

Thermal tolerance and the global redistribution of animals

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The redistribution of life on Earth has emerged as one of the most significant biological responses to anthropogenic climate warming^{1–3}. Despite being one of the most long-standing puzzles in ecology⁴, we still have little understanding of how temperature sets geographic range boundaries⁵. Here we show that marine and terrestrial ectotherms differ in the degree to which they fill their potential latitudinal ranges, as predicted from their thermal tolerance limits. Marine ectotherms more fully occupy the extent of latitudes tolerable within their thermal tolerance limits, and are consequently predicted to expand at their poleward range boundaries and contract at their equatorward boundaries with climate warming. In contrast, terrestrial ectotherms are excluded from the warmest regions of their latitudinal range; thus, the equatorward, or ‘trailing’ range boundaries, may not shift consistently towards the poles with climate warming. Using global observations of climate-induced range shifts, we test this prediction and show that in the ocean, shifts at both range boundaries have been equally responsive, whereas on land, equatorward range boundaries have lagged in response to climate warming. These results indicate that marine species’ ranges conform more closely to their limits of thermal tolerance, and thus range shifts will be more predictable and coherent. However, on land, warmer range boundaries are not at equilibrium with heat tolerance. Understanding the relative contribution of factors other than temperature in controlling equatorward range limits is critical for predicting distribution changes, with implications for population and community viability.

Climate-forced model projections forewarn of widespread invasions, extinctions and the redistribution and loss of critical ecosystem functions^{6–8}. Forecasting distributional shifts through climate niche modelling relies on the key assumption that species’ ranges are fundamentally determined by climate. The climate variability hypothesis proposes that species’ latitudinal ranges reflect their thermal tolerance⁹, whereby heat tolerance corresponds to the highest summer temperature and cold tolerance corresponds to the coldest winter temperature of their ranges (Fig. 1a). However, species may tolerate greater temperature extremes than those to which they are exposed (Fig. 1b), or may behaviourally avoid critical extremes in their thermal environment (Fig. 1c), and the extent to which these offsets occur is unknown. The relationship between thermal tolerance and latitudinal ranges of species has been quantified only in a few taxonomic groups in a few locations (European diving beetles¹⁰, South American lizards¹¹ and North American frogs¹²). Thus, the general extent to which species’ latitudinal distributions are set by thermal physiology remains an open question.

We take advantage of comprehensive data sets of species’ thermal tolerance limits, distributions and climate-related range boundary shifts to understand the importance of temperature in limiting geographic ranges at a global scale. We first test how latitudinal range limits match expectations on the basis of environmental temperature extremes and species’ thermal tolerances, with a synthesis of experimentally measured acute critical and lethal thermal tolerance limits of 142 marine and terrestrial ectotherms (plus 27 intertidal species, see Supplementary Methods). Next, we test whether species have responded equally at equatorward and poleward range boundaries to the large-scale ‘natural’ experiment of global climate change using 648 range boundaries, to evaluate the relative importance of climate-related factors in controlling them.

We find that the observed geographic range boundaries of marine ectotherms are closely matched to their potential latitudinal ranges, on the basis of thermal tolerance and extreme temperatures across latitudes (Figs 1d and 2, and see Supplementary Fig. S1 for Fig. 2 equivalent over both hemispheres). In contrast, on land, ectotherms can tolerate warmer temperatures than those experienced at their equatorward range boundary, and are thus underfilling their potential latitudinal range (Figs 1d and 2c). Equatorward underfilling increases with latitude; hence, terrestrial ectotherms at higher latitudes should occupy more equatorial latitudes on the basis of temperature alone (Supplementary Fig. S2). This suggests that some other abiotic or biotic factor(s) excludes these species from the tropics. Environmental temperatures more closely match or exceed the heat tolerance of terrestrial ectotherms found closer to the Equator; hence, they have relatively narrow thermal safety margins¹³ (Fig. 2c and Supplementary Fig. S2). At the poleward range boundary, terrestrial ectotherms live at higher latitudes than would be predicted by their measured cold tolerance alone (Fig. 1c) and consequently overfill their potential ranges at the poleward boundary (Figs 1d and 2d and Supplementary Table S1). The extent of overfilling at the poleward range boundary among terrestrial ectotherms increases at higher latitudes (Supplementary Fig. S2). Hence, cold-temperature avoidance such as diapause and hibernation is an increasingly important winter survival mechanism towards the poles¹⁴. Still, cold tolerance increases among species with more poleward range extents (Supplementary Fig. S3); therefore, both physiological cold tolerance and behavioural mechanisms together explain the capacity of terrestrial ectotherms to occupy extreme cold latitudes. These results are robust to taxonomic non-independence, variation in experimental protocols, varying quality of realized range estimates, spatial autocorrelation and non-random sampling across longitudes (see mixed-effects modelling results, Supplementary Discussion, Tables S1–S3 and Figs S4–S8).

