Greater local adaptation to temperature in the ocean than on land

Matthew Sasaki (matthew.sasaki@uconn.edu)  
University of Connecticut  https://orcid.org/0000-0001-5560-5363

Jordanna Barley  
University of Massachusetts Amherst

Sarah Gignoux-Wolfsohn  
Smithsonian Environmental Research Center

Cynthia Hays  
Keene State College

Morgan Kelly  
Louisiana State University

Alysha Putnam  
University of Massachusetts Amherst

Seema Sheth  
North Carolina State University

Andrew Villeneuve  
University of Massachusetts Amherst  https://orcid.org/0000-0001-7303-5931

Brian Cheng  
University of Massachusetts Amherst

Article

Keywords: Bogert effect, climate risk, differentiation, divergence, thermal safety margin, warming tolerance

Posted Date: October 29th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-987225/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License. Read Full License
Abstract

Warming threatens biodiversity but there is considerable uncertainty in which species and ecosystems are most vulnerable. Moreover, our understanding of organismal sensitivity is largely centered on species level assessments, which do not consider variation across populations. Here, we used meta-analysis to quantify differentiation in thermal tolerance across 413 populations from 105 species living in terrestrial, marine, and freshwater realms. Strikingly, 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 dispersal potential in the ocean should reduce intraspecific variation. Our findings are consistent with the “Bogert effect” operating in terrestrial but not marine ecosystems, which predicts that behavioral thermoregulation constrains evolution. Such adaptive differentiation in the ocean suggests that there may be standing genetic variation at the species level to buffer climate impacts. Assessments of organismal vulnerability to warming, especially in marine species, should account for variation in thermal tolerance among populations or risk under- or overestimating climate vulnerability.

Introduction

Climate warming is a major threat to the persistence of species across all realms. One key problem is that warming is variable over space and time, which has led to uncertainty in our understanding of which ecosystems and taxa may be most vulnerable to rising temperatures. 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. The oceans also exhibit higher climate velocities than on land, particularly in the tropics. However, prior work has largely focused on comparisons across species, implicitly assuming that populations within species are homogeneous and thermal tolerance from one population can be used to estimate vulnerability across a species’ range. Such an assumption may greatly under- or overestimate a species’ susceptibility to climate warming if population thermal limits are locally adapted.

Unchanging thermal tolerance across populations is a form of “niche conservatism.” In the ocean, such an assumption stems from the observation that the dispersal of marine species is often several orders of magnitude greater than terrestrial species, and characterized by rare but long distance migrants. Most marine taxa also face fewer geographic barriers to dispersal, which promotes population connectivity and the colonization of novel environments such that marine taxa appear to fully occupy their thermal niches. In theory, high dispersal and subsequent gene flow would have a homogenizing effect, swamping adaptive differentiation and limiting the potential for local adaptation. However, recent work has challenged this paradigm, suggesting that self-recruitment and high levels of larval and post-settlement selective mortality can result in less-than-predicted dispersal potential, which in turn may promote local adaptation in the oceans.
In contrast to marine taxa, terrestrial populations are typically thought to have more limited dispersal and population connectivity. However, theory also predicts that behavioral thermoregulation may reduce the strength of selection on thermal tolerance on land; this has been termed the “Bogert effect”\textsuperscript{22,23}. Many terrestrial ectotherms can moderate body temperatures by behaviorally exploiting shade, forests, crevices, or other thermal refugia\textsuperscript{23,24}. Similarly, non-mobile taxa (e.g., plants) may be able to exploit microclimatic variation, relaxing selection for thermal tolerance\textsuperscript{25}. Accordingly, variation in interspecific heat tolerance on land is only weakly associated with latitude and maximum temperature\textsuperscript{26}. However, behavioral thermoregulation is only possible if the environment is thermally heterogeneous\textsuperscript{27}. Relative to terrestrial habitats, freshwater and marine ecosystems are thermally homogeneous with limited opportunity for organisms to use refugia. Intertidal ecosystems and marine zones with strong gradients which species could exploit via sheltering or vertical migration are exceptions. Nevertheless, the relatively limited opportunity for behavioral thermoregulation in the marine ecosystem should impose stronger selection on heat tolerance\textsuperscript{28}. In support of this prediction, both marine and freshwater taxa have interspecific heat tolerances that decline sharply with increasing latitude\textsuperscript{5,6,26,29–31}. If the same pattern applies within species, differences in thermal tolerance across populations of aquatic species could buffer against the impacts of climate warming and provide standing genetic variation for the potential evolution of thermal tolerance. Despite this, broad scale analyses evaluating vulnerability to warming have largely been conducted at the species level, and it is unknown if local adaptation to thermal stress, or differences in patterns of local adaptation across aquatic and terrestrial habitats, can moderate climate risk\textsuperscript{6,32}.

