PHYSIOLOGICAL ECOLOGY

Seasonal and daily climate variation have opposite effects on species elevational range size

**Wei-Ping Chan,[1]* I-Ching Chen,[1,2]* Robert K. Colwell,[3,4,5] Wei-Chung Liu,[6]
Cho-ying Huang,[7] Sheng-Feng Shen[1]†**

The climatic variability hypothesis posits that the magnitude of climatic variability increases with latitude, elevation, or both, and that greater variability selects for organisms with broader temperature tolerances, enabling them to be geographically widespread. We tested this classical hypothesis for the elevational range sizes of more than 16,500 terrestrial vertebrates on 180 montane gradients. In support of the hypothesis, mean elevational range size was positively correlated with the scope of seasonal temperature variation, whereas elevational range size was negatively correlated with daily temperature variation among gradients. In accordance with a previous life history model and our extended versions of it, our findings indicate that physiological specialization may be favored under shorter-term climatic variability.

Changes in patterns of climatic variability with global warming are progressively more conspicuous (*1*). Increasing seasonal variability and asymmetric changes of daily maximum and minimum temperatures have altered the thermal environment that organisms experience (*2*–*4*). So far, little is known about how species respond physiologically to climate variation (*5*, *6*), yet these responses are crucial for survival in an era of rapid climate change. The climatic variability hypothesis suggests that organisms experiencing higher thermal variability, and thus having broader physiological thermal tolerances, tend to be geographically widely distributed as a consequence (*7*). This hypothesis is regarded as a broad macrophysiological principle, as it brings together climate patterns and mechanisms of adaptation to explain macroecological phenomena (*8*, *9*). Although species face environmental fluctuations on the scale of hours to days to years to decades and beyond, how the interplay between climatic variability at these various temporal scales contributes to shaping the evolution of species' physiological traits and geographical range sizes has rarely been addressed.

Consideration of how species range size relates to climatic variation has deep roots (*10*). Janzen (*11*) explained that "mountain passes are higher in the tropics" because species inhabiting tropical mountains experience relatively lower seasonal variation in temperature than species at comparable elevations at higher latitudes and may therefore evolve narrower physiological tolerances. Temperature gradients in tropical mountains thus become effective dispersal barriers and result in relatively smaller elevational range sizes (*11*, *12*). Stevens went on to propose Rapoport's rule, which postulates a positive correlation between species range size and latitude or elevation, suggesting that climatic variability may be the underlying mechanism (*13*, *14*). Empirical support for these components of the climate variability hypothesis has been equivocal (*15*–*17*), partly due to the use of latitude or elevation as a rough proxy for climatic variability (*18*–*21*). Previous studies often neglected considerable variation in climate components within latitudes (*22*), as well as associated distinct biological influences.

Here we assess how climatic variability on contrasting temporal scales—seasonal and diurnal—influences the elevational range size of terrestrial vertebrates across the world. We obtained data for climatic variables potentially associated with species range size from CRU TS2.1 and other open sources (*23*) (table S1) and adopted McCain's carefully vetted database of elevational range size for 16,592 species of rodents, bats, birds, lizards, snakes, salamanders, and frogs on 180 montane gradients spanning from 36.5°S to 48.2°N latitude (*19*) (fig. S1). We calculated mean elevational range size for each taxonomic group on each gradient. These means, not individual ranges, formed the basis for all analyses and are henceforth referred to simply as "elevational range size."

We first applied hierarchical partitioning (*24*) to select the environmental and geographic variables with the highest explanatory power for elevational range size. The nine variables retained were daily temperature maximum, diurnal temperature range (DTR), mean annual temperature, seasonal temperature range (STR), minimum and maximum monthly mean temperature, mean annual precipitation (MAP), latitude, and mountain height (fig. S2). We then applied structural equation modeling (SEM) (*25*) to assess the relationships among these variables in explaining range size. SEM is capable of including non–mutually exclusive hypotheses in a system of relationships (*25*) and, hence, is particularly suitable to structure the multiple pathways of highly correlated climatic variables that shape elevational range size (*23*) (fig. S3).