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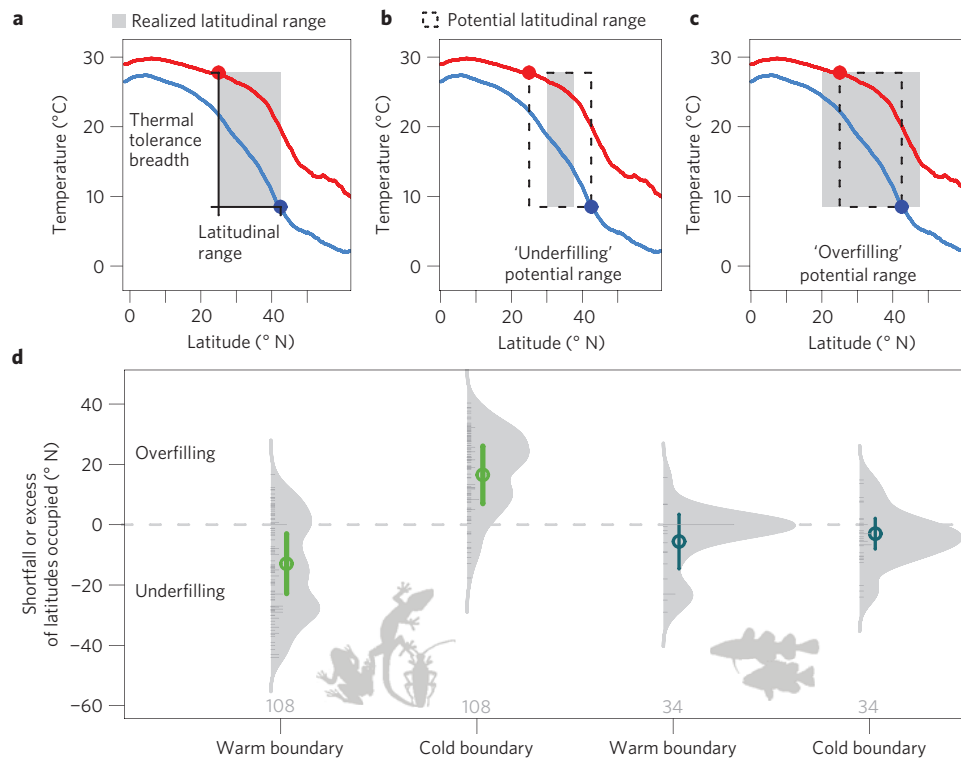


Figure 1 | Environmental temperature, thermal tolerance and potential latitudinal ranges. **a–c.** Theoretical relationships between species' realized and potential latitudinal distributions. Grey rectangles represent a species' thermal tolerance (height of rectangle) and its realized latitudinal range (width of rectangle). Realized latitudinal ranges may match (**a**), underfill (**b**) or overfill (**c**) their potential latitudinal ranges (dashed black rectangles), on the basis of species' thermal tolerances and environmental extremes with latitude (red and blue lines). **d.** Degree of offset between potential and realized latitudinal range at poleward and equatorward range boundaries of terrestrial (green) and marine (blue) ectotherms. Positive and negative values represent overfilling or underfilling of expected latitudinal ranges, respectively. Mean and 95% confidence interval from mixed-effects models that account for taxonomic and methodological non-independence are shown. Grey density plots show the distribution of raw data, with sample sizes indicated below.