\section*{Results}

\textbf{Latitudinal patterns in temperature tolerance.} To assess differences across realms in population vulnerability to warming, we compiled a meta-analytic data set from studies that examined thermal tolerance (measured as upper or lower lethal thermal limits) across populations in ectothermic animals and plants from terrestrial, marine, and freshwater realms. Our data set includes 990 heat or cold tolerance values from 413 populations of 105 species (Supplementary Fig. 1, Supp. Table 1; 633 thermal limits from terrestrial species, 108 from freshwater taxa, 169 from intertidal species, and 80 from marine species). Seven phyla are represented, and the data span a latitudinal range from 62°S to 78°N (Fig. 1). Similar to other studies, the data are largely sourced from studies evaluating populations in North America, Western Europe, and Australia (Fig. 1a). Here, we found substantial variation in heat tolerance within species (Fig. 1b-d). At the population level, we observed significant decreases in heat tolerance with increasing latitude for marine, intertidal, and freshwater taxa, but not terrestrial taxa. Intraspecific slope estimates (population heat tolerance as a function of latitude) vary in a qualitatively similar way to the interspecific patterns observed in prior studies\textsuperscript{26}, but with reduced magnitude (Fig. 1f). Strong elevational temperature gradients result in a similar absolute magnitude of differences in heat tolerance between elevational and latitudinal studies (Supplementary Fig. 2). However, because of the small latitudinal ranges these elevational gradients cover, the slope estimates generated for these studies are large and not reasonably comparable to latitudinal studies. Thus, we excluded data from studies
examining heat tolerance across elevational gradients (n = 232) from further analysis. We also examined latitudinal variation in cold tolerance for terrestrial taxa (the only group for which enough measurements have been made; n = 220; Supplementary Fig. 3). For both inter- and intraspecific comparisons, cold tolerance varies more strongly across latitude than heat tolerance, a pattern of “cold tolerance asymmetry”.

**Differentiation across ecosystems.** We used an inverse weighted meta-analytic approach to examine the strength of heat tolerance differentiation across ecosystems and potential environmental drivers of intraspecific divergence. To account for varying levels of precision in measurements across studies we estimated pairwise population differentiation in heat tolerance using a standardized effect size metric (Hedges’ $g$, Figure 2a,b,c). 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. However, this robust approach has the benefit of accounting for study level precision, decreasing the influence of small studies and is preferable to unweighted analysis. For completeness, we also conducted an unweighted analysis, which included more data and yielded similar findings as the weighted analysis (see Methods). We used a common-control approach, such that all populations (within species) were compared to a control population (specified here as the highest latitude population). Because weighted analysis resulted in a reduction in sample size, we pooled intertidal and marine taxa. We then modeled the effect size estimates with the fixed effects of ecosystem, maximum temperature difference between sites, and distance between sites, with all possible two-way and three-way interactions. We used crossed random effects of study and Phylum (or Division for plants). We also included a variance covariance matrix to account for repeated measures within species, as the data from the common control are used multiple times. Model selection yielded a single best model that excluded the two-way interaction between distance and maximum temperature difference and the three-way interaction between all moderators (Supplementary Table 2). Both this top model and a model averaging approach yielded the same conclusions, and indicate that greater maximum temperature differences are associated with greater thermal differentiation for the pooled marine and intertidal taxa but not freshwater or terrestrial taxa (Fig. 2d). Distance between populations does not predict effect size in any of the ecosystems.

