RESEARCH ARTICLE

The role of thermal tolerance in determining elevational distributions of four arthropod taxa in mountain ranges of southern Asia

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Abstract

1. Understanding the role of thermal tolerances in determining species distributions is important for assessing species responses to climate change. Two hypotheses linking physiology with species distributions have been put forward—the climatic variability hypothesis and the climatic extreme hypothesis. The climatic variability hypothesis predicts the selection of individuals with broad thermal tolerance in more variable climatic conditions and the climatic extreme hypothesis predicts the selection of individuals with extreme thermal tolerance values under extreme climatic conditions. However, no study has tested the predictions of these hypotheses simultaneously for several taxonomic groups along elevational gradients.

2. Here, we related experimentally measured critical thermal maxima, critical thermal minima and thermal tolerance breadths for 15,187 individuals belonging to 116 species of ants, beetles, grasshoppers, and spiders from mountain ranges in central and northern Pakistan to the limits and breadths of their geographic and temperature range.

3. Across all species and taxonomic groups, we found strong relationships between thermal traits and elevational distributions both in terms of geography and temperature. The relationships were robust when repeating the analyses for ants, grasshoppers, and spiders but not for beetles. These results indicate a strong role

of physiology in determining elevational distributions of arthropods in Southern Asia.

4. Overall, we found strong support for the climatic variability hypothesis and the climatic extreme hypothesis. A close association between species' distributional limits and their thermal tolerances suggest that in case of a failure to adapt or acclimate to novel climatic conditions, species may be under pressure to track their preferred climatic conditions, potentially facing serious consequences under current and future climate change.

1 | INTRODUCTION

The geographical distributions of species are influenced by the interplay among the traits of the species, biotic interactions, and the abiotic environment (Chick et al., 2020; Colwell & Rangel, 2009) Most studies investigating this interplay have focussed on temperature, precipitation, resource availability or biotic interactions (Dornelas et al., 2014; Freeman, 2016). More recently, as impacts from anthropogenic climate change have become more apparent, interest in physiology as a major driver of geographical distributions has increased substantially (Hof, 2021) and resulted in a relatively new sub-discipline of ecology: macrophysiology (Bozinovic et al., 2011; Chown et al., 2004; Chown & Gaston, 2008).

Several non-exclusive hypotheses have been proposed that link physiology and species distributions. The climatic variability hypothesis predicts that broad climatic tolerance breadths are selected for under more variable climatic conditions, enabling species to occupy variable climates and thus large geographical areas, both latitudinally and elevationally. Several studies directly or indirectly supported the predictions of the climatic variability hypothesis (Bozinovic et al., 2011; Chick et al., 2020; Khaliq et al., 2014; Letcher & Harvey, 1994). The climatic extremes hypothesis posits that species range limits are determined by their ability to tolerate extreme climatic conditions (Pither, 2003). There is an increasing body of evidence supporting the hypothesis that species capable of tolerating extreme climatic conditions can thrive in areas with harsh climatic conditions, including those found at higher latitudes and elevations (Canterbury, 2002; Gaston & Chown, 1999; Gaston & Spicer, 2001; Khaliq et al., 2017; Pither, 2003). Other studies, though mainly on endotherms, found no such relationship between thermal tolerance and elevational or latitudinal distributions (Freeman, 2016; Khaliq et al., 2017).

Both hypotheses aim to identify the mechanisms of how physiology may influence geographical distributions. It has also been suggested that physiology may not be equally important across the ranges of species (Colwell & Rangel, 2009). Indeed, several studies for both endotherms and ectotherms have highlighted that species' cold range boundaries (e.g. high elevations and latitudes) are constrained by cold extremes (Buckley et al., 2018; Khaliq et al., 2017;

Root, 1988; Sunday et al., 2012). However, current rising temperatures toward the warm edges of species ranges (e.g. low elevations and latitudes) also create challenges for species as they may turn benign conditions into extreme ones. Ectothermic species occurring at lower latitudes, for instance, are already experiencing temperatures that are close to their upper tolerance limits (Deutsch et al., 2008; Sunday et al., 2014). However, there is a lack of evidence regarding the extent to which species' warm tolerances constrains their lower elevational limits. Therefore, species' physiological limits to warm temperatures should also become more important as determinants of species' distributions at their warm edges. If this conjecture is true, then along a climatic gradient such as along elevation, physiology should limit geographic distributions toward both extremes, assuming a mechanistic link between physiological tolerance and geographic distribution.

