

Greater vulnerability to warming of marine versus terrestrial ectotherms

Malin L. Pinsky^{1*}, Anne Maria Eikeset², Douglas J. McCauley^{3,4}, Jonathan L. Payne⁵ & Jennifer M. Sunday⁶

Understanding which species and ecosystems will be most severely affected by warming as climate change advances is important for guiding conservation and management. Both marine and terrestrial fauna have been affected by warming^{1,2} but an explicit comparison of physiological sensitivity between the marine and terrestrial realms has been lacking. Assessing how close populations live to their upper thermal limits has been challenging, in part because extreme temperatures frequently drive demographic responses^{3,4} and yet fauna can use local thermal refugia to avoid extremes^{5–7}. Here we show that marine ectotherms experience hourly body temperatures that are closer to their upper thermal limits than do terrestrial ectotherms across all latitudes—but that this is the case only if terrestrial species can access thermal refugia. Although not a direct prediction of population decline, this thermal safety margin provides an index of the physiological stress caused by warming. On land, the smallest thermal safety margins were found for species at mid-latitudes where the hottest hourly body temperatures occurred; by contrast, the marine species with the smallest thermal safety margins were found near the equator. We also found that local extirpations related to warming have been twice as common in the ocean as on land, which is consistent with the smaller thermal safety margins at sea. Our results suggest that different processes will exacerbate thermal vulnerability across these two realms. Higher sensitivities to warming and faster rates of colonization in the marine realm suggest that extirpations will be more frequent and species turnover faster in the ocean. By contrast, terrestrial species appear to be more vulnerable to loss of access to thermal refugia, which would make habitat fragmentation and changes in land use critical drivers of species loss on land.

The loss of species and populations driven by a warming climate⁸ is of substantial concern, because it can deplete genetic diversity, have cascading effects on other species and alter ecosystem functioning and services^{9,10}. Ancient extinctions were often concentrated at particular latitudes and in particular ecosystems during periods of rapid climate change^{11,12}. However, there has been substantial debate over where it is that the effects of contemporary climate change will be most severe^{13,14}. Depending on the realm analysed, authors have highlighted tropical terrestrial^{14–16} or tropical marine¹⁷ species as the most vulnerable to a changing climate, but latitudinal patterns of extreme temperatures (Fig. 1a) call into question the focus on tropical sensitivity for the terrestrial realm¹³. Assessing relative vulnerability between marine and terrestrial realms has been more difficult because realm-specific analyses have used climate sensitivity measures that cannot be easily compared among studies. The correspondence between thermal limits and geographical range boundaries¹⁸, and the potential for low oxygen availability to limit thermal tolerance^{19,20}, suggests that marine species may be the most sensitive to temperature increases. Conversely, the lower acclimatization abilities^{21,22} of terrestrial species and higher thermal extremes on land (Fig. 1a) instead suggest that terrestrial species may be more sensitive to warming. Here we compare sensitivity

to warming across realms and latitudes to better guide conservation efforts.

Because proximity to acute upper thermal limits is often correlated with population-level responses to temperature^{23,24}, the difference between the upper thermal limit of a species and the hottest temperature that it experiences provides an index of the tolerance of this species for further warming^{5,15,25}. However, the temporal and spatial scales are important: short-duration extreme hot temperatures often drive the strongest responses^{3,4,13}, and small spatial refugia can allow animals to escape such extremes^{5–7}. Here we calculate the thermal safety margin (TSM) as the difference between the acute upper thermal limit of a species and the extreme hot hourly body temperature of the species in the coolest microhabitat that is available (Methods). The TSM measures the relative proximity of an organism's range of experienced temperatures to its heat-tolerance limits. Although not a direct estimate of a population response to warming (which would require knowledge of reproduction and survival as a function of sub-lethal temperatures), TSMs provide a metric for comparing warming tolerance across a wide range of species.

To compare TSMs across realms, we first compiled upper thermal limits (T_{\max}) for 406 ectothermic species (318 terrestrial and 88 marine) from 15 classes of animal (Extended Data Table 1), and calculated an adjusted T_{\max} (T_{\max}') that takes into account acclimatization²¹ to seasonal extremes (Extended Data Fig. 1, Methods). We focused on entirely terrestrial species and entirely subtidal marine species—that is, we did not include intertidal species. The highest thermal limits (in terms of T_{\max}') in marine species occurred near the equator (Fig. 2b), whereas terrestrial species had two moderate peaks in thermal tolerances at 11° S (95% confidence interval of 8–14° S) and 27° N (95% confidence interval of 23–29° N) (Fig. 2a, Extended Data Fig. 2), after accounting for realm, experimental methods and taxonomy (generalized additive mixed model (GAMM), $n = 406$ species) (Extended Data Table 2, Methods).

We then estimated body temperatures (T_b) reached by ectotherms during the hottest hours of the year. Because microhabitats strongly influence body temperatures, we estimated extreme T_b both in full sun ($T_{b, \text{exposed}}$) and in thermal refugia ($T_{b, \text{protected}}$) to characterize conditions under a range of behavioural thermoregulatory options (Extended Data Table 3, Methods). Terrestrial extreme $T_{b, \text{protected}}$ values in shaded microclimates were hottest around 18° S (95% confidence interval 10–25° S) and 25° N (95% confidence interval 21–28° N) (Fig. 2a, Extended Data Fig. 2)—near locations in which long summer days create the warmest temperatures (Fig. 1a)—and were lower than T_{\max}' across latitudes, after accounting for phylogenetic histories (GAMM, $n = 387$ species) (Extended Data Table 2). However, extreme values of $T_{b, \text{exposed}}$ for terrestrial species in full sun were frequently hotter than their thermal tolerances (Fig. 2a), which suggests that most terrestrial ectotherms must use thermal refugia to avoid harmful thermal stress⁵. Extreme T_b values in marine species peaked in the tropics, and were lower than—but roughly parallel to— T_{\max}' across latitudes (Fig. 2b),

¹Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ, USA. ²Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway. ³Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, USA. ⁴Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA, USA. ⁵Department of Geological Sciences, Stanford University, Stanford, CA, USA. ⁶Biology Department, McGill University, Montreal, Quebec, Canada. *e-mail: malin.pinsky@rutgers.edu

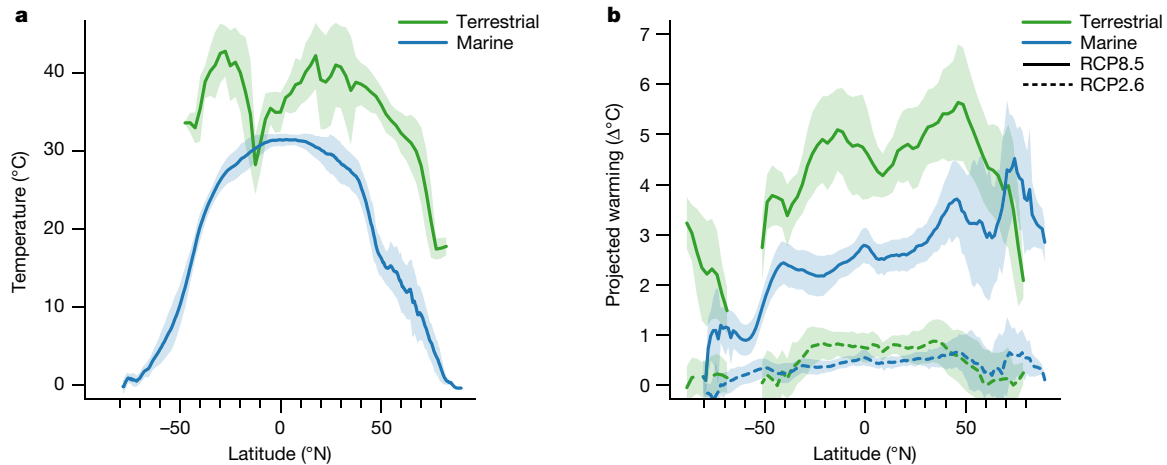


Fig. 1 | Extreme hot temperatures across latitudes in terrestrial and marine environments. Data for terrestrial environments are shown in green; data for marine environments are shown in blue. **a**, The hottest hourly air or water-surface temperatures reveal that the warmest extremes are at mid-latitudes on land and in the tropics in the ocean. $n = 1,454$ (land) or 691,150 (ocean) grid cells. **b**, Projected warming of the hottest

hour across latitudes under RCP8.5 and RCP2.6 scenarios, comparing the change in temperatures under the 1986–2005 period to the 2081–2100 period. $n = 3,106$ (land, both scenarios), 28,925 (ocean RCP2.6), or 28,965 (ocean RCP8.5) grid cells. In both plots, the line shows the mean and shaded areas show the s.d. across grid cells within each latitudinal band. Extended Data Fig. 3a shows hottest hours projected for the future.

which suggests that there are links between temperature extremes and the evolution of thermal tolerance²⁵.

We assessed sensitivity to warming by calculating the TSM as the distance between T_{\max}' and the extreme $T_{b, \text{protected}}$ for each species (Methods). Accessible thermal refugia that offer cooler conditions are important for preventing local extirpations^{6,7}; these include refugia such as shaded habitats on land or deeper waters in the ocean, for species that are mobile enough to access these microclimates (Methods). On land, the thermal safety margins were narrowest at 30° S (95% confidence interval 16–38° S) and 22° N (95% confidence interval 13–27° N), and wider towards the poles (Fig. 2c, Extended Data Fig. 2). Marine TSMs were narrowest around the equator (0° N, 95% confidence interval 19° S to 18° N), and widened towards both poles

(Fig. 2c). On average, marine species had TSMs that were only 80% as wide as those of terrestrial species, after accounting for potential effects of latitude, taxonomic group and experimental methods ($12.3 \pm 0.9^\circ\text{C}$ in the ocean and $15.4 \pm 1.3^\circ\text{C}$ on land; GAMM, $t = 2.37$ with 375.7 degrees of freedom, two-tailed $P = 0.018$, $n = 387$ species) (Fig. 2c, Extended Data Table 2). Moreover, average TSMs for tropical marine species were at least 3° C narrower than at any latitude on land.

We then used the projected warming, by the end of the twenty-first century, of the hottest hour (Fig. 1b, Extended Data Fig. 3a) to estimate the ‘remaining’ safety margins for animals that stay in place (Methods). The narrowest safety margins in either realm were projected for tropical marine species (Fig. 2c), even after accounting for the greater acclimatization abilities of marine species (Extended Data Fig. 3c, Methods).