Behavioral thermoregulation may also affect observed patterns in thermal adaptation, and may reduce the magnitude of differentiation of heat tolerance between populations. To evaluate this within our dataset, we classified all species based on their capacity to exploit heterogeneity in the thermal environment. Our classification considered two factors, 1) the availability of fine-scale variation in the thermal environment (present in terrestrial and intertidal ecosystems, but not in marine or freshwater ecosystems), 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). Stronger divergences in heat tolerance are observed in “non-motile” organisms than “motile” species that may be capable of behavioral thermoregulation (Supplementary
Fig. 4). This difference was observed for both unweighted raw mean differences and Hedges’ $d$ effect size estimates. We note, however, that the classification used here is based on qualitative characteristics, and quantitative studies of the effects of microhabitats or the utilization of thermal heterogeneity are needed. The observed cold tolerance asymmetry observed in our data set, with stronger divergence in cold tolerance than heat tolerance, may also suggest an influence of behavioral thermoregulation; nighttime thermal environments tend to be more homogenous than daytime thermal environments\textsuperscript{38}, reducing the opportunity for mobile organisms to avoid cold temperatures and the accompanying selection on cold tolerance.

**Vulnerability to climate change.** In a rapidly warming climate, vulnerability to extreme heat events depends on both the organismal heat tolerance and environmental conditions. To quantify such vulnerability, we calculated organismal warming tolerance\textsuperscript{39} as the difference between heat tolerance and mean annual maximum temperatures at the site of collection using recent remote sensed data (See Methods). Although this is not a direct forecast of vulnerability, warming tolerance serves as an index of physiological stress owing to climate change\textsuperscript{3,39}. Because organisms can adjust to rising or variable thermal environments via phenotypic plasticity (acclimation or hardening)\textsuperscript{40}, we applied a correction to heat tolerance values prior to estimating warming tolerances. As in previous analyses of vulnerability to warming\textsuperscript{3}, we accounted for the potential difference between the temperatures organisms were acclimated to prior to thermal stress assays and the mean field temperature at each collection site before calculating warming tolerance. When available, we used species-specific estimates of acclimation response ratio (change in thermal limit per degree difference in acclimation temperature)\textsuperscript{32}. If species level data were unavailable we used ecosystem-specific estimates of acclimation response ratios\textsuperscript{32}. Our analyses reveal that warming tolerances varied considerably within species, reinforcing the idea that an intra-specific perspective on vulnerability to warming is important for forecasting sensitivity to climate change (Fig. 3a-d). For marine species, we observed some evidence of curvature with low warming tolerance in a small number of high latitude populations and high warming tolerance in mid-latitude populations (Fig. 3c). However, we suggest caution in interpreting absolute values of warming tolerance estimates. The maximum temperature estimates for freshwater taxa may overestimate the temperatures experienced, particularly in large water bodies. Warming tolerance estimates for terrestrial taxa do not account for microclimatic variation and behavioural thermoregulation which can mediate climate risk\textsuperscript{27}. Further, we cannot account for the effect of co-occurring stressors, which may decrease warming tolerance\textsuperscript{41}, or how adaptation to future conditions may reduce vulnerability\textsuperscript{42}. While these 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 warming tolerance slopes indicate how vulnerability to rising temperatures changes across latitude. In marine and intertidal taxa, warming tolerance generally increased with latitude suggesting that low latitude populations are vulnerable to warming (Fig. 3b,c). Unlike for marine taxa, the relationship between warming tolerance and latitude was generally negative for terrestrial taxa, indicating that high latitude populations may be more vulnerable. However, we note that microhabitat utilization or behavioral...
thermoregulation appears to be effective enough to limit differentiation of heat tolerance between populations, and may therefore be expected to effectively increase warming tolerance of terrestrial taxa by reducing the experienced maximum temperatures. We also found substantial variation in the warming tolerance slopes within ecosystems, stemming from the interaction between patterns in population heat tolerance and spatial patterns in the thermal environment. This highlights that populations are an important unit to consider when assessing vulnerability, and that latitudinal patterns in warming tolerance are likely species-specific. Ecosystem level assessments risk over-generalizing vulnerability, limiting our ability to design effective conservation and management strategies.

Patterns in vulnerability may change as warming increases both mean and maximum temperatures. These changes will be shaped by both the spatial variability in predicted warming, and the observed intraspecific variation in thermal tolerance. Thus, we recalculated our warming tolerance estimates using mean and maximum temperatures from intermediate climate change projections (RCP 4.5 / SSP 245) for the years 2040-2050 to examine how changing temperatures may affect patterns of vulnerability. These estimates of future warming tolerance assume acclimation to the new mean habitat temperatures, and do not account for the potential for genetic adaptation or range shifts. We observed abundant intraspecific variation in predicted warming tolerances, once again reinforcing that understanding population differentiation in thermal limits is an important component of predicting species responses to climate change. The future estimates of warming tolerance also suggest decreasing warming tolerances in freshwater and terrestrial taxa versus more variable responses in marine species (Supplemental Figure 7), but again we suggest caution in interpreting the magnitude of these predicted warming tolerance values due to the potential differences between forecasted and experienced temperatures across ecosystems.

