Greater local adaptation to temperature in the ocean than on land

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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 realms¹. 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 temperatures². 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 temperatures³. The oceans also exhibit higher climate velocities than on land, particularly in the tropics⁴. 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^{5,6}. Such an assumption may greatly under- or overestimate a species’ susceptibility to climate warming if population thermal limits are locally adapted^{7–10}.

Unchanging thermal tolerance across populations is a form of “niche conservatism”¹¹. 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^{12–14}. 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^{15,16}. In theory, high dispersal and subsequent gene flow would have a homogenizing effect, swamping adaptive differentiation and limiting the potential for local adaptation^{17,18}. However, recent work has challenged this paradigm, suggesting that self-recruitment and high levels of larval and post-settlement selective mortality^{19,20} can result in less-than-predicted dispersal potential¹⁹, which in turn may promote local adaptation in the oceans²¹.

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”^{22,23}. Many terrestrial ectotherms can moderate body temperatures by behaviorally exploiting shade, forests, crevices, or other thermal refugia^{23,24}. Similarly, non-mobile taxa (e.g., plants) may be able to exploit microclimatic variation, relaxing selection for thermal tolerance²⁵. Accordingly, variation in interspecific heat tolerance on land is only weakly associated with latitude and maximum temperature²⁶. However, behavioral thermoregulation is only possible if the environment is thermally heterogeneous²⁷. 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 tolerance²⁸. In support of this prediction, both marine and freshwater taxa have interspecific heat tolerances that decline sharply with increasing latitude^{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^{6,32}.

Results

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 studies²⁶, 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”²⁸.

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 metric³⁴ (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 studies³⁵ and is preferable to unweighted analysis³⁶. 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)³⁷. 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 adaptation²², 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 environments³⁸, 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 tolerance³⁹ 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^{3,39}. Because organisms can adjust to rising or variable thermal environments via phenotypic plasticity (acclimation or hardening)⁴⁰, we applied a correction to heat tolerance values prior to estimating warming tolerances. As in previous analyses of vulnerability to warming³, 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)³². If species level data were unavailable we used ecosystem-specific estimates of acclimation response ratios³². 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 risk²⁷. Further, we cannot account for the effect of co-occurring stressors, which may decrease warming tolerance⁴¹, or how adaptation to future conditions may reduce vulnerability⁴². 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^{21,43,44}. 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 level²⁶, 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 tolerance³² 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 variation⁴⁹. 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

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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) protocol⁵⁰. 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 Intraspecific). 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 plants⁵¹), 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 WebPlotDigitizer⁵². 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.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 studies³⁴. 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^{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 v2.0⁵⁵, 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 CHELSA⁵⁶, which contains 1979-2013 monthly temperature data at 1 km spatial resolution sourced from the ERA-Interim reanalysis⁵⁷. Freshwater-specific climatologies⁵⁸ 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 mechanisms⁵⁹. 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^{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 ΔAIC 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 bias³⁶. 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 factors³². 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:

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

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.

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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

error. 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

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- [Sasaki et al 2021 supplementary.docx](#)

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