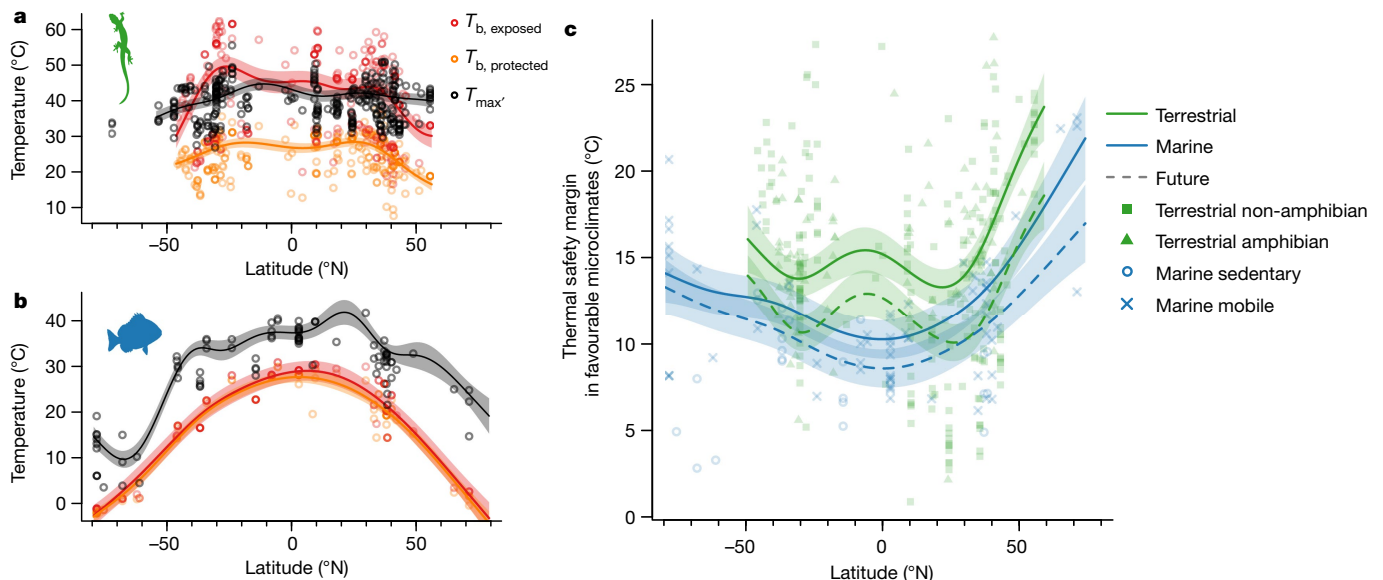


Fig. 2 | Greater thermal safety on land if thermal refugia are available. **a**, **b**, Maximum thermal-tolerance limits (T_{\max}' , black) on land (**a**) and in the ocean (**b**) compared to 95th percentile warmest hourly body temperatures (T_b) in accessible thermal refugia (orange) or in fully exposed microclimates (red). $n = 299$ (T_b on land), 318 (T_{\max}' on land) or 88 (T_b and T_{\max}' in the ocean) species. **c**, TSMs in thermal refugia for marine and terrestrial species for current and future conditions (2081–2100 under RCP8.5). $n = 299$ (land) or 88 (ocean) species. The dots

are individual ectotherm populations and the shaded ribbons show ± 1 s.e. from GAMM fits (**a–c**). Extended Data Fig. 1 shows acclimatization adjustments; Extended Data Fig. 2 shows the uncertainty in peak locations; Extended Data Fig. 3 shows future TSMs under other emission scenarios or with future acclimatization; Extended Data Fig. 4 shows alternative TSM calculations; and Extended Data Table 2 provides results of statistical modelling.

Table 1 | Contractions at warm range edges were more common in the ocean than on land

	Estimate	s.e.	z value	P value	RVI
Intercept	0.031	0.33	0.092	0.93	
Realm (terrestrial)	-1.3	0.56	-2.4	0.015	0.76
Latitude (absolute value)	0.076	0.038	2.0	0.044	0.68
Method (two surveys)	0.45	0.49	0.93	0.35	0.45
Duration	0.029	0.016	1.8	0.070	0.34

Fixed effect coefficients are from a generalized linear mixed model (GLMM) ($r^2 = 0.12$, 150 degrees of freedom, $n = 159$ species range edges) with the probability of extirpation on a logit scale as the response. 'Realm' measures the terrestrial effect compared to marine, and reveals that the chance of extirpation (expressed as log odds) were significantly lower on land (and higher in the ocean). The coefficient estimates (logit scale), z values, two-sided P values and the relative variable importance (RVI) are shown in the table. No adjustments for multiple comparisons were made. RVI indicates the relative weight of evidence in favour of including each variable. 'Method' measures the effect size for studies that conducted two surveys, compared to studies that conducted more than two surveys in time. 'Duration' refers to the time in years between the first and last survey. Random effects of nested taxonomic grouping were included to account for taxonomic non-independence.

On land, the narrowest margins were projected for mid-latitudes (Fig. 2c), which is consistent with pronounced warming projected for these locations (Fig. 1b). In scenarios of low greenhouse gas emissions (representative concentration pathway (RCP)2.6), ectotherms globally would have TSMs that were $50 \pm 10\%$ s.e. wider than under a high-emission scenario (RCP8.5)(Extended Data Fig. 3b). However, the loss on land of accessible shade or of water for evaporative cooling would erase the safety margin for most terrestrial species (Extended Data Fig. 4d).

Caution is warranted when interpreting TSMs—in part because the effects of sub-lethal temperatures often drive mortality and population extirpations before thermal safety falls to zero^{19,26,27} (Extended Data Fig. 5), and in part because acclimatization and behavioural adjustments may (for some organisms) help to reduce overheating to a greater extent than is suggested by our calculations²⁸. Full thermal performance curves and a focus on activity budgets would help to advance the field, but are not yet widely available²⁷. Additional thermal-tolerance data for equatorial species, a better understanding of behavioural thermoregulation options in the ocean and increased species-specific data on the availability and costs of using various terrestrial microhabitats are also needed to further refine our understanding of the vulnerability of marine and terrestrial ectotherms to warming²⁷.

However, despite these caveats, many extirpations that are attributable to warming have already occurred—particularly at the warm range edges of species (that is, where species are living nearest the upper limit of their thermal tolerance)⁸. The smaller TSMs for marine species suggest that—all else being equal—ongoing warming may already have driven more frequent population extirpation in the ocean. We tested for this effect in a global dataset of range-edge positions (Extended Data Table 4), and found that extirpations at the warm edges of species' ranges were twice as common in the ocean (56%) as on land (27%), after accounting for taxonomy, latitude and re-survey duration and frequency (GLMM, $n = 159$ species range edges, $z = -2.4$, two-tailed $P = 0.015$) (Table 1, Methods). High frequencies of extirpation (55%) among marine species with low adult mobility suggested that the movement of individuals alone did not explain high rates of extirpation at sea (Methods). The effect size across land and sea for ectothermic animals was stronger than—but in the same direction as—that found in a previous study of local extirpation that included endotherms and plants⁸. Lower rates of extirpation on land could result from greater access to thermal refugia, greater thermal safety in refugia, lower climate velocities or a lesser influence of temperature on range boundaries¹⁸. Overall, these data suggest that warming temperatures have already driven a higher frequency of local extirpations in the ocean.

Increased rates of local extirpation among marine species are likely to be highly consequential to ecosystem functioning and to human well-being⁹. However, local extirpations are distinct from global extinctions, which also depend on the abilities of species to colonize new

territory. Greater dispersal and colonization abilities in the ocean¹ may help some marine species to avoid global extinction, but only if habitat is available for colonization. As an example of habitat availability potentially driving extinction, the fossil record shows that high-latitude marine animals were preferentially driven to extinction during the warming and hypoxia of the mass extinction at the end of the Permian period¹², whereas low-latitude organisms were preferentially driven to extinction during the cooling of the Late Ordovician epoch and largely replaced by species from higher latitudes¹¹.

Differences in thermal safety and colonization between the ocean and land also suggest that there are differences in the ecological effects of warming. We can expect greater rates of population-level extirpation and ecological turnover in the ocean, but equal or lower rates of global extinction compared to terrestrial ecosystems if colonization successfully offsets population extirpations at sea. By contrast, limited dispersal is expected to impede colonization on land and drive range contractions for many terrestrial species²⁹. Thermal safety on land is possible only with access to thermal refugia, which highlights the interaction between warming and ongoing changes in land use⁵. With lower population connectivity and greater microclimate availability than in the oceans, responses among freshwater animals may include features of both terrestrial and marine species¹⁷.

A high sensitivity of ocean fauna to warming is of concern if oceans are to continue their substantial role in supporting human well-being, nutrition and economies. Strategic investments and policy to promote the resilience of ocean ecosystems and to coordinate across national boundaries can help to offset these risks—particularly via the mitigation of greenhouse gas emissions. The palaeobiological record shows that climate change can cause serious local and global marine extinctions, but history need not repeat itself if humanity mitigates the effects of climate change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41586-019-1132-4>.

Received: 25 January 2018; Accepted: 28 March 2019;

Published online 24 April 2019.

- Poloczanska, E. S. et al. Global imprint of climate change on marine life. *Nat. Clim. Chang.* **3**, 919–925 (2013).
- Parnesan, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**, 637–669 (2006).
- Ma, G., Rudolf, V. H. W. & Ma, C. S. Extreme temperature events alter demographic rates, relative fitness, and community structure. *Glob. Chang. Biol.* **21**, 1794–1808 (2015).
- Easterling, D. R. et al. Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074 (2000).
- 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).
- Lima, F. P. et al. Loss of thermal refugia near equatorial range limits. *Glob. Chang. Biol.* **22**, 254–263 (2016).
- Potter, K. A., Woods, H. A. & Pincebourde, S. Microclimatic challenges in global change biology. *Glob. Chang. Biol.* **19**, 2932–2939 (2013).
- Wiens, J. J. Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biol.* **14**, e2001104 (2016).
- Luck, G. W., Daily, G. C. & Ehrlich, P. R. Population diversity and ecosystem services. *Trends Ecol. Evol.* **18**, 331–336 (2003).
- IPCC. In *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Pachauri, R. K. & Meyer, L. A.) 2–34 (IPCC, 2014).
- Finnegan, S., Heim, N. A., Peters, S. E. & Fischer, W. W. Climate change and the selective signature of the Late Ordovician mass extinction. *Proc. Natl Acad. Sci. USA* **109**, 6829–6834 (2012).
- Penn, J. L., Deutsch, C., Payne, J. L., & Sperling, E. A. Temperature-dependent hypoxia explains biogeography and severity of end-Permian marine mass extinction. *Science* **362**, eaat1327 (2018).
- Vasseur, D. A. et al. Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. Lond. B* **281**, 20132612 (2014).
- Dillon, M. E., Wang, G. & Huey, R. B. Global metabolic impacts of recent climate warming. *Nature* **467**, 704–706 (2010).
- Deutsch, C. A. et al. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672 (2008).

16. Bonebrake, T. C. & Deutsch, C. A. Climate heterogeneity modulates impact of warming on tropical insects. *Ecology* **93**, 449–455 (2012).
17. Comte, L. & Olden, J. D. Climatic vulnerability of the world's freshwater and marine fishes. *Nat. Clim. Chang.* **7**, 718–722 (2017).
18. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nat. Clim. Chang.* **2**, 686–690 (2012).
19. Pörtner, H. O. & Knust, R. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97 (2007).
20. Pörtner, H. O. et al. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change* (eds Field, C. B. et al.) 411–484 (Cambridge Univ. Press, 2014).
21. Gunderson, A. R. & Stillman, J. H. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. Lond. B* **282**, 20150401 (2015).
22. Seebacher, F., White, C. R. & Franklin, C. E. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Chang.* **5**, 61–66 (2015).
23. Diamond, S. E. et al. A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology* **93**, 2305–2312 (2012).
24. Hamblin, A. L., Youngsteadt, E., López-Urbe, M. M. & Frank, S. D. Physiological thermal limits predict differential responses of bees to urban heat-island effects. *Biol. Lett.* **13**, 20170125 (2017).
25. Hoffmann, A. A. Physiological climatic limits in *Drosophila*: patterns and implications. *J. Exp. Biol.* **213**, 870–880 (2010).
26. Huey, R. B. et al. Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. Lond. B* **276**, 1939–1948 (2009).
27. Gunderson, A. R. & Leal, M. A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global change. *Ecol. Lett.* **19**, 111–120 (2016).
28. Gunderson, A. R., Dillon, M. E. & Stillman, J. H. Estimating the benefits of plasticity in ectotherm heat tolerance under natural thermal variability. *Funct. Ecol.* **31**, 1529–1539 (2017).
29. Schloss, C. A., Nuñez, T. A. & Lawler, J. J. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl Acad. Sci. USA* **109**, 8606–8611 (2012).