Conclusions

Within-species variation in heat tolerance can be substantial. However, the magnitude of these intraspecific differences in heat tolerance varies systematically across ecosystems, 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. Differences among ecosystems also reinforce that behavioral thermoregulation and the exploitation of microclimatic variation may effectively reduce the strength of selection on heat tolerance for many terrestrial taxa (i.e., the Bogert Effect). The population-level differentiation in heat tolerance documented here is qualitatively similar to that found at the interspecific level, suggesting that common factors may affect the evolution of thermal tolerance at both biological scales.

Species-level estimates of heat tolerance can highlight large-scale latitudinal patterns in climate vulnerability. However, reliance on these interspecific patterns to predict vulnerability to climate obscures both the substantial within-species variation in warming tolerance, driven by the differentiation of heat
tolerance between populations, and the systematic differences in how warming tolerance varies across latitude. The observation that equatorward populations generally have the lowest warming tolerances within marine and intertidal taxa, while poleward populations are generally more vulnerable in terrestrial species is only apparent at the intraspecific level, and sometimes conflicts with the global, cross-species patterns. Recent evidence that populations with high thermal tolerance (most often occupying low latitudes) may have diminished plasticity in thermal tolerance\(^{32}\) would also suggest that low latitude marine populations may be particularly vulnerable to the effects of warming. However, the greater population differentiation of heat tolerance observed in marine taxa suggests the potential for evolutionary rescue via gene flow\(^{45,46}\).

A focus on species-level estimates of warming tolerance reflects a general emphasis on extinction risk, rather than extirpation and defaunation. These local processes, however, are major drivers of biodiversity loss and eroding ecosystem function\(^{47,48}\). Intraspecific variation is important because the ecological effects of such variation can be equivalent and sometimes stronger than interspecific variation\(^{49}\). Inclusion of population-level assessments of vulnerability in heat and warming tolerance is crucial for our understanding of how a rapidly changing climate will affect the persistence and fate of biodiversity.

**Declarations**

**Acknowledgements**

This article arose from the Research Coordination Network, ‘Evolution in Changing Seas’ (US National Science Foundation #1764316). We thank K. Lotterhos, M. Albecker, D. Bolnick, J. Kelley, and G. Trussel for developing and organizing the network. Additional support was provided by the US National Science Foundation (#2023571). We thank H.G. Dam, E.D. Grosholz, and L.M. Komoroske for comments on earlier manuscript drafts. Finally, we are grateful to the primary authors who collected the empirical data.

**Author contributions**

All authors conceptualized and designed the paper; M.S., J.B., S.G., 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 discussion, writing, and interpretation.

**Competing financial interests**

The authors declare no competing financial interests.

**Methods**
Database Compilation

As appropriate, we followed preferred reporting items for systematic reviews and meta-analyses (PRISMA) protocol\(^5\). 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: (Thermal OR temperature) AND (Lethal OR “Thermal Tolerance” OR “Thermal Limit” OR CTmax OR LT50 OR CTmin OR “freezing tolerance”) AND (“Local Adapt” OR “Latitud* Var*” OR Intraspec). Literature searches were performed on August 24, 2019 and updated on July 28, 2020. We also included a small number of studies that we were aware of but were not returned in the search.

