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Variation in Ectotherm Thermal Tolerances With Elevation and Temperature Across Biological Scales

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ABSTRACT

Aim: Variation in thermal tolerances along environmental gradients is assumed to follow similar patterns across different biological scales, including within and between species, and across communities. However, this assumption has yet to be tested using comprehensive datasets collected through standardised methodologies.

Location: Southern Asia.

Time Period: 2017–2019.

Major Taxa Studied: Ants, beetles, grasshoppers, and spiders.

Methods: We quantified the associations between thermal tolerance traits and elevation or temperature at three biological scales (community, broad taxonomic group, and species) along two distinct elevational transects in Southern Asia. In total, we measured thermal tolerances of over 15,000 individuals from 114 arthropod species belonging to four invertebrate taxa (ants, beetles, grasshoppers, and spiders). We compared the relationships at each scale using mixed-effects models.

Results: At the community scale, across all individuals of all species, we found a consistent decline in the values of three thermal tolerance traits (upper tolerance, lower tolerance, and tolerance breadth) with elevation along the Himalayan transect but an increase in the values of upper and lower tolerance along the Sulaiman transect. The relationships of thermal tolerance traits and elevation/temperature varied among the groups and species between the Himalayan and Sulaiman transects. This suggests that factors beyond elevation, including vegetation composition, microclimate, landscape features, and local adaptation, drive observed variation in thermal tolerance traits among and within species.

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Conclusion: Our study highlights the interplay between thermal physiology and the environment across different habitats and biological scales. Our findings indicate that predicting biodiversity responses to environmental change based on thermal tolerance–environment relationships requires careful consideration of group- and species-level variation. This is essential for improving the accuracy of climate change impact assessments on biodiversity.

1 | Introduction

A central goal of macroecology is to understand how biological traits, such as thermal tolerance, vary along environmental gradients such as elevation and temperature. This variation influences species' demographic rates and distributions (Angilletta 2009; Khaliq et al. 2023) and affects biodiversity responses to climate change, particularly to rising temperatures (Cahill et al. 2013; Montejo-Kovacevich et al. 2020; Lavender et al. 2021). Ectotherms are especially sensitive to temperature changes because their body temperature depends on external conditions, directly affecting their survival and performance (Angilletta 2009). Broadly, thermal tolerances decline with temperature along elevational and latitudinal gradients (Deutsch et al. 2008; Sunday et al. 2011; Khaliq et al. 2014; Buckley et al. 2018; Lavender et al. 2021). Macroecological studies often implicitly assume that variation in the relationship between thermal tolerance and temperature, or associated gradients, in ectotherms is unimportant (Addo-Bediako et al. 2000; Sunday et al. 2011; Bennett et al. 2019). However, evidence suggests that these relationships can vary (Chown et al. 2004; Bennett et al. 2019; Bujan, Roeder, Kaspari, et al. 2020), which could challenge the accuracy of predictions on species' responses to climate change based on models that implicitly assume uniformity across scales. As temperatures rise rapidly, a comprehensive analysis is needed to understand how the relationship between thermal tolerance and environmental gradients varies within and among taxonomic groups with distinct evolutionary histories. This knowledge is crucial for improving species response predictions and refining macroecological models (Chown et al. 2003; Bennett et al. 2019).

The relationship between thermal tolerance and environmental gradients can be examined at different nested biological scales: the species scale, a broader taxonomic group scale (hereafter “group”), and the community scale (Chown et al. 2004; Chown and Gaston 2008). Species-scale analyses consider how relationships are shaped by differences among populations within a species (i.e., intraspecific variation), which may include the effects of habitat structure and microclimatic conditions on local adaptation and plasticity (Huey 1991; Battles and Kolbe 2018; Dongmo et al. 2021). Group-scale analyses compare the relationships among species within the same broad taxon groups and highlight the effects of species' traits. Variation within a clade may be influenced by the evolutionary history of species, that is, past adaptations and phylogenetic constraints on thermal tolerance (Calosi et al. 2007, 2010; Sunday et al. 2012; Warren and Chick 2013; Khaliq et al. 2014, 2015, 2017; Diamond and Chick 2017; Kingsolver and Buckley 2017). At the community scale, the relationship between thermal tolerance and elevation or temperature represents the community-average responses of multiple species and taxonomic groups, driven by a combination of species' evolutionary histories and species turnover along the gradient (Chown et al. 2004; Chown

and Gaston 2008; Gaston et al. 2009; Nowrouzi et al. 2016). While studies have explored this relationship at either species, group, or community scales (Calosi et al. 2007; Nowrouzi et al. 2018), including across multiple spatial scales (Klinges and Scheffers 2021; Terlau et al. 2023; Klinges et al. 2024), few studies have examined how trends in thermal tolerances differ between biological scales using standardised datasets (Bujan, Roeder, Kaspari, et al. 2020).

A key driver of variation within and among species in thermal tolerance is body size. Both the temperature-size rule (Angilletta and Dunham 2003; Kingsolver and Huey 2008) and the heat dissipation limitation hypothesis (Speakman and Król 2010a) suggest body size can influence thermal tolerance, with large organisms generally exhibiting broader thermal tolerance breadths. This is primarily due to their lower surface-to-volume ratios, which reduce heat loss and increase thermal inertia. This inertia is expected to have consistent effects on cold tolerance, increasing the ability of large bodies to withstand low temperatures (i.e., lowering minimal critical temperatures [CT_{min}]). By contrast, maximum critical temperatures (CT_{max}) are not necessarily higher for large bodies due to their reduced capacity to dissipate heat, which even reduces the heat tolerance compared to small bodies (Speakman and Król 2010a). Nonetheless, because increases in cold tolerance with body size tend to be more pronounced than reductions in heat tolerance (Araújo et al. 2013; Bennett et al. 2018), the net effect is often a broader thermal tolerance range. Conversely, smaller individuals heat and cool rapidly, making them more sensitive to short-term temperature extremes, though often better adapted to persistently warm temperatures (Bergmann 1847; Huey 1991; Speakman and Król 2010b).

Other environmental factors can also contribute to variation in thermal tolerance. Habitat structure, particularly vegetation, creates microclimatic variation that causes individuals to experience different thermal conditions (Duffy et al. 2015; Kaspari et al. 2015; Montejo-Kovacevich et al. 2020). Dense vegetation buffers temperature extremes and creates microclimates (Duffy et al. 2015; Montejo-Kovacevich et al. 2020), potentially weakening the direct effects of environmental variation on thermal tolerance. In contrast, more open habitats with sparse vegetation expose organisms to greater temperature extremes and fluctuations, which may strengthen the correlation between thermal tolerance and environmental gradients.