On the basis of the preliminary hierarchical partitioning and subsequent SEM analysis, we found that latitude alone explained little of the variation in elevational range size (Fig. 1, A and B), in accord with other studies that used latitude as a proxy for climatic variability (*15*, *17*, *19*). However, when we considered all possible combinations of proxies, drivers, and relevant climate components, the final model retained latitude, MAP, STR, and DTR as the best model (Fig. 1, A and C). In this model, STR had a significantly positive relationship with elevational range size for our vertebrate data set (correlation coefficient $R = 0.29$, probability $P = 0.006$) (Fig. 1A and table S3). Not surprisingly, latitude had a strong and significant positive relationship with STR ($R = 0.88$, $P < 0.001$) (Fig. 1A and fig. S4A) and thus indirectly influenced elevational range size through its effect on STR in the model. Together, these results support the climate variability hypothesis and corroborate previous results (*11*, *12*, *19*).

However, elevational range size had a significantly negative relationship with DTR ($R = -0.25$, $P = 0.012$) (Fig. 1, A and D). Moreover, DTR and STR are each negatively correlated with MAP (fig. S4, D and E; $R = -0.54$, $P < 0.001$ and $R = -0.07$, $P = 0.025$, respectively; panels A, B, and C in fig. S4 display the global patterns between each climatic factor and latitude). In contrast, MAP showed only a weak correlation with elevational range size itself (Fig. 1E), as demonstrated previously by McCain (*19*). Our final model fits better than a model with only latitude and STR [root mean square error of approximation = 0.076; comparative fit index = 0.981; standard root mean square residual = 0.073 (table S2); note that SEM penalizes for each additional parameter]. When we used climate variables for which climate data are currently available at finer spatial resolutions (5 arc min and 30 arc sec) (fig. S5), the structured relationships remained robust, except that the effect of STR became insignificant in one model variant.

In our analysis, latitude and MAP emerged as the geographical and environmental factors that indirectly shape elevational range size through their influence on climatic variability (DTR and STR). We used a stationary bootstrap method to assess whether STR and/or DTR is more explanatory than expected at random along latitude and MAP gradients (*23*). We found that MAP gradients, but not latitude, influenced the relative importance of DTR versus STR with regard to the elevational range size (Fig. 2, A and B). The explanatory

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[1]Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan. [2]Department of Life Sciences, National Cheng Kung University, Tainan 70101, Taiwan. [3]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA. [4]University of Colorado Museum of Natural History, Boulder, CO 80309, USA. [5]Departmento de Ecologia, Universidade Federal de Goiás, CP 131, 74.001-970 Goiânia, Goiás, Brazil. [6]Institute of Statistical Science, Academia Sinica, Taipei 11529, Taiwan. [7]Department of Geography, National Taiwan University, Taipei 10617, Taiwan.
*These authors contributed equally to this work. †**Corresponding author. E-mail: shensf@sinica.edu.tw**