We screened papers based on several criteria for inclusion, retaining only studies that: reported upper or lower thermal limits in °C (e.g., rather than units of time), quantified thermal limits for at least two populations (as defined by authors), recorded organismal scale measurements of thermal limits (e.g. - CTmax or LD50, with the exception of electrolyte leakage methods for plants\(^5\)), 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 from the main or supplemental text, tables, and/or raw data associated with the study. When required, data was extracted from figures using WebPlotDigitizer\(^5\). In some cases, we contacted authors to acquire data or metadata that was not reported in the study. At the beginning of the data extraction process, a random subset of studies was processed by multiple authors to verify consistent data extraction. All errors reported in the studies were converted to standard deviations. Each thermal tolerance measurement was classified as either an upper or lower thermal limit. We also classified each study as examining “latitudinal” or “elevational” patterns, and 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) motility of the species, and 2) the scale of environmental heterogeneity relative to that motility. The number of thermal limits retained after the main filtering steps is summarized in Supplementary Fig. 1. A list of the studies included in the data set is provided in Supplementary Table 1.
Latitudinal Patterns

Using this thermal tolerance data set, we examined latitudinal patterns in thermal adaptation across the four major ecosystems (Fig. 1). To compare intra-specific patterns with inter-specific data, 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 examined in a study. We then compared these intra-specific patterns with the inter-specific values reported in Sunday et al.\textsuperscript{26} (i.e., the latitudinal slope estimates from the non-covariate model for critical thermal limits). These latitudinal patterns were examined for upper thermal limits of taxa from all four ecosystems, and for lower thermal limits of terrestrial taxa. There was substantial variation in thermal limits over elevational gradients, but data from these studies was excluded from the latitudinal slope estimates as the short horizontal distance covered by these studies resulted in inflated latitudinal slope values.

Differentiation across ecosystems

To examine differentiation across ecosystems and potential environmental drivers of divergence we used an unweighted and weighted approach. First, we used unweighted pairwise thermal limits within each study, only comparing within-study groupings (sex, life-stage, acclimation temperature). We used a common control design when generating these pairs, comparing all populations within a study to the population from the highest latitude sampling site. For each population pair, we calculated the difference in thermal limits (i.e., unweighted raw mean differences in thermal limits between populations), the linear distance in km between sites, and the difference in maximum annual temperatures. We modelled pairwise differences in thermal limits using a linear mixed effects model with the distance between populations and the difference in maximum temperatures between the sites as factors. The two-way interactions between these factors and environment were also included, along with random effects of species nested within phylum. Data was restricted to just population pairs that were <4000 km apart, as all marine population pairs were less than 4000 km apart and only a small proportion of terrestrial, freshwater, or intertidal population pairs fell beyond that threshold (n = 32 beyond compared to n = 371 below).

Second, we used inverse weighted meta-regression to account for varying levels of precision in tolerance estimates across studies\textsuperscript{34}. This analysis included only studies that have sample size greater than one and reported a measure of spread (e.g. standard deviation, standard error, variance) and examined the relationship between thermal limit contrasts and two moderators, distance between sites and difference in maximum temperature. Note that these criteria result in the exclusion of studies that used thermal tolerance metrics like LD50, which was commonly estimated from a single survivorship curve per
population in our data set. Intertidal and marine taxa were lumped together for this analysis to account for the smaller number of studies that met the necessary sample size criteria. Effect sizes were estimated as pairwise standardized mean differences (Hedges’ $g$) using the ‘metafor’ package in R\textsuperscript{53,54}, using common-control pairwise contrasts within a study. Effect sizes were estimated for each within-study group (acclimation temperature, life stage, sex, etc.) separately. We account for the repeated use of the common control by implementing a variance covariance matrix to address non-independence.

To test for environmental drivers of differentiation among populations, we extracted climate data (mean annual temperature and annual maximum temperature) for each collection site. For marine species we used Bio-Oracle v2.0\textsuperscript{55}, 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.edu). For terrestrial, freshwater, and intertidal species we used CHELSA\textsuperscript{56}, which contains 1979-2013 monthly temperature data at 1 km spatial resolution sourced from the ERA-Interim reanalysis\textsuperscript{57}. Freshwater-specific climatologies\textsuperscript{58} closely matched the data extracted from CHELSA (Supplementary Fig. 5). Because the freshwater-specific data set returned environmental data for fewer sites, we used CHELSA derived temperatures for all freshwater sites. We recognize that intertidal species generally experience high body temperatures driven by multiple factors including aerial and water temperature, as well as conductive and convective heat transport mechanisms\textsuperscript{59}. 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\textsuperscript{60,61}. Temperature data was averaged over a 1 km region around coordinates for each site. If the 1 km region failed to return environmental data (e.g., coastal studies) we used a 2 km region.