Recent research has documented variation in thermal tolerance along elevational and temperature gradients, but inconsistencies in data sources and methodologies pose significant challenges for cross-study comparisons (Addo-Bediako et al. 2000; Sunday et al. 2019; Bujan, Roeder, Yanoviak, and Kaspari 2020; Chick et al. 2020). Many studies rely on large datasets compiled from diverse sources, including published literature with varying spatial and temporal coverage (Addo-Bediako et al. 2000; Sunday et al. 2011; Khaliq et al. 2014).

Moreover, the use of different study designs and methodologies for collecting field samples and measuring individual thermal tolerances complicates efforts to compare findings or evaluate the influence of factors across biological scales (Roeder et al. 2021). There is a need for large-scale studies with standardised field sampling and laboratory methodologies to assess thermal tolerance patterns along environmental gradients (including elevation, temperature, and habitat), at multiple biological scales.

In this study, we investigated the associations of body size, elevation, and temperature with thermal tolerance traits across three biological scales, using one of the largest thermal tolerance datasets collected to date for ectotherms (including over 15,000 individuals across 113 species belonging to ants, beetles, grasshoppers, and spiders). We sampled along two elevational transects in southern Asia that vary in vegetation cover: the Himalayan transect is covered with dense vegetation, and our sampling sites were predominantly covered with forests, while the Sulaiman transect covered more open habitat. (1) We aimed to assess consistency in the relationships between thermal tolerance traits and elevation/temperature across biological scales; that is, whether the relationships for populations of the same species match those for species in the same clade and those for the community as a whole. (2) Overall, we expected a negative relationship between thermal tolerance traits and elevation, but that the strength of this relationship would differ across biological scales and by transect. (3) We expected the weakest relationships between thermal tolerance and elevation/temperature at the community scale, as the relationship might be weakened by species turnover along the gradient, variation in the ecological strategies of different taxon groups, and population-level differences in thermal environments. At the group level, we expected stronger relationships between thermal tolerance and the environmental gradients as species of the same group are more similar. We expected the strongest relationships at the species level, where local adaptations and phenotypic plasticity may drive strong effects of elevation/temperature on thermal tolerance. However, overall, we expected that both the strength and direction of these relationships would vary among different taxonomic groups and species because differences in body size influence thermal inertia and coupling to environmental temperatures, while habitat use alters the degree of microclimate buffering. (4) We also expected, overall, a positive relationship between body size and thermal tolerance across the three biological scales. (5) Finally, we expected that differences in vegetation cover along the survey transects would influence the relationship between thermal tolerance and elevation or temperature, possibly due to differences in exposure to extreme temperatures. Hence, at the Sulaiman transect, we expected stronger relationships between thermal tolerance and elevation or temperature than at the Himalayan transect.

2 | Material and Methods

2.1 | Field Sampling

We measured thermal tolerances in ectotherms along two elevational transects in Pakistan. The Sulaiman transect was set up in the Sulaiman Mountain range (central Pakistan) and

the Himalaya transect was set up in the Himalayas (northern Pakistan). The Sulaiman transect ranged from 135–2100 m a.s.l., whereas the Himalaya transect ranged from 897–2900 m a.s.l. Temperatures at the two transects ranged from 17.2°C – 36.8°C at the Sulaiman range and from 14.9°C to 38.4°C at the Himalayan range. The details of the study sites can be found in Figure 1.

We sampled arthropods at 25 different sites (16 sites along the Sulaiman transect and 9 sites along the Himalaya transect) between 2017 and 2019. The Sulaiman transect was principally sampled in March, April, September, and October, while the Himalayan transect was principally sampled from May to August. At each site, we set up three quadrats of 50 × 50 m containing six pitfall traps, each with two traps in the middle and four at the four corners of the quadrat. Traps were left in the field for 24 h and were regularly checked and emptied during daylight hours. In addition to pitfall trapping, we hand-collected ants, beetles, grasshoppers, and spiders, sampling during sunny days from 8 am until 4 pm across the whole quadrat. We visited each site at least twice in a year. In total, we spent 92 days in the field.

After collection, the animals were taken to the laboratory for thermal tolerance measurements, with minimal acclimatisation time (see next section). Temporary laboratories were set up near the sampling sites to start measurements promptly upon sample arrival. The duration between collection and measurements was approximately 1 h.

For species identification, we referred to specific sources depending on the arthropod group. To identify grasshoppers, we followed the guidelines provided by Sultana and Wagan (2015). Ant identification was done using keys from AntWiki (www.antwiki.org). Spider identification followed the methodology outlined in Ashfaq et al. (2019), while beetle identification was based on Azadbakhsh and Rafi (2017) and Ali et al. (2018).

To measure air temperatures, we placed one Tinytag TGP-4017 temperature logger at each sampling site, in the shade to avoid overheating and faulty readings. We measured temperatures every 10 min from 2018 to 2019 at each site during the field days. The accuracy of the data loggers was $\pm 0.6^\circ\text{C}$. In the analyses, we used the mean daily temperature of the sampling day for each site. For context, we also measured ground temperatures using standard mercury thermometers (to support interpretation of our results).

2.2 | Thermal Tolerance and Body Size Measurements

To determine individual critical thermal limits, we measured both the upper critical temperature (CT_{max}) and the lower critical temperature (CT_{min}) for each individual, with a total of 15,156 individuals measured (Table S1). We measured CT_{min} first to ensure the animals were alive for the second measurement, as CT_{min} is typically less detrimental to the individuals. After allowing a minimum recovery time of 4 h following the CT_{min} measurement, we measured CT_{max} . Measuring CT_{min} first has no effect on measurements of CT_{max} (Khaliq

