

Global analysis of thermal tolerance and latitude in ectotherms

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A tenet of macroecology is that physiological processes of organisms are linked to large-scale geographical patterns in environmental conditions. Species at higher latitudes experience greater seasonal temperature variation and are consequently predicted to withstand greater temperature extremes. We tested for relationships between breadths of thermal tolerance in ectothermic animals and the latitude of specimen location using all available data, while accounting for habitat, hemisphere, methodological differences and taxonomic affinity. We found that thermal tolerance breadths generally increase with latitude, and do so at a greater rate in the Northern Hemisphere. In terrestrial ectotherms, upper thermal limits vary little while lower thermal limits decrease with latitude. By contrast, marine species display a coherent poleward decrease in both upper and lower thermal limits. Our findings provide comprehensive global support for hypotheses generated from studies at smaller taxonomic subsets and geographical scales. Our results further indicate differences between terrestrial and marine ectotherms in how thermal physiology varies with latitude that may relate to the degree of temperature variability experienced on land and in the ocean.

Keywords: macroecology; macrophysiology; thermal tolerance breadth; latitude; thermal niche; climate variability hypothesis

1. INTRODUCTION

Latitudinal changes in temperature and other associated climatic variables are marked, both on land and in the surface waters of the ocean, and have been invoked to explain global patterns in species distribution and diversity [1–4]. Broadly speaking, seasonal temperature variation is relatively low at the equator and increases with latitude (figure 1). Seasonal temperature variation is thought to have an adaptive influence on the range of temperatures physiologically tolerated by species occupying different latitudes. This principle has led to a large body of work seeking to understand how thermal tolerance of individual species varies with latitudinal location. Nearer to the equator, where seasonal variation is minimal, breadths of thermal tolerance are expected to be relatively narrow compared with species at higher latitudes, where seasonal variation is more extreme. Such links between physiology and large-scale geography are the focus of the emerging field of macrophysiology [1,5,6], and have received renewed attention for their implications in understanding species' relative vulnerabilities to anthropogenic climate change [7–10].

Taken together, empirical evidence that species' thermal tolerance breadths (TTB) increase with latitude are persuasive [11–17], but the generality of support is unclear, largely owing to a number of analytical challenges widely recognized in the macroecological literature [1,18]. We address five of these here, and

show how they may be overcome with the use of larger datasets and modern statistical techniques to simultaneously account for multiple sources of variation. First, studies often focus on patterns within a continent, raising questions as to whether an emergent pattern is the result of the specific geometry, climatology and biogeographical history of separate land masses. A notable exception is the global synthesis of thermal tolerances in insects by Addo-Bediako *et al.* [11], in which upper and lower thermal limits were compiled across a broad range of latitudes such that Northern and Southern Hemispheres could be compared (though a formal test could not be made; see below). Second, taxonomic scope is often restricted, with the most broad-scale comparative studies limited to the level of class (Insecta [11]; Actinopterygii [12]; Amphibia [16]). While restricting taxonomic scope allows for comparison of species that are similar in body types and physiology, this approach represents a missed opportunity to test for differences among taxonomic groups and, as a consequence, between terrestrial and marine species (figure 2). Third, upper and lower thermal tolerance data are not always sampled from the same species, leaving two datasets that can be compared only by latitudinal location. In these cases, latitude becomes the unit by which thermal tolerance range is studied, rather than species (e.g. [11,12]; but see [14,16,17]), which weakens the strength of inference about species' thermal tolerance breadths. Fourth, some broad-scale studies do not account for phylogenetic or taxonomic non-independence among species [11,12,17], calling into question the degree to which the macroecological pattern may be an artefact of the taxonomically non-random species subset available for analysis

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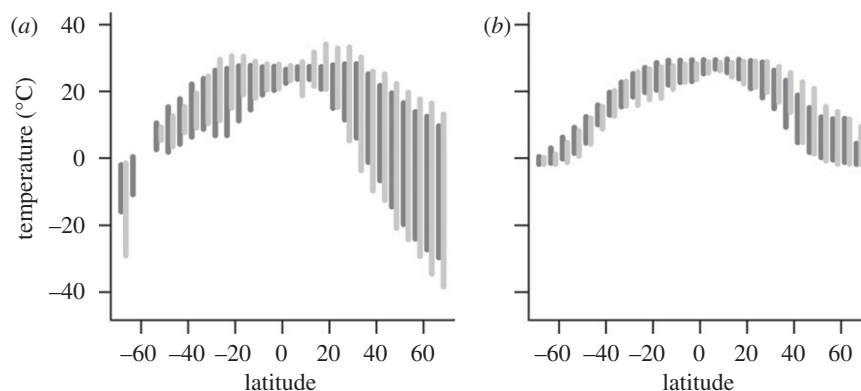