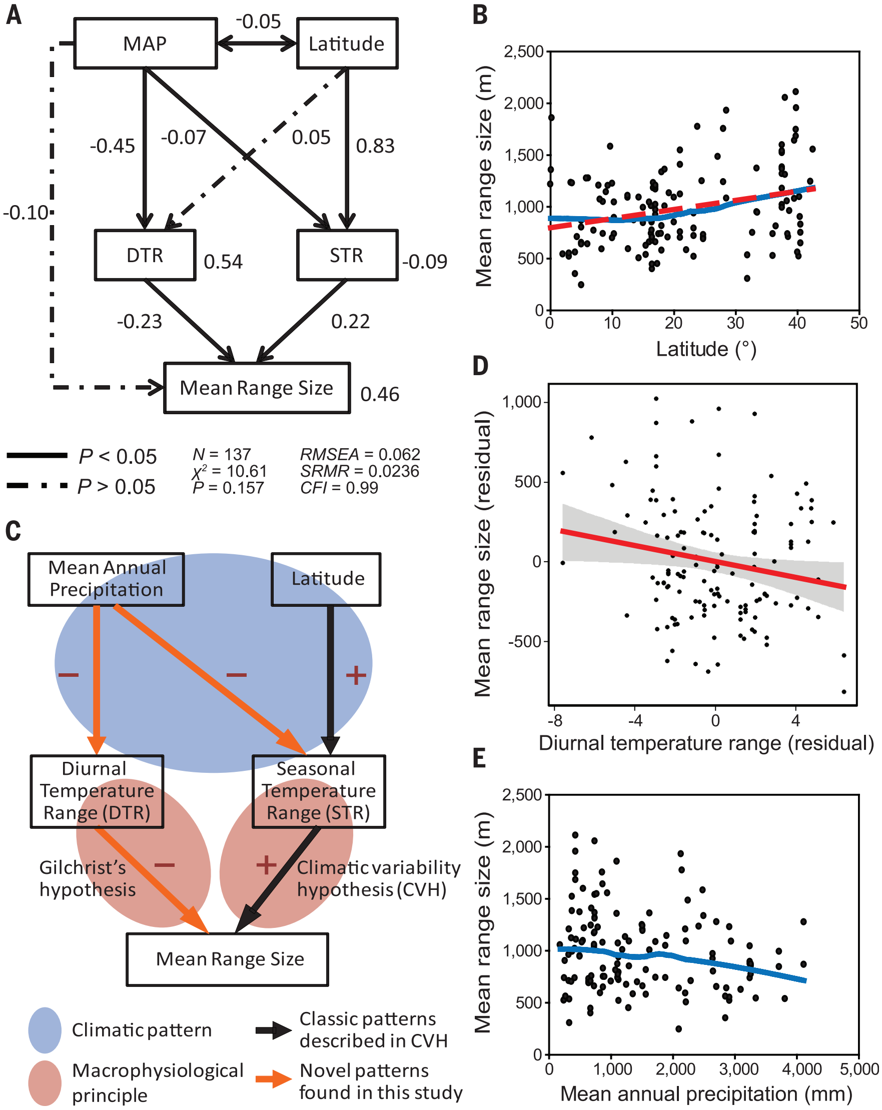

Fig. 1. Relationships among MAP, DTR, latitude, and STR in explaining the elevational range sizes of terrestrial vertebrates. (**A**) Structural equation statistical model. *N*, number of mountain gradients; RMSEA, root mean square error of approximation; SRMR, standard root mean square residual; CFI, comparative fit index. (**B**) Direct relationship between elevational range size and latitude. The blue line represents the LOESS mean; the red dashed line represents a significant linear relationship. (**C**) Conceptual scheme of this study. Plus and minus symbols represent positive and negative relationships, respectively. (**D**) Partial residual plots of elevational range size and DTR. The red line represents the regression curve, which controls for the effect of STR and the interaction between DTR and STR. The gray shaded area represents the smoothed 95% confidence interval. (**E**) Direct relationship between elevational range size and MAP. The blue line represents the LOESS mean. In (A), the structural equation model, numbers next to arrows and boxes are unstandardized slopes and intercepts, respectively. The double-headed arrow indicates correlations between factors. For this analysis, taxonomic differences were statistically controlled by setting taxon as a variable, but taxa were also analyzed separately (fig. S11). For details, see tables S3 to S5.

power of MAP was generally higher than random expectation along the precipitation gradient, whereas latitude showed considerably less deviation from random expectations. Because precipitation influences global energy flow through its correlation with cloudiness and latent heat flux, MAP has been identified as a dominant factor governing Earth's thermodynamics (*26*). At lower precipitation levels, DTR was the dominant influence on geographic variation in mean elevational range size, whereas STR dominated at moderate precipitation levels. At high precipitation levels, the effects of both DTR and STR were diminished (Fig. 2A). This complex relationship was generally concealed when the proxy approach was directly applied. As shown by the blue lines in Fig. 2, A and B, the locally weighted scatterplot smoothing (LOESS) lines for elevational range size did not respond noticeably to either gradient.

Our structural equation model demonstrated that STR and DTR have opposite effects on species elevational range size. Although organisms must evolve to survive all conditions that they experience (tolerance range), they can nonetheless focus reproductive activity on a narrow range of conditions (optimum performance range), as long as they experience those conditions often enough within their life span (*27*). Using a phenotypic optimality model, Gilchrist (*27*) demonstrated that greater among-generation temperature variation should favor a wider performance range (thermal generalists), whereas a narrower performance range (thermal specialists) will be favored by selection when within-generation temperature variation is great. Recent empirical studies also show that the scope of tolerance range limits for motor function and survival, as determined experimentally, may be a poor predictor of elevational range size for thermal generalists (*28*).

Nevertheless, because Gilchrist's model focused on within- and among-generation environmental variation, an organism's life span should have a pronounced influence on the evolution of thermal performance range. Thus, it is perhaps surprising to see the strong relationships among STR, DTR, and range size for the vertebrate species in our analysis, given that most have multiyear generation times. We therefore extended Gilchrist's approach to general forms of environmental variation to investigate the expected effects of longer- and shorter-term environmental variations on the expected evolution of performance range (*23*) (figs. S6 to S9). We found that Gilchrist's principal predictions still hold, even when we replaced among- and within-generation variations with a more general form of longer- and shorter-term variation, respectively. This result arises simply because longer-term variation (including STR) occurs more frequently among generations than within generations, whereas shorter-term variation (e.g., DTR) tends to occur within generations (*23*). Moreover, we found that average STR was highly correlated with multiyear temperature variation ($R = 0.87$, $P < 0.001$) (*23*) (fig. S10). Together, these results help to explain the important roles of STR and DTR in shaping the elevational range sizes of the vertebrate species in this study.