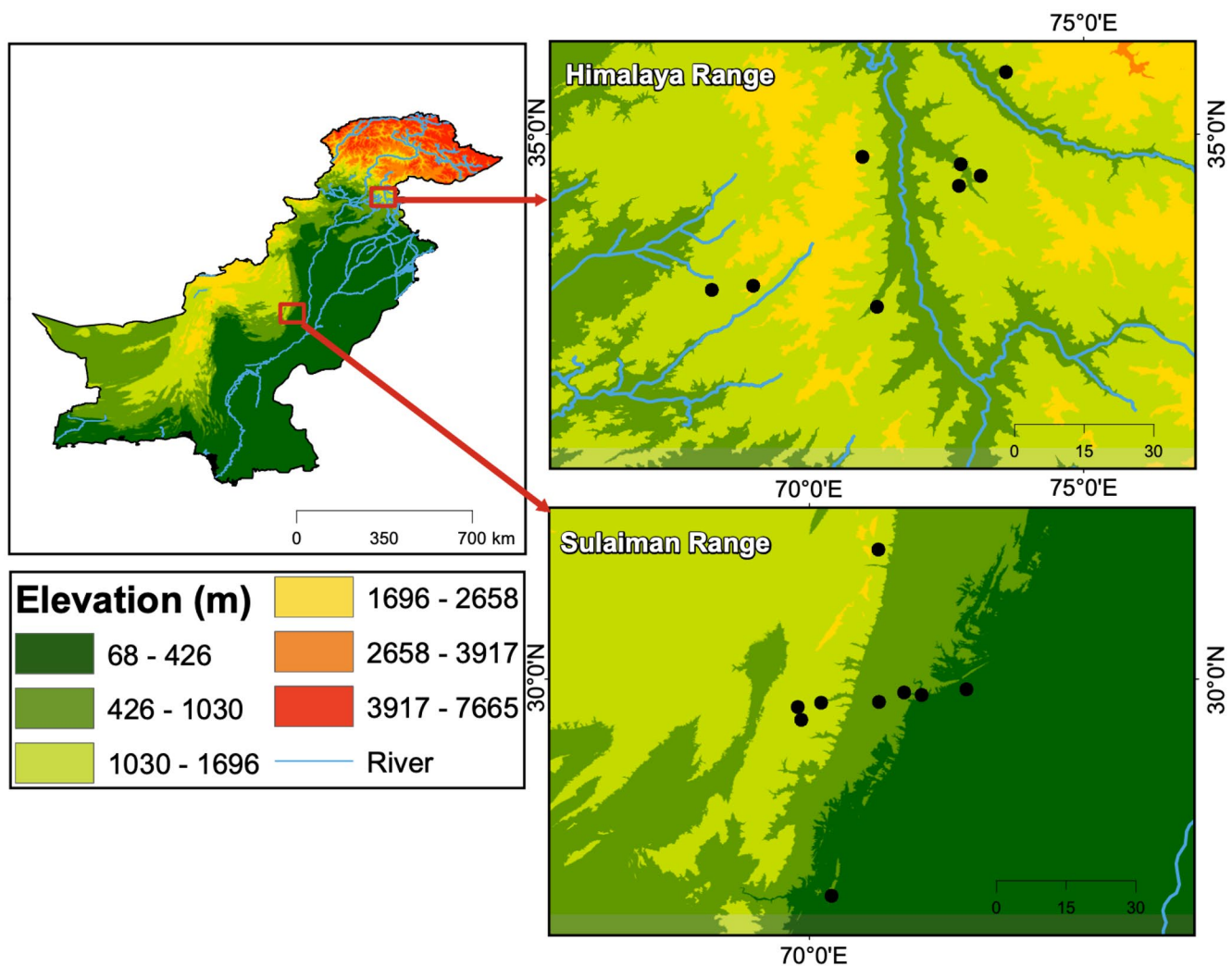


FIGURE 1 | Sampling sites. The Himalaya and Sulaiman ranges are shown in rectangles on the map of Pakistan. Sampling sites along the two transects are shown as black dots. Some of the points are not visible due to overlap of other sampling sites. We sampled 16 sites in the Sulaiman transect, collecting 7458 individuals, and 9 sites in the Himalaya transect, collecting 7698 individuals.

et al. 2023). We did not measure CT_{min} in 2017 at the Sulaiman transect.

For the measurements, we used an XMTD-204 digital thermostat water bath. Animals were placed in either 1.5 mL Eppendorf tubes or 50 mL Falcon tubes, depending on their size. We avoided using cotton plugs in the tubes to prevent individuals from using them as a thermal refuge. The tubes were equilibrated at 20°C for 5 min, and then the temperature was lowered or increased at a rate of 1°C/min to measure CT_{min} and CT_{max} , respectively (Moretti et al. 2017). We monitored water temperatures with three thermometers and used ice to maintain temperatures below 0°C. We recorded the temperature as CT_{min} or CT_{max} at which the individual stopped moving even after tapping the tubes for 3 s. Thermal tolerance breadth was defined as the difference between CT_{max} and CT_{min} . After measurement, individuals were returned to ambient temperatures, and animals resumed normal behaviour after approximately 30 min.

We measured individual body size using a Vernier calliper. We measured from the head to the end of the abdomen for ants,

beetles, and grasshoppers. For spiders, we took the length from the head to the end of the abdomen, ignoring the legs.

2.3 | Statistical Analysis

Our analysis focused on species for which we had sampled at least five individuals ($n = 114$ species). We examined the association between thermal tolerance traits (i.e., CT_{min} , CT_{max} , and thermal tolerance breadth), environmental variables (elevation and temperature), and species characteristics (body size) at three biological scales, using linear mixed-effects models. We were interested in how the strength and direction of the relationships between thermal traits and environmental (elevational/temperature) gradients vary across different biological scales and with body size. At each biological scale, we fitted two batches of models, one including elevation (and other predictors) and one including temperature instead of elevation (with an otherwise identical model structure) because of collinearity (Figure S1). Model equations are given for the first batch of models.

In the community-scale analysis, we modelled each thermal tolerance trait (denoted y) as a function of covariates, according to the equation:

$$\begin{aligned} y_i \sim N(\mu_i, \sigma^2) \mu_i = & \beta_0 + \beta_1 \text{year}_i^{(2)} + \beta_2 \text{year}_i^{(3)} \\ & + \beta_3 \text{size}_i + \beta_4 \text{elevation}_i + \beta_5 \text{transect}_i^{(2)} \\ & + \beta_6 (\text{elevation}_i \times \text{transect}_i^{(2)}) + u_{m(i)} + u_{o(i)} + u_{f(i)} \\ & + u_{g(i)} + u_{s(i)} u_{m(i)} \sim N(0, \sigma_{\text{month}}^2) u_{o(i)} \\ & \sim N(0, \sigma_{\text{order}}^2) u_{f(i)} \sim N(0, \sigma_{\text{family}}^2) u_{g(i)} \\ & \sim N(0, \sigma_{\text{genus}}^2) u_{s(i)} \sim N(0, \sigma_{\text{species}}^2) \end{aligned} \quad (1)$$

where i indexes observations (individuals), $m(i)$, $o(i)$, $f(i)$, $g(i)$ and $s(i)$ map each observation to its month, taxonomic order, family, genus and species, respectively; β denotes coefficients; and u denotes random effects. Fixed-effect factors (year and transect) are denoted by the variable name and a superscript ((2), (3), ... etc.) that denotes the category (e.g., “2018” or “2019”). These terms are ordered alphanumerically and coded as 1 (for the defined category) and 0 otherwise. We centred and scaled all continuous variables. This model thus estimates the average effect of elevation on the trait across the entire community for each transect, alongside the average effect of body size. The nested random effects for species/genus/family/order account for phylogenetic relatedness.