Our analysis includes a full model with effect size as a function of ecosystem, maximum temperature difference, distance, and included all interactions and crossed random effects of study and Phylum (or Division for plants). Covariates were centered and scaled prior to 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 $\Delta$AIC value < 2). The best model excluded the two-way interaction between distance and maximum temperature difference and the three-way interaction between all moderators (Supplementary Table 2). We used this model to estimate the effects of distance and temperature difference on our effect size response. We note that a model averaging approach yielded the same conclusions. We used funnel plots to evaluate the possibility of publication bias. Funnel plots depict effect sizes as a function of precision (error) (Supp. Fig. 8). Asymmetrical funnel plots would suggest the possibility of publication bias\textsuperscript{36}. Analyses with the entire data set indicated some skew (Supp. Fig. 8a) but removal of these outliers revealed a balanced funnel plot and no change in the analysis outcomes.
The effect of motility on the divergence of thermal limit measurements was examined using two separate analyses, one for unweighted raw mean differences and another for the Hedges’ $d$ effect size estimates. In both cases, the absolute magnitude of divergence was compared between taxa classified as motile and non-motile using a one-way ANOVA. All divergences were examined together, rather than separated out by ecosystem because the proportion of studies dropped between the unweighted mean difference analysis and the Hedges’ $d$ effect size analysis was not equal across ecosystems. No non-motile species are retained from terrestrial studies for example. Only for marine taxa was there a large enough sample size in both analyses for a robust comparison between motile and non-motile taxa. The results of this comparison did not differ from what was observed across the pooled data points.

Vulnerability to climate change

For each population, we estimated a warming tolerance, defined as the difference between upper thermal limits and the maximum temperature at the site of collection origin. To account for potential field acclimatization (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. 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. 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 modeled as a function of thermal tolerance and ecosystem as interacting factors. This model was then used to predict an ARR value for each population based on its thermal tolerance and the ecosystem. This predicted ARR is then used to adjust thermal tolerance (TT) based on the difference between acclimation temperature and the mean temperature of each population's collection location:

$$\text{Adj. TT} = \text{Raw TT} + (\text{ARR} \times (\text{Mean Field Temp.} - \text{Acclimation Temp}))$$

These two approaches are illustrated in schematic form in Supplementary Fig. 6.

Predictions of near-term (2040-2050) environmental data (mean temperature and maximum temperature of the warmest month) were retrieved for an intermediate climate scenario (RCP 4.5 / SSP 245) from Bio-
Oracle marine sites, and WorldClim for terrestrial, freshwater, and intertidal sites. We note that while the current and future temperature data for marine sites has the same spatial resolution, the predicted future air temperature data set has a spatial resolution of ~4 km (2.5 minutes), rather than the ~1 km resolution (30 arc sec) of the recent climate data. The resolution of the future air temperature data is still high enough to differentiate climates for different populations, as no populations from latitudinal studies were less than 10 km apart. Future mean and maximum temperatures were used to estimate a warming tolerance in the same way as for current temperatures. Briefly, thermal limits were adjusted to account for the difference between acclimation temperature and the mean temperature at the site of collection using either species-specific estimates of ARR or ecosystem-specific estimates of ARR based on the population's thermal limit. This adjusted thermal limit was then compared with the predicted maximum temperature (max. temp. – adjusted limit) to estimate a warming tolerance under future conditions.

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* (2009) doi:10.1038/nature08649.
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. Burrows, M. T. *et al.* The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science* **334**, 652–655 (2011).
5. Hughes, A. R. *et al.* Predicting the sensitivity of marine populations to rising temperatures. *Frontiers in Ecology and the Environment* **17**, 17–24 (2019).
6. Bennett, S., Duarte, C. M., Marbà, N. & Wernberg, T. Integrating within-species variation in thermal physiology into climate change ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180550 (2019).
7. Kelly, M. W., Sanford, E. & Grosberg, R. K. Limited potential for adaptation to climate change in a broadly distributed marine crustacean. *Proceedings of the Royal Society B: Biological Sciences* **279**, 349–356 (2012).
8. Valladares, F. *et al.* The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* **17**, 1351–1364 (2014).
9. Moran, E. V., Hartig, F. & Bell, D. M. Intraspecific trait variation across scales: Implications for understanding global change responses. *Global Change Biology* **22**, 137–150 (2016).
10. Razgour, O. *et al.* Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 10418–10423 (2019).
11. Wiens, J. J. *et al.* Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**, 1310–1324 (2010).
12. Kinlan, B. P & Gaines, S. D. Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. *Ecology* **84**, 2007–2020 (2003).