Our findings lead to testable hypotheses as to the relative sensitivities of species' range boundaries to climate forcing. Marine species are thermal-range conformers: their latitudinal ranges correspond to their thermal tolerance (Fig. 1a). The ultimate driver of this relationship may lie as much with temperature as it does with factors closely correlated with temperature, such as dissolved oxygen availability (oxygen limitation hypothesis¹⁵). Regardless, the close coupling between thermal tolerance and environmental temperature suggests that marine species will be sensitive to temperature change at both their poleward and equatorward range boundaries. In contrast, terrestrial species' latitudinal ranges are likely to respond to warming more strongly at their cold range margins, where their present ranges extend to higher latitudes than are predicted from their cold tolerance, but may be less sensitive at their equatorward range margins, owing to the decoupling between temperature tolerance and heat experienced at their equatorward range boundary, particularly among higher-latitude species^{3,16}.

We tested these hypotheses using an extensive compilation of recent climate-related range shifts at poleward and equatorward range boundaries, both on land and in the ocean. We compiled two data sets of range shift observations in marine and terrestrial ectotherms: local assemblage-scale studies that document shifts at both poleward and equatorward range boundaries in multiple species using a consistent methodology; and species-level studies of changes at a single range boundary (see Methods). Our review revealed nine assemblage-scale analyses: seven marine (invertebrates and fishes) and two terrestrial assemblages (dragonflies and butterflies; Table 1). These studies were conducted mainly at temperate latitudes (Fig. 3a). As we predicted, in ocean assemblages, both poleward and equatorward range boundaries have shifted

towards higher latitudes with similar frequency ($\chi^2 = 0.0009$, 1 d.f., $P = 0.98$, Table 1), whereas on land, equatorward-boundary contractions have been less frequent than poleward-boundary expansions (Fig. 3b,c, $\chi^2_{(1, n=120)} = 5.51$, 1 d.f., $P = 0.02$, Table 1). Among single-species studies in the ocean, the relative frequencies of poleward-boundary expansions and equatorward-boundary contractions have been within the same order of magnitude. On land, observations of poleward-boundary expansions have been three orders of magnitude more frequent than equatorward-boundary contractions (Fig. 3c).

The greater asymmetry in range shifts on land is not easily explained by latitudinal variation in climate velocities in the regions included in our study¹⁷, nor by range shift detection bias, demographic compensation at equatorward range boundaries or evolutionary adaptation, because there is no reason to expect these processes to be less influential in the ocean (for further discussion of these points see Supplementary Discussion). Instead, the available data suggest equatorward range boundaries of terrestrial ectotherms are less sensitive to climate change when compared with the poleward boundary, and are consistent with the predictions that follow from the pattern of range underfilling on land. Our findings are consistent with two other lines of evidence. Similar assemblage-scale asymmetries have been observed in climate-associated latitudinal range shifts of birds¹⁸, and elevational range shifts in insects¹⁹, birds²⁰ and herptiles²¹, whereby trailing range boundaries (minimum latitude or elevation) were lower in frequency when compared with the leading (maximum latitude or elevation) range boundaries. These observations are also consistent with terrestrial phylogeographic evidence showing that equatorward range boundaries have been relatively stable