We also fitted a group-scale model. The purpose of this model was to estimate the relationship between the thermal tolerance traits and both environmental and body-size gradients across species within taxonomic groups (ants, beetles, spiders, and grasshoppers) and to examine how group-scale patterns vary between groups. To this end, we modified Equation (1) as follows to include a fixed effect for taxonomic group and interactions between group, elevation and transect:

$$\begin{aligned} y_i \sim N(\mu_i, \sigma^2) \mu_i = & \beta_0 + \beta_1 \text{year}_i^{(2)} + \beta_2 \text{year}_i^{(3)} + \beta_3 \text{size}_i + \beta_4 \text{elevation}_i + \beta_5 \text{transect}_i^{(2)} \\ & + \beta_6 (\text{elevation}_i \times \text{transect}_i^{(2)}) + \sum_{j=2}^4 \left[\beta_{5+j} \text{group}_i^{(j)} + \beta_{8+j} (\text{group}_i^{(j)} \times \text{size}_i) + \beta_{11+j} (\text{group}_i^{(j)} \times \text{elevation}_i) \right. \\ & \left. + \beta_{14+j} (\text{group}_i^{(j)} \times \text{transect}_i^{(2)}) + \beta_{17+j} (\text{group}_i^{(j)} \times \text{elevation}_i \times \text{transect}_i^{(2)}) \right] + u_{m(i)} + u_{o(i)} + u_{f(i)} + u_{g(i)} + u_{s(i)} \end{aligned} \quad (2)$$

where all terms are as previously described. In this way, we estimated the expected relationship between thermal tolerances and both elevation and body size across all species in each taxonomic group.

In our species-scale analysis, we modelled the relationship between the thermal tolerance traits and both elevation and body size explicitly for each species using fixed effects. In this analysis, we focused on six species (≤ 2 species per taxonomic group) that were present on both transects and most widely distributed along the elevational gradient. The species were *Crematogaster subnuda* (ant), *Monomorium indicum* (ant), *Acrida gigantea* (grasshopper), *Coccinella septempunctata* (beetle), *Agelastica alni* (beetle) and *Evipa* sp. (spider). (The remaining species lacked sufficient observations along the elevation gradients on both transects). Our species-scale models took the form:

$$\begin{aligned} y_i \sim N(\mu_i, \sigma^2) \mu_i = & \beta_0 + \beta_1 \text{year}_i^{(2)} + \beta_2 \text{year}_i^{(3)} + \beta_3 \text{size}_i \\ & + \beta_4 \text{elevation}_i + \beta_5 \text{transect}_i^{(2)} + \beta_6 (\text{elevation}_i \times \text{transect}_i^{(2)}) \\ & + \sum_{k=2}^6 [\beta_{5+k} \text{species}_i^{(k)} + \beta_{10+k} (\text{species}_i^{(k)} \times \text{size}_i) \\ & + \beta_{15+k} (\text{species}_i^{(k)} \times \text{elevation}_i) + \beta_{20+k} (\text{species}_i^{(k)} \times \text{transect}_i^{(2)}) \\ & + \beta_{25+k} (\text{species}_i^{(k)} \times \text{elevation}_i \times \text{transect}_i^{(2)})] + u_{m(i)}. \end{aligned} \quad (3)$$

We repeated the earlier community-scale analyses for the same subset of six species to validate the robustness of our results to data selection and facilitate comparisons. (We did not repeat the group-scale analyses due to the presence of only one species for beetles and spiders).

To examine the variation in thermal tolerance along the elevational temperature gradient, we refitted the same set of models but with the elevation variable replaced by the mean temperature at each site (averaged over the relevant day of sampling). For simplicity, we will use the terms ‘elevation model’ and ‘temperature model’ hereafter to describe the two sets of models.

We compared the slopes of the thermal traits–environment relationships across three biological scales, using the degree of overlap between their confidence intervals to evaluate whether the strength and direction of these relationships differed. Model fitting, visualisation, and standard diagnostic checks were implemented using the lme4 package in R, version 4.3.0 (R Core Team 2024). We used the function r^2 GLMM from the MuMIn package to calculate the marginal R^2 and conditional R^2 values (Nakagawa and Schielzeth 2013). There were some issues with residual diagnostics, and in some of the models, the residual distribution was slightly skewed (mainly for upper critical temperature, Figure S2, Supplement

R-Markdown file). However, linear mixed-effects models can be robust to violation of the distributional assumptions (Schielzeth et al. 2020), and our results were broadly consistent across alternative modelling approaches. All code is provided in the [Supporting Information](#).

3 | Results

3.1 | Influence of Elevation and Temperature on the Himalayan Transect

Across the Himalayan transect, thermal traits generally showed negative relationships with elevation, but the strength and direction of these relationships varied by biological scale. As expected, the relationships between thermal traits and

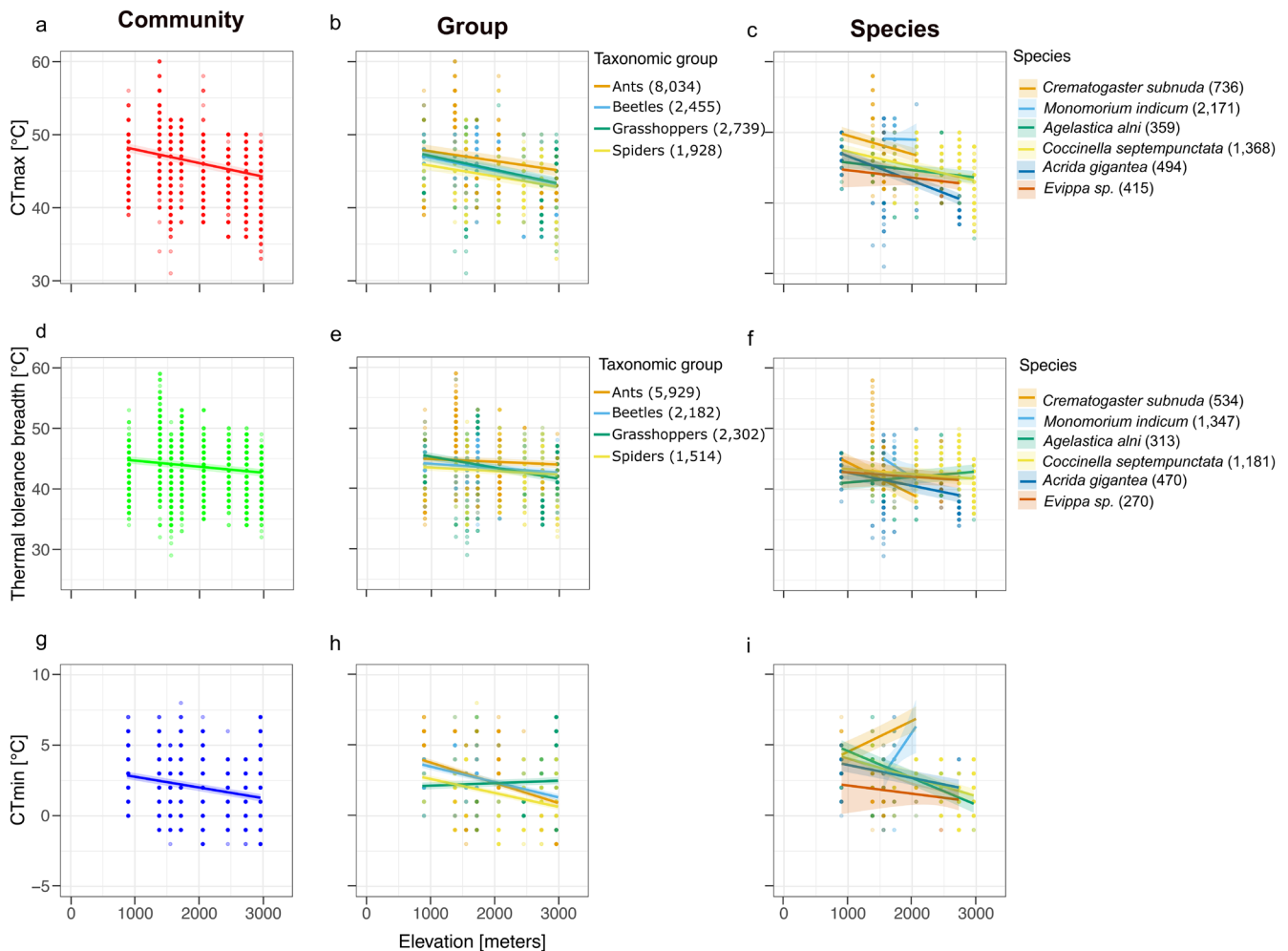


FIGURE 2 | Relationships between thermal tolerance traits and elevation along the Himalayan transect at three biological scales. Each panel shows the relationship between a thermal tolerance trait (rows) and elevation for a selected biological scale (columns). Predictions are shown along the range of elevation spanned by the relevant data while holding other variables at the first factor level or the mean value. The shaded areas along the regression lines represent the 95% confidence intervals and include uncertainty in the mean as well as the effect of elevation. Many data points are overlapping, indicated by different colour intensities. Numbers in parentheses represent the sample size. Panels (a, d, g) correspond to the community scale, panels (b, e, h) to the group scale, and panels (c, f, i) to the species scale. Within each column, the rows correspond to CT_{max}, thermal tolerance breadth and CT_{min}, from top to bottom.

environmental gradients at the group and species scales differed from those observed at the community scale, with slopes ranging from positive to negative and the confidence intervals are showing limited overlap (details are given below, Figure S3). The greatest variation occurred at the species scale (SD of slopes: CT_{max} = 0.91, thermal tolerance breadth = 2.84, CT_{min} = 2.45), followed by the group scale (SD of slopes: CT_{max} = 0.18, thermal tolerance breadth = 0.46, CT_{min} = 0.48).

3.1.1 | Community Scale

All statistics in the following sections are per 100m for elevation, 1 degree temperature rise for temperature, and 1 mm for body size.

At the community scale, consistent with the expectations, we observed a consistent decline in all three thermal tolerance

trait values with increasing elevation on the Himalayan transect (Table S2; Figure 2a,d,g), with slopes ranging from -0.10°C (CT_{min}) to $-0.21^{\circ}\text{C}/100\text{m}$ (CT_{max}). In line with this result, CT_{min} and CT_{max} increased (by 0.01°C – $0.25^{\circ}\text{C}/^{\circ}\text{C}$) with rising temperatures on the Himalayan transect, but the relationship between thermal tolerance breadth and temperature was not statistically significant (Table S3; Figure 3a,d,g). These results remained consistent when we focused on the six species included in the species-scale analysis (see below and Supplement R-Markdown file).

3.1.2 | Group Scale

At the group-scale, all three thermal tolerance traits declined with increasing elevation (by -0.17 to $-0.28^{\circ}\text{C}/100\text{m}$) in all taxonomic groups in the Himalayas, except CT_{min} in grasshoppers (Table S4; Figure 2b,e,h). CT_{max} and CT_{min} increased

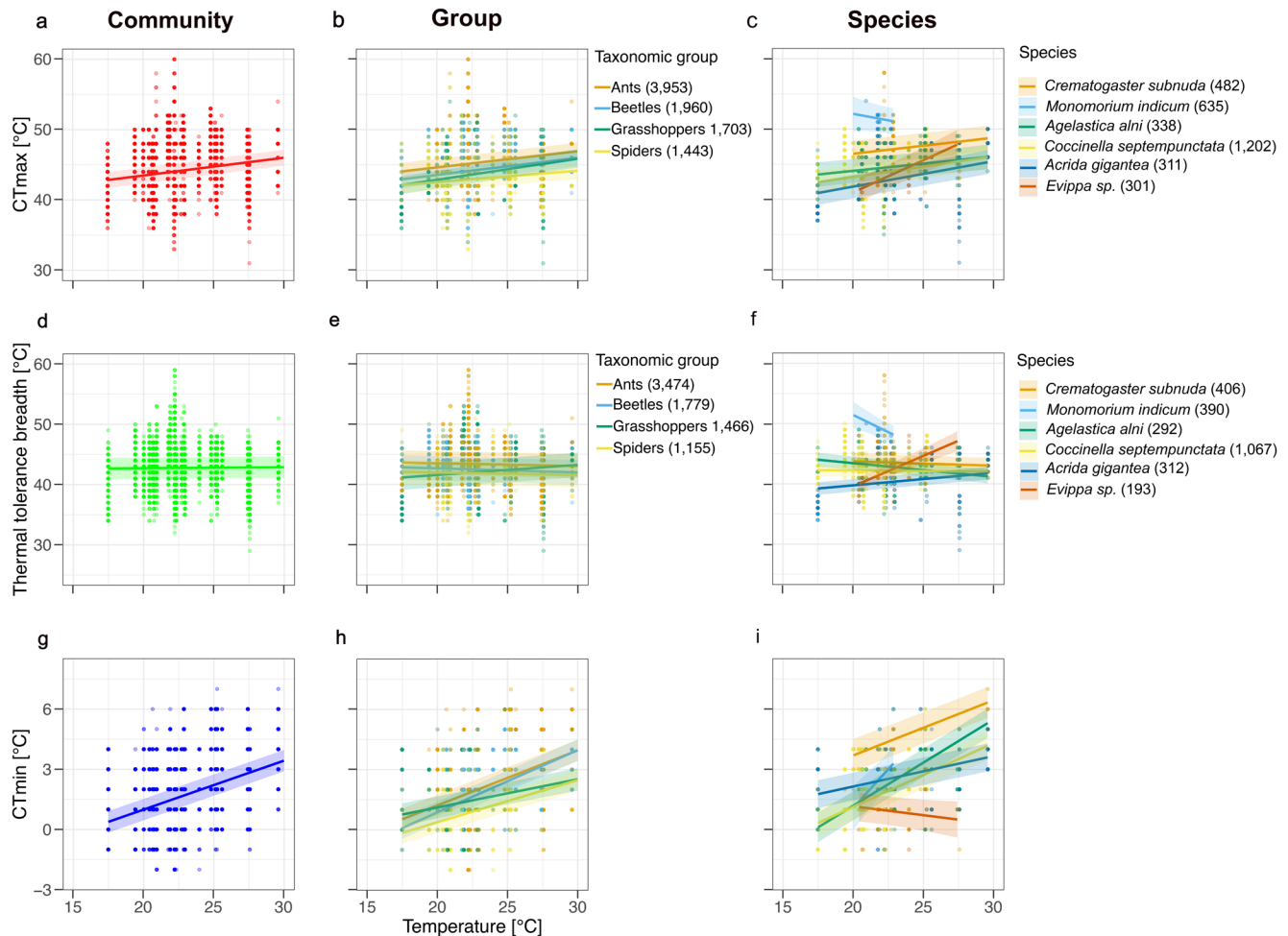


FIGURE 3 | Relationships between thermal tolerance traits and temperature along the Himalayan transect at three biological scales. Each panel shows the relationship between a thermal tolerance trait (rows) and temperature for a selected biological scale (columns). Predictions are shown along the range of elevation spanned by the relevant data while holding other variables at the first factor level or the mean value. The shaded areas along the regression lines represent the 95% confidence intervals and include uncertainty in the mean as well as the effect of elevation. Many data points are overlapping, indicated by different colour intensities. Numbers in parentheses represent the sample size. Panels (a, d, g) correspond to the community scale, panels (b, e, h) to the group scale and panels (c, f, i) to the species scale. Within each column, the row correspond to CT_{max}, thermal tolerance breadth and CT_{min}, from top to bottom.

with temperature along the Himalayan transect for all taxonomic groups, but thermal tolerance breadth showed mixed patterns: for ants there was a slight decline of $-0.04^{\circ}\text{C}/^{\circ}\text{C}$ in thermal tolerance breadth and for grasshoppers there was an increase of $+0.15^{\circ}\text{C}/^{\circ}\text{C}$ in thermal tolerance breadth (Table S5; Figure 3b,e,h). These directions and the magnitude differed from the community-scale results in both transects (Figure S3a–f).

3.1.3 | Species Scale

At the species scale, trends in thermal tolerance traits with elevation and temperature along the Himalayan transect were mixed, from strongly negative to strongly positive (Table S5; Figure 2c,f,i). We observed moderate declines (by $<0.09^{\circ}\text{C}/100\text{m}$) in CT_{max} for all species. We observed mixed trends for thermal tolerance breadth along elevation, with expected breadths moderately increasing ($+0.08^{\circ}\text{C}/100\text{m}$) for *A. alni* and decreasing for *M. indicum* (over a restricted elevational range) (Figure 2f). The

trends for CT_{min} were also mixed, with increases for *C. subnuda* ($+0.12^{\circ}\text{C}/100\text{m}$) and *M. indicum* ($+0.16^{\circ}\text{C}/100\text{m}$) and decreases for *A. alni* ($-0.18^{\circ}\text{C}/100\text{m}$) (Figure 2i). In the temperature models, we generally observed positive relationships between temperature and CT_{max}/CT_{min}, except for *Evippa* sp. and *M. indicum* (Table S6; Figure 3c). Thermal tolerance breadth broadly decreased with the increase of temperature, except in *Evippa* sp. (Figure 3d) and *A. gigantea* (Figure 3f).

As with the group scale, many species-scale patterns differed in direction and magnitude from those at the community scale (Figure S2a–f).

3.2 | Influence of Transect

Contrary to our expectation, relationships between thermal tolerance traits and elevation were generally weaker at the Sulaiman transect. At the community scale, changes differed

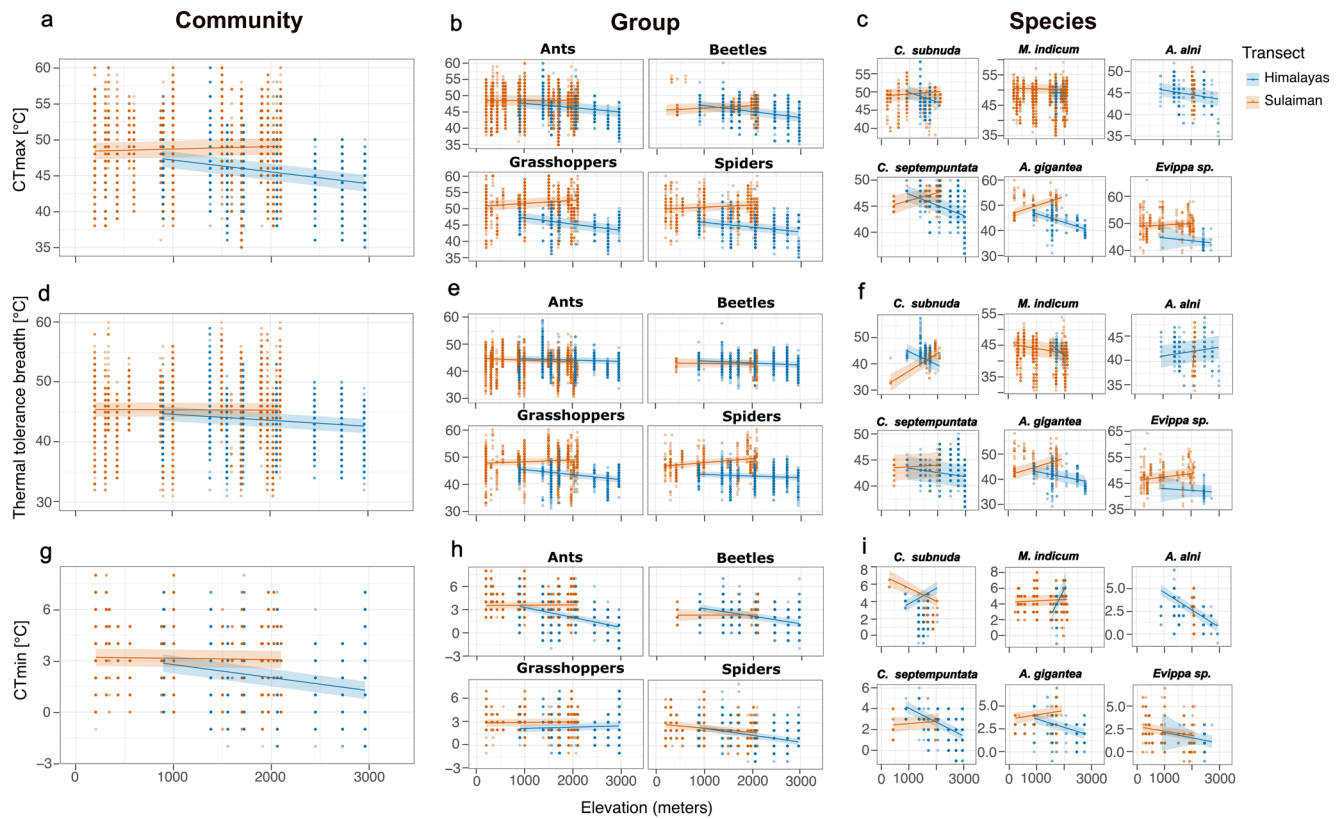


FIGURE 4 | Relationship of thermal tolerance traits with elevation along two contrasting transects at three biological scales. For each thermal tolerance trait, the effect of elevation is shown for both transects at the community scale (column one, a, d, g), at the group scale for each taxonomic group (column two, b, e, h), and at the species scale (column three, c, f, i) for each of the six selected species. The shaded areas along the regression lines represent the 95% confidence intervals. Many data points are overlapping, indicated by different colour intensities.

significantly between the transects for all thermal traits: the Himalayan transect showed declines in thermal tolerance with elevation, whereas the Sulaiman transect showed weak increases (Table S2; Figure 4a,d,g). At the group scale, we found contrasting patterns between transects in most cases (Figure 4b,e,h). At the species scale, CT_{max} and thermal tolerance breadth also showed contrasting elevational associations between transects, except in *A. alni* and *M. indicum*, which had similar trends in both transects (Table S5; Figure 4c,f,i). For CT_{min} , three species (*C. subnuda*, *A. gigantea*, and *C. septempunctata*) showed contrasting patterns along elevation at two transects (Table S5; Figure 4c,f,i). In contrast, *M. indicum* showed similar patterns between transects for CT_{max} , CT_{min} , and thermal tolerance breadth (Figure 4c,f,i).

3.3 | Influence of Body Size

Consistent with our predictions, we observed an increase in CT_{max} with increasing body size at all biological scales, ranging from +0.06 to +0.46°C/mm in the elevation models (Tables S2, S4 and S6) and +0.003 to +0.44°C/mm in the temperature models (Tables S3, S5 and S7) over a body-size range of 0.4 to 70.7 mm. CT_{min} declined with increasing body size (−0.008°C to −0.04°C/mm) in both elevation and temperature models, except for the elevation model at the group scale, which showed a +0.07°C/mm change (Tables S2–S7). Thermal tolerance breadth generally increased with increasing body size (+0.06 to +0.22°C/mm in the

elevation models), though at the community scale in the temperature model it declined slightly (−0.01°C/mm), while group and species scales showed increases (+0.07°C and +0.39°C/mm, respectively, Tables S3 and S5).

4 | Discussion

Using one of the largest thermal tolerance datasets for ectotherms to date, we investigated whether the strength and direction of the relationships between thermal tolerances and elevation or temperature vary across three biological scales and two transects with different habitat structures. Consistent with our expectation, we found that these relationships differed in both strength and direction between community, group, and species scales, as well as between two transects. At the community scale, all three thermal tolerance traits along the Himalayan transect decreased with increasing elevation and increased with increasing temperature, indicating that individuals at low elevations and high ambient temperatures have, on average, a greater ability to tolerate extreme temperatures. In contrast, and contrary to our expectation of uniformly negative associations with elevation, thermal tolerances slightly increased with elevation along the Sulaiman transect. At the group scale, all thermal traits decreased along the Himalayas, except for the CT_{min} of grasshoppers, which showed a positive association with elevation. At the species scale, we observed more variable relationships between thermal traits and elevation or temperature than

predicted, suggesting that local ecological strategies such as microhabitat use and population-level adaptations strongly influence thermal tolerance. Together, these results highlight that while broad-scale patterns exist, they are not always consistent across biological scales, aligning only partially with our initial predictions.

At the community scale, our study reveals complex patterns in thermal tolerance traits along elevational gradients in the Himalayan and Sulaiman mountains. At the Himalayan transect, CT_{max} and thermal tolerance breadth declined with elevation, whereas at the Sulaiman transect, thermal tolerances were either unrelated or positively associated with elevation. These contrasting patterns only partly support our predictions: rather than being the weakest, community-level patterns were strong in the Himalayas. This divergence between transects likely reflects the differences in local microclimatic conditions, habitat structure, and species composition between the two transects. For example, the Himalayan transect includes more closed-canopy forest, and hence species may be adapted to shaded, cooler environments. In contrast, the Sulaiman transect includes more open and arid habitats, where species are more exposed to these conditions. Furthermore, air temperatures at the Sulaiman transect are cooler at higher elevation in comparison to lower elevation, yet warmer in comparison to the Himalayan transect (Figure S4). While our findings partially align with those of Sunday et al. (2019), who found weak or no global-scale relationships between CT_{max} and elevation, the associations revealed by our fine-resolution dataset emphasize the importance of local context in shaping thermal trait variation along elevational gradients (Sunday et al. 2019).

The observed increase in values of CT_{max} , CT_{min} , and thermal tolerance breadth with elevation along the Sulaiman transect at the community scale is somewhat surprising and runs counter to our initial expectations of declining tolerances with elevation. The Sulaiman transect is drier, hotter, and mostly barren (with limited vegetation) compared to the Himalayan transect, and in such exposed environments, we expected thermal traits to show a clearer decline with elevation (due to limited buffering from vegetation). We discuss a possible mechanism that could explain this result.

This possible mechanism relates to the insolation hypothesis, which suggests that diurnal thermal variation increases with elevation due to thinner air, resulting in more rapid daytime warming and nighttime cooling (Sunday et al. 2019). While this mechanism could theoretically apply to both transects, the extent of diurnal temperature variation is likely influenced by differences in microclimatic conditions. At Sulaiman, the lack of vegetation and rugged, exposed terrain allow higher elevations to heat up more rapidly because of higher radiation compared to the Himalayas, where dense vegetation and greater moisture provide thermal buffering (Sunday et al. 2019). This effect has been demonstrated in ants, with a decline in CT_{max} of subterranean species with elevation (Baudier et al. 2018). While the insolation hypothesis predicts CT_{max} values to be disproportionately influenced by rare extreme thermal events rather than mean temperature, our study suggests that this effect may be more relevant in drier, less buffered environments like Sulaiman,

and less pronounced in thermally buffered regions like the Himalayas.

Our analysis at the group scale reveals that thermal tolerance traits exhibit varied associations with elevation across different transects and taxonomic groups. For example, the CT_{min} of grasshoppers in the Himalayas, contrary to other taxonomic groups, increased with elevation, highlighting the potential influences of biotic interactions, life history, and behavioural differences (Angilletta 2009; Sunday et al. 2014; Bishop et al. 2017). While variation in thermal traits was more consistently associated with elevation, associations of thermal traits with temperature were also present. These findings align with our objective of testing temperature–thermal trait associations and support the idea that temperature plays a role in driving thermal tolerance traits in ectotherms (Angilletta 2009; Bujan, Roeder, Kaspari, et al. 2020). The variation between taxonomic groups may result from biotic interactions (Jankowski et al. 2013; Paquette and Hargreaves 2021), their distinct life histories, and behavioural strategies. For instance, ants and beetles often rely on sheltered or subterranean microhabitats that buffer extreme temperature fluctuations, which could allow them to maintain relatively stable thermal traits across elevations. In contrast, grasshoppers are diurnally active and more exposed to ambient conditions, particularly at higher elevations where vegetation is sparse and cooler thermal refuges are limited during the daytime. This greater exposure may increase daytime heat stress, while also reducing exposure to cooler nighttime temperatures due to behavioural thermoregulation. This could be one explanation for the apparent increase in CT_{min} with elevation in grasshoppers, as reduced cold exposure may relax selection for cold tolerance (Terlau et al. 2023). Spiders, with their varied habits ranging from web-building to ground-dwelling species, may also differ in their capacity to avoid extreme temperatures through behavioural adaptations (Malmos et al. 2021). These species-specific thermal responses are further influenced by activity patterns and foraging behaviours, which can buffer or amplify environmental stress depending on the time of day and habitat structure (Bennett et al. 2019; Bujan, Roeder, Yanoviak, and Kaspari 2020). Overall, the interactions between life history traits, behaviour (Sunday et al. 2014), and habitat structure likely contribute to the divergent patterns observed across biological scales and between transects.

At the species scale, our study reveals substantial variability in how thermal tolerance traits relate to elevation and temperature, demonstrating that patterns observed at community scales may not fully capture the complex responses of individual species to environmental gradients (Start and Gilbert 2019). For instance, on the Sulaiman transect, CT_{max} and thermal tolerance breadth values of *Monomorium indicum* decreased with elevation and increased with temperature, while those of other species showed opposite trends. Between the two transects, thermal tolerance traits of most analysed species showed contrasting patterns. Our study highlights how variation in thermal tolerance along elevation and temperature, likely influenced by microclimatic refugia, leads to contrasting patterns across taxonomic groups and species. As we expected, we show that from group and species scales, thermal tolerance patterns do not always scale up to the community level due to species-specific thermal responses and

habitat differences. This variability means that it is important to account for differences at the various biological scale levels, if possible, when investigating ecological responses to temperature changes.

Our analysis reveals that body size significantly influences thermal tolerance traits, with larger individuals exhibiting greater tolerance to both high and low temperatures, which may enhance their resilience to temperature extremes and climate change. For example, CT_{max} increased with body size at a rate of $0.47^{\circ}\text{C}/\text{mm}$ (averaged across all biological scales). These findings align with studies on ectotherms that also reported a positive relationship between body size and CT_{max} (von May et al. 2019; Weaving et al. 2023; Jones et al. 2024); however, other studies focusing on bees reported no significant influence of body size on thermal tolerance traits (Oyen and Dillon 2018; Gonzalez et al. 2022). Larger individuals often exhibit higher CT_{max} due to greater thermal inertia, meaning they heat up and cool down more slowly compared to smaller individuals (Abou-Shaara 2015). Additionally, larger body sizes retain more water, potentially enabling individuals to tolerate higher temperatures (Jones et al. 2024). Values of CT_{min} decreased at a rate of $0.035^{\circ}\text{C}/\text{mm}$, suggesting larger individuals are better equipped to withstand colder conditions, consistent with the temperature-size rule and previous studies (Kingsolver and Huey 2008; von May et al. 2019; Weaving et al. 2023). As a result, the thermal tolerance breadth increased with increasing body size at a rate of $0.17^{\circ}\text{C}/\text{mm}$. The broader thermal tolerance breadth of larger individuals may make them less vulnerable to climate change in comparison to smaller individuals as they have relatively higher CT_{max} and lower CT_{min} in this study (Gardner et al. 2011; von May et al. 2019), especially at the Sulaiman transect, which already experiences ground temperatures close to 60°C (Khaliq et al. 2023).

Several caveats need to be borne in mind when interpreting the findings of our study. (1) Sampling was limited to during summer. In the Sulaiman transect, we avoided May–August due to extreme heat, while in the Himalayan transect, we sampled during this period as temperatures were mild. Nights outside this period were very cold in the Himalayan transect. While seasonal fluctuations can influence ectotherm thermal tolerances, our findings should be robust for summer when invertebrates are most active. (2) We used a ramping speed of $1^{\circ}\text{C}/\text{min}$ for measuring thermal tolerance in the laboratory, which can be considered relatively fast and potentially lead to an overestimation of thermal tolerances. However, similar thermal tolerance values have previously been reported for the same taxa and our measured values are within the reported ranges (Nascimento et al. 2022). (3) We acknowledge the potential presence of cryptic species along two transects, which may have different thermal tolerances. The identification of cryptic species in these systems is only possible using DNA barcoding, which was beyond the scope of this study. However, there were very few congeneric species in our data and, therefore, our results should be robust to cryptic species. (4) We acknowledge that we did not explicitly apply a phylogenetic framework to account for species relatedness, which may have influenced our trend estimates. However, due to the lack of a molecular-dated phylogeny for all species and the relatively low number of beetle ($n=18$) and grasshopper ($n=22$) species in our dataset, this was not possible. Having said this, to partially account for species-related variation, we

included a nested random intercept structure with order/family/genus/species in our models. Lastly, we acknowledge that we cannot definitively explain all observed patterns. We suggest some mechanisms that may contribute towards explaining our results, but these are not exhaustive and we recognize these may represent important avenues for future research.

5 | Conclusions

Our study examines thermal tolerance patterns at multiple biological scales, revealing significant variability that may impact estimates of biodiversity responses to ongoing and projected climate change. By quantifying thermal tolerance patterns along elevation and temperature gradients for ectotherms across three biological scales in a region with limited biodiversity data, we highlight that aggregative (community and group-scale) analyses often mask critical species variation. Our findings highlight the necessity of considering taxon-specific life histories and behavioral strategies when interpreting thermal tolerance patterns, as different arthropod groups may respond differently to environmental gradients due to their unique ecological and physiological traits. This oversight may lead to inaccurate estimates of range shifts, vulnerability, and extinction risk. Therefore, it is crucial to consider species variation in thermal tolerance traits when developing climate change mitigation strategies (Bolnick et al. 2011; Cahill et al. 2013), as species responses to environmental changes are not uniformly predictable.

Author Contributions

Imran Khaliq and Christian Hof designed the research. Imran Khaliq analysed the data and wrote the first draft. Imran Khaliq, Haseeb Kamran, Muhammad Junaid Shahid, Muhammad Sheraz, Muhammad Awais, Mehtab Shabir, Muhammad Yasir, Abdul Hameed, Muhammad Asgher, and Abdul Rehman conducted the field work. Christian Hof, Maria Riaz, Diana E. Bowler, and Edward Lavender contributed to analysis and writing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The associated data and R code to generate the results and figures are provided as [Supporting Information](#) and uploaded on Figshare repository: <https://figshare.com/s/8567d729c1a864e6e0ca>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1.** geb70135-sup-0001-DataS1.zip.