Acknowledgements We thank P. Falkowski, A. Gunderson, R. Huey, H. John-Alder, F. Joyce, G. Saba, B. Seibel, M. Tingley and members of the Pinsky laboratory for discussions; and D. L. Forrest for assistance with data

compilation. This research was partially conducted on a research exchange at the University of Oslo, supported by the Nordforsk-funded project 'Green Growth Based on Marine Resources: Ecological and Socio-Economic Constraints (GreenMAR)'. We also acknowledge support from the Alfred P. Sloan Research Fellow program, National Science Foundation projects OCE-1426891, DEB-1616821 and EAR-1151022, the Benioff Ocean Initiative, the Natural Sciences and Engineering Research Council of Canada and the Biodiversity Research Centre at the University of British Columbia. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling (which was responsible for producing CMIP5) and thank the climate modelling groups for making the output of their models available. The US Department of Energy's Program for Climate Model Diagnosis and Intercomparison provided coordinating support and led the development of software infrastructure for CMIP5, in partnership with the Global Organization for Earth System Science Portals.

Reviewer information *Nature* thanks Michael Burrows, Mark Payne, Anthony Richardson and the other anonymous reviewer(s) for their contribution to the peer review of this work.

Author contributions M.L.P. conceptualized and administered the project, visualized the data and wrote the original draft of the manuscript. M.L.P., A.M.E., D.J.M. and J.M.S. acquired funding. J.M.S. and M.L.P. wrote the software, and performed data curation and formal analysis. M.L.P., J.M.S. and D.J.M. developed the methodology. M.L.P., D.J.M., J.M.S. and J.L.P. reviewed and edited the manuscript.

Competing interests The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41586-019-1132-4>.

Supplementary information is available for this paper at <https://doi.org/10.1038/s41586-019-1132-4>.

Reprints and permissions information is available at <http://www.nature.com/reprints>.

Correspondence and requests for materials should be addressed to M.L.P.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2019

METHODS

No statistical methods were used to predetermine sample size.

Global environmental temperatures. Extreme heat events are often more important for long-term population persistence than annual, seasonal or monthly means^{5,5,30}. We therefore examined extreme hourly air and water temperatures. For air, we used the warmest extreme daily maximum temperature (TXx) recorded in the HadEX2 dataset (<https://www.climdex.org/>) for 1986–2005³¹. Extreme daily maximum temperatures in this dataset are derived from meteorological stations across the land areas of the world (excluding Antarctica). We averaged the values in this dataset within latitudinal bands for plotting in Fig. 1a.

A global dataset of extreme warm hours is not directly available for the ocean. We instead found the warmest daily mean temperatures in NOAA's Optimum Interpolation Sea Surface Temperature (OISST) dataset for 1986–2005³². To estimate the hottest hour, we then added half of the diurnal temperature range as recorded in the HadDTR climatology³³. The estimate of diurnal variation in the HadDTR dataset is an average across years, and therefore did not allow us to account for potential inter-annual variation in diurnal temperature range. Our extreme hourly ocean temperatures may, therefore, be underestimates.

We note that our calculations of extreme organismal operative and body temperatures examined microclimate variation in extreme temperatures (see 'Operative and body temperatures').

Thermal-tolerance data. To study thermal tolerance, we used integrative measures of performance that are anticipated to be more closely related to whole-organism and ecological consequences than lower-level measures such as enzyme activity. We expanded previously compiled databases of published experimental measurements of upper thermal limits^{5,18,34} by adding records of heat tolerance limits from the literature^{35–43} that had either not been included in previous analyses owing to their focal questions (for example, a focus on cold and heat limits¹⁸) or that have been published subsequently to the compilation of these earlier databases. The data were originally compiled by searching the ISI Web of Science for studies on ectothermic animals that estimated upper thermal limits for a species, excluding specimens collected from laboratory culture, agriculture, aquaculture, regions outside their native range or locations that we could not geo-reference. We only focused on terrestrial and subtidal marine organisms (including benthic, demersal and pelagic animals), and we excluded intertidal, anadromous, catadromous, amphidromous and freshwater species. The dataset excluded measurements from early life stages (eggs, larvae, gametes and so on) and focused on measurements from adult organisms, which helped to avoid effects from potential differences in thermal tolerance across life stages. Future work will be needed to resolve whether and how the patterns that we report vary for early life stages. The dataset included pre-experimental acclimatization or collection temperatures from each study, as well as latitude, longitude and altitude.

For upper thermal limits (T_{max}), the dataset compiled information on the critical maximum temperature or the lethal temperature. Critical maximum temperature is the ramping temperature at which motor function is lost⁴⁴. Lethal temperature is a fixed temperature at which a given percentage (usually 50%) of individuals survives a given duration of exposure (usually 24 h). Both measures are relatively short-term (minutes to hours) temperature-tolerance metrics that are relevant for exposure to acute high-temperature events; we therefore included both metrics (critical and lethal), but accounted for potential differences between them as a factor in statistical models. We assumed that differences in ramping rates and durations of exposure—which can affect final T_{max} estimates—were not biased with regards to latitude and realm. Methodological approaches and definitions of critical motor function (for the critical maximum temperature) tend to vary among taxonomic groups (for example, righting responses of reptiles, maintenance of vertical body position in fish and ability to hold onto a wall in insects). To help to account for this, we included taxonomic classification as a random effect in our analytical models, which simultaneously accounted for taxonomic relatedness and helped to address potentially different methodological approaches among major taxonomic groups.

The final thermal-tolerance dataset included 88 marine species ($n = 47$ fish, 22 molluscs, 11 crustaceans and 8 other invertebrates) and 318 terrestrial species ($n = 122$ reptiles, 91 insects, 89 amphibians and 16 spiders) (Extended Data Table 1). The samples were collected from 77° S to 71° N in the ocean, and from 71° S to 55° N on land. T_{max} values are sometimes assumed to be the same across the full range of a species⁴⁵. However, because T_{max} can represent the influence of local adaptation, we did not extrapolate it here to the full species range⁴⁵.

The acclimatization temperatures used in each experimental study ($T_{acc, experimental}$) were sometimes far from the seasonal extreme temperatures (Extended Data Fig. 1). However, organisms in the wild can acclimatize to local conditions; this often affects their thermal-tolerance limits²¹. A recent synthesis suggests that acclimatization abilities are greater in marine compared to terrestrial ectotherms, but do not vary strongly across latitudes²¹. We therefore accounted for the effects of acclimatization on maximum thermal tolerance during seasonal extremes by

including an adjustment to the reported T_{max} values under a simulated ideal acclimatization regime. We assumed that an appropriate acclimatization temperature ($T_{acc, ideal}$) would be the average summer temperature at each site (Extended Data Fig. 1). We calculated average summer temperatures for 1986–2005 from NOAA's 1/4° OISST AVHRR-only v.2 dataset³², and from the University of Delaware's terrestrial air temperature gridded monthly time series v.4.01⁴⁶. To account for potential differences between the elevation of the temperature grid cell (calculated at 0.25° spatial resolution using the GMTED2010 dataset⁴⁷) and the study-reported elevation at which an animal had been collected, we adjusted the summer temperatures from the University of Delaware's dataset using a lapse rate of 0.0055°C m⁻¹.

We then used the mean acclimatization response ratio (ARR), which was empirically derived from species-level data in each realm, to adjust each observed thermal-tolerance limit (T_{max}) to the thermal limit that an organism would be likely to have if it was exposed to conditions in the field, rather than to experimental conditions^{5,17}: $T_{max'} = T_{max} + ARR \times (T_{acc, ideal} - T_{acc, experimental})$. The ARR is the degree to which thermal-tolerance limits (T_{max}) increase or decrease with changes in the acclimatization temperature²¹. We used mean ARR for marine and terrestrial species from a previous²¹ synthesis of acclimatization experiments: mean ARR was 0.11 for terrestrial species and 0.24 for marine species (estimate derived from the previously published²¹ top model fit to a database of 394 estimates of thermal-tolerance plasticity; see table 1a of the study²¹). This approach toward accounting for acclimatization retained variability in the T_{max} data, and the studies with more-appropriate acclimatization temperatures were changed the least. This adjustment factor led to minor changes from T_{max} to $T_{max'}$ (a decrease of 0.32 ± 0.046°C (± s.e.) on land, and a decrease of 0.23 ± 0.090°C (± s.e.) in the ocean) (Extended Data Fig. 1). We note that our results were not sensitive to whether or not we included the acclimatization adjustment (Extended Data Table 2).

However, assuming an average ARR across all marine and across all terrestrial species may hide variation in acclimatization abilities among species within a realm. We therefore conducted a sensitivity test using the previously published²¹ species-specific ARRs. For the 69 species in our dataset with species-specific ARRs, we found that using species-specific ARRs increased $T_{max'}$ very slightly—by 0.04 ± 0.07°C (± s.e.)—compared to using an average ARR. The two values were also highly correlated ($r^2 = 0.998$, Extended Data Fig. 1c). We chose to use the average ARR for the remainder of our analysis so as to maintain a larger sample size.

We used a GAMM to calculate latitudinal gradients of $T_{max'}$ (smoothed interaction term between latitude and habitat) while accounting for fixed differences among habitats (ocean versus land), a fixed effect of experiment type (critical versus lethal T_{max} measurement) and taxonomic non-independence (phylum, class, order, family and genus as nested random effects). We fit the model using the mgcv package version 1.8–24⁴⁸ in R version 3.4.2. Reported P values are two-sided. We report r^2 calculations from the summary.gam() function in the mgcv package. We fit all possible models with subsets of these variables and ranked them with Akaike's information criterion with the finite sample size correction (AICc)⁴⁹. AICc uses information theory to identify well-fitting models that have relatively few explanatory variables. We then calculated Akaike weights for each model and the relative variable importance for each variable⁴⁹. The latter is the sum of Akaike weights across all models that included a particular variable, and indicates the relative weight of evidence in favour of including each variable.

To detect peaks in the GAMM fits, we searched for temperatures at which the first derivative of the fitted function switched from positive to negative (or negative to positive for detecting a valley), and in which the fit was also the highest point within ± 4° N (or lowest for detecting a valley). To detect uncertainty in the number and location of the peaks, we drew 1,000 multivariate normal samples from the posterior-fitted GAMM parameter vector, multiplied these by the linear predictors⁴⁸ and detected peaks in each sampled fit (Extended Data Fig. 2).

These $T_{max'}$ calculations were the first step in TSM calculations. Importantly, TSM model results using acclimatization-temperature-corrected $T_{max'}$ values were quantitatively similar to those in which raw T_{max} values were used or to those in which raw T_{max} values were used and acclimatization temperature was included as a fixed effect (Extended Data Table 2). We show results in the paper using acclimatization-temperature-adjusted $T_{max'}$ values because they more fully account for factors that are known to be important, and allowed for easier visualization of differences in acclimatized T_{max} values and TSM.

Operative and body temperatures. Steady-state operative environmental temperatures (T_e) of ectotherms in different microhabitats can be predicted using physical models or manikins⁵⁰, or calculated with biophysical models^{51,52}. Considering T_e instead of air temperature is particularly important because the complex interplay of radiation, convection, conduction and evaporation can make the surface temperature of a terrestrial ectotherm diverge sharply from the surrounding air temperature^{5,52}.

