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Analysis

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Greater evolutionary divergence of thermal limits within marine than terrestrial species

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There is considerable uncertainty regarding which ecosystems are most vulnerable to warming. Current understanding of organismal sensitivity is largely centred on species-level assessments that do not consider variation across populations. Here we used meta-analysis to quantify upper thermal tolerance variation across 305 populations from 61 terrestrial, freshwater, marine and intertidal taxa. We found strong differentiation in heat tolerance across populations in marine and intertidal taxa but not terrestrial or freshwater taxa. This is counter to the expectation that increased connectivity in the ocean should reduce intraspecific variation. Such adaptive differentiation in the ocean suggests there may be standing genetic variation at the species level to buffer climate impacts. Assessments of vulnerability to warming should account for variation in thermal tolerance among populations (or the lack thereof) to improve predictions about climate vulnerability.

Climate warming is a major threat to the persistence of species across all realms[1]. Variation in the rate and intensity of warming over space and time contributes to uncertainty in which ecosystems and taxa may be most vulnerable to rising temperatures[2]. Previous work suggests that marine species may be at great risk because they live close to their thermal limits and have limited capacity to cope with rising temperatures[3]. However, these studies have largely focused on comparisons across rather than within species[3–5]. This may misrepresent a species' overall susceptibility to climate warming if thermal limits (and the proximity of these limits to maximum temperatures) vary among populations[6–11]. Predictions of vulnerability can therefore be strengthened by a population-level perspective on variation in thermal limits, which better incorporates how thermal limits vary in relation to spatial patterns in extreme temperatures.

Within species, spatial patterns in thermal limits will be shaped by the balance between selection and gene flow, along with the availability of adaptive genetic diversity. Phenotypic plasticity can also have strong, but variable, effects on thermal limits[12–15]. Many marine and intertidal taxa with planktonic larvae face fewer geographic barriers to dispersal, which may promote long-distance migration and increased population connectivity[16–20]. In theory, the subsequent gene flow would have a homogenizing effect, constraining adaptive differentiation and limiting the potential for local adaptation[21,22]. However, self-recruitment and high levels of larval and post-settlement selective mortality[23,24] can result in smaller-than-predicted dispersal potential, which, in turn, may promote local adaptation in the oceans[25]. While dispersal and population connectivity may be difficult to generalize across realms[26–32], terrestrial and freshwater taxa may have relatively limited dispersal between populations due to the presence of geographic barriers, increasing the potential for local adaptation.

Previous work has shown that across species, heat tolerance decreases more strongly with increasing latitude in marine and intertidal than terrestrial or freshwater taxa[5,33–35]. A similar pattern within species would have major implications for predicting vulnerability

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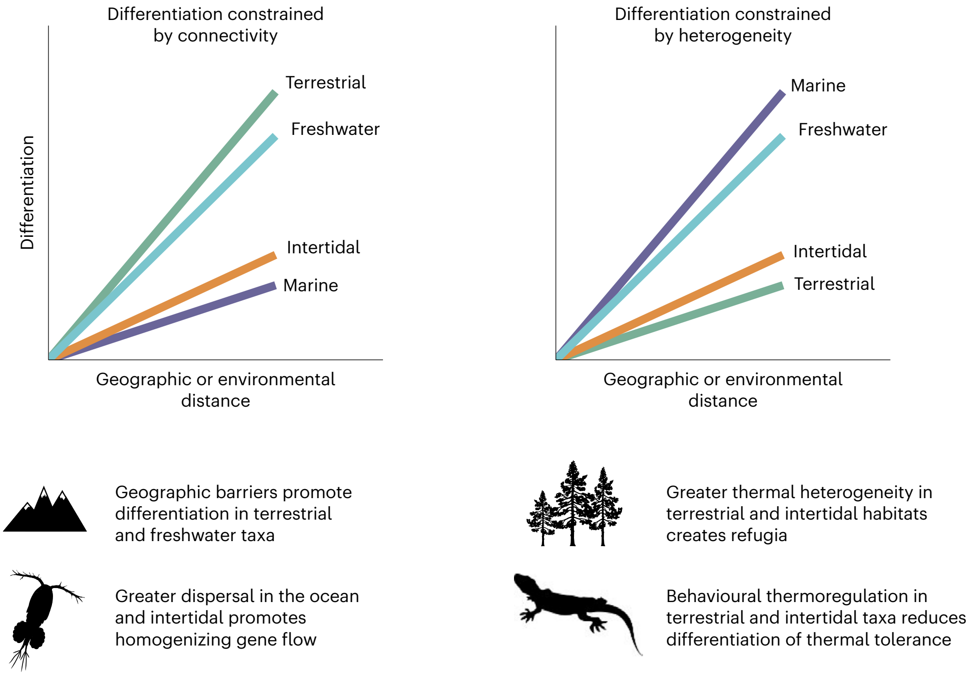

Fig. 1 | Conceptual figure outlining hypotheses predicting population-level divergence in thermal limits across realms. Pairwise population differentiation across all realms increases with greater geographic and environmental distance, consistent with an isolation by distance model. However, realms may differ in the rate of divergence owing to relative balance of population connectivity (dispersal and gene flow) and local-scale environmental heterogeneity, which can create thermal refugia. Credits: copepod and lizard icons, T. Sotis; tree icon, Gabriele Midolo, Phylopic under a Creative Commons license CC0 1.0.

across a species' range. This difference in the magnitude of thermal limit variation may reflect differences in the structure of aquatic and terrestrial habitats; while terrestrial and intertidal taxa may be able to exploit fine-scale heterogeneity in the thermal environment to avoid extreme temperatures[36,37], freshwater and marine habitats are relatively more thermally homogeneous with limited accessible refugia[38–40]. This leads to two competing hypotheses regarding the magnitude of divergence in thermal limits within species (Fig. 1): (1) a scenario where increased connectivity and gene flow between populations leads to weaker differentiation over environmental gradients or, alternatively, (2) that the exploitation of fine-scale heterogeneity in the thermal environment reduces exposure to extreme temperatures, resulting in weaker selective pressures and less divergence in thermal limits. While the relative impact of population connectivity and environmental heterogeneity may vary across realms (leading to stronger divergence in terrestrial and freshwater or marine and intertidal taxa, respectively), these hypotheses are not mutually exclusive, and variation within realms may be affected by differences in life history, dispersal traits and motility.

Developing an understanding of the large-scale patterns in within-species variation in thermal limits is important because this variation could provide a buffer against the near-term impacts of climate warming and standing genetic variation for the evolution of thermal tolerance over longer timescales. Differentiation among populations may also be a key factor in determining species range shifts and contractions in response to rapid warming[41,42]. Here we examine how patterns in thermal limit divergence within species vary across realms to better understand which taxa may be most vulnerable to a rapidly changing climate.

Latitudinal patterns in temperature tolerance

To assess differences in population vulnerability to warming across realms, we compiled a dataset from 90 studies that examined thermal tolerance (measured as upper or lower lethal thermal limits) across populations in ectothermic animals and plants from terrestrial, marine, intertidal and freshwater realms. Importantly, these studies acclimated organisms to common conditions before measurement of thermal limits, reducing the influence of phenotypic plasticity on observed differences. Our dataset includes 1,193 heat- or cold-tolerance values from 506 populations of 123 species (Extended Data Fig. 1 and Supplementary Table 1; 742 thermal limits from terrestrial species, 165 from freshwater taxa, 202 from intertidal species and 84 from marine species). Seven phyla are represented, and the data span a latitudinal range from 62° S to 78° N (Fig. 2a). The analyses we describe here focus on a subset of the full dataset, examining 598 upper thermal limits of 305 populations distributed across latitudinal (rather than elevational) thermal gradients (245 thermal limits from terrestrial species, 115 from freshwater taxa, 160 from intertidal taxa and 78 from marine taxa; Extended Data Fig. 1). While there is substantial variation in heat tolerance within species in all realms (Fig. 2b–e), heat tolerance consistently decreased with latitude within marine and intertidal taxa but not within terrestrial or freshwater taxa (Fig. 2f). This is similar to the interspecific patterns observed in prior studies[5,43] but with reduced magnitude (Fig. 2f). For terrestrial taxa, there is stronger divergence in lower thermal limits between populations than in upper thermal limits (Extended Data Fig. 2). This is a common observation, known as Brett's Rule or 'cold tolerance asymmetry'[44] and may reflect the tendency for cold tolerance to evolve faster than heat tolerance[43]. Lower thermal limit measurements were abundant only in terrestrial taxa, however, preventing cross-realm comparisons of patterns in this metric.