To date, analyses for multiple species have been carried out at global as well as local levels to test the role of physiological tolerance (Buckley et al., 2018; Khaliq et al., 2017). At regional scales, such studies have mostly been carried out for a single taxonomic group and different studies have shown contradictory results for different taxa (Chick et al., 2020; Freeman, 2016; Slatyer et al., 2016). Several recent synthesis studies have provided convincing empirical evidence that species with broader thermal tolerances tend to occupy larger geographic ranges both along latitudinal and elevational gradients (but see Khaliq et al., 2017) and also have a larger range of experienced temperature conditions. These analyses often use data on thermal tolerances that were compiled from a wide range of studies using different methods for different taxa and regions (Roeder et al., 2021; Sunday et al., 2019). However, the choice of methodology may have an effect on the thermal tolerance data generated (Roeder et al., 2021). Hence, in addition to global synthesis studies, valuable insights can be provided by field-based studies that test the predictions of different hypotheses across different taxonomic groups sampled at the same locality and that follow a standardized methodology (Roeder et al., 2021).

Here, we investigate the variation of thermal traits of 116 arthropod species across four taxa (ants, beetles, grasshoppers and spiders) in central and northern Pakistan, based on experimental measurements of more than 15,000 individuals. Specifically, we

tested for relationships between species' thermal tolerances and their elevational ranges or the range of temperatures they experienced (temperature range hereafter) over 2 years (2018–2019). We expected (i) a positive relationship between species' thermal tolerance breadth (difference between upper and lower thermal tolerance limits) and their elevational or temperature range, as predicted by the climatic variability hypothesis; (ii) a relationship between species' thermal tolerance limits and their elevational distribution limits or the limits of their temperature range, as predicted by the climatic extreme hypothesis.

2 | MATERIALS AND METHODS

2.1 | Field sampling

We sampled along two contrasting elevational transects in the Sulaiman mountain range in central Pakistan and around Nathia Gali within the Himalaya mountain range in northern Pakistan (Sulaiman transect and Himalaya transect hereafter) from 2017 to 2019

(Figure 1). We covered the entire elevational range of the mountains at both transects to make sure that we covered the complete elevational distribution of the species. The Sulaiman transect was sampled in all 3 years, while the Himalaya transect was established in 2018; therefore, only 2 years of data were available for this transect. The transects range from 135 to 2100 m a.s.l. elevation (Sulaiman) and from c. 900 to c. 3000 m a.s.l. (Himalaya); thus, while the elevational ranges are similar (c. 2000 m), the minimum and maximum elevations differ. The sampled area of the Sulaiman transect is very dry with very little vegetation. The air temperatures could reach 50°C at lower-elevation sites over the course of a year, with surface temperatures sometimes reaching 58°C or higher and could reach 0°C at high-elevation sites. Along the Himalaya transect, temperatures are much less extreme, ranging from about −5 to 30°C over the course of a year across different elevations. This region also receives more precipitation than the Sulaiman transect, so the areas we sampled were forest, with Blue Pine, Oaks and Silver Firs as dominant tree species.