For each terrestrial species in our dataset, we used the biophysical modelling package NicheMapR⁵³ to estimate T_e at each collection location. NicheMapR is a

set of microclimate and ectotherm models. The microclimate models use a global dataset of monthly climate conditions, topography and location to simulate hourly environmental conditions, including solar radiation, infrared radiation, humidity, air pressure, surface temperatures, air temperatures and wind speed profiles⁵². The models simulate hourly temperatures from daily averages and data on diurnal temperature ranges⁵³. To consider extreme events, we added daily anomalies for daily minimum and maximum temperature from 1986–2005, as calculated from the nearest Global Historical Climatology Network-Daily meteorological station with no more than 20% missing data^{54,55}. We allowed up to 30% missing data for locations between 3° S and 3° N because climate records were less consistently available in this region. Although meteorological station sites were not immediately adjacent to organismal sampling sites, assuming similar extreme temperature anomalies between the sites was useful because such anomalies are correlated over hundreds of kilometres⁵¹. The ectotherm models then used the hourly environmental calculations to simulate the operative temperature of ectotherms exposed to these conditions by solving coupled energy and mass balance equations. The microclimate and ectotherm models have been extensively tested against field observations^{52,53}.

We used the ectotherm models to calculate T_e for each hour for each species in our dataset⁵². For each collection site (with specified latitude and longitude), we simulated the T_e values of non-thermoregulating, lizard-shaped objects with 90% solar absorptivity in open habitats (full sun $T_{e, \text{exposed}}$) or full shade at 2 m ($T_{e, \text{protected}}$). We chose these two habitats as one of the harshest (full sun) and as one of the most sheltered microclimates (full shade) considered to be broadly available⁵. The full shade microclimate has similar temperatures to 20-cm-deep burrows⁵. In our simulations of extreme operative temperatures in each microclimate, we assumed dry skin (for non-amphibians in both environments and for amphibians in the exposed environment) or wet skin (for amphibians in shaded or protected environments) over 100% of the skin surface area.

Operative temperature (T_e) estimates the instantaneous surface temperature of an organism, which may be different from core temperatures—particularly for large organisms with substantial heat capacity and slow equilibration times. We therefore modelled transient core body temperatures (T_b) as a function of body size and thermal history following a previous publication⁵⁶:

$$T_{b2} = T_{e2} + e^{-\frac{t}{\tau}}(T_{b1} - T_{e2})$$

in which T_{b1} and T_{b2} are core body temperatures at time points 1 and 2, t is duration of time (60 min) at the new operative temperature (T_{e2}), and τ is the mass-dependent thermal time constant. We estimated separate heating- and cooling-specific values of τ from body mass⁵⁷. We initialized T_b at time 0 as the mean T_e in a given microclimate (protected or exposed) over the entire time series, and iterated T_b forward for 20 years (175,200 h) in that same microclimate. By assuming organisms stayed in a given microclimate, we delineated the extreme warm and extreme cool body temperatures an organism could achieve, limited by the transience in their body temperatures as they equilibrate to temporal fluctuations. Body sizes of the organisms in our dataset were generally small (median 7 g, third quartile 27 g and maximum 10 kg) and therefore body temperatures equilibrated quickly for most species. From these simulations, we extracted the 95th percentile warmest hourly T_b for a given site and microhabitat to guard against outliers and associated sampling issues with extreme values.

In the ocean, high rates of convective and conductive heat transfer between an ectotherm and its environment cause body temperatures to equilibrate rapidly with water temperatures⁵⁸. Marine species in our dataset were primarily inshore and coastal benthopelagic species, and none of the species were found in deep habitats. We therefore used the 95th percentile hottest hour calculated from sea surface temperature at the location of collection (see ‘Global environmental temperatures’) as an approximation for marine ectotherm $T_{b, \text{exposed}}$. However, habitat temperatures generally decline with depth and we expect that both upper thermal limits and maximum habitat temperatures will generally be lower for marine species that live deeper than those in our dataset. For example, compared to the ocean surface, global ocean temperatures decline by 0.9 °C at 50 m, by 6.1 °C at 300 m and by 11.2 °C at 1,000 m—on average—as computed from the World Ocean Atlas 2013 v.2⁵⁹.

Although the ocean provides fewer microclimates than do terrestrial ecosystems, behavioural thermoregulation is possible in the ocean for more mobile animals^{60–62}. For example, cod (*Gadus morhua*) in southern Norway avoid shallow waters when temperatures climb above 16 °C and instead choose deeper waters up to 5 °C cooler^{60,62}. Bigeye tuna (*Thunnus obesus*)⁶¹ forage in 14–17 °C waters, but return to surface waters to re-warm at 27 °C. Movements of dentex (*Dentex dentex*)⁶³, bonefish (*Albula vulpes*)⁶⁴ and sharks⁶⁵ across depths also appear to help to regulate body temperatures up or down. Larger arthropods—such as lobster (*Homarus americanus*) and horseshoe crabs (*Limulus polyphemus*)—move in the field in relation to temperatures, especially at seasonal timescales^{66,67}. Crawling

ectotherms—such as abalone and snails—also move along short thermal gradients (in a laboratory or in the intertidal zone, for example)^{68,69}, but at rates (<20 cm/h) that provide little capacity for behavioural thermoregulation in the subtidal environment. Mobility in many—but not all—marine species scales positively with body size⁷⁰, and so behavioural thermoregulatory capacity is often greater for larger marine species. However, in a pelagic environment, even small species can often access much cooler environments by moving deeper. For example, zooplankton that conduct diel vertical migrations can access deeper and cooler water below the thermocline, and can adjust their behaviour based on their thermal environment^{71,72}.

To help to account for differences in thermoregulatory abilities among marine species, we categorized species based on their mode of movement (swimming, crawling or sessile), their habitat (demersal, pelagic–neritic and pelagic–oceanic) and their body size (Extended Data Table 3). We obtained habitat, movement and maximum reported length data for species in our dataset from Fishbase (<http://www.fishbase.org>), Sealifebase (<http://www.sealifebase.org>) and the literature^{73,74}. Body size was categorized in a binary fashion as greater than or less than 50-cm total length. We note that our approach does not account for territoriality, which could restrict the ability of even relatively large species to access cooler thermal refugia and which could render our adjustments here overly generous.

Cooler waters at depth are typically found below the thermocline, whereas surface waters in the mixed layer are of relatively homogenous and usually warmer temperatures. Based on research in tuna and zooplankton^{61,71}, behavioural thermoregulation could allow the most-mobile species (for example, both small and large pelagic–oceanic species as well as all large pelagic–neritic species) to access waters 10 °C cooler than the surface. We assumed that sessile species would not be able to thermoregulate behaviourally. Species that crawl, those that are constrained by shallow water or those that are already living on the bottom (demersal) have intermediate thermoregulatory abilities, because their slow speeds of movement or limited opportunities for moving deeper constrain their options for finding cooler water. We note that our approach to marine behavioural thermoregulation is relatively coarse, mirroring the coarse data available to quantify the spatial and temporal patterns of ocean temperatures. There is a need for better understanding of both vertical and horizontal thermal microclimates in the ocean, as well as for improved understanding of animal abilities to reach these microclimates.

To calculate marine $T_{b, \text{protected}}$ s we subtracted a behavioural thermoregulation adjustment (Extended Data Table 3) from $T_{b, \text{exposed}}$. As a sensitivity test, we also examined whether using a 50%-larger or 50%-smaller behavioural thermoregulation adjustment affected our results (see ‘TSM’). We made sure that $T_{b, \text{protected}}$ was no lower than the freezing point of seawater (−2 °C), which was only a consideration at very high latitudes.

To examine patterns in extreme T_b across habitats and latitudes, we used a GAMM to calculate latitudinal gradients (smoothed interaction term between latitude and habitat) while accounting for fixed differences among habitats (ocean versus land), and taxonomic non-independence (phylum, class, order, family and genus as nested random effects). Reported P values are two-sided. We also used a model choice framework⁴⁹ to calculate the relative variable importance for each variable⁴⁹, and calculated the location and uncertainty in location of peaks in the GAMM fit (see statistical methods description in ‘Thermal tolerance data’).

TSM. The TSM is a previously established measure of an organism’s excess thermal tolerance above regularly experienced environmental temperatures^{5,15,17,25}, and—if calculated carefully—it can be a comparable proxy for the relative amount of warming that an organism in a location can tolerate. TSM is often defined as the difference between the upper temperature an organism experiences and its physiological thermal-tolerance maximum, but different studies use slightly different definitions for experienced temperature and thermal tolerance^{5,15,17,25,45}. Most differences among studies relate to the temporal and spatial scales over which the experienced temperature is calculated; this calculation has often been limited by the resolution of temperature data available (typically gridded and monthly). Because extreme events are likely to drive the strongest responses^{3,4,13}, here we focus on extreme hot body temperatures from hourly records in microclimate environments ($T_{b, \text{protected}}$) and acute physiological thermal-tolerance maxima (T_{max}). However, we note that precise tolerance will probably differ from our calculations for individual species because T_{max} (and therefore TSM) can change with ontogenetic stage, duration of exposure, rate of warming, experimental methods and thermal history; and because our calculated $T_{b, \text{protected}}$ and $T_{b, \text{exposed}}$ values may differ from actual body temperatures depending on specific body shapes, sizes, behaviours and spatial availability of microhabitats⁵⁶.

Absolute TSM based on laboratory measurements is likely to be an overestimate of an organism’s ability to withstand heating in nature. Organisms in the wild need to eat, avoid being eaten, reproduce and perform other energy- and oxygen-consuming tasks; failure of any of these could lead to sub-lethal effects of warming on organismal fitness and population growth rates. Therefore, declining performance is expected and generally observed well before TSMs shrink to zero^{15,24,75,76}.

We therefore consider TSM as a relative rather than an absolute measure, particularly for survival during acute heat extremes. Fully connecting thermal tolerance to organismal fitness in the wild is an active research area^{45,77}. More complex measures of performance that are more directly relevant to fitness are possible if the full population growth rate–thermal performance curve is available^{13,78}, but these curves are limited in availability to a relatively small number of species, which precludes a comprehensive comparison across ecosystems at this time. Further efforts to measure and compare thermal performance curves across species will be important going forward.

Nevertheless, thermal performance curves tend to have common shapes across species. Optimal temperature (T_{opt} , the peak of the performance curve) is closely related to T_{max} such that the two are related with an r^2 of 0.77 in comparisons using data from species for which both have been measured ($P < 10^{-15}$, $n = 312$) (Extended Data Fig. 5). This relationship suggests that the rate of decline from T_{opt} to T_{max} is similar across species, such that proximity to T_{max} provides useful information about the degree of thermal stress and the degree of decline in performance. Therefore, keeping the above caveats in mind, TSM provides a useful index for large-scale comparisons across species⁷⁷.

Because our measures of T_{max} were from acute exposures during short-term challenge experiments (see ‘Thermal tolerance data’), we focused on TSMs during acute high body temperatures (T_b)—that is, the 95th percentile hottest hour of body temperatures. Microrefugia that offer cooler, but accessible, thermal conditions are important for preventing local extirpations of populations^{6,7}, and previous analyses indicate that they are necessary for a broad range of terrestrial ectotherms to persist in the locations in which they are currently found⁵. Extended use of microrefugia (such as shade) may incur a cost—such as reduced time for foraging⁷⁹—but organisms that are avoiding acute high temperatures may only need to use microrefugia for a short period of time (for example, the duration of the extreme event, such as during midday sun), with consequently lower costs. To account for the possibility of behavioural thermoregulation and for the ability of organisms to seek out cooler microhabitats during acute high temperature events, we therefore compare the extreme body temperature from a cool microhabitat ($T_{b, \text{protected}}$; see ‘Operative and body temperatures’) to an organism’s physiological upper thermal tolerance (T_{max} ; see ‘Thermal tolerance data’). We calculated $\text{TSM} = T_{\text{max}} - T_{b, \text{protected}}$ for each paired measurement of T_{max} and calculation of extreme $T_{b, \text{protected}}$.

For comparison, we also calculated TSM using various versions of chronic environmental temperatures, including temperatures averaged across the warmest month, across the summer season and across the year (Extended Data Fig. 4a, b). Because acute high temperature measurements—such as the hottest hour—are a more-appropriate comparison to acute physiological thermal limits (T_{max}) measured in the laboratory, these coarser-scale averages serve to demonstrate how other patterns in TSM may appear if coarser timescales are used (particularly, the annual scale).