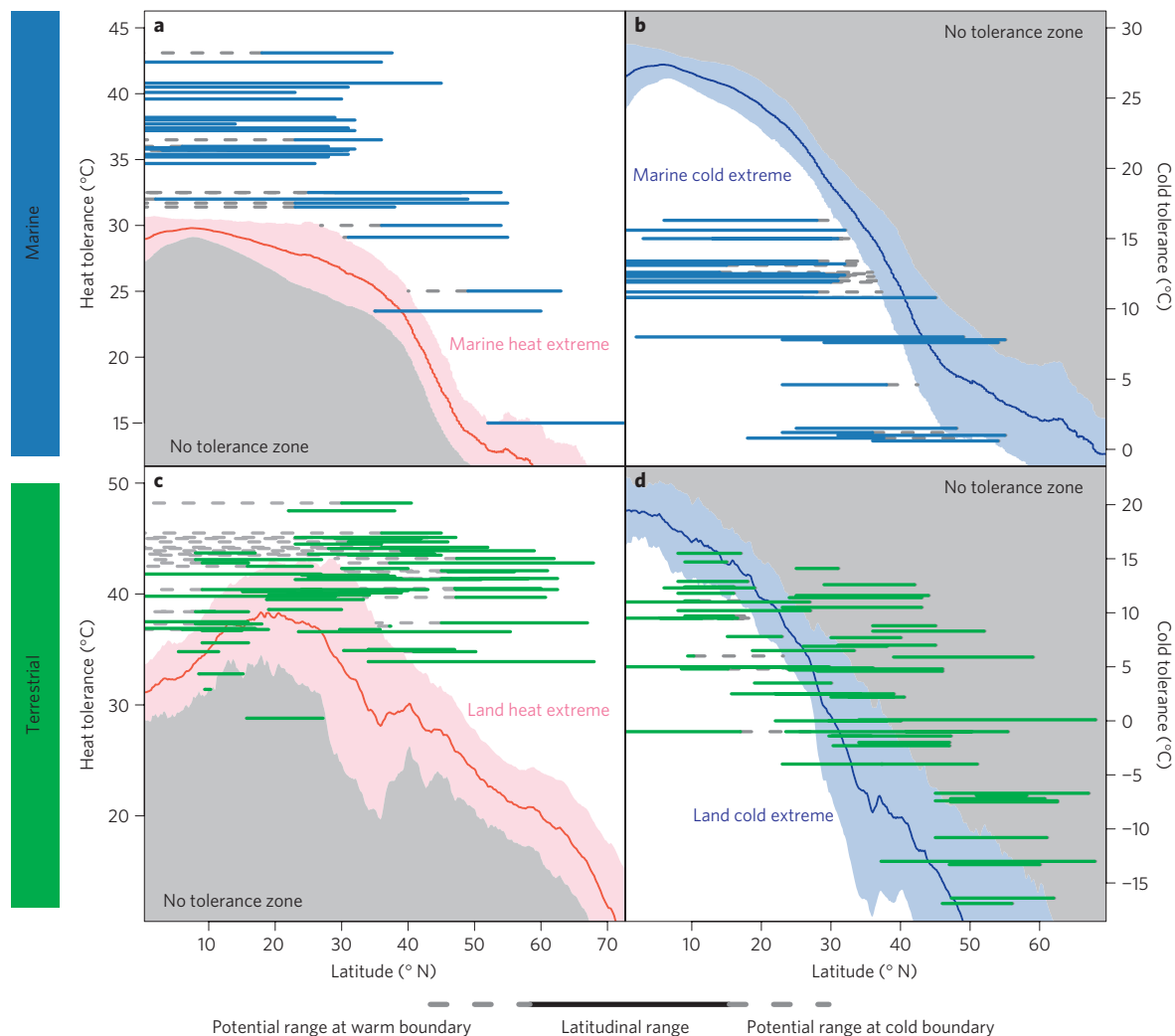


Figure 2 | Potential and realized latitudinal range boundaries of ectotherms. **a–d**, The realized latitudinal ranges of marine (**a,b**) and terrestrial (**c,d**) ectotherms represented as solid horizontal bars along the x axis, versus species' heat (**a,c**) and cold (**b,d**) tolerance limits on the y axis. The mean temperature of the warmest (red) or coldest (blue) month for each latitude from long-term climate data is shown, with shaded regions showing standard deviation across longitude. Grey shaded regions show where species' critical thermal tolerance would be insufficient to remain active in extreme warm (**a,c**) and cold (**b,d**) temperatures. Dashed grey horizontal lines show the extent of latitudes that species could potentially occupy on the basis of thermal tolerance alone.

through glacial history when compared with recent expansions at poleward range boundaries¹⁶.

We offer three, non-mutually exclusive, explanations as to why terrestrial ectotherms underfill their potential equatorward ranges, each of which addresses why equatorward range boundaries are less sensitive to climate warming. First, precipitation and moisture availability, a constraint unique to terrestrial ectotherms, may set the equatorward range boundary, particularly around the driest latitudes ($\sim 22^\circ$, Supplementary Fig. S9). If so, equatorward range boundaries may not shift in a poleward direction at the same rate as poleward range boundaries because the predicted changes in precipitation and temperature differ²².