Differentiation across realms

Adaptation to different thermal environments should shape spatial patterns in the divergence of heat tolerance. We used an inverse weighted meta-analytic approach to examine patterns across realms in how heat tolerance differentiation varied in relation to differences in the maximum temperature between sites. Weighted meta-analytic approaches have the benefit of accounting for study-level precision, decreasing the influence of studies with smaller sample sizes and are preferable to unweighted analysis[45,46]. To account for varying levels of precision

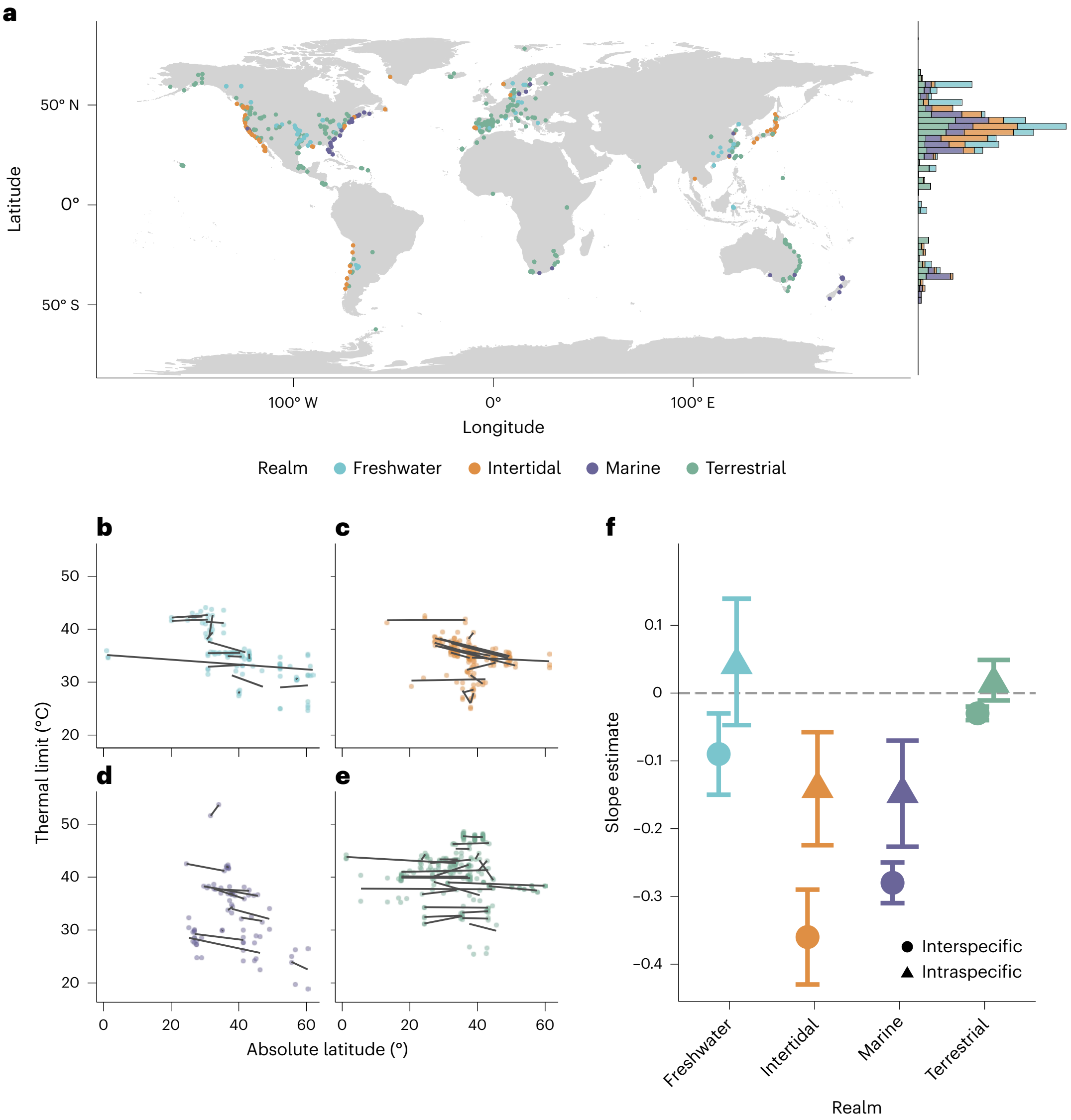

Fig. 2 | Population-level patterns in heat tolerance. a, Map of populations included. Points are coloured by realm. The marginal histogram shows the latitudinal distribution of tolerance measurements. **b**–**e**, Latitudinal variation in heat tolerance. Each point represents the heat tolerance of one population. Grey regression lines show patterns within species. **f**, Comparison between mean (± standard error) inter- and intraspecific slopes. Interspecific slopes are from previous work examining these patterns[5]. Intraspecific slopes represent the mean of the slopes of the grey lines in **b**–**e** (number of slopes; freshwater = 16; intertidal = 17; marine = 14; terrestrial = 23). A slope of zero (indicated by the grey horizontal line) indicates no variation in thermal limits with latitude. Intraspecific variation in heat tolerance is generally less strong than interspecific estimates. Basemap in **a** from Natural Earth.

in measurements across studies, we estimated pairwise population differentiation in heat tolerance using a standardized effect-size metric[47] (Hedges' *g*; Fig. 3). Effect sizes were estimated using a common-control approach, where populations within a study were compared to the population from the highest latitude, rather than using all pairwise comparisons[48]. We then modelled the effect size estimates with interacting fixed effects of realm and difference in maximum temperature between sites. Model selection yielded a single best model that included the two-way interaction (Supplementary Table 2). This model indicated that greater maximum temperature differences are associated with greater thermal tolerance differentiation for marine and intertidal taxa but not freshwater or terrestrial taxa (Fig. 3a,b).