We then used a GAMM to calculate latitudinal gradients of TSM (smoothed interaction term between latitude and habitat) while accounting for fixed differences among habitats (ocean versus land), a fixed effect of experiment type (critical versus lethal T_{max} measurement) and taxonomic non-independence (phylum, class, order, family and genus as nested random effects). Reported P values are two-sided. We also used a model choice framework⁴⁹ to calculate the relative variable importance for each variable⁴⁹, and calculated the location and uncertainty in location of valleys in the GAMM fit (see ‘Thermal tolerance data’ for details of statistical methods).

We also tested whether excluding marine behavioural thermoregulation had a large effect on our results, and we found that thermoregulation primarily helped increase thermal safety for tropical species in our dataset (Extended Data Fig. 4c). In addition, we tested whether using a 50%-larger or 50%-smaller behavioural thermoregulation adjustment affected our results (see ‘Operative and body temperatures’). We found that doing so decreased the marine–terrestrial difference in thermal safety to 2.57 °C ($P = 0.087$) or increased it to 3.47 °C ($P = 0.00003$), respectively, compared to 3.1 °C ($P = 0.018$) from our base model (Extended Data Table 2). In all cases, marine thermal safety was less than on land but our ability to confidently detect this marine–terrestrial difference would be limited if marine behavioural thermoregulation were 50% larger than our base case.

Future TSMs. As an estimate of future change in TSMs, we used the surface warming expected for maximum air and ocean temperatures across the ensemble mean from the CMIP5 set of global climate models used in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change⁸⁰. We calculated change in temperature from 1986–2005 to 2081–2100 under RCP2.6 or RCP8.5. RCP2.6 is a scenario roughly similar to that envisioned by the Paris Agreement with twenty-first century warming of about 1 °C. RCP8.5 is a high greenhouse gas emissions scenario with approximately 4 °C warming. On land, we calculated change in the maximum TXx (extreme daily maximum surface-air temperature) between the two 20-year periods⁸¹. Changes in daily maximum ocean-surface temperatures are not

available from the CMIP5 archive; instead, we calculated the change in monthly temperature of the ocean surface from the hottest month at each location. Our calculations therefore do not account for potential changes in the diurnal temperature range of the future ocean, which could (for example) arise from changes in wind strength (the largest diurnal warming occurs on days with low wind)⁸². We downloaded the Fifth Assessment Report CMIP5 ensemble means from the KNMI Climate Explorer (<http://climexp.knmi.nl>).

We calculated future safety margins as $\text{TSM}_{\text{fut}} = T_{\text{max}} - (T_{b, \text{protected}} + \Delta_{\text{fut}})$, which simplifies to $\text{TSM}_{\text{fut}} = \text{TSM}_{\text{current}} - \Delta_{\text{fut}}$, in which Δ_{fut} is the amount of expected warming over the twenty-first century under RCP2.6 or RCP8.5 at each location. This is a relatively crude calculation that assumes each degree increase in environmental temperatures translates to a degree of increase in body temperatures. This assumption is probably reasonable for dry-skinned ectotherms in the shade and for ocean ectotherms but may have been an overestimate of the change for wet-skinned amphibians that make use of evaporation. We may therefore have overestimated the degree to which amphibian TSMs will decline when they have access to wet habitats.

Evidence exists for the ability of organisms to modify their T_{max} after exposure to warm temperatures, as might be expected for organisms faced with long-term climate change. In addition, acclimatization abilities are different among marine and terrestrial species²¹. To test whether accounting for acclimatization would alter our results, we calculated a modified TSM that includes a factor for acclimatization, $\text{TSM}_{\text{fut}} = (T_{\text{max}} + \text{ARR} \times \Delta_{\text{fut}}) - (T_{b, \text{protected}} + \Delta_{\text{fut}})$, which simplifies to $\text{TSM}_{\text{fut}} = \text{TSM}_{\text{current}} - \Delta_{\text{fut}} \times (1 - \text{ARR})$, in which ARR is the acclimatization response ratio for within-species change in thermal-tolerance limits (see ‘Thermal tolerance data’). This calculation has the effect of reducing—through acclimatization—the effective amount of warming to which a species is exposed. Other considerations that may influence ability of some species to cope with warming include developmental acclimatization, transgenerational acclimatization and evolution^{83–86}, although we did not attempt to account for these processes because of limited understanding of their relative magnitude across the tree of life, and between marine and terrestrial species.

We also conducted a sensitivity test by calculating TSM_{fut} with the previously compiled²¹ species-specific ARRs. For the species in our dataset with species-specific ARRs, we found that using species-specific ARRs decreased TSM_{fut} slightly—by 0.17 ± 0.05 °C (\pm s.e.) by 2081–2011 under RCP8.5—compared to using an average ARR. The two values were also highly correlated ($r^2 = 0.989$).

Climate-related local extirpations. To examine rates of local extirpations, we compiled studies from the published literature that quantify latitudinal shifts in the warm range edges of ectothermic animals that were attributed to climate warming. Reviews of range shifts summarizing only shifts in the expected climate-related direction (towards higher latitudes) were not included, because these studies had biased sampling against species showing no response. We also excluded single-species studies that may be more prone to this bias. Studies that examined climatic cycles—such as the North Atlantic Oscillation—and those that investigated range shifts in exotic species were excluded from the dataset. Our dataset also excluded studies of commercially harvested marine fish that had range contractions at both equatorward and poleward boundaries, to avoid attributing an excess of range contractions to climate change. Range shifts were defined as statistically significant changes in latitudinal range boundaries (if a statistical test was conducted by the original study authors) or as a shift >30 km (if a statistical test was not conducted).

We identified sources for this database in three ways. First, we examined references from a previous paper on range shifts¹⁸ but excluded studies that documented only changes in abundance, because we focused on extirpation for the current analysis. In addition, we examined references that studied latitudinal range limits in marine or terrestrial ectothermic animals identified in a previous publication⁸. Finally, we searched the Web of Science Core Collection on 28 August 2017 for newer studies that would have been missed by earlier compilations (that is, we searched for studies published 2016–2017). We used the keywords ‘Topic = (global warm* OR climate change) AND Topic = (extinction* OR contraction* OR range shift*)’. A total of 2,107 results were returned. We sorted the results by relevance and examined the first 800 (40%). We found two more relevant studies to add to our database. The final 250 references that we examined did not include any that were relevant to our study.

Our final compilation covered 108 marine ectotherms and 51 terrestrial ectothermic animal populations, including 46 species of insects, 5 reptiles, 29 fishes, 18 molluscs and 15 crustaceans. Most studies (153 out of 159) had been conducted in the Northern Hemisphere. Most studies (137) were from temperate latitudes (35–66.5°) with an additional 15 at subtropical latitudes (23–35°) and 7 at the edge of the tropics (~22°).

For each population, we recorded information on whether it was marine or terrestrial, the latitude of the warm range edge in the first survey, the duration between the first and last re-survey and whether the population was surveyed twice or more than twice. Duration was included to test whether populations re-surveyed

after longer intervals were more likely to detect a local extirpation. The re-survey frequency was included to test whether populations re-surveyed only twice were more likely to record a local extirpation (for example, by failing to detect a population that was actually present).

We tested whether marine or terrestrial species had a higher proportion of local extirpations with a GLMM with binomial errors and a logit link (function `glmer()` in the `lme4` version 1.1-18-1 package⁸⁷ for R v.3.2.4). We included taxonomic levels as nested random effects to help to account for taxonomic non-independence, and included duration, method (two surveys versus more than two surveys), habitat (marine or terrestrial) and the absolute value of latitude as fixed effects. Reported *P* values are two-sided. We calculated marginal r^2 (which only considers the fixed effects) by approximating observation variance with a second-order Taylor series expansion⁸⁸, as coded in the `rsquared()` function of the `piecewiseSEM` version 2.0.3 package for R⁸⁹. We also used a model choice framework⁴⁹ to identify whether habitat was an important predictor of differences in probability of local extirpation at species' warm range edges. We fit all 20 possible models with subsets of these variables, and ranked them with AICc. We then calculated Akaike weights for each model and the relative variable importance for each variable⁴⁹.

Finally, we classified marine species according to their mobility mode as adults (swimming, crawling or sessile) and examined the frequency of extirpations by mobility class. We report high-mobility (swimming) versus low-mobility (crawling or sessile) results in the main text, but note that frequencies were similar across all mobility classes: 56% of swimming taxa, 57% of crawling taxa and 50% of sessile taxa had extirpations at warm range edges.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

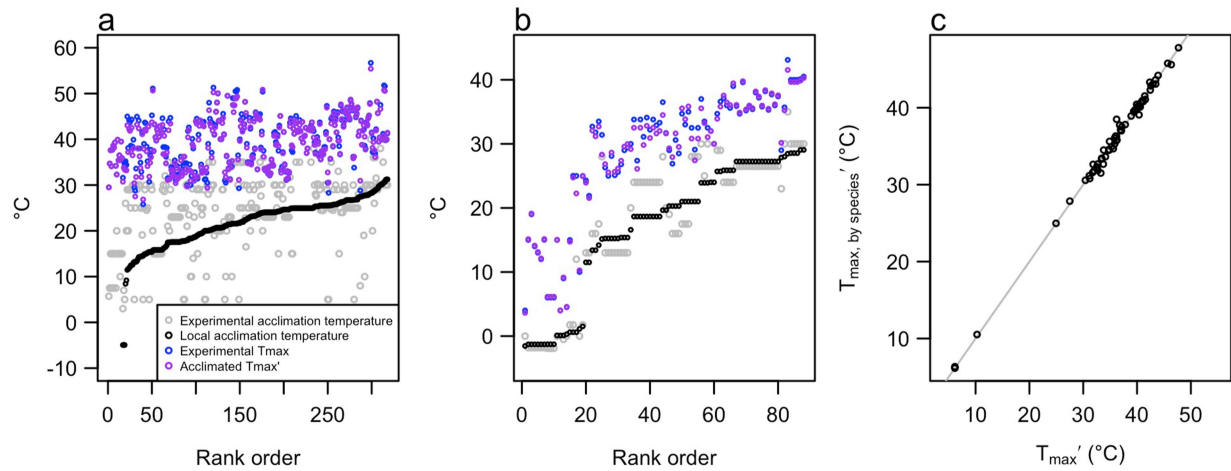
The upper thermal-tolerance data and extirpation data that support the findings of this study are available at Zenodo under the identifier: <https://doi.org/10.5281/zenodo.2576197>. Any other relevant data are available from the corresponding author upon reasonable request.

Code availability

Custom analysis scripts are available at Zenodo under the identifier: <https://doi.org/10.5281/zenodo.2576197>.