13. Benestan, L. *et al.* Restricted dispersal in a sea of gene flow. *Proceedings of the Royal Society B: Biological Sciences* **288**, 20210458 (2021).

14. Palumbi, S. R. & Pinsky, M. L. Marine dispersal, ecology, and conservation. in *Marine community ecology and conservation* 57–84 (Sinauer Associates, 2014).

15. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nature Climate Change* **2**, 686–690 (2012).

16. Grummer, J. A. *et al.* Aquatic Landscape Genomics and Environmental Effects on Genetic Variation. *Trends in Ecology & Evolution* **34**, 641–654 (2019).

17. Mayr, E. *Animal Species and evolution.* (Harvard University Press, 1963).

18. Haldane, J. The relation between density regulation and natural selection. *Proceedings of the Royal Society of London. Series B - Biological Sciences* (1956) doi:10.1098/rspb.1956.0039.

19. 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).

20. 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).

21. Sanford, E. & Kelly, M. W. Local Adaptation in Marine Invertebrates. *Annual Review of Marine Science* **3**, 509–535 (2011).

22. 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).

23. Bogert, C. M. Thermoregulation in Reptiles, a Factor in Evolution. *Evolution* **3**, 195–211 (1949).

24. Kearney, M., Shine, R. & Porter, W. P. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *PNAS* **106**, 3835–3840 (2009).

25. 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**, (2020).

26. Sunday, J. *et al.* Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20190036 (2019).

27. Huey, R. B. *et al.* Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 1665–1679 (2012).

28. Marais, E. & Chown, S. L. Beneficial acclimation and the Bogert effect. *Ecology Letters* **11**, 1027–1036 (2008).

29. Cereja, R. Critical thermal maxima in aquatic ectotherms. *Ecological Indicators* **119**, 106856 (2020).

30. Vinagre, C. *et al.* Upper thermal limits and warming safety margins of coastal marine species – Indicator baseline for future reference. *Ecological Indicators* **102**, 644–649 (2019).
31. Sasaki, M. & Dam, H. G. Global patterns in copepod thermal tolerance. *Journal of Plankton Research* **43**, 598–609 (2021).

32. Barley, J. M. *et al.* Limited plasticity in thermally tolerant ectotherm populations: evidence for a trade-off. *Proceedings of the Royal Society B: Biological Sciences* **288**, 20210765 (2021).

33. Herrando-Pérez, S. *et al.* Heat tolerance is more variable than cold tolerance across species of Iberian lizards after controlling for intraspecific variation. *Functional Ecology* **34**, 631–645 (2020).

34. Cooper, H., Hedges, L. V. & Valentine, J. C. *The handbook of research synthesis and meta-analysis*. (Russel Sage Foundation, 2009).

35. Button, K. S. *et al.* Power failure: why small sample size undermines the reliability of neuroscience. *Nat Rev Neurosci* **14**, 365–376 (2013).

36. Gurevitch, J., Koricheva, J., Nakagawa, S. & Stewart, G. Meta-analysis and the science of research synthesis. *Nature* **555**, 175–182 (2018).

37. Gleser, L. & Olkin, I. Stochastically dependent effect sizes. in *The handbook of research synthesis and meta-analysis* 357–376 (Russell Sage Foundation, 2009).

38. Muñoz, M. M. & Bodensteiner, B. L. Janzen’s Hypothesis Meets the Bogert Effect: Connecting Climate Variation, Thermoregulatory Behavior, and Rates of Physiological Evolution. *Integrative Organismal Biology* **1**, (2019).

39. Deutsch, C. A. *et al.* Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* **105**, 6668–6672 (2008).

40. Seebacher, F., White, C. R. & Franklin, C. E. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* **5**, 61–66 (2015).

41. Todgham, A. E. & Stillman, J. H. Physiological Responses to Shifts in Multiple Environmental Stressors: Relevance in a Changing World. *Integrative and Comparative Biology* **53**, 539–544 (2013).

42. Hoffmann, A. A. & Sgró, C. M. Climate change and evolutionary adaptation. *Nature* **470**, 479–485 (2011).

43. Pespeni, M. H. & Palumbi, S. R. Signals of selection in outlier loci in a widely dispersing species across an environmental mosaic. *Molecular Ecology* **22**, 3580–3597 (2013).