Our results show that heat tolerance does not vary consistently with latitude or differences in maximum environmental temperatures in terrestrial taxa. Behavioural thermoregulation may play a large role in shaping this pattern, termed the 'Bogert effect'[49,50]. Many terrestrial ectotherms can moderate body temperatures by behaviourally exploiting shade, forest understories, crevices or other thermal refugia[50,51]. Similarly, non-motile taxa (for example, plants) may be able to exploit microclimatic variation[52]. This would decrease spatial variation in selection on heat tolerance, dampening spatial patterns as we have observed here. Using a coarse classification of species in our dataset based on their relative capacity to exploit thermal heterogeneity in the environment (described in detail in Methods), we observed larger divergences in heat tolerance in 'non-motile' organisms than 'motile' species that may be capable of behavioural thermoregulation (Extended Data Fig. 3). This is also observed within intertidal taxa (Extended Data Fig. 3)—the mixture of both motile and non-motile taxa may explain the relatively small overall parameter estimates for this realm in the meta-regression model (Fig. 3b). The cold tolerance asymmetry observed in our dataset, with stronger divergence in cold tolerance than heat tolerance in terrestrial taxa, may also suggest an influence of behavioural thermoregulation; for example, nighttime thermal environments tend to be cooler and more homogenous than

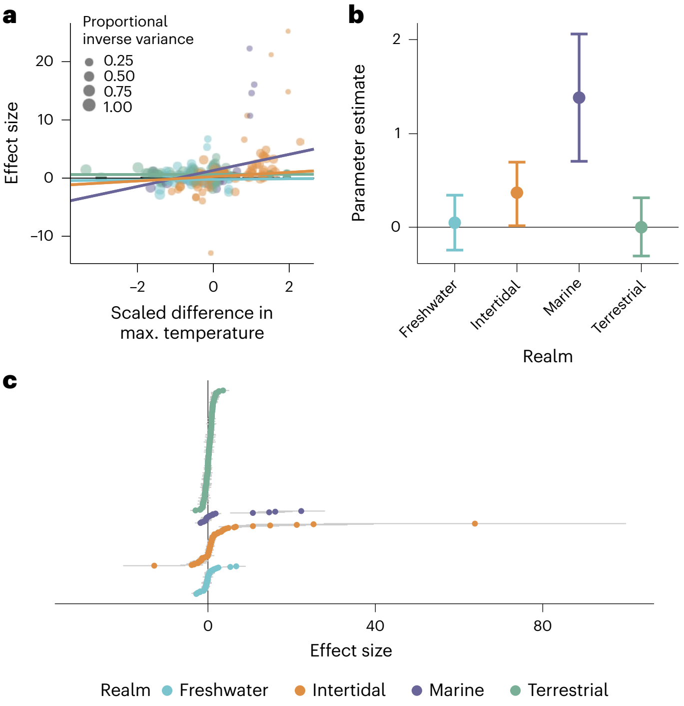

Fig. 3 | Pairwise heat tolerance comparisons between populations using Hedges' *g*. Larger effect sizes indicate greater differentiation in heat tolerance. **a**, Relationship between effect size and scaled difference in maximum temperature. Regression slopes are derived from the meta-regression model. Point size is inversely related to variance. Axis extent is restricted for clarity. **b**, Meta-regression model parameter estimates (± 95% confidence interval) indicate that difference in maximum temperature predicts effect sizes for marine and intertidal taxa but not freshwater or terrestrial taxa (number of effect-size estimates: freshwater = 45, intertidal = 68, marine = 20, terrestrial = 192). Slopes different from zero indicate a significant predictor of thermal limit differentiation between populations. **c**, Caterpillar plot depicting pairwise contrasts (± 95% confidence interval).

daytime thermal environments[37], reducing the opportunity for motile organisms to avoid cold temperatures and the accompanying selection on cold tolerance.

Vulnerability to warming

In a rapidly warming climate, vulnerability to extreme heat events is determined by both organismal heat tolerance and the proximity of these limits to environmental temperatures. To quantify this vulnerability, we calculated warming tolerance[53] for each population as the difference between heat tolerance and mean annual maximum temperatures at the site of collection. Although this is not a direct forecast of vulnerability, warming tolerance serves as an index of potential physiological stress owing to climate change[3,53,54]. Similar to previous analyses of vulnerability to warming[3], we accounted for the effects of phenotypic plasticity[12] on heat tolerance before calculating warming tolerance. These effects stem from potential differences between the temperatures organisms were acclimated to before thermal tolerance assays and the mean field temperature at each collection site. As heat tolerance plasticity varies both between- and within-species[14,15], where possible, we used population-specific estimates of acclimation response ratio (change in thermal limit per degree difference in acclimation temperature). If population-level data were unavailable, we estimated acclimation response ratios using a model based on the realm and population thermal limit[15], which was then used to adjust the thermal limit before estimating warming tolerance.

Our analyses reveal substantial warming tolerance variation across latitude within species (Fig. 4a–d). The change in warming tolerance across latitude within species also varied strongly (Fig. 4e–h). Warming tolerance generally increased with latitude within species in marine and intertidal taxa (Fig. 4f,g), suggesting that populations near the Equatorward range edge of a species' distribution are relatively more vulnerable to warming. Within-species patterns were highly variable in both freshwater and terrestrial taxa (Fig. 4e,h), highlighting that vulnerability to warming is likely both population- and species-specific.

Our results illustrate that latitudinal patterns in warming tolerance are important to consider across all realms. However, we suggest caution in interpreting absolute values of warming tolerance estimates. Thermal limits may vary systematically by method used (measuring critical thermal maxima (CTmax) versus lethal temperatures (LD50), for example), which would affect the magnitude of estimates of warming tolerance. Additionally, while there is often a strong correlation between air and freshwater temperatures[55], the maximum temperature estimates for freshwater realms may overestimate the temperatures experienced, particularly in large water bodies. Warming tolerance estimates for terrestrial taxa also do not account for microclimatic variation and potential behavioural thermoregulation, which, as we have seen, may be effective enough at reducing thermal stress to dampen spatial patterns in adaptation of heat tolerance and may therefore play an important role in reducing vulnerability to warming. Further, we cannot account for the effect of co-occurring stressors, which may decrease warming tolerance[56] or how adaptation to future conditions may reduce vulnerability[57]. However, while these factors may bias the magnitude of warming tolerance estimates, we expect that latitudinal patterns in warming tolerances provide insight into the relative vulnerability of populations to near-term extreme heat events. The substantial variation observed within species highlights that populations are important to consider to avoid over-generalized estimates of vulnerability to climate change and promote effective conservation and management strategies.

Conclusions

Within-species variation in heat tolerance, while generally weaker than across-species variation, can be substantial. The magnitude of these intraspecific differences in heat tolerance varies across realms, with stronger variation in marine and intertidal taxa than in terrestrial and freshwater taxa. This finding conflicts with the historical paradigm that highly dispersive life history traits homogenize marine populations, indicating that processes like local retention and 'adaptation with gene flow' can produce strong differentiation between populations[25,58,59], with implications for the response of these taxa to climate change. Differences among realms also suggest that the exploitation of microclimatic variation may effectively reduce the strength of selection on heat tolerance for many terrestrial taxa (that is, the Bogert effect). The population-level differentiation in heat tolerance documented here is qualitatively similar to that found at the interspecific level[5], suggesting that common factors may affect the evolution of thermal tolerance at both biological scales.

Species-level estimates of heat tolerance highlight large-scale latitudinal patterns in climate vulnerability[3]. However, reliance on these interspecific patterns to predict vulnerability to climate change obscures how substantial variation in thermal limits results in spatial variation in warming tolerance within species. Rectifying the relative paucity of studies examining intraspecific spatial variation in thermal limits in the tropics and polar regions should be a priority for future work. As species and populations with high thermal tolerance may have diminished plasticity in thermal tolerance[15], low latitude populations may be particularly vulnerable to warming in marine and intertidal taxa. However, the greater population differentiation of heat tolerance observed in these taxa also suggests the potential for