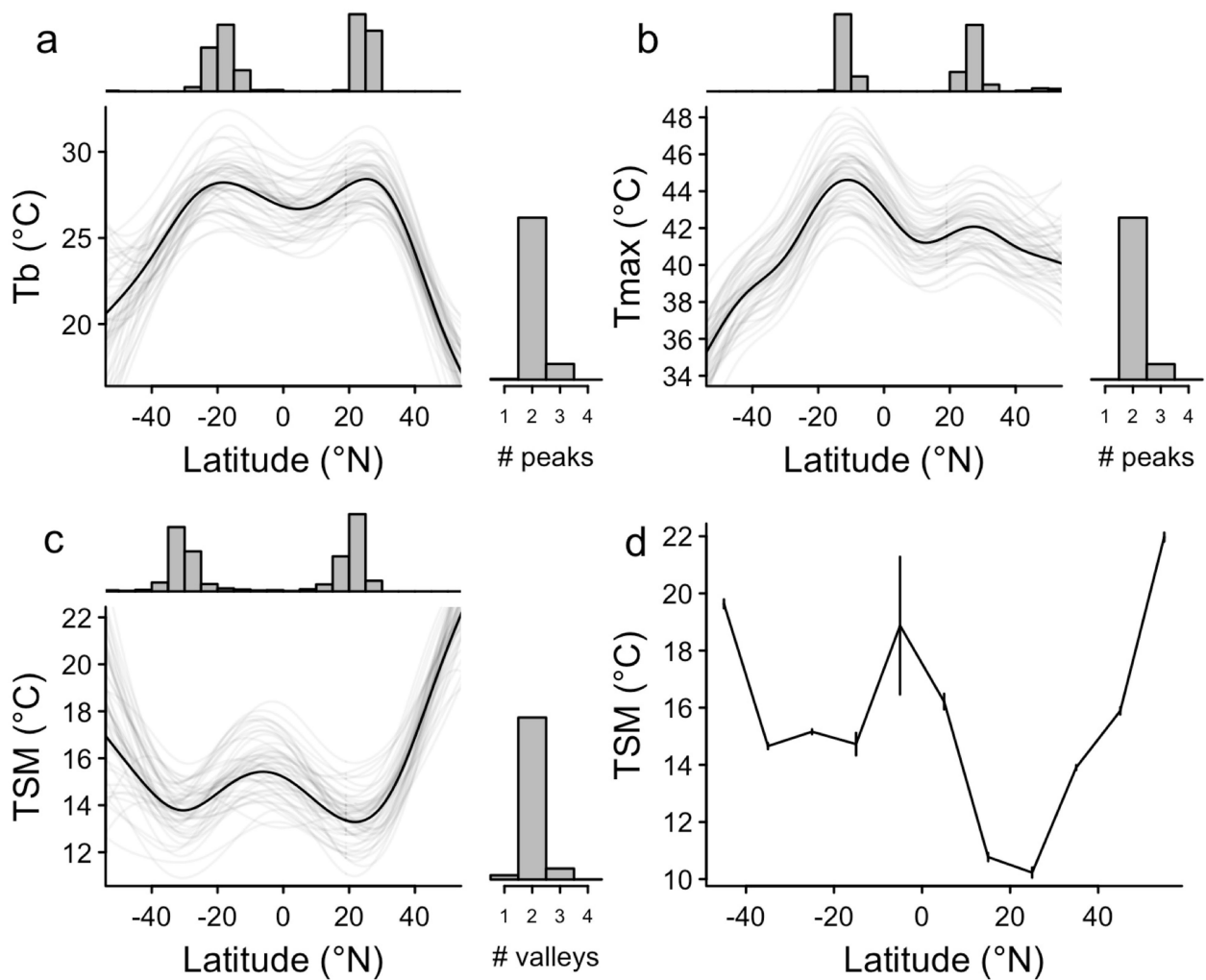
30. Parmesan, C., Root, T. L. & Willig, M. R. Impacts of extreme weather and climate on terrestrial biota. *Bull. Am. Meteorol. Soc.* **81**, 443–450 (2000).
31. Donat, M. G. et al. Updated analyses of temperature and precipitation extreme indices since the beginning of the twentieth century: the HadEX2 dataset. *J. Geophys. Res.* **118**, 2098–2118 (2013).
32. Reynolds, R. W. et al. Daily high-resolution blended analyses for sea surface temperature. *J. Clim.* **20**, 5473–5496 (2007).
33. Kennedy, J. J., Brohan, P. & Tett, S. F. B. A global climatology of the diurnal variations in sea-surface temperature and implications for MSU temperature trends. *Geophys. Res. Lett.* **34**, 1–5 (2007).
34. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. Lond. B* **278**, 1823–1830 (2011).
35. Scholander, P. F., Flagg, W., Walters, V. & Irving, L. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* **26**, 67–92 (1953).
36. Morley, S. A. et al. Rates of warming and the global sensitivity of shallow water marine invertebrates to elevated temperature. *J. Mar. Biol. Assoc. U.K.* **96**, 159–165 (2016).
37. Urban, H. J. Upper temperature tolerance of ten bivalve species off Peru and Chile related to El Niño. *Mar. Ecol. Prog. Ser.* **107**, 139–145 (1994).
38. Zerebecki, R. A. & Sorte, C. J. B. Temperature tolerance and stress proteins as mechanisms of invasive species success. *PLoS ONE* **6**, e14806 (2011).
39. Ansell, A. D. & McLachlan, A. Upper temperature tolerances of three molluscs from South African sandy beaches. *J. Exp. Mar. Biol. Ecol.* **48**, 243–251 (1980).
40. Madeira, D., Narciso, L., Cabral, H. N. & Vinagre, C. Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. *J. Sea Res.* **70**, 32–41 (2012).
41. Vinagre, C. et al. Effect of temperature in multiple biomarkers of oxidative stress in coastal shrimp. *J. Therm. Biol.* **41**, 38–42 (2014).
42. Prentice, E. F. & Schneider, D. E. Respiration and thermal tolerance of the Dungeness crab, *Cancer magister* Dana. *Comp. Biochem. Physiol. A* **63**, 591–597 (1979).
43. Kennedy, V. S. & Mihursky, J. A. Upper temperature tolerances of some estuarine bivalves. *Chesap. Sci.* **12**, 193–204 (1971).
44. Lutterschmidt, W. I. & Hutchison, V. H. The critical thermal maximum: history and critique. *Can. J. Zool.* **75**, 1561–1574 (1997).
45. Sinclair, B. J. et al. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol. Lett.* **19**, 1372–1385 (2016).
46. Willmott, C. J. & Matsuura, K. Terrestrial air temperature: 1900–2014 gridded monthly time series (v.4.01) http://climate.geog.udel.edu/~climate/html_pages/download.html#T2014, accessed September 2016.
47. Danielson, J. J. & Gesch, D. B. *Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010)*. Report No. 2011-1073 (U.S. Geological Survey, 2011).
48. Wood, S. N. *Generalized Additive Models: An Introduction with R* 2nd edn (Chapman and Hall/CRC, Boca Raton, 2017).
49. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* 2nd edn (Springer, New York, 2002).
50. Bakken, G. S. Measurement and application of operative and standard operative temperatures in ecology. *Am. Zool.* **32**, 194–216 (1992).
51. Kearney, M. & Porter, W. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334–350 (2009).
52. Kearney, M., Shine, R. & Porter, W. P. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proc. Natl Acad. Sci. USA* **106**, 3835–3840 (2009).
53. Kearney, M. R. & Porter, W. P. NicheMapR – an R package for biophysical modelling: the microclimate model. *Ecography* **40**, 664–674 (2017).
54. Chamberlain, S. rnoaa: 'NOAA' Weather Data from R R package version 0.7.0. <https://CRAN.R-project.org/package=rnoaa>. (2017).
55. Menne, M. J., Durre, I., Vose, R. S., Gleason, B. E. & Houston, T. G. An overview of the global historical climatology network-daily database. *J. Atmos. Ocean. Technol.* **29**, 897–910 (2012).
56. Sears, M. W. et al. Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proc. Natl Acad. Sci. USA* **113**, 10595–10600 (2016).
57. Grigg, G. C., Drane, C. R. & Courtice, G. P. Time constants of heating and cooling in the eastern water dragon, *Physignathus lesuerui*, and some generalizations about heating and cooling in reptiles. *J. Therm. Biol.* **4**, 95–103 (1979).
58. Denny, M. W. *Air and Water: The Biology and Physics of Life's Media* (Princeton Univ. Press, Princeton, 1993).
59. Locarnini, R. A. et al. *World Ocean Atlas 2013, Volume 1: Temperature* (National Oceanographic Data Center, Silver Spring, 2013).
60. Freitas, C., Olsen, E. M., Knutsen, H., Albretsen, J. & Moland, E. Temperature-associated habitat selection in a cold-water marine fish. *J. Anim. Ecol.* **85**, 628–637 (2016).
61. Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R. & Fournier, D. A. Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358**, 410–412 (1992).
62. Freitas, C., Olsen, E. M., Moland, E., Ciannelli, L. & Knutsen, H. Behavioral responses of Atlantic cod to sea temperature changes. *Ecol. Evol.* **5**, 2070–2083 (2015).
63. Aspillaga, E. et al. Thermal stratification drives movement of a coastal apex predator. *Sci. Rep.* **7**, 526 (2017).
64. Brownscombe, J. W., Cooke, S. J. & Danylchuk, A. J. Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia* **183**, 689–699 (2017).
65. Hight, B. V. & Lowe, C. G. Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? *J. Exp. Mar. Biol. Ecol.* **352**, 114–128 (2007).
66. Watson, W. H., III, Schaller, S. Y. & Chabot, C. C. in *Biology and Conservation of Horseshoe Crabs* (eds Tancredi, J. T. et al.) 131–147 (Springer US, Boston, 2009).
67. Jury, S. H. & Watson, W. H. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. *Can. J. Fish. Aquat. Sci.* **70**, 1650–1657 (2013).
68. Herrera, F. D., Ramirez, F. B., Sevilla, B. B. & Farfán, C. Behavioral thermoregulation of *Bulla gouldiana* (Gastropoda: Opisthobranchia: Cephalaspidea). *J. Therm. Biol.* **21**, 319–322 (1996).
69. Díaz, F. et al. Thermal preference and tolerance of green abalone *Haliotis fulgens* (Philippi, 1845) and pink abalone *Haliotis corrugata* (Gray, 1828). *Aquacult. Res.* **37**, 877–884 (2006).
70. McCauley, D. J. et al. Marine defaunation: animal loss in the global ocean. *Science* **347**, 1255641 (2015).
71. Elder, L. E. & Seibel, B. A. The thermal stress response to diel vertical migration in the hyperiid amphipod *Phronima sedentaria*. *Comp. Biochem. Physiol. A* **187**, 20–26 (2015).
72. Werner, T. & Buchholz, F. Diel vertical migration behaviour in Euphausiids of the northern Benguela current: seasonal adaptations to food availability and strong gradients of temperature and oxygen. *J. Plankton Res.* **35**, 792–812 (2013).
73. Froese, R. & Pauly, D. FishBase version 12/2017 <http://www.fishbase.org>, accessed December 2017.
74. Boettiger, C., Chamberlain, S., Temple Lang, D. & Wainwright, P. rfishbase: R Interface to 'FishBase'. R package version 2.1.0.1 <https://github.com/ropensci/rfishbase> (2016).
75. Diamond, S. E. et al. A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology* **93**, 2305–2312 (2012).
76. Dong, Y.-w. et al. Untangling the roles of microclimate, behaviour and physiological polymorphism in governing vulnerability of intertidal snails to heat stress. *Proc. R. Soc. Lond. B* **284**, 20162367 (2017).
77. Huey, R. B. et al. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Phil. Trans. R. Soc. Lond. B* **367**, 1665–1679 (2012).
78. Kingsolver, J. G., Diamond, S. E. & Buckley, L. B. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct. Ecol.* **27**, 1415–1423 (2013).
79. Sinervo, B. et al. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899 (2010).