Figure 1. Range of surface temperatures for (a) land and (b) sea. Bars indicate the inner 95% quantile of mean monthly temperatures from long-term climatologies, sampled over all longitudes, on a $5^{\circ} \times 5^{\circ}$ grid basis (land: 1961–1990 [26]; sea: 1960–1989 [27]). (a) Data from New World (North and South America, and adjacent polar regions) and Old World (other continents and adjacent polar regions) land areas are shown separately (dark and light grey bars, respectively). Data from the Pacific Ocean (and adjacent Southern Ocean and polar waters) and combined Atlantic and Indian Oceans (and adjacent Southern Ocean and polar waters) are shown separately (dark and light grey bars, respectively).

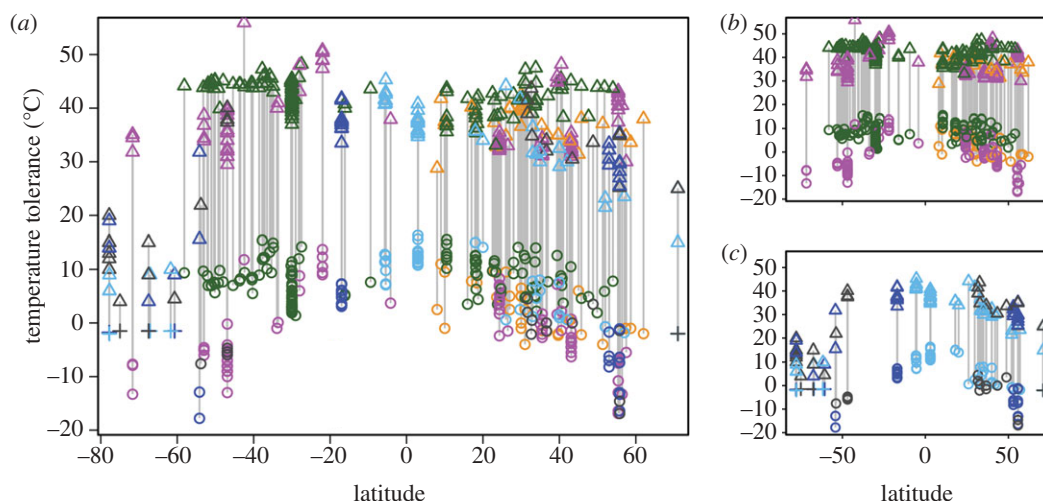


Figure 2. Thermal tolerance limits of ectotherms (a) by taxonomic group, and for (b) terrestrial and (c) marine species. Grey lines link paired upper (triangles) and lower (circles) thermal tolerance limits of species by collection location, corrected for altitude (see text). Crosses indicate cold tolerances estimated by the freezing point of sea water. Southern latitudes are represented by negative x -axis values. Yellow, amphibian; green, reptile; pink, terrestrial arthropod; navy blue, mollusc; sky blue, fish; black, marine arthropod.

at any given latitudinal band [19]. Fifth, the numerous methodologies used for measuring and defining thermal physiological limits appear to constrain comparative analysis. Thermal history, such as season of collection or temperature acclimation prior to experiments, has known effects on temperature tolerance estimates [20,21]. In addition, studies differ in the tolerance metric selected (e.g. lethal versus sublethal endpoints) and the rate at which temperature is changed (e.g. static versus dynamic techniques [21,22]) to the extent that some researchers are reluctant to make comparisons between studies [22]. While these different methods of estimating thermal tolerance introduce variability, this is likely to be small compared with large-scale patterns across species, and can be controlled for statistically in order to quantify the strength and the direction of macrophysiological relationships.