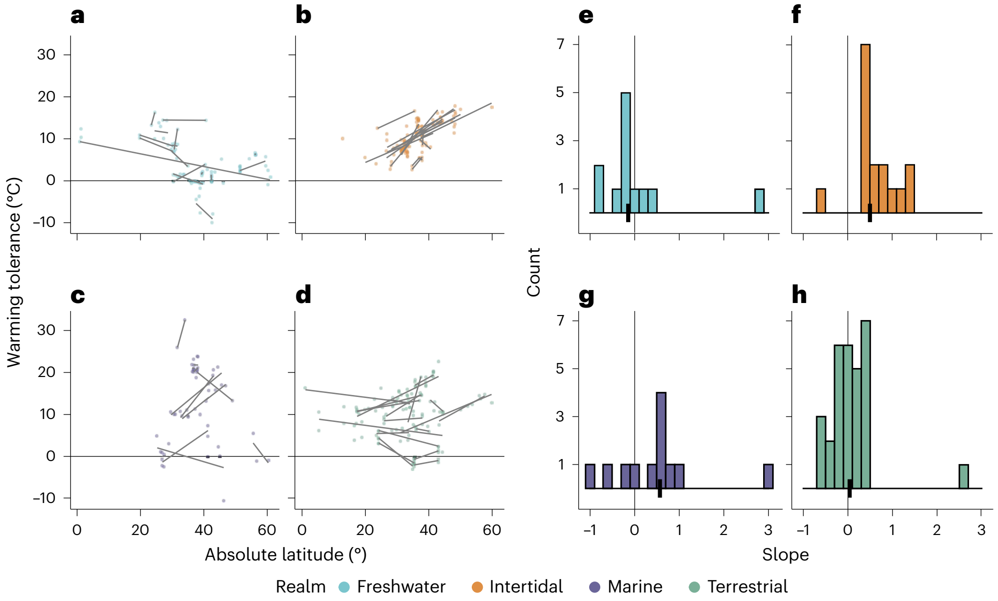

Fig. 4 | Estimated warming tolerance. a–d, Warming tolerance against latitude. Regression lines for individual studies are shown in grey. **e–h**, Histograms of slope estimates (change in warming tolerance per degree latitude). Median values are indicated by bars above the main axis.

evolutionary rescue via gene flow in mid- and poleward range extent populations.

A focus on species-level estimates of warming tolerance reflects a general emphasis on extinction risk, rather than extirpation and defaunation in climate change biology. These processes, however, are major drivers of biodiversity loss and the erosion of ecosystem function[60,61]. Inclusion of population-level assessments of vulnerability in heat and warming tolerance is crucial for a robust understanding of how a rapidly changing climate will affect the persistence of biodiversity. Our results highlight the importance of creating or maintaining thermal refugia for mitigating thermal stress, particularly in terrestrial habitats[62]. Our work also suggests that maintaining population connectivity to facilitate adaptive gene flow should be a priority in the oceans[63].

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-022-01534-y.

References

1. Urban, M. C. Accelerating extinction risk from climate change. *Science* **348**, 571–573 (2015).
2. Loarie, S. R. et al. The velocity of climate change. *Nature* **462**, 1052–1055 (2009).
3. Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L. & Sunday, J. M. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* **569**, 108–111 (2019).
4. Hughes, A. R. et al. Predicting the sensitivity of marine populations to rising temperatures. *Front. Ecol. Environ.* **17**, 17–24 (2019).
5. Sunday, J. et al. Thermal tolerance patterns across latitude and elevation. *Philos. Trans. R. Soc. B* **374**, 20190036 (2019).
6. Bennett, S., Duarte, C. M., Marbà, N. & Wernberg, T. Integrating within-species variation in thermal physiology into climate change ecology. *Philos. Trans. R. Soc. B* **374**, 20180550 (2019).
7. Sasaki, M. C. & Dam, H. G. Integrating patterns of thermal tolerance and phenotypic plasticity with population genetics to improve understanding of vulnerability to warming in a widespread copepod. *Glob. Change Biol.* **25**, 4147–4164 (2019).
8. Kelly, M. W., Sanford, E. & Grosberg, R. K. Limited potential for adaptation to climate change in a broadly distributed marine crustacean. *Proc. R. Soc. B* **279**, 349–356 (2012).
9. Valladares, F. et al. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol. Lett.* **17**, 1351–1364 (2014).
10. Moran, E. V., Hartig, F. & Bell, D. M. Intraspecific trait variation across scales: implications for understanding global change responses. *Glob. Change Biol.* **22**, 137–150 (2016).
11. Razgour, O. et al. Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. *Proc. Natl Acad. Sci. USA* **116**, 10418–10423 (2019).
12. Seebacher, F., White, C. R. & Franklin, C. E. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Change* **5**, 61–66 (2015).
13. Somero, G. N. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.* **213**, 912–920 (2010).
14. Gunderson, A. R. & Stillman, J. H. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B* **282**, 20150401 (2015).
15. Barley, J. M. et al. Limited plasticity in thermally tolerant ectotherm populations: evidence for a trade-off. *Proc. R. Soc. B* **288**, 202110765 (2021).
16. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nat. Clim. Change* **2**, 686–690 (2012).
17. Grummer, J. A. et al. Aquatic landscape genomics and environmental effects on genetic variation. *Trends Ecol. Evol.* **34**, 641–654 (2019).
18. Kinlan, B. P. & Gaines, S. D. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84**, 2007–2020 (2003).
19. Lester, S. E., Ruttenberg, B. I., Gaines, S. D. & Kinlan, B. P. The relationship between dispersal ability and geographic range size. *Ecol. Lett.* **10**, 745–758 (2007).