44. Hoey, J. A. & Pinsky, M. L. Genomic signatures of environmental selection despite near-panmixia in summer flounder. *Evolutionary Applications* **11**, 1732–1747 (2018).

45. Howells, E. J. *et al.* Enhancing the heat tolerance of reef-building corals to future warming. *Science Advances* **7**, eaba6070 (2021).

46. Bay, R. A., Rose, N. H., Logan, C. A. & Palumbi, S. R. Genomic models predict successful coral adaptation if future ocean warming rates are reduced. *Science Advances* **3**, e1701413 (2017).

47. Dirzo, R. *et al.* Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).

48. 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).
49. Des Roches, S. et al. The ecological importance of intraspecific variation. *Nat Ecol Evol* 2, 57–64 (2018).
50. Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G. & Grp, P. Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *Plos Medicine* 6, (2009).
51. Lancaster, L. T. & Humphreys, A. M. Global variation in the thermal tolerances of plants. *PNAS* 117, 13580–13587 (2020).
52. Rohatgi, A. *WebPlotDigitizer*. (2020).
53. Viechtbauer, W. Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software* 36, 1–48 (2010).
54. R Core Team. *R: A language and environment for statistical computing*. (R Foundation for Statistical Computing, 2020).
55. Assis, J. et al. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography* 27, 277–284 (2018).
56. Karger, D. N. et al. Climatologies at high resolution for the earth’s land surface areas. *Sci Data* 4, 170122 (2017).
57. Dee, D. P. et al. The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society* 137, 553–597 (2011).
58. Domisch, S., Amatulli, G. & Jetz, W. Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. *Sci Data* 2, 150073 (2015).
59. Helmuth, B. et al. Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298, 1015–1017 (2002).
60. Bell, E. C. Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga Mastocarpus papillatus Kützing. *Journal of Experimental Marine Biology and Ecology* 191, 29–55 (1995).
61. Helmuth, B. Thermal biology of rocky intertidal mussels: Quantifying body temperatures using climatological data. *Ecology* 80, 15–34 (1999).

**Figures**
Figure 1

Population-level patterns in heat tolerance. **a**, Map of studies included in our dataset. Points are colored by ecosystem. The marginal histogram shows the latitudinal distribution of thermal tolerance measurements. **b-e**, latitudinal variation in heat tolerance. Each point represents the heat tolerance of one population and small grey regression lines are for populations within each species, with the global regression for each ecosystem in color. **f**, comparison between inter- and intra-specific slopes (interspecific slope estimates are from Sunday et al. 2019). Point estimates depict mean slope ± standard
Heat tolerance generally decreases with latitude both between and within species. Intra-specific variation in heat tolerance is generally less strong than inter-specific estimates.

**Figure 2**

Pairwise heat tolerance comparisons between populations using effect size estimates based on inverse weighted Hedges’ d (standardized mean differences). A greater effect size indicates greater differentiation in heat tolerance. Positive values refer to a population that has a greater heat tolerance as
compared to the reference population (highest latitude). Scatterplots show the relationships between effect size and scaled distance (a) or maximum temperature difference (b). Regression line slopes are derived from the metaregression model. Point size is inversely related to variance, reflecting the diminished influence of smaller studies in the model. In the forest plot (c), each point represents a pairwise population contrast (arranged along y-axis) and points with greater effect size estimates indicate greater differentiation (along x-axis). Greater effect size estimates are seen in the marine than terrestrial and freshwater realms. Meta-regression model parameter estimates, (d), indicate that distance between populations does not predict effect size estimates. Error bars represent standard error estimates from the meta-regression model. Difference in maximum temperature predicts effect sizes for pooled marine and intertidal taxa, but not freshwater or terrestrial taxa. Slopes different from zero indicate a significant predictor of thermal limit differentiation between populations.

Figure 3

Estimated warming tolerance. a-d, Warming tolerance against latitude. Regression lines for individual studies are shown in grey, with a GAM smoother for all data from each ecosystem in color. e-h, Histograms of slope estimates (change in warming tolerance per degree latitude). Median values are indicated by bars above the main axis.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Sasakietal2021supplementary.docx
• suppdatatable1.csv
• suppdatatable2.csv
• suppdatatable3.csv