Second, the temperature climatologies used in our analyses may not represent the critical bottlenecks for long-term species persistence of terrestrial species at their equatorward boundaries. Interannual anomalies or short periods of high temperatures not captured by the monthly averages used here may be critical for limiting long-term occupancy at warm range boundaries (Supplementary Fig. S10). Both spatial¹⁷ and temporal²³ variability in environmental temperature are greater on land when compared with the ocean. If extreme events set the equatorward boundary on

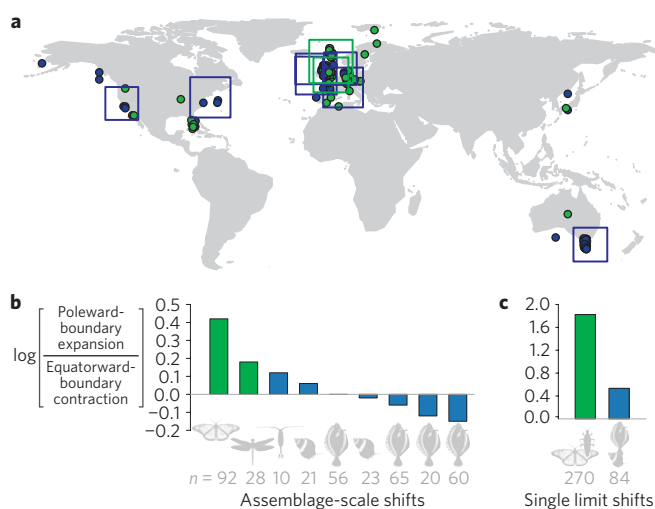
land, range contractions would not be expected until a threshold, or tipping point, is breached at a species' equatorward boundary²⁴.

Third, biotic interactions may be more important in setting species' equatorward range boundaries when compared with their poleward range boundaries, such that species may be biotically excluded from realizing their full potential equatorward range^{4,25}. Darwin proposed this hypothesis on the basis of greater species richness, and the expectation of greater diffuse competition, towards the Equator⁴. Biotic exclusion at equatorward range boundaries may be more prominent on land when compared with the ocean for two reasons. First, the marked increase in species richness towards the Equator is less pronounced in the ocean²⁶, suggesting that the potential for diffuse competition and other complex biotic interactions may not scale with latitude in the ocean as strongly as they do on land. Second, trophic interactions and spatial dynamics in the ocean tend to be based to a greater extent on individuals' size, rather than on species identity, whereas for terrestrial species identity plays a greater role^{27,28}. Under this biotic limitation hypothesis, terrestrial species should be more sensitive to the encroachment of competitors and enemies rather than to temperature directly²⁹, and thus

Table 1 | Summary of studies comparing climate-related range shifts of poleward and equatorward range boundaries in marine and terrestrial ectotherm assemblages, in which both poleward and equatorward range limits were sampled.

Taxon	Shift type	Equatorward-boundary contractions/number sampled	Poleward-boundary expansions/number sampled	log (poleward-boundary/equatorward-boundary shifts) [†]	χ^2 test P value
Marine assemblages					
Shore invertebrates ³²	Range limits [‡]	12/17	4/6	−0.02	0.94
Pelagic copepods ³³	Range limits	3/5	4/5	0.12	0.84
Shore invertebrates ³⁴	Abundance	5/8	10/14	0.06	0.87
Demersal fish ³⁵	Range limits	6/12	3/8	−0.12	0.94
Demersal and pelagic fish ³⁶	Range limits [§]	7/27	5/27	−0.15	0.83
Demersal fish ³⁷	Abundance	11/14	33/42	0.00	0.82
Demersal fish ³⁸	Abundance	15/25	21/40	−0.06	0.92
Marine assemblages pooled		49/101	37/73	0.02	0.98
Terrestrial assemblages					
Dragonflies ³⁹	Range limits [‡]	2/4	18/24	−0.18	1.00
Butterflies ⁴⁰	Range limits	10/40	34/52	−0.42	0.03*
Terrestrial assemblages pooled		12/44	52/76	−0.40	0.02*

[†]Number of range limits shifts in predicted direction were standardized by the number of species sampled at each range boundary, respectively, in a study. [‡]In the absence of a significance test, range shifts less than 30 km were not counted. [§]Harvested stocks with range contractions at both poleward and lower limits were removed. ^{||}Every species was counted once. Ref. 37 data were not included in pooled tally because species identity were not available.