20. Kinlan, B. P., Gaines, S. D. & Lester, S. E. Propagule dispersal and the scales of marine community process. *Diversity Distrib.* **11**, 139–148 (2005).
21. Mayr, E. *Animal Species and Evolution* (Harvard Univ. Press, 2014).
22. Haldane, J. B. S. The relation between density regulation and natural selection. *Proc. R. Soc. Lond. B* **145**, 306–308 (1956).
23. Marshall, D. J., Monro, K., Bode, M., Keough, M. J. & Swearer, S. Phenotype–environment mismatches reduce connectivity in the sea. *Ecol. Lett.* **13**, 128–140 (2010).
24. Burgess, S. C., Treml, E. A. & Marshall, D. J. How do dispersal costs and habitat selection influence realized population connectivity? *Ecology* **93**, 1378–1387 (2012).
25. Sanford, E. & Kelly, M. W. Local adaptation in marine invertebrates. *Annu. Rev. Mar. Sci.* **3**, 509–535 (2011).
26. Caplat, P. et al. Looking beyond the mountain: dispersal barriers in a changing world. *Front. Ecol. Environ.* **14**, 261–268 (2016).
27. Nickols, K. J., Wilson White, J., Largier, J. L. & Gaylord, B. Marine population connectivity: reconciling large-scale dispersal and high self-retention. *Am. Nat.* **185**, 196–211 (2015).
28. Pinsky, M. L., Comte, L. & Sax, D. F. Unifying climate change biology across realms and taxa. *Trends Ecol. Evol.* https://doi.org/10.1016/j.tree.2022.04.011 (2022).
29. Fourcade, Y. et al. Habitat amount and distribution modify community dynamics under climate change. *Ecol. Lett.* **24**, 950–957 (2021).
30. Kappes, H., Tackenberg, O. & Haase, P. Differences in dispersal- and colonization-related traits between taxa from the freshwater and the terrestrial realm. *Aquat. Ecol.* **48**, 73–83 (2014).
31. Kinlan, B. P. & Gaines, S. D. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84**, 2007–2020 (2003).
32. Kappes, H. & Haase, P. Slow, but steady: dispersal of freshwater molluscs. *Aquat. Sci.* **74**, 1–14 (2012).
33. Sasaki, M. & Dam, H. G. Global patterns in copepod thermal tolerance. *J. Plankton Res.* **43**, 598–609 (2021).
34. Cereja, R. Critical thermal maxima in aquatic ectotherms. *Ecol. Indic.* **119**, 106856 (2020).
35. Vinagre, C. et al. Upper thermal limits and warming safety margins of coastal marine species – Indicator baseline for future reference. *Ecol. Indic.* **102**, 644–649 (2019).
36. Muñoz, M. M. The Bogert effect, a factor in evolution. *Evolution* **76**, 49–66 (2022).
37. Muñoz, M. M. & Bodensteiner, B. L. Janzen's hypothesis meets the Bogert effect: connecting climate variation, thermoregulatory behavior, and rates of physiological evolution. *Integr. Org. Biol.* **1**, oby002 (2019).
38. Spence, A. R. & Tingley, M. W. The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. *Ecography* **43**, 1571–1590 (2020).
39. Burrows, M. T. et al. The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652–655 (2011).
40. Steele, J. H., Brink, K. H. & Scott, B. E. Comparison of marine and terrestrial ecosystems: suggestions of an evolutionary perspective influenced by environmental variation. *ICES J. Mar. Sci.* **76**, 50–59 (2019).
41. Sexton, J. P., McIntyre, P. J., Angert, A. L. & Rice, K. J. Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.* **40**, 415–436 (2009).
42. Chuang, A. & Peterson, C. R. Expanding population edges: theories, traits, and trade-offs. *Glob. Change Biol.* **22**, 494–512 (2016).
43. Bennett, J. M. et al. The evolution of critical thermal limits of life on Earth. *Nat. Commun.* **12**, 1198 (2021).
44. Gaston, K. J. et al. Macrophysiology: a conceptual reunification. *Am. Nat.* **174**, 595–612 (2009).
45. Button, K. S. et al. Power failure: why small sample size undermines the reliability of neuroscience. *Nat. Rev. Neurosci.* **14**, 365–376 (2013).
46. Gurevitch, J., Koricheva, J., Nakagawa, S. & Stewart, G. Meta-analysis and the science of research synthesis. *Nature* **555**, 175–182 (2018).
47. Cooper, H., Hedges, L. V. & Valentine, J. C. *The Handbook of Research Synthesis and Meta-Analysis* (Russel Sage Foundation, 2009).
48. Gleser, L. & Olkin, I. in *The Handbook of Research Synthesis and Meta-Analysis* (eds Cooper, H. et al.) Ch. 19 (Russel Sage Foundation, 2009).
49. Huey, R. B., Hertz, P. E. & Sinervo, B. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* **161**, 357–366 (2003).
50. Bogert, C. M. Thermoregulation in reptiles, a factor in evolution. *Evolution* **3**, 195–211 (1949).
51. 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* **10**, 3835–3840 (2009).
52. Denney, D. A., Jameel, M. I., Bemmels, J. B., Rochford, M. E. & Anderson, J. T. Small spaces, big impacts: contributions of micro-environmental variation to population persistence under climate change. *AoB Plants* **12**, plaa005 (2020).
53. Deutsch, C. A. et al. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672 (2008).
54. Clusella-Trullas, S., Garcia, R. A., Terblanche, J. S. & Hoffmann, A. A. How useful are thermal vulnerability indices? *Trends Ecol. Evol.* **36**, 1000–1010 (2021).
55. Wanders, N., van Vliet, M. T. H., Wada, Y., Bierkens, M. F. P. & van Beek, L. P. H. High-resolution global water temperature modeling. *Water Resour. Res.* **55**, 2760–2778 (2019).
56. Todgham, A. E. & Stillman, J. H. Physiological responses to shifts in multiple environmental stressors: relevance in a changing world. *Integr. Comp. Biol.* **53**, 539–544 (2013).
57. Hoffmann, A. A. & Sgró, C. M. Climate change and evolutionary adaptation. *Nature* **470**, 479–485 (2011).
58. Pespeni, M. H. & Palumbi, S. R. Signals of selection in outlier loci in a widely dispersing species across an environmental mosaic. *Mol. Ecol.* **22**, 3580–3597 (2013).
59. Hoey, J. A. & Pinsky, M. L. Genomic signatures of environmental selection despite near-panmixia in summer flounder. *Evolut. Appl.* **11**, 1732–1747 (2018).
60. Dirzo, R. et al. Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
61. Young, H. S., McCauley, D. J., Galetti, M. & Dirzo, R. Patterns, causes, and consequences of Anthropocene defaunation. *Annu. Rev. Ecol. Evol. Syst.* **47**, 333–358 (2016).
62. Morelli, T. L. et al. Managing Climate Change refugia for climate adaptation. *PLoS ONE* **11**, e0159909 (2016).
63. Cowen, R. K. & Sponaugle, S. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* **1**, 443–466 (2009).

Methods

Database compilation

We followed preferred reporting items for systematic reviews and meta-analyses (PRISMA) protocol[64–66]. We compiled data from studies that experimentally quantified thermal tolerance across populations by searching the published literature using the Web of Science (Clarivate Analytics) with the following search string: ('Heat tolerance' OR 'Heating tolerance' OR 'Temperature limit' OR 'Heat coma' OR 'Thermal Tolerance' OR 'Thermal Limit' OR CTmax OR LD50 OR CTmin OR 'freezing tolerance') AND (geographic OR 'within species' OR 'between site' OR 'between population' OR Intraspecific). Similar to CTmax, CTmin is the critical thermal minimum and a commonly used metric for lower thermal limits. The literature search was performed on 1 February 2022. We also included a small number of studies that we were aware of but were not returned in the search. This approach was similar to that used to assemble comparable datasets[67].

We screened papers based on several criteria for inclusion, retaining only studies that: experimentally determined upper or lower thermal limits in °C (for example, rather than units of time), quantified thermal limits for at least two populations (as defined by authors), recorded organismal scale measurements of thermal limits (for example, CTmax or LD50, with the exception of electrolyte leakage methods for plants[68]), reported sample size for each population (as the number of thermal tolerance measurements made) and quantified tolerance in individuals that were acclimated to common conditions across all populations. We excluded studies that measured thermal limits in populations that arose from cultivars, domesticated species, non-native populations or post-selection generations of experimental evolution studies.

For studies that met the above criteria, we extracted thermal tolerance values and metadata (for example, realm, population latitude and longitude, whether populations covered latitudinal or elevational gradients, acclimation time and temperature and so on) from the main or supplemental text, tables and/or raw data associated with the study. When required, data were extracted from figures using WebPlotDigitizer[69]. In some cases, we contacted authors to acquire data or metadata that was not reported in the study. Studies were excluded when key information (for example, geographic coordinates of sampling sites) could not be ascertained and could not be obtained from authors. At the beginning of the data-extraction process, a random subset of studies was processed by multiple authors to verify consistent data extraction. All error estimates reported in the studies were converted to standard deviations. Each thermal tolerance measurement was classified as either an upper or lower thermal limit. The number of thermal limits retained after the main filtering steps is summarized in Extended Data Fig. 1.

This dataset contained a mixture of both upper and lower thermal limits. Our analyses focused specifically on upper thermal limit data from studies examining latitudinal patterns. Data for lower thermal limits, from studies examining differentiation over elevational gradients, and populations separated by less than 1° latitude were excluded to ensure maximal comparability across realms. Cold tolerance was excluded as only terrestrial taxa had sufficiently abundant measurements (Extended Data Fig. 2). Data from elevational studies and studies covering very small latitudinal ranges were excluded as the small latitudinal ranges covered by these studies resulted in inflated latitudinal slope values (Supplementary Fig. 1). Studies from the four realms include populations that span similar differences in the magnitude of spatial or environmental gradients covered. Studies from each of the four realms included populations separated by similar distances and environmental gradients (Supplementary Fig. 2).