There is considerable variation in the degree to which local climate varies between land and sea, and between

hemispheres, which provides opportunities for testing the role of climate variability in patterns of TTB [23]. At a broad scale, seasonal temperature variability is dampened in marine habitats compared with terrestrial habitats, and seasonal variability in the sea is remarkably stable at polar latitudes (figure 1). Likewise, landmasses in the Southern Hemisphere experience a relatively ocean-buffered climate because they are smaller in size when compared with landmasses in the Northern Hemisphere ([2,11,24]; figure 1). TTBs of terrestrial insects appear to reflect this difference between hemispheres [11], though the extent to which this pattern extends to other taxa is unknown. Oxygen limitation and ventilation capacities of water- and air-breathing species are known to differ [25], but explicit comparisons between marine and terrestrial thermal limits are rare.

Here, we test predictions about TTB and latitude using all available paired thermal tolerance estimates of metazoan ectotherms from marine and terrestrial

habitats, while accounting for additional explanatory variables. We first explore the relationship between TTB and latitude of collection, and next examine the extent to which upper and lower thermal limits vary independently with latitude. We use a linear mixed-effects modelling approach to investigate differences between marine and terrestrial species, and between the Northern and Southern Hemispheres, while accounting for the effects of study methodology and taxonomic affinity. By comparing species from different habitats and hemispheres, we simultaneously test specific hypotheses pertaining to the dampened seasonality in marine habitats [23], and the greater maritime influence on terrestrial habitats in the Southern Hemisphere [2,11,24].

2. MATERIAL AND METHODS

Two common metrics of upper and lower thermal tolerance are: (i) lethal limits (upper lethal temperature, ULTx; lower lethal temperature, LLTx), defined as temperatures at which a predefined percentage (x) of individuals die after a fixed duration of exposure (also called ‘static’ method; reviewed by Lutterschmidt & Hutchison [22]), and (ii) critical temperature limits (CT_{max} and CT_{min}), defined as the mean temperature at which individuals lose some essential motor function corresponding to a slow increase or decrease in body temperature, also termed points of ‘ecological death’ [28] (also called ‘dynamic’ method; see [22]). The endpoint is an observable loss of coordination or motor response (e.g. righting response, motor response to a stimulus and maintenance of upright body orientation), or as the onset of muscle spasms [22].

We searched ISI Web of Science for studies on ectothermic animals that estimated both upper and lower thermal limits for a given species. We included both critical and lethal limits, as defined above. Studies in which specimens were collected from laboratory culture, agriculture, aquaculture or regions outside their native range were discarded to avoid the confounding issues of unnatural selective history.

Thermal tolerance can be modified by acclimation and varies seasonally [20]. For studies that used laboratory-based acclimation, or when collections and experiments were undertaken at different times of the year, the lower thermal limit from the lowest acclimation temperature and the upper thermal limit from the highest acclimation temperature were taken to more closely reflect species’ potential adaptation to inter-annual temperature variation (hereafter ‘acclimation’ studies). Studies that did not include multiple acclimation temperatures prior to measuring upper and lower limits were categorized as ‘no acclimation’ studies.

Where separate studies of the same species were encountered ($n = 19$ cases), a single study was selected that most closely met the following criteria: it either (i) documented thermal tolerance temperatures in both summer and winter, (ii) included the greatest range of high and low acclimation temperatures, or (iii) if it was a ‘no acclimation’ study, it had the largest sample size.

Latitude of collection for each species was noted and corrected when the elevation of collection was greater than 600 m. Anurans and lizards were given a correction factor of an absolute increase of 1.75° latitude for every 200 m of elevation as derived by Cruz *et al.* [14] from South American

lizards. A correction factor of 4° latitude for every 305 m in latitude was applied to insects [29]. Results were qualitatively robust to these correction factors (see electronic supplementary material, table S1 and figure S1).

(a) Data analysis

We used a mixed-effects modelling approach in three separate analyses to test how thermal envelope breadth, and upper and lower limits of thermal tolerance relate to latitude of collection. For each analysis, we began with a full model based on *a priori* hypotheses for inclusion of terms and higher-order interactions, and identified the minimum adequate model by step-wise removal of non-significant terms using likelihood ratio tests [30] (see electronic supplementary material, table S2). Linear model assumptions were met by including and competing variance structures according to Zuur *et al.* [30], and checking normalized residual plots for homogeneity of variance. Marine intertidal and subtidal species were grouped together as a single habitat category because of low levels of latitudinal and taxonomic sampling within each group.

A phylogeny was not available for the resulting diverse dataset that spanned 11 animal classes within three phyla, so we accounted for shared evolutionary history using taxonomy, which is preferable to ignoring evolutionary history entirely [31,32]. To account for taxonomic non-independence, therefore, we included a nested grouping structure based on taxonomy (Phylum, Class, Order, Family and Genus; Tax_{P/C/O/F/G}) as a random effect on the intercept [33]. In all cases, the mixed-effects model including taxonomic signal had a significantly greater log-likelihood score (see electronic supplementary material, table S1) than the linear model that excluded taxonomy. All analyses were done using the nLME package in R v. 2.8.1 [34].

The freezing of sea water at -2°C introduces a hard boundary to cold tolerance that reflects a physical (rather than physiological) limit and generates a nonlinear pattern in thermal tolerance at highest latitudes. While we report data for polar marine species, we restrict our statistical analyses to the linear portion of the dataset by excluding data above 60° absolute latitude ($n = 24$ species).

(b) Thermal envelopes and latitude

The following fixed effects were included in the full model of TTB variation: absolute latitude of collection (corrected for altitude; Lat_{col}), habitat (marine/terrestrial; Hab), hemisphere (Hem), acclimation history (acclimated or not; Acc) and thermal limit metric (lethal or critical; Met). A third-order interaction between hemisphere, habitat and latitude was included to test for a difference in patterns among terrestrial species in the Northern and Southern Hemispheres. Any significant interaction between habitat or hemisphere with latitude was explored post hoc, to determine if 95 per cent confidence intervals (CIs) of slopes within habitats and hemispheres overlapped with zero.

$$\text{TTB} \sim (\text{Lat}_{\text{col}} \times \text{Hab} \times \text{Hem}) + \text{Acc} + \text{Met} + \text{Tax}_{\text{P/C/O/F/G}}$$

(c) Upper and lower thermal limits with latitude

Variation in upper (T_{max}) and lower thermal limits (T_{min}) was explored separately with the following predictive variables in the full model: latitude of collection (corrected for altitude), habitat, acclimation history and thermal limit

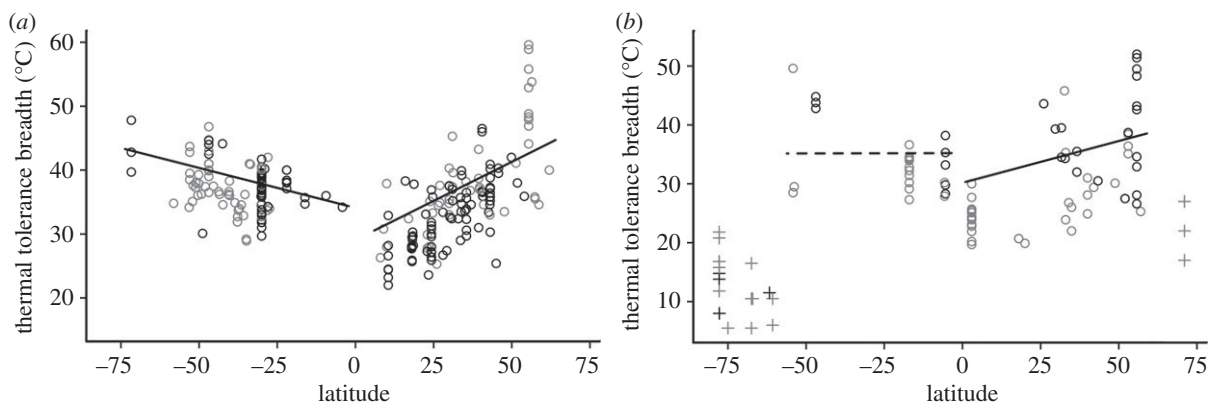


Figure 3. Thermal tolerance breadth (TTB) by latitude of specimen collection for (a) terrestrial and (b) marine species. Points indicate studies in which upper and lower thermal limits were measured after acclimation to different temperatures (black; $n = 129$) or to the same temperature (grey; $n = 188$). Crosses indicate TTBs bounded by the freezing point of sea water. Best-fit regression lines for each habitat and hemisphere from the linear mixed-effects model, accounting for acclimation history and taxonomic affinity (table 1) are shown; solid lines represent relationships significantly different from zero. Latitudes of collection are corrected for altitude (see text).

metric. An interaction between habitat and latitude was included to test for differences in the relationship among habitats.

$$T_{\max} \sim (\text{Lat}_{\text{col}} \times \text{Hab}) + \text{Acc} + \text{Met} + \text{Tax}_{\text{P/C/O/F/G}}$$

$$\text{and } T_{\min} \sim (\text{Lat}_{\text{col}} \times \text{Hab}) + \text{Acc} + \text{Met} + \text{Tax}_{\text{P/C/O/F/G}}$$

3. RESULTS

We obtained TTB data for 341 species (see electronic supplementary material, appendix S1). The major animal groups sampled in each system were as follows. Terrestrial: reptiles ($n = 128$), arthropods (81) and amphibians (30); marine: fish (46), molluscs (28) and arthropods (28). There were more terrestrial species (239) than marine (102), though marine species had a wider taxonomic coverage. The spread of samples across latitudes from 60° S to 60° N was relatively even, although most taxonomic groups were better represented in the Northern Hemisphere (see electronic supplementary material, figure S1 for breakdown by major animal group). Marine species above 60° in absolute latitude were mainly collected from Southern seas.

In terrestrial species, TTB increased overall with latitude and did so at a greater rate in the Northern Hemisphere compared with the Southern Hemisphere (figure 3; table 1). By contrast, in marine species, TTB increased with latitude up to 60° , but decreased near the poles, where cold tolerance was assumed to be equal to the freezing point of sea water (figure 3). Even when these polar species were excluded from the dataset, the rate of increase remained lower in marine when compared with terrestrial species (figure 3; table 1). Examining the covariates associated with methodology, we found that TTBs were approximately 2.0°C broader in studies that acclimated animals to different temperatures (warm and cold, respectively) prior to testing their upper and lower tolerance limits, compared with studies that measured both limits using specimens acclimated to the same temperature (see electronic supplementary material, figure S2 for a breakdown of tolerance limit methodologies). Thermal breadth did not differ significantly between studies that used lethal versus critical thermal metrics (although

see results below for the effect of thermal tolerance metric on upper and lower limits separately; see also electronic supplementary material, figure S2). Variation within taxonomic groups was greatest at the levels of order followed by class (table 1; see electronic supplementary material, figure S3 for patterns across major animal groups). Variation of TTBs increased somewhat with latitude in both hemispheres, and was more pronounced in the Northern Hemisphere (figure 3). We tested this explicitly by incorporating a variance structure that allowed the residual variation to increase as a function of the latitude, which significantly improved model fit (delta AIC = 24.4, likelihood ratio₂ = 28.4, $p < 0.001$).

Considering upper and lower thermal limits separately revealed that upper thermal limits decreased little, though significantly, with latitude in terrestrial species (approx. 0.3°C decrease for every 10° of latitude; table 1; figure 4), and decreased at a greater rate in marine species (approx. 1.7°C for every 10° of latitude; table 1; figure 4). Lower thermal limits also decreased towards the poles, and did so coherently in both marine and terrestrial habitats when polar marine species were excluded (approx. 2.4°C per 10° of latitude; table 1; figure 4). In terrestrial species, the rate of decline was an order of magnitude lower in upper versus lower thermal limits (slope $\pm 95\%$ CI, upper: -0.03 ± 0.02 ; lower: -0.24 ± 0.04). However, in marine species, the rates of decline in the two tolerance limits with latitude were not significantly different from each other as indicated by the overlap in confidence intervals (slope $\pm 95\%$ CI, upper: -0.17 ± 0.08 ; lower: -0.30 ± 0.07). Upper and lower thermal limits were more extreme among studies that used differential acclimation, significantly so for lower thermal limits (see table 1 and electronic supplementary material, figure S2). Both lower and upper limits were lower among studies that used lethal versus critical thermal limits (more extreme lower limits, but less extreme upper limits; table 1 and electronic supplementary material, figure S2). While variance in cold tolerance appears to increase with latitude in both hemispheres and habitats (figure 2), this pattern was not statistically supported (model fit was not improved when variance was allowed

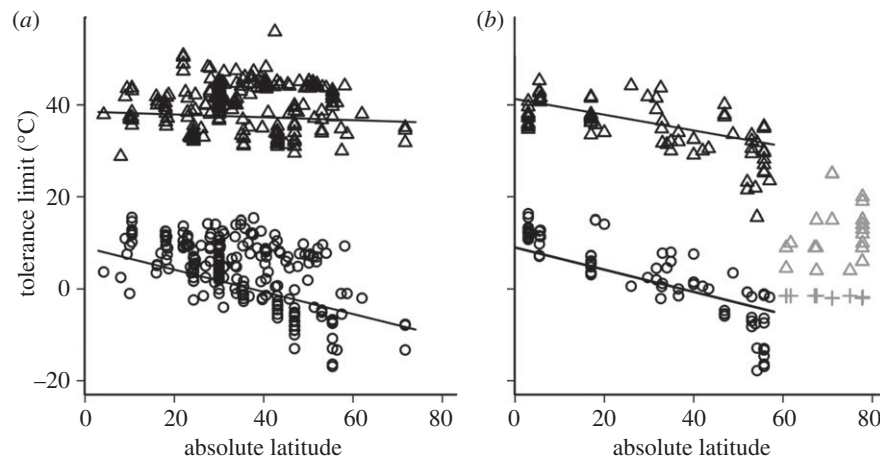


Figure 4. Upper and lower thermal tolerance limits by absolute latitude of collection, for (a) terrestrial and (b) marine species. Points indicate upper (triangles) and lower (circles) tolerance limits. Data not included in the linear model are in grey, crosses indicate cold limits estimated by the freezing point of sea water. Best-fit regression lines from linear mixed-effects model are shown. Latitudes of collection are corrected for altitude (see text).

Table 1. Model summaries. Fixed effects: treatment contrast coefficients and diagnostics (*t*- and *p*-values) indicate the effect of each parameter level on the reference level, denoted as reference. The reference levels for each term are: latitude, zero; habitat, terrestrial; hemisphere, northern; acclimation, true; thermal limit metric, critical (see text for definition of variables). Random effects: phylum (P), class (C), order (O), family (F) and genus (G).

| fixed effects | | | | | | random effects | |
|------------------------------------|-------------|-------|------|-----------------|-----------------|-------------------------------|-----------------------|
| effect | effect type | coef. | s.e. | <i>t</i> -value | <i>p</i> -value | taxon level (no. observation) | within-group variance |
| (a) thermal tolerance breadth | | | | | | | |
| reference | intercept | 30.1 | 2.3 | 13 | 0.000 | P (3) | 4.8 |
| habitat (marine) | intercept | 1.1 | 2.7 | 0.4 | 0.7 | C/P (11) | 5.5 |
| hemisphere (S) | intercept | 5.0 | 1.4 | 5.1 | 0.000 | O/C/P (33) | 6.2 |
| acclimation history (no acc.) | intercept | -2.0 | 0.6 | -3.2 | 0.002 | F/O/C/P (95) | 5.0 |
| latitude | slope | 0.24 | 0.03 | 8.3 | 0.000 | G/F/O/C/P (162) | 1.8 |
| latitude × habitat (marine) | slope | -0.13 | 0.05 | -2.5 | 0.013 | residual | 1.1 |
| latitude × hemisphere (S) | slope | -0.12 | 0.03 | -3.7 | 0.000 | | |
| (b) upper thermal tolerance | | | | | | | |
| reference | intercept | 40.4 | 1.3 | 32.1 | 0.000 | P (3) | 0.0 |
| habitat (marine) | intercept | 2.8 | 2.2 | 1.2 | 0.22 | C/P (11) | 3.1 |
| thermal limit metric (lethal lim.) | intercept | -3.7 | 0.7 | -5.0 | 0.00 | O/C/P (33) | 5.0 |
| latitude | slope | -0.03 | 0.01 | -2.6 | 0.01 | F/O/C/P (95) | 7.2 |
| latitude × habitat (m) | slope | -0.14 | 0.04 | -3.2 | 0.002 | G/F/O/C/P (162) | 3.6 |
| | | | | | | residual | 5.1 |
| (c) lower thermal tolerance | | | | | | | |
| reference | intercept | 9.0 | 1.9 | 4.9 | 0.000 | P (3) | 7.0 |
| acclimation history (no acc.) | intercept | 1.9 | 0.5 | 3.4 | 0.001 | C/P (11) | 0.9 |
| thermal limit metric (lethal lim.) | intercept | -1.87 | 0.79 | -2.4 | 0.02 | O/C/P (33) | 1.9 |
| latitude | slope | -0.24 | 0.02 | -13.7 | 0.000 | F/O/C/P (95) | 8.7 |
| | | | | | | G/F/O/C/P (162) | 2.0 |
| | | | | | | residual | 10.0 |

to increase with latitude; delta AIC = -3.9, likelihood ratio₂ = 1.92, *p* = 0.165), and normalized residual variance did not increase with latitude in the final fitted model.