80. Collins, M. et al. 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* (eds Stocker, T. F. et al.) 1029–1136 (Cambridge Univ. Press, 2013).
81. Sillmann, J., Kharin, V. V., Zwiers, F. W., Zhang, X. & Bronaugh, D. Climate extremes indices in the CMIP5 multimodel ensemble: part 2. Future climate projections. *J. Geophys. Res.* **118**, 2473–2493 (2013).
82. Gentemann, C. L. & Minnett, P. J. Radiometric measurements of ocean surface thermal variability. *J. Geophys. Res.* **113**, C08017 (2008).
83. Munday, P. L., Donelson, J. M. & Domingos, J. A. Potential for adaptation to climate change in a coral reef fish. *Glob. Chang. Biol.* **23**, 307–317 (2017).
84. Donelson, J. M. Development in a warm future ocean may enhance performance in some species. *J. Exp. Mar. Biol. Ecol.* **472**, 119–125 (2015).
85. Donelson, J. M., Munday, P. L., McCormick, M. I. & Pitcher, C. R. Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nat. Clim. Chang.* **2**, 30–32 (2012).
86. Hoffmann, A. A. & Sgrò, C. M. Climate change and evolutionary adaptation. *Nature* **470**, 479–485 (2011).
87. Bates, D., Maechler, M., Bolker, B. M. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
88. Nakagawa, S., Johnson, P. C. D. & Schielzeth, H. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* **14**, 20170213 (2017).
89. Lefcheck, J. S. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).
90. Chen, B. Patterns of thermal limits of phytoplankton. *J. Plankton Res.* **37**, 285–292 (2015).
91. Beaugrand, G., Luczak, C. & Edwards, M. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob. Chang. Biol.* **15**, 1790–1803 (2009).
92. Hiddink, J. G., Burrows, M. T. & García Molinos, J. Temperature tracking by North Sea benthic invertebrates in response to climate change. *Glob. Chang. Biol.* **21**, 117–129 (2015).
93. Nye, J. A., Link, J. S., Hare, J. A. & Overholtz, W. J. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* **393**, 111–129 (2009).
94. Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915 (2005).
95. Pitt, N. R., Poloczanska, E. S. & Hobday, A. J. Climate-driven range changes in Tasmanian intertidal fauna. *Mar. Freshw. Res.* **61**, 963–970 (2010).
96. Rubal, M., Veiga, P., Cacabelos, E., Moreira, J. & Sousa-Pinto, I. Increasing sea surface temperature and range shifts of intertidal gastropods along the Iberian Peninsula. *J. Sea Res.* **77**, 1–10 (2013).
97. Franco, A. M. A. et al. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Glob. Chang. Biol.* **12**, 1545–1553 (2006).
98. Hickling, R., Roy, D. B., Hill, J. K. & Thomas, C. D. A northward shift of range margins in British Odonata. *Glob. Chang. Biol.* **11**, 502–506 (2005).
99. Parmesan, C. et al. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583 (1999).
100. Wu, J. Detecting and attributing the effects of climate change on the distributions of snake species over the past 50 years. *Environ. Manage.* **57**, 207–219 (2016).
101. Wu, J. Can changes in the distribution of lizard species over the past 50 years be attributed to climate change? *Theor. Appl. Climatol.* **125**, 785–798 (2016).



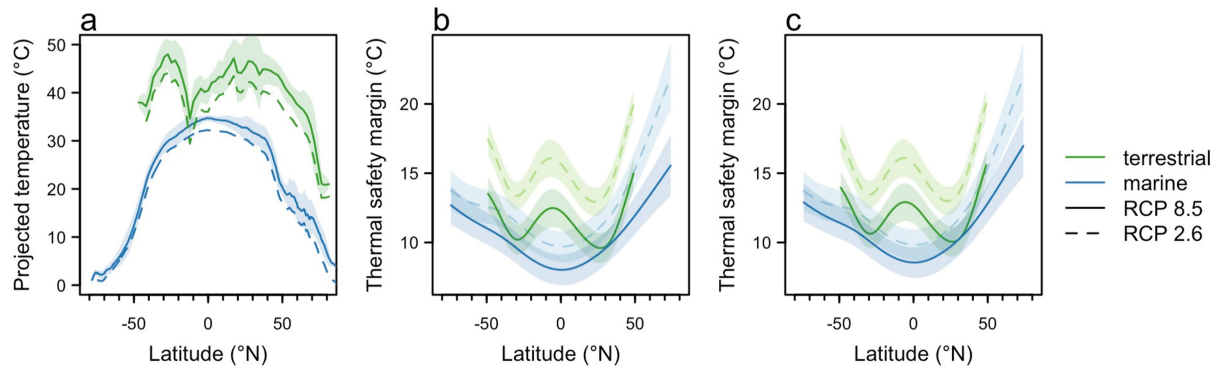
Extended Data Fig. 1 | Adjustment to account for the acclimatization temperatures used in laboratory experiments. **a, b,** For land (**a**) and ocean (**b**) separately, the points show the average summer temperature used for acclimatization calculations (black) at each collection site, ordered from smallest to largest, the experimental acclimatization temperature

(grey), the experimentally measured thermal-tolerance maximum (T_{\max} , blue) and the acclimatization-adjusted thermal-tolerance maximum (T_{\max}' , purple). **c,** T_{\max}' adjusted with species-specific acclimatization response ratios (ARRs, $n = 69$ species) is compared against T_{\max}' adjusted with ARR averaged within realms. The grey line is a 1:1 line.



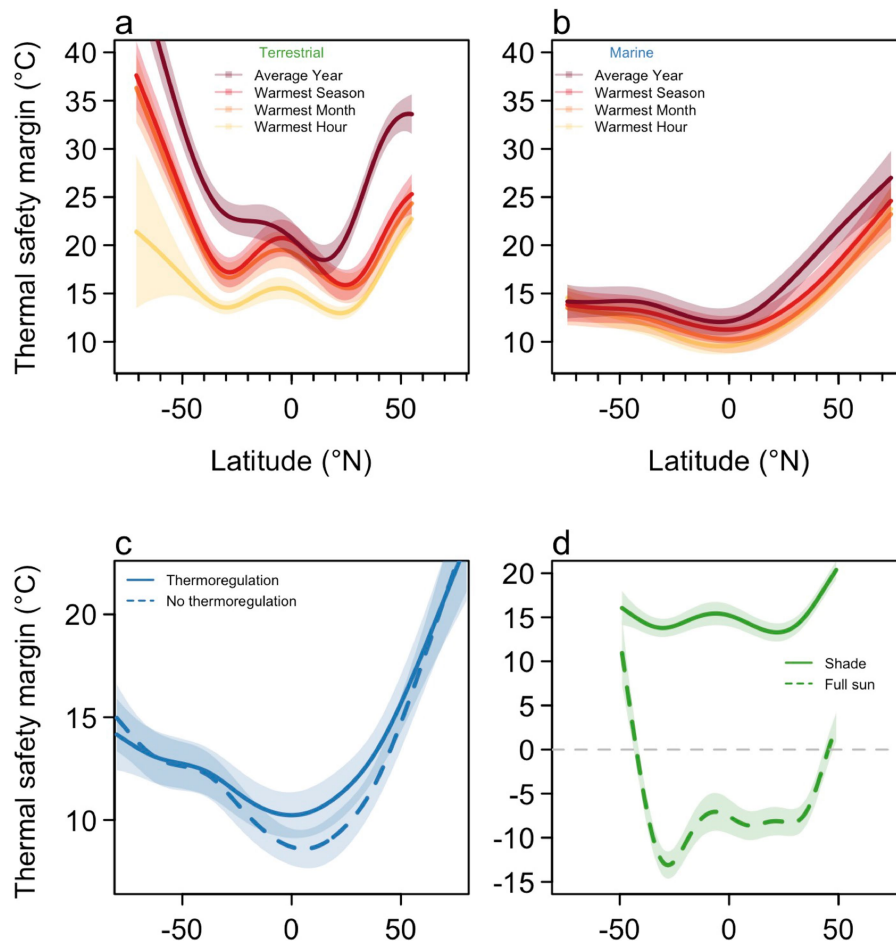
Extended Data Fig. 2 | Uncertainty in the location of peaks or valleys in GAMM fits for terrestrial ectotherms. a–c, Clusters of graphs for extreme hot values of body temperatures in thermal refugia ($T_{b, \text{protected}}$) (a), hot thermal-tolerance limits (T_{max}) (b) and TSM (c) across latitudes. Each cluster of graphs has three parts: (1) the centre graph shows the fitted effect against latitude from a GAMM (dark line), and 50 samples from the fitted smoother (grey lines); (2) the top histogram shows uncertainty

in the locations of the peaks (a, b) or valleys (c) detected from 1,000 samples from the fitted smoother; and (3) the right-hand histogram shows uncertainty in the number of peaks or valleys detected. d, Average TSM is plotted against the mid-point of each 10° latitude band. Error bars show s.e.m. Fewer data points create larger error bounds near the equator. $n = 299$ species.



Extended Data Fig. 3 | Effects of alternative emission scenarios and acclimatization on TSMs for the end of the twenty-first century (2081–2100). **a**, Projected extreme hot hourly air- or water-surface temperatures from RCP8.5 or RCP2.6 scenarios. Shaded regions

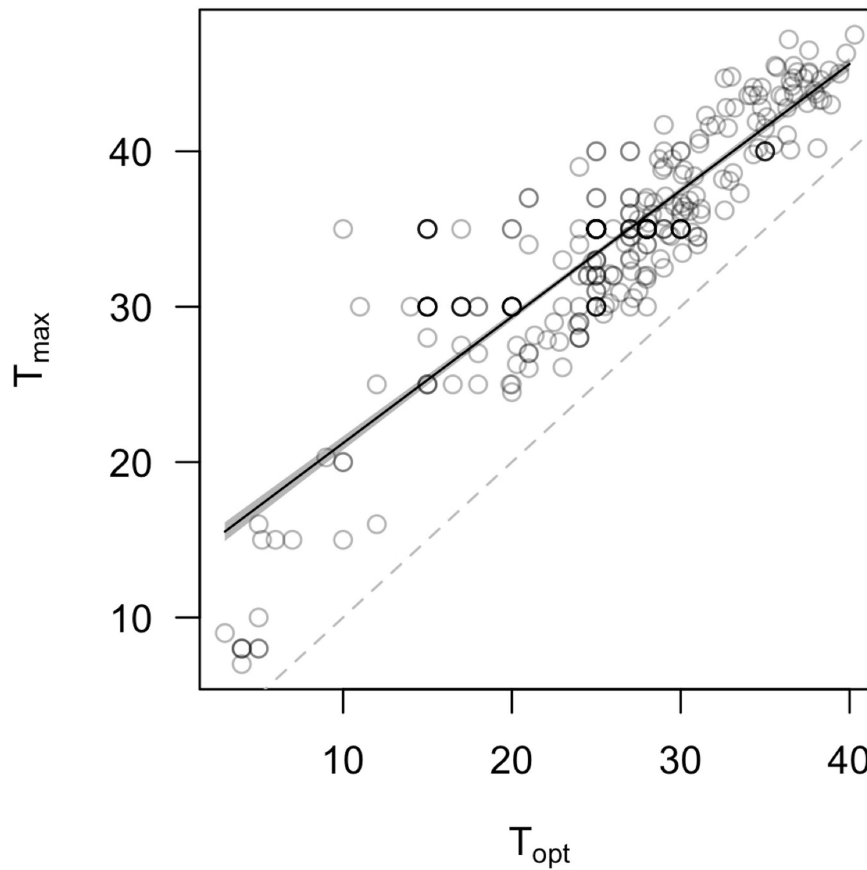
show ± 1 s.d. $n = 1,454$ (terrestrial), 689,769 (ocean RCP8.5) or 689,381 (ocean RCP2.6) grid cells. **b**, Future TSMs without acclimatization. **c**, Future TSMs with acclimatization. Shaded ribbons show ± 1 s.e. from GAMM fits (**b**, **c**). $n = 382$ species for GAMM fits (**b**, **c**).