In addition, taxon-specific analysis showed that MAP and DTR synergistically shape elevational range sizes of rodents and birds (but not bats, the third endotherm group considered), with increasing range size associated with greater MAP (fig. S11). For endotherms, water availability is crucial for evaporative cooling in a hot environment (*29*). The role of water in adaptation to cold remains largely unexplored in ecological studies, but water may be important in blood circulation and metabolic heat (*30*). Further studies of the relationship between water availability and shorter-term temperature variation could prove fruitful, especially for endotherms, including bats (see supplementary text and fig. S12).

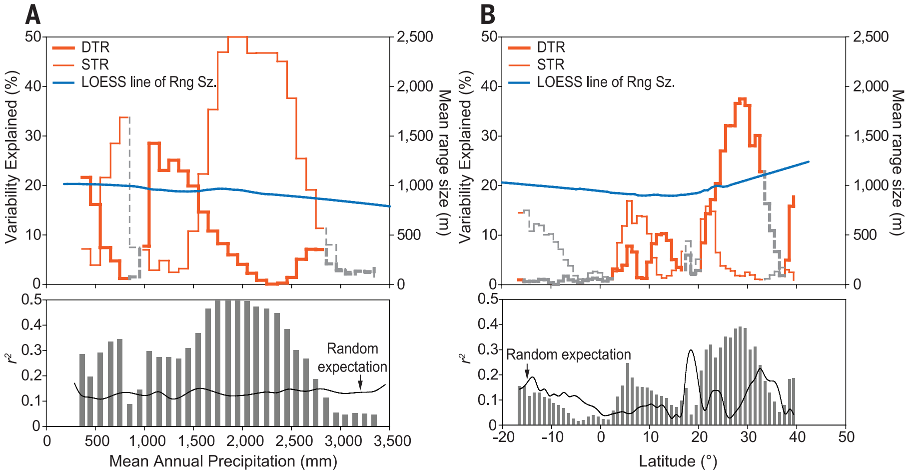

Fig. 2. Influence of DTR and STR along environmental gradients. Panels show the relative explanatory power of DTR and STR for elevational range size along (**A**) the MAP gradient and (**B**) the latitudinal gradient. In the upper panels, blue lines represent LOESS lines of the plots in Fig. 1, B and E. Total explanatory power is indicated by bars in the lower panels, plotted against random expectations (black lines). Rng Sz., range size; r^2, coefficient of determination.

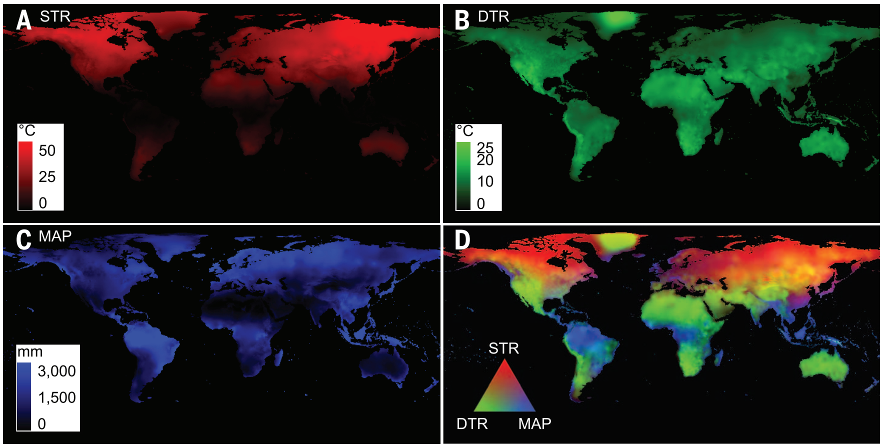

Fig. 3. Global maps of temperature variability. (**A**) Seasonal temperature range (STR). (**B**) Diurnal temperature range (DTR). (**C**) Mean annual precipitation (MAP). (**D**) RGB (red-green-blue) color spectra presenting STR, DTR, and MAP. For example, the northern Amazon basin within the tropical region has very high MAP with low STR and DTR, yielding bluish pixels in (D). All maps are at 0.5° spatial resolution.