In total, we sampled arthropods from 25 sites along these two transects (16 along the Sulaiman transect and 9 along the Himalaya
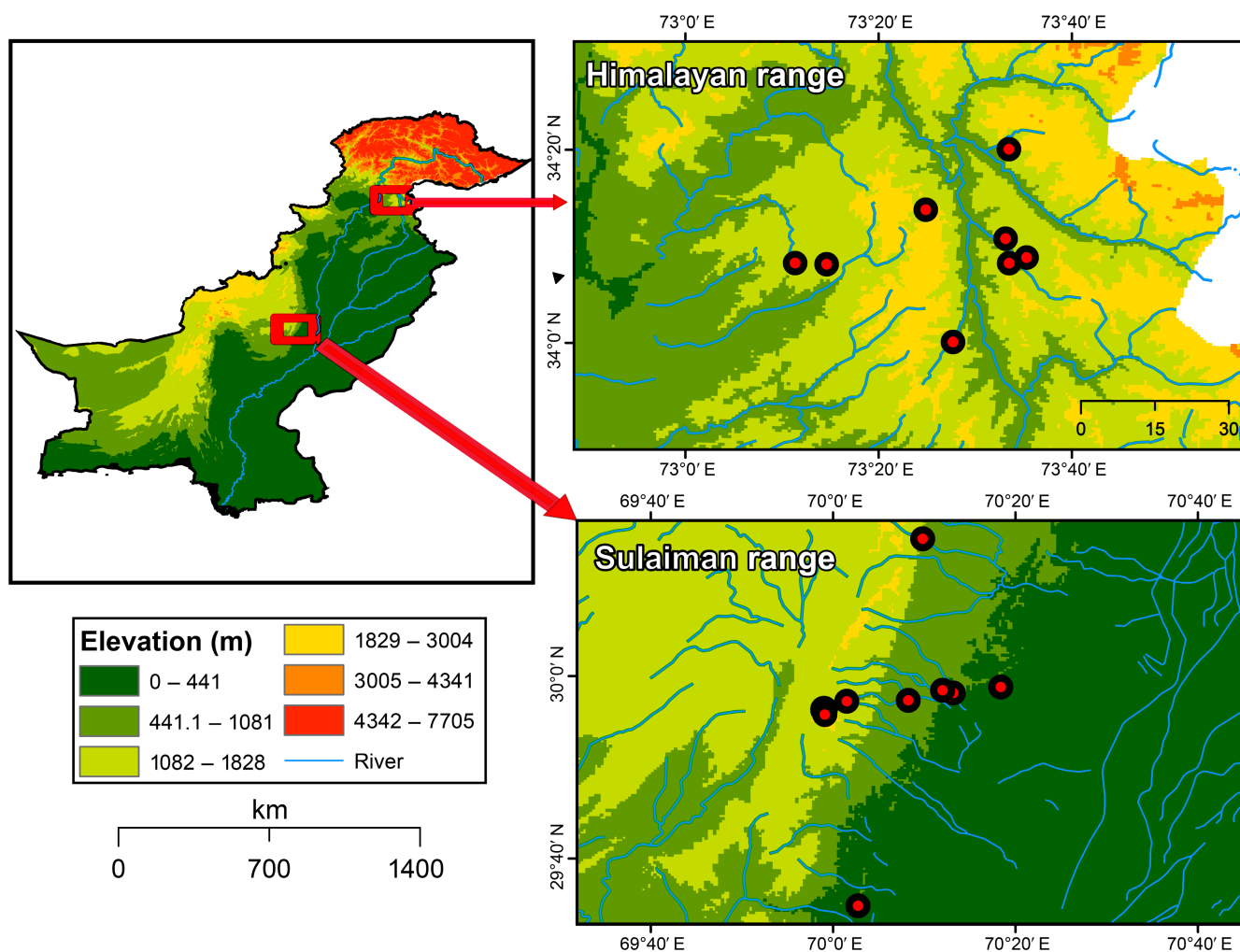
FIGURE 1 Location of the study sites. The two areas with the sampling transect are shown as red rectangles on the map of Pakistan. The red points indicate the locations of the sampling sites. A few of the points are not shown due to close proximity of other sampling sites.

transect) with minimum distance of 200 m between two sites within a transect. We always collected samples on sunny days between 8 am and 4 pm, avoided overcast conditions, and sampled when temperatures ranged from 20 to 35°C. However, at the Sulaiman transect, temperatures were above 35°C during a few of the sampling days. At each site along each transect, we placed three 50 × 50 m quadrats that were 5 to 10 m apart from each other at a similar elevation. Within each quadrat, we placed 6 pitfall traps of 7 cm diameter each. Each pitfall trap had wax on the top to keep the trapped animals inside and was left in the field for 24 h. We placed the traps randomly within the quadrat but at least five m apart from each other. Each site had 18 pitfalls in total. During daytime, we periodically kept on checking the traps and emptied them if arthropods were found in any of the traps. We also hand-collected arthropods (with a focus on ants, beetles, grasshoppers, and spiders) for 16 person hours of effort per quadrat per visit. We kept all captured species separately in boxes having soil at the bottom, without feeding them. We visited each site at least twice per year at the Himalaya transect and three times at the Sulaiman transect. At the Sulaiman transect, sampling frequency was higher and spread across a longer time period of each year, while avoiding the months with the most extreme temperature conditions, that is we collected samples in March, April, September and October. Along the Himalaya transect, we sampled during the summer months only, that is from May to August. Although we sampled the two transects during different months, temperature conditions of the transects were similar in these months. In total, we spent 92 sampling days in the field (36 days at Himalaya transect and 56 days at Sulaiman transect).

After collecting the samples, we brought the animals back to the lab for thermal tolerance measurements. We avoided keeping animals overnight to reduce the potential effect of acclimatization. We established ad-hoc labs close to the sampling sites whenever possible, and we started measuring as soon as samples arrived in the lab. Generally, it took approximately 1 h to reach the laboratory from the sampling site and to start the measurements. To identify grasshoppers, we followed Sultana and Wagan (2015), for ants we followed keys taken from AntWiki (www.antwiki.org), for spiders we followed Ashfaq et al. (2019) and for beetles we followed Ali et al. (2018) and Azadbakhsh and Rafi (2017).

2.2 | Temperature data

We collected temperature data using dataloggers. We placed Tinytag TGP-4017 data loggers at each site at the ground in shade during the sampling period and set the recording interval time at 10 min. We calculated the mean minimum temperature and mean maximum temperature at each site after pooling the data of 2 years (i.e. 2018 and 2019). We took the difference of minimum and maximum temperatures recorded as the temperature range. We avoided using readily available temperature such as Chelsa or the Worldclim dataset (Harris et al., 2020; Karger et al., 2017) because the data are available at a resolution of 1 km², which may not capture the

thermal environment that surface-active individuals experience. Additionally, several of our sites at both transects fall, although they are elevationally separated, within one grid cell. We conducted field surveys on two transects during the months with extreme temperatures and observed very few individuals. At higher elevations, we did not find any individuals at some sites. Consequently, we restricted our analyses to the temperature data that we collected during our sampling period. This ensured that we used only temperature information that we were confident the species had experienced. Therefore, we used the temperature data that we recorded from the data loggers.

2.3 | Thermal tolerance measurement

We used the temperatures at which individuals lost voluntary muscle control to identify temperatures that were the critical thermal limits (Angilletta, 2009). We measured upper critical temperatures (CT_{max}) and lower critical temperatures (CT_{min}) on the same individuals, measuring 15,187 individuals in total (Table S1 in Figshare at https://doi.org/10.6084/m9.figshare.23744610). To make sure that the animals were alive for the second measurement, we measured CT_{min} first. CT_{min} usually is farther from the lethal limits than CT_{max} and thus less damaging to the individuals. Before the CT_{max} measurements, we allowed a minimum of 4 h recovery time for each individual after measuring CT_{min}.