Environmental data

Climate data (mean annual temperature and mean annual maximum temperature) were collected from large-scale datasets for each collection site. For marine species, we used Bio-Oracle v2.0 (ref. [70]), which contains 2000–2014 monthly sea surface temperatures at 9.2 km spatial resolution sourced from the Global Observed Ocean Physics Reprocessing product (http://marine.copernicus.eu). For terrestrial, freshwater and intertidal species, we used the CHELSA database[71], which contains 1979–2013 monthly temperature data at 1 km spatial resolution sourced from the ERA-Interim reanalysis dataset[72]. We used values from the entire period covered by the respective datasets to estimate both climatic parameters. Previous studies have also shown that there is a correlation between air temperature and water temperature in freshwater systems[55]. Because several of the studies included in our dataset examined organisms living in small or ephemeral freshwater habitats that are not contained in the larger freshwater datasets, we used CHELSA-derived temperatures for all freshwater sites to ensure sufficient coverage. We also recognize that intertidal species generally experience high body temperatures driven by multiple factors including aerial and water temperature and conductive and convective heat transport mechanisms[73]. We used aerial temperature for intertidal sites as a proxy because there is little body temperature data derived from biomimetic loggers or mechanistic models for species in our dataset[74,75]. Temperature data were averaged over a 1 km region around coordinates for each site. If the 1 km region failed to return environmental data (for example, coastal studies), we used a 2 km region.

Latitudinal patterns

We used the statistical program R (version 4.0.3) for all analyses[76]. Using the upper thermal tolerance dataset, we examined latitudinal patterns in thermal adaptation across the four realms (Fig. 1). To compare intraspecific patterns with interspecific data[5], we estimated the change in thermal tolerance per degree latitude for each study by regressing thermal tolerance data against latitude. These regressions included no random effects or interaction terms. Separate regressions were estimated for each species, sex, life stage and so on examined in a study. For studies examining only two populations, these slopes are simply the difference in thermal limits divided by the latitudinal separation. We then compared the intraspecific patterns (mean latitudinal slope for each realm) with the interspecific values reported in a previous study (the latitudinal slope estimates from the non-covariate model for critical thermal limits)[5].

Differentiation across realms

To examine a potential environmental driver of divergence, we used inverse weighted meta-regression, allowing us to account for varying levels of precision in tolerance estimates across studies[47]. This slightly reduced the number of studies included in this analysis ($n = 258$ population pairs from 29 studies of 30 species) because analysis required replicate heat tolerance values within each population, thus excluding most studies that used metrics like LD50, which is a population- rather than individual-level metric of heat tolerance. Effect sizes were estimated as pairwise standardized mean differences (Hedges' g) using the 'metafor' package in R[77], using common-control pairwise contrasts within a study, comparing all populations within a study to the population from the highest-latitude sampling site. We also calculated the difference in mean annual maximum temperatures between sites using the environmental data described above. As in the examination of latitudinal slopes, we again used the within-study groupings (sex, life stage, acclimation temperature) when generating the pairwise contrasts.

Our analysis includes a full model with effect size as a function of realm and maximum temperature difference, along with the interaction and crossed random effects of study and phylum (or division for plants). We accounted for the repeated use of the common control by calculating a variance covariance matrix, which was implemented in the meta-regression model. Maximum temperature difference was centred and scaled before analysis. We then used model selection to compare the full model and all possible iterations, which yielded a single-best model (no other models had a difference in Akaike information criterion (ΔAIC) value <2). The best model included the two-way interaction between realm and maximum temperature difference (Supplementary Table 2). We used this model to estimate the effect of temperature difference on our effect-size response. We used funnel plots to evaluate the possibility of publication bias. Funnel plots depict effect sizes as a function of precision (error) (Supplementary Fig. 3). Asymmetrical funnel plots would suggest the possibility of publication bias[46]. Analyses with the entire dataset indicated some skew (Supplementary Fig. 3a), but removal of these outliers revealed a more balanced funnel plot and no change in the analysis outcomes (Supplementary Table 2).

Putative Bogert effects

We also classified each taxon as either motile or non-motile. We based this classification on an individual's ability to exploit thermal heterogeneity in the surrounding environment, which, in turn, has two components: (1) the presence of fine-scale variation in the thermal environment (present in terrestrial and intertidal realms but not in marine or freshwater realms) and (2) the motility of the organism relative to the spatial scale of this variability (high in terrestrial animals like lizards and intertidal animals like snails and crabs, while low in plants and sessile intertidal animals like mussels).

In general, larger divergences in heat tolerance are observed in 'non-motile' organisms than 'motile' species that may be capable of behavioural thermoregulation (Extended Data Fig. 3). The effect of motility on the divergence of thermal limit measurements was examined using both raw differences in thermal limits and Hedges' *g* effect size estimates. In both cases, divergence was compared between taxa classified as motile and non-motile. This classification is coarse, and while it is a reasonable first approximation for exploring general differences across realm, quantitative studies of the effects of microhabitats or the utilization of thermal heterogeneity are needed.

Vulnerability to climate change

For each population, we estimated a warming tolerance, defined as the difference between upper thermal limits and the mean annual maximum temperature at the site of collection origin. To account for potential field acclimation (phenotypic plasticity), we estimated a corrected thermal tolerance value that accounts for differences between the mean temperature at the site of collection and the acclimation temperature used before thermal tolerance measurements were made. Mean temperature was used to represent the average temperature an individual would have been acclimated to at that site. If studies included thermal tolerance data for multiple acclimation temperatures, thermal tolerance in the field was predicted directly from the thermal tolerance reaction norm for each population. These norms were estimated by regressing thermal tolerance against acclimation temperature and then using this regression to predict thermal tolerance at an acclimation temperature equal to the mean temperature at the site of collection. There were no systematic differences in acclimation temperatures used across studies (Supplementary Fig. 4). For studies that did not evaluate the potential for acclimation capacity to affect thermal tolerance, we used the reaction norms described above to predict acclimation response ratios (ARRs) for each population. ARR values were estimated as the slope of each reaction norm, which were then modelled as a function of thermal tolerance and realm as interacting factors[15] (Supplementary Table 3). This model was then used to predict an ARR value for each population based on its thermal tolerance and the realm. This predicted ARR was then used to adjust thermal tolerance based on the difference between acclimation temperature and the mean temperature of each population's collection location: adjusted thermal tolerance = raw thermal tolerance + (ARR × (mean field temperature − acclimation temperature)). The two distinct approaches are illustrated in schematic form in Supplementary Fig. 5. Latitudinal variation in warming tolerance within species was then examined in the same way as thermal limits, with warming tolerance data for each group within a study regressed against latitude. For groups that included only two populations, the latitudinal slope was simply the difference in warming tolerance divided by the latitudinal difference.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The thermal tolerance data that support the findings of this study are available in a figshare repository[78].

Code availability

Custom analysis scripts are available in a figshare repository[78].

References

64. Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G. & PRISMA Group Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *Ann. Internal Med.* **151**, 264–270 (2009).
65. O'Dea, R. E. et al. Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biol. Rev*. https://doi.org/10.1111/brv.12721 (2021).
66. Page, M. J. et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* **372**, 89 (2021).
67. Bennett, J. M. et al. GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci. Data* **5**, 180022 1198 (2018).
68. Lancaster, L. T. & Humphreys, A. M. Global variation in the thermal tolerances of plants. *Proc. Natl Acad. Sci. USA* **117**, 13580–13587 (2020).
69. Rohatgi, A. WebPlotDigitizer (2020); https://automeris.io/WebPlotDigitizer
70. Assis, J. et al. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* **27**, 277–284 (2018).
71. Karger, D. N. et al. Climatologies at high resolution for the Earth's land surface areas. *Sci. Data* **4**, 170122 (2017).
72. Dee, D. P. et al. The ERA–interim reanalysis: configuration and performance of the data assimilation system. *Q. J. R. Meteorolog. Soc.* **137**, 553–597 (2011).
73. Helmuth, B. et al. Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298**, 1015–1017 (2002).
74. Helmuth, B. Thermal biology of rocky intertidal mussels: quantifying body temperature using climatological data. *Ecology* **80**, 15–34 (1999).
75. Bell, E. C. Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga *Mastocarpus papillatus* Kützing. *J. Exp. Mar. Biol. Ecol.* **191**, 29–55 (1995).
76. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2020).
77. Viechtbauer, W. Conducting meta-analyses in R with the metafor package. *J. Stat. Software* **36**, 1–48 (2010).
78. Sasaki, M. et al. Data for 'greater local adaptation to temperature in the ocean than on land'. figshare https://doi.org/10.6084/m9.figshare.20173571 (2022).