4. DISCUSSION

Our analysis represents the widest coverage of latitudes, taxonomic groups and habitats in a single analysis of thermal tolerance breadth (TTB) and latitude conducted to date. We provide comprehensive support for the view that TTBs increase with latitude among

ectothermic animals, reinforcing previous studies conducted at smaller taxonomic and geographical scales [11–17]. As expected, the rate of increase is greater in habitats and hemispheres where climate variability is more pronounced. Our results extend previously observed macroecological patterns to a global scale, implicate mechanisms driving habitat-related differences in upper thermal tolerance variation, and inform our understanding of relative vulnerabilities of ectothermic animals under anthropogenic climate change. We conclude with some caveats and suggestions for future research.

The results of this study build upon previous work showing that TTBs generally increase with latitude [11–17], lending support for this pattern as a macrophysiological rule [1], but highlight that latitudinal trends in thermal tolerance are less pronounced and more complex in marine species [12]. Overall, the observed relationships between TTB with latitude are in keeping with expectations based on differences in climate variability between land and sea [23], and between the two hemispheres [2,11,35]. On land, temperature variability increases with latitude at a greater rate in the Northern versus the Southern Hemisphere, which is mirrored by a greater rate of increase in TTBs with latitude in terrestrial species from the Northern compared with Southern Hemisphere [2,11,35]. The lower rate of increase in TTB with latitude in marine species, as well as the narrowing of thermal limits towards the poles, is likewise consistent with the decrease in seasonal temperature variation with latitude (figure 1 [12,23]). The difference in the thermal tolerances among marine species between the hemispheres may be attributable to slightly greater temperature variability in the Northern Hemisphere (figure 1), although the power to detect an increase in TTB with latitude was low because data from the Southern Hemisphere are sparse (figures 2 and 3).

Our synthesis provides comprehensive support for previous observations in terrestrial species that lower thermal limits decline at a greater rate towards the poles than upper thermal limits [2,11,15–17]. However, the upper and lower thermal limits of marine species declined at nearly the same rate towards the poles. Thus, our data indicate that relatively rapid poleward declines in cold tolerance can only be considered a rule (as suggested by Gaston [1]) on land, and suggest that caution be used when assuming that macroecological patterns can be transferred across systems [36]. We identify three possible mechanisms for the near-invariance of upper thermal tolerances with latitude in terrestrial species, and highlight possible driving mechanisms that are consistent with differences between marine and terrestrial climate patterns. First, thermal limits may accurately reflect the range of temperatures experienced by ectothermic animals at each latitude. Summer temperatures vary less over latitude than winter temperatures (figure 1 [2,35]), and extreme high-temperature events, despite being infrequent or short-lived, may be particularly important in shaping adaptive physiology at all latitudes [37]. The observed difference in the relationship between upper thermal tolerance and latitude in marine and terrestrial species is consistent with seasonal temperature extremes as an underlying mechanism: mean summer temperatures decline with latitude at a greater rate over sea than over land [38], and rare high-temperature events are likely to be more buffered by the greater heat capacity of water. Second, thermoregulatory behaviour by ectotherms may decouple body temperatures from environmental temperatures, such that maximum body temperatures are more constant across latitudes [15,39,40]. For instance, the upper thermal tolerances of lizards *increase* with latitude, possibly because species at higher latitudes bask more [15]. In addition, terrestrial systems presumably offer a greater range of microhabitat temperatures than ocean habitats. This thermal variability can be exploited behaviourally by ectothermic animals to maintain body

temperature within a preferred window of temperatures that is narrower than environmental temperatures. Thus, finding that upper temperature limits do not vary greatly across latitude in terrestrial ectotherms is consistent with thermoregulatory behaviour as a driving mechanism. Finally, upper thermal tolerance limits may be evolutionarily conserved among terrestrial ectotherms, resulting in heat tolerance thresholds at higher latitudes that exceed survival requirements. Extant ranges of organisms were heavily shaped by Quaternary climate shifts [41], and it is probable that adaptation to cold tolerance set ‘entry rules’ for range expansion towards the poles from equatorial refugia. If heat tolerance is not energetically costly to maintain, invariance in heat tolerance across latitudes may represent a latent artefact of ancestral thermal regimes, in which all extant species tolerated similar high temperatures, as opposed to adaptation to current experienced temperatures.

Though the above mechanisms may not be mutually exclusive, teasing out a mechanistic explanation for the invariance in heat tolerance across latitude in terrestrial ectotherms is critical for generalizing about latitudinal variation in survival vulnerabilities under climate warming [6]. If thermal tolerance accurately reflects the warmest temperatures experienced by a species, increases in environmental temperatures may similarly challenge animals across a range of latitudes. By contrast, if behaviours such as basking, habitat choice and timing of activity are responsible for the low variation in upper thermal tolerance, the ability to modify these behaviours should be an important predictor of climate warming vulnerability [35,40]. Finally, if the low variation in upper thermal tolerance is owing to evolutionary conservatism or latency, temperate species may have upper thermal limits that surpass their maximum encountered temperatures and may be at an intrinsic advantage in terms of acute heat survival (i.e. greater intrinsic ‘warming tolerance’ [7,15]). Further analyses of temperature variation and experienced body temperatures with latitude will help to distinguish among these important mechanisms, which may vary on a species-by-species basis.

We identify three caveats to our findings, which can serve to guide future research. First is the grouping of intertidal and subtidal species in the ‘marine’ category. Depending upon the height occupied in the intertidal, and thus exposure to air, high intertidal species may experience temperature variability nearing that of strictly terrestrial systems. In addition, many intertidal species can be tested for cold tolerance out of water, and therefore at temperatures below -2°C . However, the difference between intertidal and subtidal species is most pronounced at high latitudes, and trends in their TTBs were similar within the bounds of our linear analyses (see electronic supplementary material, figure S4). In addition, intercept differences between intertidal and subtidal habitats were accounted for inadvertently by the inclusion of taxonomy in our analyses, since all marine molluscs and arthropods were sampled from intertidal locations, while marine fish (92%) were primarily subtidal (see electronic supplementary material, figure S1). Second, while we were able to account statistically for some differences in methodologies, additional factors may have contributed to

inter-study variability. For example, the rate of temperature increase selected during critical limit studies, the sub-lethal endpoint used to define critical limits (e.g. muscles spasms and loss of motor function) and the extent of the difference between acclimation temperatures for upper and lower thermal limits all varied among studies. Interestingly, there was not always a clear difference between the methods for which we were able to account. We found no significant difference between TTBs using lethal versus critical limits, for example. While this was a surprise, the two metrics measure different aspects of the physiological response: body temperatures in lethal-limit studies are typically ramped up or down at a faster rate (near-instant) than in critical-limit studies (approx. $1^{\circ}\text{C min}^{-1}$), and organisms need to tolerate longer periods of exposure (e.g. 24 h versus 1 min; reviewed in [22]). Critical temperature limits may be either less [42] or more extreme [3] than lethal limits, and this relationship can change depending on the acclimation temperature [43]. Nevertheless, standardization of both acclimation and thermal limit methodologies will be helpful for future comparative analyses. Finally, while accounting for taxonomic affinity can help account for common evolutionary histories of species [31,32], a molecular phylogeny may better account for common evolutionary histories, as soon as such a large-scale phylogeny becomes available.

Macroecology encompasses some of the most fundamental processes underlying the abundance, distribution and diversity of life on Earth [44]. However, the search for generalities in these patterns has been fraught with limited data quality and quantity, and a preponderance of univariate hypothesis testing [45,46]. We show how modern statistical methods can be used to discriminate among multiple hypotheses while accounting for several covariates. The search for general ecological laws and rules of life, particularly those relating to thermal performance, has become ever more important in the era of rapid anthropogenic climate change. We show clear differences between marine and terrestrial habitats in how heat tolerance varies with latitude, and present three alternative mechanisms with differing consequences for relative species vulnerabilities under climate warming.

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