**Figure 3 | Asymmetry in recent geographic range shifts of ectotherms.**

a, Location of latitudinal range shift studies at the scale of assemblages (squares) and single species (points) for terrestrial and marine species (green and blue, respectively). **b**, Ratio of the relative frequency of range shifts towards higher latitudes at poleward versus equatorward range boundaries of terrestrial (green) and marine (blue) assemblages, ranked by magnitude of ratio, log-transformed. A log-ratio of zero represents the null expectation of equal observations at both range limits, and a log-ratio > 0 indicates an excess of poleward-boundary expansions. Numbers denote sample size of study. Diagrams indicate taxonomic composition. **c**, Ratio of poleward range shifts at poleward versus equatorward range boundaries from single-range-limit studies, log-transformed. Numbers denote total number of observations.

equatorward-boundary contractions will be less predictable using climate variables alone.

The different relationships between potential and realized thermal ranges among marine and terrestrial ectotherms can be used to understand predictions of future range shifts and

ecosystem change within the latitudes sampled (~60° N–60° S). In the ocean, because species' present ranges conform more closely to their thermal limits, species distribution modelling will yield more accurate forecasts of range shifts. On land, poleward range boundaries will also respond predictably with climate warming, subject to the challenges of accounting for species' dispersal and establishment rates, and availability of habitat. However, there are at least three potential mechanisms that may limit the equatorward boundary—moisture availability, extreme heat and competitive exclusion. Although distribution models generally incorporate precipitation and maximum environmental temperature, changes in the equatorward boundary will be more challenging to predict owing to the uncertainty in future projections of precipitation and extreme events, as well as the unknown relative importance of biological mechanisms. Consequently, our data suggest that the impacts of climate change will be more context dependent and less certain on land than in the ocean, and that the mechanisms controlling range boundaries need to be better understood. As terrestrial species' ranges stretch towards the poles, owing to poleward expansions and more-stagnant equatorward boundaries, this raises concern for the potentially harmful consequences of shifting population connectivity and viability, new species combinations and ecological surprises.

Methods

Species' thermal tolerance and latitudinal range limits. Potential latitudinal ranges were calculated using a data set of published experimental estimates of heat and cold tolerance limits of ectotherms³⁰. These included both lethal and critical (loss of motor function) thermal limits, and our results were robust to metric type (Supplementary Discussion). We defined potential cold and warm range boundaries as the latitudinal limits at which a species could survive the mean temperature of the most extreme month given its thermal tolerance (Fig. 1). Realized latitudinal range extents were determined using primary literature and online data providers, mainly the Global Biodiversity Information Facility³¹ (data and references available on request). Species with latitudinal range boundaries occurring at the edge of a continent or island, within freshwater or sampled at elevations above 2,000 m (where latitude is expected to be a poor proxy for thermal regime) were excluded; thus, the resulting data set included species that tended to be broadly distributed (Fig. 2). We used mixed-effects linear models to test for differences between expected and realized range boundaries, while taking into account different experimental methodologies and taxonomic non-independence,

using taxonomy as a nested random effect. We also tested for linear relationships between cold tolerance and poleward range boundaries, and heat tolerance and equatorward range boundaries, with the expectation that more extreme thermal tolerances can allow for more extreme latitudinal boundaries. See Supplementary Methods for treatment of intertidal species.

Climate-related range shifts. We searched the published literature for studies quantifying latitudinal range shifts in ectothermic animals within a region attributed to climate warming, in which both poleward and equatorward range boundaries were sampled (see Supplementary Fig. S11). We defined range shifts as either changes in latitudinal range boundaries or changes in species abundance at regions close to their poleward or equatorward range limits. For each study, we extracted the number of significant poleward shifts, or increases/decreases in abundance that would correspond to a poleward shift, relative to the total number of poleward or equatorward range boundaries that were sampled. We also sampled the published literature for climate-attributed range shifts at range margins of single species. We used combinations of the following keywords: range shift, contraction, expansion, temperature and climate change, in searches using ISI Web of Knowledge and Google Scholar up until December of 2011. All range shift studies were screened according to inclusion rules (see Supplementary Information) and are listed in Supplementary Table S5.

See Supplementary Information for full methods.

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Author contributions

All authors contributed to the study design and formulation of hypotheses. J.M.S. collected latitudinal range and thermal tolerance data and performed the data analyses. A.E.B. reviewed the literature of temperature-driven range shifts and J.M.S. compiled these data for presentation. All authors wrote the manuscript.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.M.S.