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Author contributions

All authors conceptualized and designed the paper. M.S., J.M.B., S.G.-W., C.G.H., M.W.K., A.B.P., S.N.S., A.R.V. and B.S.C. assembled the data; M.S. analysed the data and produced figures. M.S. and B.S.C. drafted the paper; all authors contributed to discussion, writing and interpretation.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41558-022-01534-y.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41558-022-01534-y.

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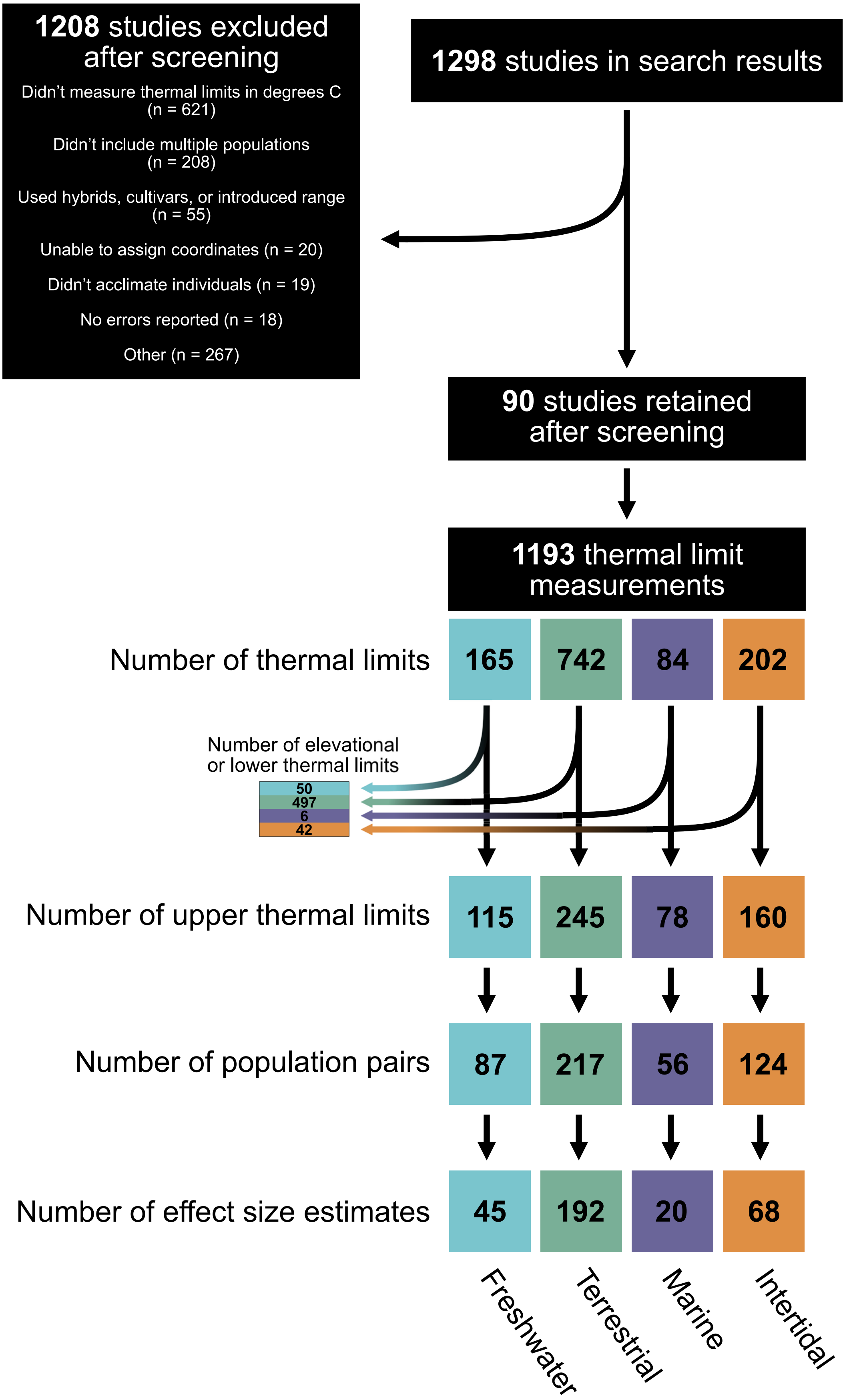
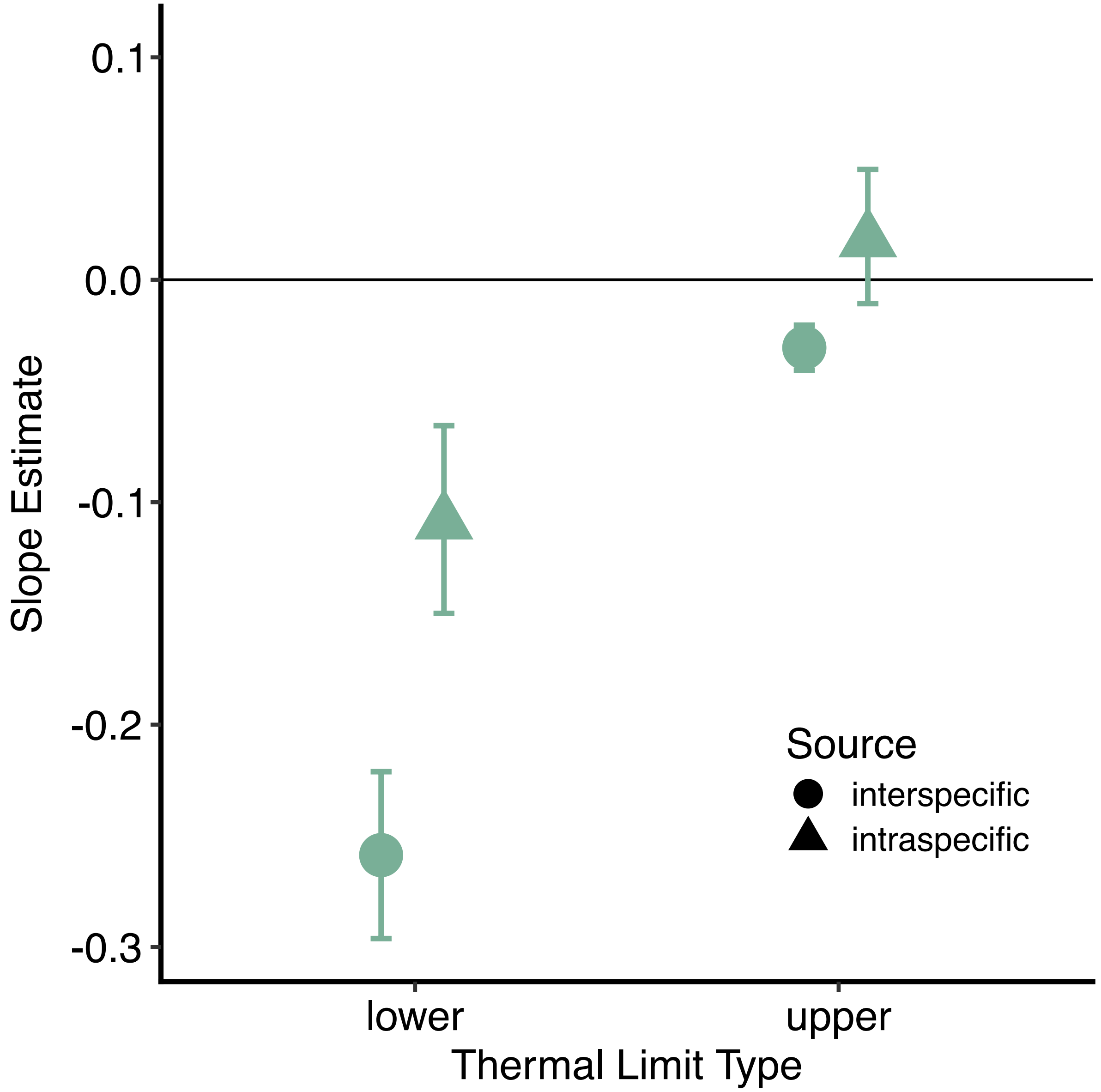
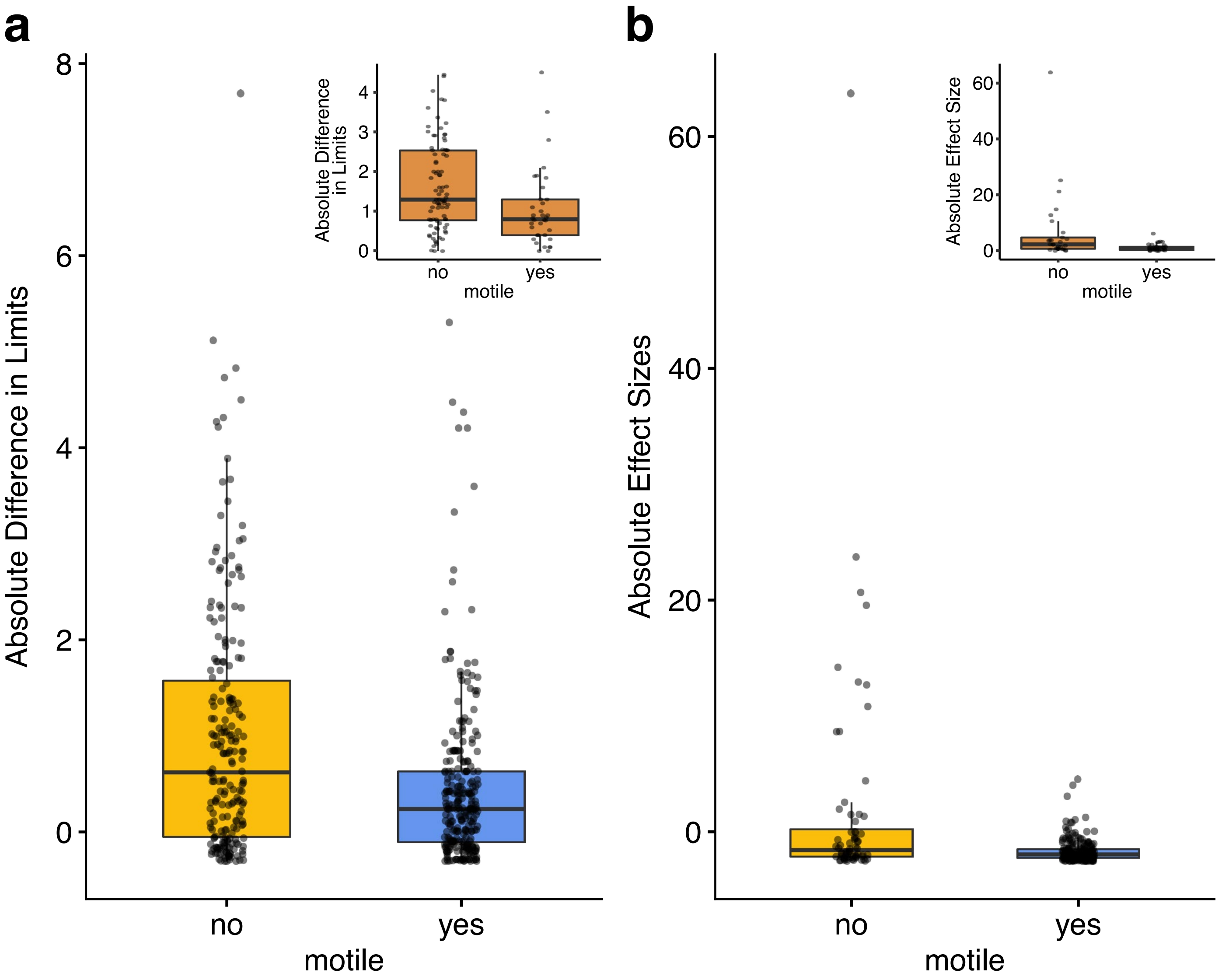


