spatial residual autocorrelation. There were no differences in the residuals among biogeographic realms (Supplementary Fig. 3), suggesting that inclusion of realms as random effects would not improve the parameter estimates of the models.

Controlling for the sampling effect in observed climate extremes. A potential sampling effect exists in the observed climate extremes: a species with a large range may have more chances to experience greater climate extremes than a small one simply because it occupies more grids (for example, more samples). We controlled for this sampling effect by including the expected climate extremes from the random range simulations into the predictors in the models. The inclusion of independent variables between which correlation existed in multiple regressions will generate unbiased parameter estimates³⁷.

We generated a random range within the spatial boundaries of the biogeographic realm(s) that a species actually occupied and based on the range size of the species using a method of completely random simulation³⁸. We set the biogeographic realm(s) that a species actually occupied as constraining boundaries first, then selected the starting cell at random within the realm(s) and then selected the second cell in an unoccupied area until the observed range size was reached.

For each species, we simulated the random range 1,000 times, and calculated the expected extremes. Owing to the lower power of controlling for the sampling effect in small-range species, we excluded species with <5 grid cells (15 species) from our data set for the consequent analysis¹⁵.

We did not apply the approach of calculating standardized values ((observed value—mean of simulated values)/(standard deviation of simulated values)) of the observed climate extremes to control for the sampling effect because the standard deviations of the simulated climate extremes would be highly influenced by the range size. Large range size would always have nearly the same extremes but small standard deviation, which makes the standardized values very large and unreliable. The use of a standard value might result in the loss of some information of observed climate extremes.

The relative importance of predictors. We performed multimodel inference based on information theory¹⁴ to quantify the relative importance of predictors for range sizes of the terrestrial vertebrates. We ranked the PGLS models based on AICc (Akaike's information criterion corrected for small sample sizes), and calculated the relative importance of each variable by summing Akaike weights over all of the models that contained that particular variable¹⁴. Model averaging was used to estimate average parameters from the PGLS regressions. We report the top ten models based on the lowest AICc values. The models that were within 2 AIC units (that is, $\Delta\text{AICc} \leq 2$) of the top models were considered highly supported models¹⁴. We conducted all analyses in R version 3.0.3 (ref. 39), using the `pgls` function in the `caper` package⁴⁰ and the `dredge` and `model.avg` functions in the `MuMIn` package⁴¹.

As the sample bias in records of distribution of species might affect the results of analysis, and larger resolution might reduce the sample bias, we also performed the multimodel inference at a coarser resolution (approximately $1^\circ \times 1^\circ$ at the Equator) to evaluate the generality of the relative importance of each predictor at different resolutions.

Comparison with null models. We performed null PGLS models to test whether the results of model averaging might be statistical artefacts arising by chance¹⁵. We generated a random range of a given range size within biogeographic realm(s) that a species actually occupied for each species using a method of completely random simulation³⁸ (also see Controlling for the sampling effect in observed climate extremes). Then we performed null PGLS models with range size as the response variable and with climate variables and continent width obtained from the random range and other potential factors as predictors. We performed two types of test, one for each of the important predictors and one for combinations of the important predictors. We repeated this process 1,000 times for each test. If the r^2 for observed data was larger than 95% of the 1,000 simulated values (one-tailed), we rejected the null hypothesis that the relationship between range size and observed variables was an artefact due to chance (Supplementary Tables 26–29).

References

- Bird Species Distribution Maps of the World* Version 2.0 (BirdLife International and NatureServe, 2012).
- Olson, D. M. *et al.* Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience* **51**, 933–938 (2001).
- Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T. & Ferrier, S. Space can substitute for time in predicting climate-change effects on biodiversity. *Proc. Natl Acad. Sci. USA* **110**, 9374–9379 (2013).
- Norman, G. R. & Streiner, D. L. *Biostatistics: The Bare Essentials* (B. C. Decker, 2007).
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
- Loarie, S. R. *et al.* The velocity of climate change. *Nature* **462**, 1052–1055 (2009).
- Garrard, G. E., McCarthy, M. A., Vesk, P. A., Radford, J. Q. & Bennett, A. F. A predictive model of avian natal dispersal distance provides prior information for investigating response to landscape change. *J. Anim. Ecol.* **81**, 14–23 (2012).
- Liu, X. *et al.* Congener diversity, topographic heterogeneity and human-assisted dispersal predict spread rates of alien herpetofauna at a global scale. *Ecol. Lett.* **17**, 821–829 (2014).
- Baselga, A., Lobo, J. M., Svenning, J. C. & Araujo, M. B. Global patterns in the shape of species geographical ranges reveal range determinants. *J. Biogeogr.* **39**, 760–771 (2012).
- Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884 (1999).
- Fritz, S. A., Bininda-Emonds, O. R. P. & Purvis, A. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**, 538–549 (2009).
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
- Freckleton, R. P. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* **71**, 542–545 (2002).
- Jetz, W. & Rahbek, C. Geometric constraints explain much of the species richness pattern in African birds. *Proc. Natl Acad. Sci. USA* **98**, 5661–5666 (2001).
- R Core Team R: *A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2014).
- Orme, D. *et al.* *Caper: Comparative Analyses of Phylogenetics and Evolution in R* R package version 0.5.2 (R Foundation for Statistical Computing, 2013).
- Bartoń, K. *MuMIn: Multi-Model Inference* R package version 1.10.0 (R Foundation for Statistical Computing, 2014).