On the basis of our empirical and modeling results, we propose a new macroecological principle. Introducing temporal scale offers a new perspective on the physical influence of climatic variability. STR dominates the thermal profile at high latitudes in the Northern Hemisphere, whereas tropical areas with high amounts of rainfall weaken the contrast between DTR and STR (Fig. 3). DTR dominates the majority of the rest of the land surface, including arid land masses, mountainous areas, and most of the terrestrial Southern Hemisphere (Fig. 3D). We conclude that the relevance of each climatic factor to the range size of species should be carefully evaluated for organisms of different taxonomic groups, characterized by different generation times and thermoregulatory systems.

Our study may have implications for understanding biological responses to climate change. For example, tropical species are expected to be thermal specialists because they are adapted to low STR (*5*, *6*). Nevertheless, because of their adaptation to higher DTR, both tropical and temperate montane species (of some groups) may be thermal specialists and, thus, vulnerable to changing climates.

REFERENCES AND NOTES

1. IPCC, "Summary for policymakers," in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. F. Stocker *et al*., Eds. (Cambridge Univ. Press, 2013), pp. 1–30.
2. D. R. Easterling *et al*., *Science* **277**, 364–367 (1997).
3. T. R. Karl *et al*., *Geophys. Res. Lett.* **18**, 2253–2256 (1991).
4. G. Wang, M. E. Dillon, *Nat. Clim. Chang.* **4**, 988–992 (2014).
5. I. Khaliq, C. Hof, R. Prinzinger, K. Böhning-Gaese, M. Pfenninger, *Proc. Biol. Sci.* **281**, 20141097 (2014).
6. D. A. Vasseur *et al*., *Proc. Biol. Sci.* **281**, 20132612 (2014).
7. J. Spicer, K. Gaston, *Physiological Diversity and Its Ecological Implications* (Blackwell Science, 1999).
8. F. Bozinovic, P. Calosi, J. I. Spicer, *Annu. Rev. Ecol. Evol. Syst.* **42**, 155–179 (2011).
9. K. J. Gaston *et al*., *Am. Nat.* **174**, 595–612 (2009).
10. K. J. Gaston, *The Structure and Dynamics of Geographic Ranges* (Oxford Univ. Press, 2003).
11. D. H. Janzen, *Am. Nat.* **101**, 233–249 (1967).
12. C. K. Ghalambor, R. B. Huey, P. R. Martin, J. J. Tewksbury, G. Wang, *Integr. Comp. Biol.* **46**, 5–17 (2006).
13. G. C. Stevens, *Am. Nat.* **133**, 240–256 (1989).
14. G. C. Stevens, *Am. Nat.* **140**, 893–911 (1992).
15. K. J. Gaston, S. L. Chown, *Oikos* **84**, 309–312 (1999).
16. C. M. McCain, K. Bracy Knight, *Glob. Ecol. Biogeogr.* **22**, 750–759 (2013).
17. F. J. Whitton, A. Purvis, C. D. L. Orme, M. Á. Olalla-Tárraga, *Glob. Ecol. Biogeogr.* **21**, 179–190 (2012).
18. A. Addo-Bediako, S. L. Chown, K. J. Gaston, *Proc. Biol. Sci.* **267**, 739–745 (2000).
19. C. M. McCain, *Ecol. Lett.* **12**, 550–560 (2009).
20. A. Ruggiero, V. Werenkraut, *Glob. Ecol. Biogeogr.* **16**, 401–414 (2007).
21. J. M. Sunday, A. E. Bates, N. K. Dulvy, *Proc. Biol. Sci.* **278**, 1823–1830 (2011).
22. K. S. Sheldon, J. J. Tewksbury, *Ecology* **95**, 2134–2143 (2014).
23. Materials and methods are available as supplementary materials on *Science* Online.
24. U. Grömping, *J. Stat. Software* **17**, 1 (2006).
25. J. B. Grace, *Structural Equation Modeling and Natural Systems* (Cambridge Univ. Press, 2006).
26. J. T. Kiehl, K. E. Trenberth, *Bull. Am. Meteorol. Soc.* **78**, 197–208 (1997).
27. G. W. Gilchrist, *Am. Nat.* **146**, 252–270 (1995).
28. J. M. Sunday *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **111**, 5610–5615 (2014).
29. L. B. Buckley, A. H. Hurlbert, W. Jetz, *Glob. Ecol. Biogeogr.* **21**, 873–885 (2012).
30. C. M. Beall, N. G. Jablonski, A. Steegmann, *Human Biology: An Evolutionary and Biocultural Perspective* (Blackwell Science, 2012).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/351/6280/1437/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S12
Tables S1 to S5
References (*31*–*37*)

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