Extended Data Fig. 1 | Flowchart breaking down the number of studies processed during screening, and the number of thermal limits used in our analyses. A summary of the number of studies processed during screening, the number of thermal limits before and after major filtering, and the number of population pairs and effect size estimates used in our analyses.



Extended Data Fig. 2 | Comparison of within- and between-species latitudinal patterns in upper and lower thermal limits. Comparison of mean intraspecific slope estimates (± SE) for upper and lower thermal tolerance values against latitude for terrestrial taxa (n = 37 lower thermal limit slopes; n = 43 upper thermal limit slopes). Studies examining elevational differences are excluded. For comparison, interspecific slope estimates are included from Sunday et al.[5].



Number of Population Pairs		
	Non-Motile	**Motile**
Freshwater	66	21
Intertidal	88	36
Marine	56	0
Terrestrial	5	212

Number of Effect Size Estimates		
	Non-Motile	**Motile**
Freshwater	24	21
Intertidal	35	33
Marine	20	0
Terrestrial	0	192

Extended Data Fig. 3 | Comparison of thermal limit divergence between motile and non-motile taxa. Absolute difference in upper thermal limits between motile and non-motile taxa (motility defined here as whether or not an individual could control their microhabitat sufficiently to regulate body temperature using environmental thermal heterogeneity), calculated using both (a) unweighted raw mean differences (n = 215 non-motile & 269 motile) and (b) inverse-weighted standardized mean differences (Hedges' *g*; n = 79 non-motile & 246 motile). Inset plots show the values for intertidal taxa alone. In all cases, the box plot's horizontal line represents the median, while box limits illustrate the first and third quartiles. Whiskers extend from the box limits to the minimum and maximum values (not including outlier values that are more than 1.5 times the interquartile range from the box limits). Tables underneath each plot show the number of population pairs or effect size estimates for each realm and motility type.

nature research

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Reporting Summary

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Software and code

Policy information about availability of computer code

Data collection	When not reported in the text of the study, thermal tolerance values were manually extracted from figures using WebPlotDigitizer v4.4.
Data analysis	We used the statistical program R 4.0.3 to analyze the data in this study. As described in the code accessibility statement, scripts for data analysis are available in a Figshare repository.

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Life sciences study design

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

Sample size	Sample size was equal to the number of thermal tolerance values reported in studies that measured thermal tolerance in multiple populations of the same species.
Data exclusions	We excluded thermal tolerance measurements from studies that used conditions or organisms that limited comparability across studies. Specifically, we excluded studies that measured thermal limits in populations that arose from cultivars, domesticated species, non-native populations, or post-selection generations of experimental evolution studies. Studies were also excluded if we were unable to assign coordinates to sampling locations, or if organisms were not acclimated to common conditions prior to thermal limit measurements.
Replication	This study does not include the results of experimental work, and therefore there is no replication strategy.
Randomization	As this study does not report the results of new experimental work, no randomization strategy is reported.
Blinding	The initial literature search, study screening, and data extraction steps were performed before data analysis. During this process studies were randomly assigned to co-authors. All data was compiled from the literature before undertaking the main analyses.

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Methods

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