Extended Data Fig. 4 | Alternative approaches to TSM calculations.

a, b, Warm TSMs across latitudes for terrestrial (**a**) and marine (**b**) species with alternative temperature calculations (annual average, summer average, warmest month and warmest hour). Physiological tolerance measurements were from acute laboratory exposures (minutes to hours), and acute environmental temperature extremes are therefore arguably most-appropriate for calculating TSM. TSMs from the most-acute temporal scale (hours) revealed a different latitudinal pattern than from the more-aggregated scales, in part because they better capture short-duration thermal extremes. However, in all calculations marine species had narrower TSMs. **c, d,** Warm TSM calculations for marine species (**c**) or for terrestrial species (**d**), with (solid line) or without

(dashed line) accounting for behavioural thermoregulation. The latter case is appropriate if behavioural thermoregulation is not possible (for example, thermal refugia are not accessible). Negative thermal safety on land indicates that these habitats are not habitable during midday heat for durations that bring body temperatures close to equilibrium. Note that calculations in **a** and **b** do not account for acclimatization or behavioural thermoregulation, to enable clear comparison across timescales. Calculations in **c** and **d** include acclimatization to summer temperatures. In all plots, shaded ribbons show \pm s.e. from GAMM fits. $n = 387$ (warmest hour, no marine thermoregulation, or exposed or full sun) or 390 (warm month, summer average or annual average) species for GAMM fits.



Extended Data Fig. 5 | Relationship between physiological maximum (T_{\max}) and optimum (T_{opt}) temperature across species. Data are shown from studies^{15,26,90} that measured T_{\max} and T_{opt} across species of phytoplankton, insects and lizards. The line is from a linear model with T_{\max} as the response variable and T_{opt} as the explanatory term (linear

regression $r^2 = 0.77$, $F = 1,036$ with 1 and 310 degrees of freedom, two-sided $P < 10^{-15}$ with no corrections for multiple comparisons, $n = 312$ species). All data are plotted in transparent grey so that overlapping data points appear as darker circles. The dashed line is a 1:1 relationship.

Extended Data Table 1 | Thermal-tolerance maximums (T_{max}) were compiled from 406 species in 15 classes

Realm	Phylum	Class	Species with T_{max}
Terrestrial	Arthropoda	Arachnida	16
Terrestrial	Arthropoda	Entognatha	3
Terrestrial	Arthropoda	Insecta	88
Terrestrial	Chordata	Amphibia	89
Terrestrial	Chordata	Reptilia	122
Marine	Arthropoda	Malacostraca	11
Marine	Brachiopoda	Rhynchonellata	2
Marine	Chordata	Actinopterygii	43
Marine	Chordata	Ascidiacea	3
Marine	Chordata	Elasmobranchii	1
Marine	Echinodermata	Asteroidea	1
Marine	Echinodermata	Echinoidea	3
Marine	Echinodermata	Ophiuroidea	2
Marine	Mollusca	Bivalvia	18
Marine	Mollusca	Gastropoda	4

Extended Data Table 2 | Statistical model results for maximum thermal-tolerance limits (T_{max}), extreme body temperatures ($T_{b,protected}$) and TSM of marine and terrestrial ectothermic animals

Model	Variable	Smth	Coefficient	SE	t	EDF	F	p	RVI
Tmax	Intercept		33.74	1.38	24.37			2.80×10^{-80}	
Tmax	Realm (Terrestrial)		6.74	1.79	3.76			0.0002	1
Tmax	Method (Lethal)		-2.34	0.95	-2.48			0.014	0.84
Tmax	Latitude:Marine	Yes				7.94	45	1.80×10^{-61}	
Tmax	Latitude:Terrestrial	Yes				6.65	11.07	2.20×10^{-12}	1
Tb	Intercept		20.75	0.94	21.98			2.50×10^{-69}	
Tb	Realm (Terrestrial)		4.60	1.55	2.97			0.0032	1
Tb	Latitude:Marine	Yes				5.29	133.32	5.50×10^{-124}	
Tb	Latitude:Terrestrial	Yes				5.68	24.64	2.20×10^{-22}	1
TSM	Intercept		12.33	0.93	13.19			6.40×10^{-33}	
TSM	Realm (Terrestrial)		3.1	1.31	2.37			0.018	1
TSM	Method (Lethal)		-2.13	0.94	-2.27			0.024	0.74
TSM	Latitude:Marine	Yes				3.42	6.88	0.0001	
TSM	Latitude:Terrestrial	Yes				4.85	13.04	1.70×10^{-10}	1
TSMnoacc	Intercept		12.38	0.71	17.36			5.40×10^{-50}	
TSMnoacc	Realm (Terrestrial)		3.06	0.88	3.48			0.00057	1
TSMnoacc	Method (Lethal)		-2.59	0.90	-2.88			0.0042	0.82
TSMnoacc	Latitude:Marine	Yes				3.54	10.62	2.40×10^{-7}	
TSMnoacc	Latitude:Terrestrial	Yes				5.00	15.86	2.20×10^{-14}	1
TSMaccterm	Intercept		8.42	1.12	7.51			5.30×10^{-13}	
TSMaccterm	Realm (Terrestrial)		2.71	0.98	2.77			0.0058	1
TSMaccterm	Method (Lethal)		-2.35	0.92	-2.56			0.011	0.8
TSMaccterm	Acclimation temp.		0.20	0.04	5.40			1.20×10^{-7}	1
TSMaccterm	Latitude:Marine	Yes				4.03	14.96	2.10×10^{-11}	
TSMaccterm	Latitude:Terrestrial	Yes				4.79	16.02	3.70×10^{-12}	1
TSMARRbyspp	Intercept		12.45	1.59	7.85			5.90×10^{-11}	
TSMARRbyspp	Realm (Terrestrial)		2.57	1.72	1.49			0.14	0.3
TSMARRbyspp	Method (Lethal)		3.87	2.75	1.41			0.16	0.24
TSMARRbyspp	Latitude:Marine	Yes				1	10.54	0.0018	
TSMARRbyspp	Latitude:Terrestrial	Yes				1	0.36	0.55	0.24
TSM_marBTmore	Intercept		12.84	1.02	12.54			2.30×10^{-30}	
TSM_marBTmore	Realm (Terrestrial)		2.57	1.5	1.71			0.087	1
TSM_marBTmore	Method (Lethal)		-1.74	0.96	-1.81			0.071	0.45
TSM_marBTmore	Latitude:Marine	Yes				3.17	6.16	0.00039	
TSM_marBTmore	Latitude:Terrestrial	Yes				4.88	12.57	2.70×10^{-10}	1
TSM_marBTless	Intercept		11.74	0.74	15.83			1.30×10^{-43}	
TSM_marBTless	Realm (Terrestrial)		3.47	0.82	4.23			0.00003	1
TSM_marBTless	Method (Lethal)		-2.71	0.86	-3.15			0.0018	0.89
TSM_marBTless	Latitude:Marine	Yes				3.82	9.02	1.10×10^{-6}	
TSM_marBTless	Latitude:Terrestrial	Yes				4.72	16.85	7.50×10^{-13}	1

Coefficients are from GAMMs fit to data on acclimatization-adjusted T_{max} data ($r^2 = 0.63$, $n = 406$ species), extreme T_b in thermal refugia ($T_{b,protected}$, $r^2 = 0.66$, $n = 387$ species) and acclimatization-adjusted TSM in thermal refugia ($r^2 = 0.29$, $n = 387$ species). As sensitivity tests, TSM models are shown that used raw T_{max} (TSMnoacc, $r^2 = 0.30$, $n = 387$ species), that used raw T_{max} and included a fixed effect for acclimatization temperature (TSMaccterm, $r^2 = 0.37$, $n = 351$ species), that adjusted T_{max} with a species-specific acclimatization response ratio (TSMARRbyspp, $r^2 = 0.17$, $n = 69$ species), that used 50%-larger marine behavioural thermoregulation adjustments (TSM_marBTmore, $r^2 = 0.25$, $n = 387$ species) or that used 50%-smaller adjustments (TSM_marBTless, $r^2 = 0.33$, $n = 387$ species). By focusing on thermal refugia, $T_{b,protected}$ and TSM account for thermoregulatory behaviour that can mitigate the consequences of extreme but short-duration temperatures. Table shows coefficients with standard errors (SE), two-sided P values and relative variable importance from a model-choice approach. No adjustments for multiple comparisons were made. Relative variable importance indicates the relative weight of evidence in favour of including each variable. Table also shows empirical degrees of freedom (EDF) for smooth (Smth) terms. Realm measures the terrestrial effect, compared to marine. Method measures the effect of measuring lethal thermal-tolerance limits, as opposed to critical limits.

Extended Data Table 3 | Marine behavioural thermoregulation adjustments

Mobility	Habitat	Size (cm)	Behavioral thermoregulation adjustment (°C)	# species
swim	pelagic-oceanic	>50	10	0
swim	pelagic-oceanic	<50	10	2
swim	pelagic-neritic	>50	10	0
swim	pelagic-neritic	<50	3	4
swim	demersal	>50	3	7
swim	demersal	<50	1	40
crawl	demersal	>50	1	0
crawl	demersal	<50	0.5	12
sessile	demersal	>50	0	0
sessile	demersal	<50	0	23

Some marine species can behaviourally thermoregulate; we therefore included adjustments to extreme hot body temperatures to account for the fact that many marine species could access cooler waters during the hottest times of the year. We also accounted for the fact that larger or more-mobile animals from the open ocean could better access cooler waters than smaller, less-mobile or coastal animals that were constrained by movement abilities or habitat availability.

Extended Data Table 4 | Synthesis of range contraction prevalence in multi-species studies

Habitat	Taxon	Average latitude	Duration (years)	Range edges sampled (species)	Proportion contracted
Marine	Marine invertebrates ⁹¹	49.4	39	5	1
Marine	Marine invertebrates ⁹²	55	14	65	0.55
Marine	Fishes ⁹³	38.3	39	17	0.41
Marine	Fishes ⁹⁴	59	24	12	0.5
Marine	Marine invertebrates ⁹⁵	-41.3	52	6	0.67
Marine	Molluscs ⁹⁶	37.7	80	3	0.67
Terrestrial	Butterflies ⁹⁷	55	20	2	1
Terrestrial	Dragonflies ⁹⁸	55	25	4	0.5
Terrestrial	Butterflies ⁹⁹	39.9	71	40	0.25
Terrestrial	Reptiles ¹⁰⁰	28	40	2	0
Terrestrial	Reptiles ¹⁰¹	34.3	40	3	0

Summary of studies⁹¹⁻¹⁰¹ that document whether the warm range edges of marine and terrestrial ectotherms contracted across latitudes over time, related to climate change. Latitude refers to the average latitude of the warm range edge at the beginning of the study.

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection

No software used for data collection.

Data analysis

We used the statistical program R 3.4.2 to analyze the data in this study. Scripts for data analysis are available in a GitHub repository archived at Zenodo doi:10.5281/zenodo.2576197

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data reported in the paper are available from the GitHub repository archived at Zenodo doi:10.5281/zenodo.2576197

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	Upper thermal tolerance data consisted of the 406 species for which measurements were available from the literature. We used generalized linear mixed models (GLMMs) and generalized additive mixed models (GAMMs) to determine whether sample size was sufficient.
Data exclusions	We excluded upper thermal tolerance data for specimens collected from laboratory culture, agriculture, aquaculture, regions outside their native range, or locations that we could not georeference. We only focused on terrestrial and subtidal marine organisms (including benthic, demersal, and pelagic animals), and we excluded intertidal, anadromous, catadromous, amphidromous, and freshwater species. The dataset excluded measurements from early life stages (eggs, larvae, gametes, etc.) and focused on measurements from adult organisms, which helped to avoid effects from potential differences in thermal tolerance across life-stages. These were pre-established data exclusions.
Replication	This study does not include new experimental findings.
Randomization	As a study that does not include new experimental findings, we did not allocate samples/organisms/participants into experimental groups.
Blinding	The data were collected from the literature before analysis and the provenance of each data point can be traced back to its original source.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging