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High thermal variation in maximum temperatures invert Brett's heat-invariant rule at fine spatial scales

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Abstract

Discovering how species' thermal limits evolve and vary spatially is crucial for predicting their vulnerability to ongoing environmental warming. Current evidence indicates that heat tolerance is less spatially variable than cold tolerance among species, presenting a major concern for organismal vulnerability in a rapidly warming world. This asymmetry in thermal limits has been supported by large-scale geographic studies, across latitudinal and elevational gradients (known as Brett's heat-invariant rule). Yet, how critical limits vary across finer spatial scales (e.g., across microenvironments) is less understood. Here, we show that minimum temperatures are more variable than maximum temperatures at large geographic scales (across latitude/elevation) but are less variable at local scales (within sites), in turn guiding spatial asymmetries in thermal tolerances. Using thermal tolerance measurements from amphibians, insects, and reptiles, we confirm the invariance of heat tolerance at large spatial scales and also find more variable heat than cold tolerances at local scales (an inverted Brett's heat-invariant rule at fine spatial scales). Our results suggest that regional- or global-level studies will likely obscure fine-scale structuring in thermal habitats and corresponding patterns of local heat tolerance adaptation. We emphasize that inferences based on broadscale geographic patterns obscure fine-scale variation in thermal physiology. For instance, a genetic basis for fine-scale variation in thermal physiology may reshuffle spatial and phylogenetic patterns of vulnerability.

KEYWORDS

Brett's heat-invariant rule; elevation; latitude; local scale; macrophysiology; microclimate; spatial scales, amphibians, reptiles, insects; thermal tolerance limits

INTRODUCTION

Physiological limits, like heat and cold tolerance (CT_{\max} and CT_{\min}), dictate the range of environmental conditions

suitable for vital activity; correspondingly, these features structure how organisms are distributed across space and time (Araújo et al., 2013; Calosi et al., 2010; Sunday et al., 2011, 2019). As such, understanding variation in

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critical thermal limits across different geographical scales (and the mechanisms underpinning those patterns) is a central topic in biogeography, macroecology, and global change biology (e.g., Chown & Gaston, 2016; Deutsch et al., 2008; Gaston et al., 2009; Sunday et al., 2019). At broad geographic scales (i.e., across latitude and elevation), heat tolerance is less spatially variable than cold tolerance, a result echoed across both terrestrial and freshwater systems at both interspecific (Araújo et al., 2013; Bozinovic et al., 2014; Sunday et al., 2019; but see Sunday et al., 2011, 2019 for marine systems) and intraspecific levels (Sasaki et al., 2022). This biogeographic asymmetry in physiological tolerance, more formally recognized as Brett's rule or cold-tolerance asymmetry (Brett, 1956; Gaston et al., 2009), arises from the fact that maximum temperatures decline less sharply than minimum temperatures with elevation and latitude; the shallower shifts in maximum temperature facilitate behavioral buffering for upper physiological limits through thermoregulation (a phenomenon known as the Bogert effect; Bogert, 1949; Huey et al., 2003; Muñoz, 2022). Over broad geographic distances, such asymmetric behavioral buffering favors greater clinal variation in cold tolerance than in heat tolerance (Buckley et al., 2013; Muñoz, 2022; Sunday et al., 2011). As global warming marches on, limited acclimation responses and low evolutionary potential for adaptation in upper physiological limits present a proximate concern for species' resilience (Araújo et al., 2013; Bennett et al., 2021; Kellermann, Loeschke, et al., 2012; Qu & Wiens, 2020; Rubalcaba et al., 2023; van Heerwaarden et al., 2016).

Whereas latitudinal and elevational patterns in critical thermal limits have been widely documented (Sunday et al., 2011, 2014, 2019), far less is known about how temperature and physiological tolerance structure locally (but see Bodensteiner et al., 2024; Leahy et al., 2022; Pintanel et al., 2019, 2022; Scheffers, Edwards, et al., 2017). As we explain below, we might expect Brett's rule to invert at local scales; within sites, we expect upper physiological limits to be more variable than lower physiological limits. Central to interpreting Brett's rule is Janzen's (1967) *climate variability hypothesis* (CVH), which predicts a positive relationship between an organism's thermal tolerance breadth and the climatic variability that it experiences (Janzen, 1967; Stevens, 1989, 1992). In its original conception, the CVH postulates that by living in thermally stable environments, tropical species should be more physiologically specialized (i.e., narrower tolerance range between CT_{max} and CT_{min}) than counterparts in more thermally seasonal climates with wider temperature ranges, particularly colder winter temperatures (Figure 1A; Ghalambor et al., 2006; Janzen, 1967).

When we apply the principles of the CVH to finer spatial scales, such as *within* a locality, patterns of

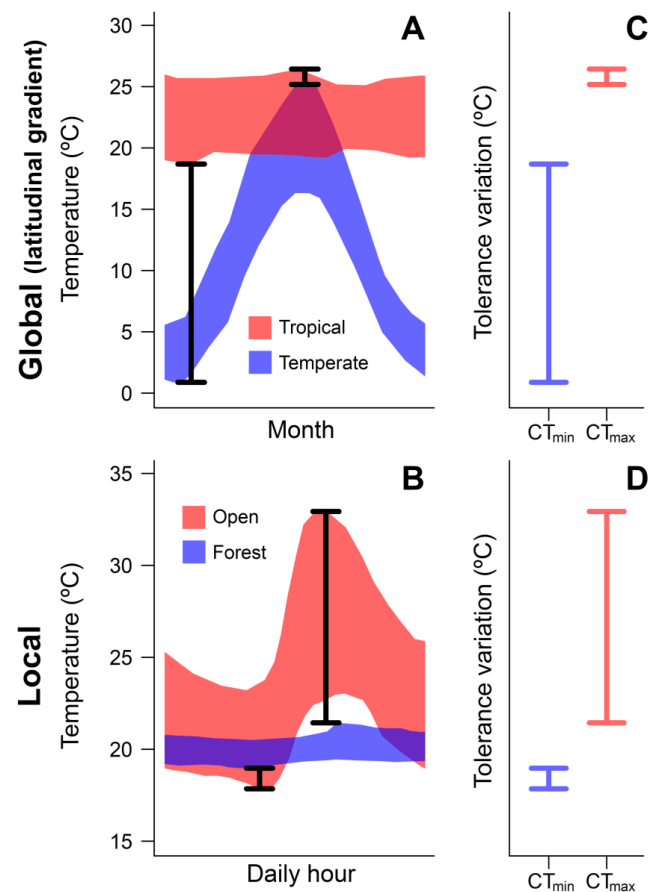


FIGURE 1 Hypothetical variation in environmental temperatures at large (A) and local (B) geographic scales with their predicted species thermal tolerance variation according to each scale (C, D). Black brackets in the temperature variation (A, B) indicate the variation in minimum (left) and maximum (right) extreme temperatures as a function of each location. Blue and red brackets on the right represent the equivalent variation in CT_{min} and CT_{max} we expect to find in the thermal tolerance variation according to each geographical scale. (A, B) Environmental temperature is plotted against month, from January to December (A), and against daily hour, from midnight to midnight (B). Note that within site, thermal patterns are consistent when sampled over a calendar year (Appendix S1: Figure S1).

environmental and physiological variation might be predicted to invert. Whereas shifts in minimum (rather than maximum) temperatures largely shape thermal variation across latitudinal and elevational scales (Janzen, 1967), at local scales, thermal variation mainly reflects fine-scale heterogeneity in maximum (rather than minimum) temperatures in daytime environments, for example, between the exposed forest edge and the sheltered forest interior (Figure 1B; Appendix S1: Figure S1). Correspondingly, species restricted to canopy-covered areas should be more physiologically specialized (i.e., have a narrower thermal breadth) than species found in

more thermally heterogeneous, open or edge habitats (Figure 1B; Bota-Sierra et al., 2022; Muñoz et al., 2016; Muñoz & Bodensteiner, 2019; Pintanel et al., 2019). Putting these pieces together, we can predict contrasting asymmetries in thermal tolerance variability that should show a scale-dependent relationship (Guo et al., 2023). Specifically, we hypothesize that at local scales, greater variation in maximum environmental temperatures will promote higher variation in upper thermal tolerances (“heat-tolerance asymmetry” sensu Herrando-Pérez et al., 2020; Pintanel et al., 2019; “inverted Brett’s heat-invariant rule,” here). By contrast, across latitude or elevation, steeper shifts in minimum environmental temperatures should promote higher variation in lower thermal tolerances between lineages (“cold-tolerance asymmetry” sensu Herrando-Pérez et al., 2020; “Brett’s heat-invariant rule” Brett, 1956; Gaston et al., 2009) (Figure 1).

We address these ideas in three different groups of terrestrial ectotherms: amphibians, reptiles, and insects. We begin by evaluating how maximum and minimum environmental temperatures structure across local (within-site) and regional (across latitude and elevation) scales. We then created a database of thermal tolerance for 578 species of amphibians, reptiles, and insects that we extracted from the literature (available in Pintanel et al., 2025, on Figshare at <https://doi.org/10.6084/m9.figshare.28845968.v2>). We then assessed geographic patterns in thermal tolerance in order to explore patterns of heat- and cold-tolerance asymmetry across local and broad spatial scales. Our results indicate that Brett’s rule inverts at local scales: heat tolerance is more locally variable than cold tolerance, reflecting steeper within-site variation in maximum than minimum environmental temperatures. Consistent with Brett’s rule, such local variation in heat tolerance is eroded at broad geographic scales, as cold tolerance is much more spatially variable than heat tolerance at regional ranges. Such fine-scale diversity in heat tolerance implies that resilience to warming should vary substantially among sympatric species exposed to environments with contrasting maximum temperatures. Likewise, substantial local variation in heat tolerance weakens regional generalizations about vulnerability to warming, even among close relatives.

MATERIALS AND METHODS

Climatic variation at different spatial scales

First, we evaluated how maximum and minimum environmental temperatures vary across different spatial scales.

We chose microenvironments at a local scale that were as different as possible, as well as microenvironments that were similar, but as distant as possible, in a regional scale. We obtained microenvironmental thermal records from previous studies (Gutiérrez-Pesquera et al., 2016; Pintanel et al., 2022) and from unpublished data. Briefly, these records comprise seven aquatic habitats (two streams and five temporary ponds) and three terrestrial habitats (one open area and two forested areas) from eight locations in Ecuador, as a representative of an aseasonal tropical climate, and two locations in Spain, as a representative of a seasonal temperate climate (see Figure 2). Thermal records were measured in situ using temperature data loggers (HOBO UA-002-64) to obtain continuous records of habitat temperatures (every 15 min) across several months of sampling at each site. For aquatic habitats, data loggers were placed at the bottom of each aquatic habitat. For terrestrial habitats, data loggers were placed within shelters used by frogs during the daytime (underneath rocks, fallen leaves, or logs). We assumed that these locations could be selected by either tadpoles or frogs to avoid extreme heat and cold (Duarte et al., 2012; Pintanel et al., 2019). These datasets were selected to visually show how the thermal microclimate varies between local and large scales in freshwater and terrestrial habitats. Figure 2 depicts examples of variation in maximum and minimum temperatures of aquatic and terrestrial habitats across different spatial scales. Most fine-scale thermal data are collected over relatively short periods (days to weeks); to evaluate whether the same thermal patterns manifest over longer sampling periods, we gathered thermal data for more than a year from Caamaño Park in the Dominican Republic (dates of sampling: 07/07/2022 to 01/10/2023). Specifically, three data loggers were deployed in “open” microsites (5%–15% canopy cover) and three loggers were deployed in “closed” microsites (85%–95% canopy cover). The loggers were placed at randomly chosen heights ranging from 0 to 190 cm, and they sampled temperature every 30 min during this period.

Physiological adaptation

We used the most comprehensive database available with experimentally derived thermal tolerance data (Globtherm; Bennett et al., 2018) and included additional data extracted from literature (available in Pintanel et al., 2025, on Figshare at <https://doi.org/10.6084/m9.figshare.28845968.v2>). Because critical thermal limits are not fully comparable across studies due to methodological differences (e.g., ramping rate, acclimation temperature) (Agudelo-Cantero & Navas, 2019; Sinclair et al., 2016), each

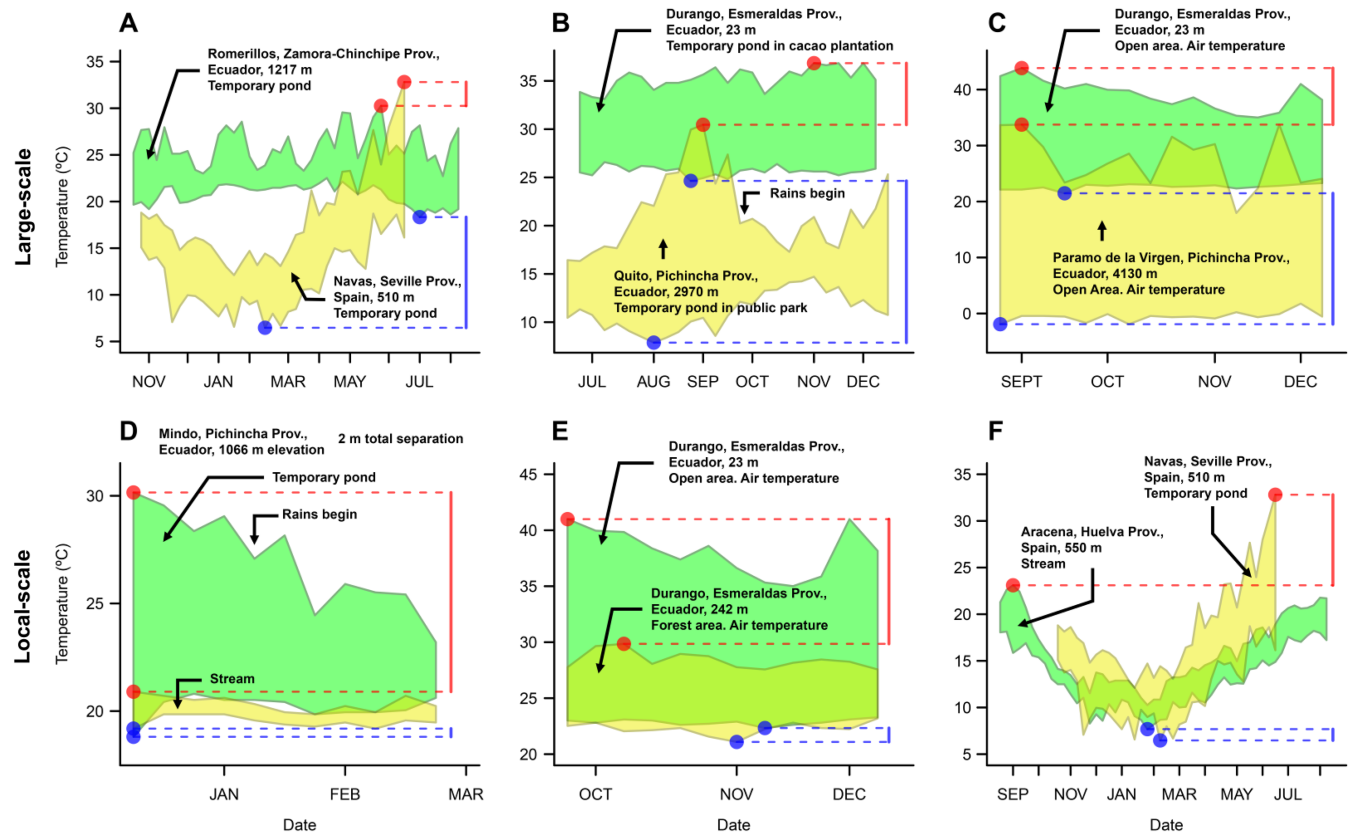


FIGURE 2 Representative temperature regimes comparing three large-scale variation sites (differing latitude or elevation) (upper row panels A–C). (A) Latitude, temperate versus tropical ponds, Romerillos, Ecuador (4.164°S, 78.944°W, 1217 m above sea level [asl]), and Navas del Berrocal, Spain (37.7830°N, 6.0846°W, 510 m asl) (Gutiérrez-Pesquera et al., 2016; Pintanel et al., 2022). (B) Elevation, lowland versus upland tropical ponds, Durango, Ecuador (1.165°N, 78.753°W, 23 m asl), and Quito Metropolitan Park, Ecuador (0.187°S, 78.464°W, 2970 m asl) (Pintanel et al., 2022). (C) Elevation, lowland versus upland open forest, Durango, Ecuador (1.165°N, 78.753°W, 23 m asl), and Páramo de la Virgen (0.322°N, 78.200°W, 4130 m asl) (Pintanel, Tejedo and Merino, unpublished). Three local-scale variation sites (comparing differing habitats) (lower row panels, D–F). (D) Aquatic habitats, tropical pond versus tropical stream, Mindo, Ecuador (0.018°N, 78.808°W, 1066 m asl) (Pintanel et al., 2022). (E) Terrestrial habitats, tropical open versus forest, Durango, Ecuador (1.165°N, 78.753°W, 23 m asl), and Durango, Ecuador (1.034°N, 78.624°W, 242 m asl) (Pintanel, Tejedo, and Merino, unpublished). (F) Aquatic habitats, temperate pond versus stream, Navas del Berrocal, Spain (37.7830°N, 6.0846°W, 510 m asl), and Aracena, Spain (37.9175°N, 6.5690°W, 550 m asl) (Gutiérrez-Pesquera et al., 2016). Each graph figures two regimes. Solid green and yellow lines trace the weekly extreme maximum and minimum temperatures. Red and blue points represent the absolute maximum and minimum temperatures for each regime. Red and blue lines represent the total variation in maximum and minimum temperatures between the two regimes, respectively.

study was analyzed separately (hereafter referred to as different “samples”). In some cases, the lead author(s) included more species in a second study or analyzed CT_{max} and CT_{min} separately in two different studies; therefore, we consolidated such studies into a single “sample” (see data repository). We only used samples that included at least five species with matching metrics of critical thermal limits. For the variance calculations, we used the mean CT_{max} and CT_{min} for each species. For our analysis of thermal tolerance across broad geographic scales, we restricted samples to those studies spanning a range of at least 20 absolute latitudinal degrees (latitudinal range) and/or at least a difference of 2000 m in elevation (elevational range). For local geographic scales, we

used samples limited to a specific region and with an elevation range not exceeding 500 m. While our data provide valuable insights into patterns of thermal variability, we acknowledge that the environmental data used do not correspond to all species collection sites. As most studies in thermal physiology do not include detailed microclimatic data, achieving this correspondence is challenging.

Statistical analysis

To test our hypothesis that local and large scales show different patterns of thermal tolerance asymmetry, we considered a null scenario (i.e., symmetry) and two

alternative scenarios, as proposed by Herrando-Pérez et al. (2020): (1) “cold-tolerance asymmetry” (or heat-invariant hypothesis), in which variation in upper thermal tolerance is lower than variation in lower thermal tolerance ($\sigma^2_{CTmax} < \sigma^2_{CTmin}$), and (2) “heat-tolerance asymmetry,” in which variation in upper thermal tolerance is higher than variation in lower thermal tolerance ($\sigma^2_{CTmax} > \sigma^2_{CTmin}$). We calculated variances (σ^2) using the var function in R, and for each sample, we obtained variance ratios as $\sigma^2_{CTmax}/\sigma^2_{CTmin}$.

To examine whether thermal tolerance variance ratios (i.e., log-transformed variance ratios) differ between local and global scales, while accounting for phylogenetic non-independence, we used a linear mixed-effects model (LMM) using the lme4 package (Bates et al., 2015) in R. Since phylogenetic relatedness may be associated with geographical distance, we incorporated taxa age (in million years) as a continuous variable, ranging from 6 to 692 million years. We extracted the estimates of taxa age from the evolutionary time tree of life available at <http://www.timetree.org> (Hedges et al., 2006), following Bennett et al. (2021). To reduce heteroscedasticity and account for nonlinear relationships, we applied a log-transformation. The model included log-transformed taxa age and geographical scale as fixed effects, with taxon (amphibians, reptiles, and invertebrates) as a random intercept to control for phylogenetic structure, reducing potential biases due to phylogenetic autocorrelation. We inspected the model’s residuals for normality and homoscedasticity using diagnostic plots and assessed the significance of fixed effects through type III ANOVA using the car package (Fox & Weisberg, 2019).

To assess the robustness of our findings and evaluate potential biases introduced by sample selection, we conducted a resampling analysis. We generated 10,000 random subsamples, each consisting of five observations per study that were drawn from the full dataset, and we then fitted the same linear mixed-effects model. We extracted p-values for the fixed effects across all subsamples. To further account for potential pseudoreplication, we repeated the resampling procedure by randomly selecting a single observation per publication in each iteration, ensuring that each study contributed only one data point per resampled dataset. All analyses were conducted in R ver. 4.4.2 (R Core Team, 2024).

RESULTS

The linear mixed-effects model revealed significant effects of both geography and phylogeny on the variance of thermal tolerance. Geographic scale exhibited a strong effect ($\chi^2 = 20.718$, $p < 0.001$), indicating that thermal

tolerance variance ratios differ between local and global scales. Additionally, log-transformed taxa age was also significant ($\chi^2 = 11.178$, $p < 0.001$), suggesting that phylogenetic relatedness contributes to the observed variance (see Appendix S1: Table S1).

The resampling analysis supported these findings, with 9871 out of 10,000 subsamples showing significant effects of geographic scale ($p < 0.05$), despite a completely random selection of species within each sample. A subsequent resampling procedure, restricting each iteration to a single randomly selected observation per publication to minimize pseudoreplication, produced similarly consistent results, with 9683 out of 10,000 subsamples showing significant effects of geographic scale ($p(\text{subsamples}) = 0.0317$), thus further reinforcing the robustness of our findings. Nevertheless, interpretations should acknowledge data limitations.

DISCUSSION

Over the past half century, studies of the “climate variability hypothesis” have almost exclusively centered on the effects of latitudinal (i.e., seasonal) and elevational variation in temperatures on species’ thermal tolerance (Janzen, 1967; Sheldon et al., 2018). Those studies have generally found that thermal breadth (i.e., the range of temperatures between critical thermal limits) is broader in species found at temperate latitudes and high tropical elevations in comparison with tropical latitudes and tropical lowlands, respectively (e.g., Muñoz et al., 2014; Pintanel et al., 2022; Polato et al., 2018). In response to stronger shifts in minimum (rather than maximum) environmental temperatures, the increase in thermal breadths at higher elevations and latitudes can be largely explained by enhanced cold tolerance, as predicted by *Brett’s heat-invariant rule* (Araújo et al., 2013; Chown & Gaston, 2016). Across both latitudinal and elevational gradients, minimum environmental temperatures are more variable than maximum temperatures either because of the extreme minimum winter temperatures at temperate latitudes or because of the higher reduction in minimum than maximum temperatures with elevation (Ghalambor et al., 2006; Gutiérrez-Pesquera et al., 2016; Pintanel et al., 2022, Figure 2B,C).

At local scales, by contrast, proportional variation in the maximum temperature (as compared to minimum temperature) is greater than across latitudinal or elevational gradients (panels Figure 2D–F vs. panels Figure 2A–C). These trends hold true for short- and long-term sampling periods, though the magnitude of the disparity in maximum temperatures is higher in summer than in winter, even in the tropics (Appendix S1:

Figure S1). At finer spatial scales, correspondingly, physiological patterns are inverted: thermal heterogeneity is more strongly driven by variation in maximum daily temperatures (rather than minimum daily temperatures) (Figure 2), and local shifts in thermal tolerance breadth strongly reflect variation in heat tolerance (rather than cold tolerance) (Figure 3). As such, asymmetry in thermal limits across different geographic scales reflects congruent physiological responses to scale-dependent variation in thermal extremes.

Higher variability in upper thermal tolerances at local scales may reflect fine-scale thermal habitat partitioning. Such partitioning may occur, for example, between closed-canopy forest and nearby edge/open habitats (Gunderson et al., 2018; Kaspari et al., 2015; Muñoz et al., 2016; Muñoz & Bodensteiner, 2019; Pintanel et al., 2019), between the more thermally buffered ground and more exposed canopy (Leahy et al., 2022; Scheffers, Edwards, et al., 2017; Scheffers, Shoo, et al., 2017), between ponds in closed-canopy versus open forests

(Duarte et al., 2012; Gutiérrez-Pesquera et al., 2016), or between ponds and stream habitats (Pintanel et al., 2021, 2022). High thermal heterogeneity in maximum temperatures at local scales, in turn, may be an engine promoting microgeographic thermal adaptation (Bodensteiner et al., 2021; Muñoz, 2022). Among sympatric lizard species, for example, those with a behavioral preference for basking in exposed, sunny habitats also exhibited higher heat tolerances than close relatives preferring shade in more closed-canopy environments (Bodensteiner et al., 2024; Gunderson et al., 2018; Muñoz et al., 2016). Arboreal ants experience hotter, more thermally variable temperatures than their terrestrial counterparts and, correspondingly, have higher heat tolerance and wider performance breadths (Leahy et al., 2022). Interspecific interactions, such as competition and predation, may further act as a catalyst for physiological specialization (see da Silva et al., 2023). For instance, recent within-community studies suggest that predatory species are more heat tolerant than their prey (Franken et al., 2018;

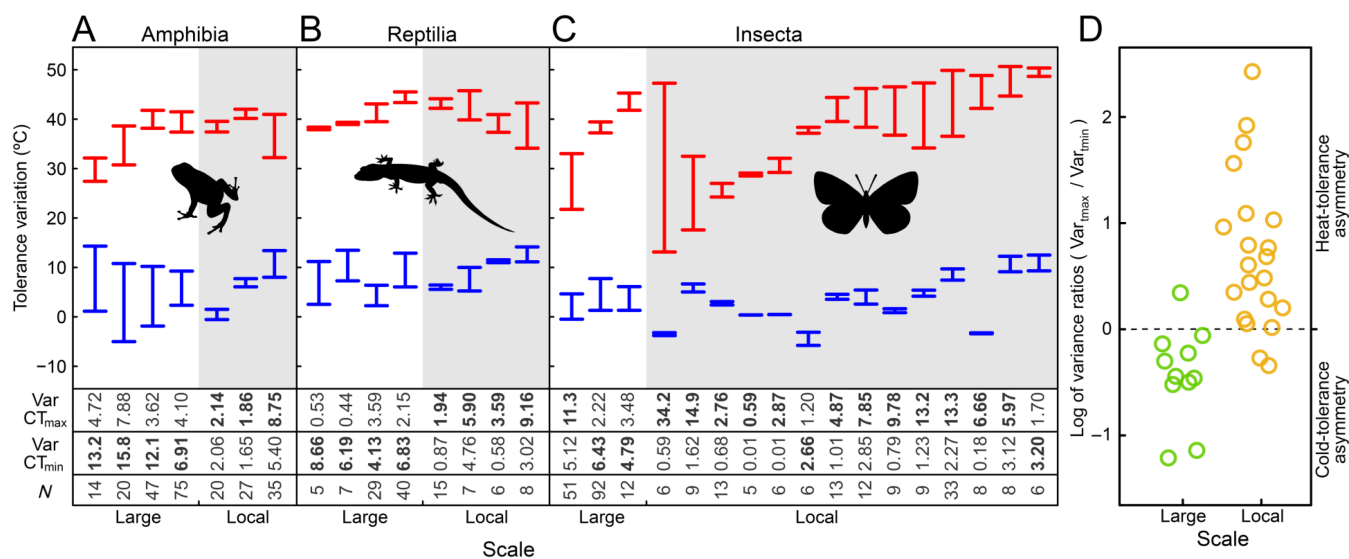


FIGURE 3 Scale-based asymmetries in the variance of thermal tolerance limits. Variance in critical thermal maxima (CT_{max}, red) and minima (CT_{min}, blue) and sample size and species count (N) across (A) amphibians, (B) reptiles, and (C) insects at large and local climatic scales (available in Pintanel et al., 2025, on Figshare at <https://doi.org/10.6084/m9.figshare.28845968.v2>). The bars represent the mean CT values for each sample \pm the observed variance. (D) Variance ratios ($\sigma^2_{CT_{max}}/\sigma^2_{CT_{min}}$) on a logarithmic scale for each large- (green) and local-scale (yellow) samples (see *Materials and methods*). Dashed line represents thermal tolerance symmetry, while values above represent heat-tolerance asymmetry and values below represent cold-tolerance asymmetry. Amphibians, from left to right: large scale, von May et al. (2017); Pintanel et al. (2019); Gutiérrez-Pesquera et al. (2016); Pintanel et al. (2022). Local scale: Gutiérrez-Pesquera et al. (2016), only temperate species; Gutiérrez-Pesquera et al. (2016), only tropical species; von May et al. (2019). Reptiles, from left to right: large scale, Huang et al. (2006) and Huang et al. (2007); Muñoz et al. (2014); Spellerberg (1972); Cruz et al. (2005); and Cruz et al. (2009). Local scale: Herrando-Pérez et al. (2020); Bennett and John-Alder (1986); Huey et al. (2009); van Berkum (1986) and (1988). Insects, from left to right: large scale, Shah et al. (2017); Kellermann, Overgaard, et al. (2012) and Kellermann, Loeschcke, et al. (2012); Pintanel et al. (2021). Local scale: Rendoll-Cárcamo et al. (2020); Shah et al. (2017) tropical 1; Shah et al. (2017) tropical 2; Shah et al. (2017) tropical 3; Shah et al. (2017) temperate; Klok and Chown (2003); Bishop et al. (2017) subsample 1, 1500 m elevation; Bishop et al. (2017) subsample 2, 1800 m elevation; Bishop et al. (2017) subsample 3, 2400 m elevation; Leahy et al. (2022) upland; Leahy et al. (2022) lowland; Käfer et al. (2020); Marsh (1985); Roberts et al. (1991). Silhouette illustrations were taken from PhyloPic (<http://phylopic.org>), under public domain license “CC0 1.0 Universal Public Domain Dedication.”

Katzenberger et al., 2021; Pintanel et al., 2021), whereas cold tolerance did not differ (Pintanel et al., 2021).

That such high variability at local scales in upper tolerances has been largely unnoticed may be because this same variation is “masked” at larger spatial scales. Broad-scale contrasts, for example, across latitudinal and elevational gradients, reflect long-term temporal processes, which can mask the fine-scale variability observed at smaller spatial and temporal scales. This distinction is critical for understanding how local environments may experience heightened thermal variability, which may not be apparent when only considering broader spatial patterns. As Bozinovic et al. (2014) put it, “species and populations with larger heat tolerances do live in the warmest environments and also are found at cooler high latitudes and altitudes.”

Future studies could also benefit from considering generation time and biogeographic range size as covariates to account for the differential exposure to thermal variability across species. Relative to species with longer generation times, those with shorter generation times may be more responsive to fine-scale thermal variation; fluctuating selection can maintain higher levels of adaptive genetic variation within the population, and selection may favor the evolution of increased plasticity, both of which favor acclimation to thermal heterogeneity (Bitter et al., 2021). Likewise, species with larger range sizes could be more exposed to broad-scale temperature gradients, also potentially influencing their thermal adaptation patterns.

By contrast, there is higher variability in lower thermal tolerances over large climatic scales, which is consistent with *Brett's heat-invariant rule*. This pattern may arise as a consequence of thermal selection on cold tolerance at the local scale. Extreme cold temperatures exhibit narrower variation than hotter temperatures between environments at local scales (Figure 1B). Additionally, at local scales, thermal heterogeneity for minimum temperatures is low (Figure 2D–F), limiting opportunities for behavioral compensation. Correspondingly, narrow local variation in minimum temperatures should expose organisms to strong selection on cold tolerance, in turn promoting rapid evolution (Barrett et al., 2011; Diamond et al., 2018), and substantial variation at large geographical gradients (elevation and latitude) (e.g., Gutiérrez-Pesquera et al., 2016; Muñoz et al., 2014; Pintanel et al., 2019; Sunday et al., 2011, 2019). Spatial asymmetries in thermal extremes likely operate in conjunction with other factors, such as biochemical constraints (which might hinder selection), to guide patterns of physiological specialization (Angilletta, 2009; Clarke, 2003). For example, maximum temperatures observed in a habitat often exceed species' upper critical limits, likely

reflecting (in part) thermal constraints on protein stability (Somero et al., 2017).

While our focus has been on terrestrial lineages, thermal heterogeneity varies among terrestrial, subterranean, and aquatic systems, with implications for physiological specialization. In species restricted to more thermally homogenous environments (e.g., subterranean species), variation in heat tolerance may show a similar response to cold tolerance, with higher variation at broad spatial scales (Baudier et al., 2018; Mammola et al., 2019). By contrast, broadly distributed species may increase cold tolerance variation locally, which may blur the local asymmetric pattern. Given that geographic range size is positively correlated with absolute latitude (*Rappoport's rule*; Stevens, 1989), this blurring pattern may be stronger in temperate regions (but see the inverse Rappoport's rule observed in equatorial marine fishes with larger geographical ranges: Pie et al., 2021; Stuart-Smith et al., 2017). However, if there is local adaptation or plasticity in cold tolerance, the impact of wide-ranging species on local cold tolerance variation would be reduced as community members adjust phenotypes in response to the experienced environment. The notion that variation in thermal tolerances should correlate with exposure to extreme temperature variation should generally apply to any ectotherm. Knowledge about the variation in thermal tolerances in marine ectotherms or lineages restricted to thermally stable habitats, such as subterranean species, would be useful for testing this hypothesis.

In a warming world, microgeographic variation in physiological specialization limits spatial generalizations about vulnerability to rising temperatures. For example, species restricted to closed-canopy forests will be more vulnerable to heat stress owing to a more cool-adapted thermal physiology, whereas relatives in nearby edge/open habitat might be more heat tolerant and resilient (Huey et al., 2009). Moreover, local microclimatic variation may remove the necessity for some species to migrate upslope or to higher latitudes as temperatures continue to warm (Battey et al., 2019), which could help explain the asymmetries observed in species range shift patterns (e.g., Chen et al., 2011; Parmesan & Yohe, 2003). Aside from the effects of rising temperatures, we expect that local extinctions of less heat-tolerant species may be considerably tied to (or compounded by) habitat thermal homogenization due to changes in land use and deforestation (Frishkoff et al., 2015). Indeed, in the Caribbean, deforestation has expanded the availability of relatively warm open habitats (like pastures) at the expense of relatively cool closed-canopy habitat (like cloud forest): heat-adapted lowland lizard species are found at high elevations where cloud forest—and its

complement of endemic, cool-adapted species—previously persisted (Frishkoff et al., 2019). Notably, these lizard species are close relatives that vary primarily in thermal habitat use, with corresponding differences in physiological specialization (Bodensteiner et al., 2024). Therefore, although climate-driven extinctions are likely to be severe at the lowland tropics (Colwell et al., 2008; Duarte et al., 2012; Huey et al., 2009), from a global perspective, the most vulnerable species would be those that are locally distributed in less variable habitats, regardless of latitude. To get a better picture of species' vulnerability to warming, global studies should also focus on how functional diversity at local scales may be affected by rising temperatures.

CONCLUDING REMARKS

Previous studies have analyzed how physiological thermal traits vary across large climatic scales. The goal of this study was to connect climate variation and physiological thermal variation at different spatial scales so as to understand how physiological tolerances relate to environmental variation at both fine-scale and broadscale spatial scales. Using a large number of studies with terrestrial ectotherms, we show that, at local scales, inter-specific variation in upper thermal tolerances is greater than that in lower thermal tolerances, which is contrary to the variability pattern seen at large climatic scales. We propose that differences in extreme temperature variation across scales may promote this contrasting pattern (Figure 1). Local thermal heterogeneity promotes higher variation in maximum temperatures, while seasonality (latitude) and/or adiabatic lapse rate (elevation) at larger climatic scales promotes higher variation in minimum temperatures. Incorporating microclimatic data will likely unveil fine-scale patterns in physiological diversity, even among close relatives, in turn sharpening our inferences about how vulnerability to warming is spatially and phylogenetically structured.

AUTHOR CONTRIBUTIONS

Pol Pintanel, Miguel Tejedo, Urtzi Enriquez-Urzelai, and Martha M. Muñoz conceived the ideas and designed the methodology. Pol Pintanel, Miguel Tejedo, Saúl F. Domínguez-Guerrero, and Martha M. Muñoz obtained the data. Pol Pintanel analyzed the data. Pol Pintanel led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Pintanel et al., 2025) are available on Figshare at <https://doi.org/10.6084/m9.figshare.28845968.v2>.

ETHICS STATEMENT

This study did not involve researchers who collected the original data. All data used for the analyses were taken from a previous data compilation (Bennett et al., 2018), and the original references on which all analyses were built are quoted.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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