To measure critical thermal limits, we used a XMTD-204 digital thermostat water-bath. We placed the animals in either 1.5 mL Eppendorf tubes or 50 mL Falcon tubes, depending on how big the individuals were. We avoided plugging tubes with cotton as we observed that some individuals were using the cotton as thermal refuge. We discarded all these measurements and found out that Eppendorf tube caps worked fine. No individual was observed hiding in the lid of the tubes. We placed the tubes in the water at 20°C for 5 min so that the tubes' temperatures were equilibrating to the temperature of the water and animals could settle down. After that we started lowering the temperature and at a rate of 1°C per minute. We kept checking the individuals after every minute without taking out the tubes from the water. We noted the temperature as CT_{min} when individuals stopped moving. Once we had measured CT_{min}, we put the individuals back to ambient temperatures. Generally, animals began behaving normal after about 30 min. We measured CT_{max} in the same manner, starting at 20°C, increasing the temperature at a rate of 1°C per minute, and noting CT_{max} as the temperature when the individuals stopped moving. In order to monitor water temperature, we additionally placed three thermometers inside the water baths and continuously monitored the temperatures. For temperatures below 0°C we maintained four containers that were placed in ice and kept the temperatures at −1, −2, −3 and −4°C for these four containers because our water bath equipment could not maintain temperatures below zero. At the Sulaiman transect, we were not able to measure CT_{min} for the samples that were collected in 2017. Therefore, there are no CT_{min}

values for nine spider species and four ant species that were collected only in year 2017 (Table S2). We also measured the body size of all individuals using a Vernier calliper to account for the effect of body size on thermal traits due to the influence of body size on life history traits (Brown & Sibly, 2006). For ants, beetles, grasshoppers and spiders, body size was measured from the tip of the head to the end of the abdomen.

2.4 | Statistical analysis

We included only those species for which we sampled five or more individuals. For each species, we calculated the thermal tolerance breadth as the difference between the mean of the five highest CT_{max} values and the mean of the five lowest CT_{min} values (Chick et al., 2020). As an additional measure of thermal tolerance range, we calculated the standard deviation of the temperatures experienced at all the sites where each species was observed, following the approach of Arnan et al. (2015). This provided a species-specific measure of thermal tolerance range. To calculate the range of the elevational distribution ('elevational range' hereafter), we took the difference between the maximum and the minimum elevations at which a species was sampled. For the minimum elevation for each species, we stopped sampling when we reached the edges of urban areas. We calculated the elevational range for each species separately for each of the two transects as well as after combining the data. Similarly, we calculated the range of experienced ambient temperatures (temperature range), that is as the difference between the maximum temperature and minimum temperature recorded across the elevational range of each species. To compare the mean thermal tolerance range (difference of CT_{max} and CT_{min}), mean CT_{max} and mean CT_{min} among the four taxa, we applied analysis of variance (ANOVA). To test for the relationships between the limits and range of elevational distribution and temperature with thermal tolerance breadth and limits, we applied ordinary least squares (OLS) models. Specifically, we modelled elevational range, maximum elevation, minimum elevation, temperature range, minimum temperature or maximum temperature as a function of body size and the respective thermal trait measure, that is thermal tolerance breadth, CT_{min} or CT_{max}, as well as taxon and transect. For the entire dataset we ran six different regression models: (i) elevational range as a function of body size, thermal tolerance breadth, taxon and transect; (ii) elevational maximum as a function of body size, CT_{min}, taxon and transect; and (iii) elevational minimum as a function of body size, CT_{max}, taxon and transect; (iv) temperature range as a function of body size, thermal tolerance breadth, taxon and transect; (v) minimum temperature as a function of body size, CT_{min}, taxon and transect; and (vi) maximum temperature as a function of body size, CT_{max}, taxon and transect. We also added interaction terms between the respective thermal tolerance variable as well as transect and taxa to the model. We then repeated the analyses for all four taxa separately.

3 | RESULTS

We included 116 species (30 ant, 21 beetle, 17 grasshopper and 48 spider species, Table S2) for our analysis out of 142 species we sampled. Overall, we found the distributions of CT_{min} and CT_{max} to be very similar across all 3 years (Figure S1). On average, spiders showed the broadest elevational range (mean = 1580 m, CI: 1350–1810), and on average ants showed the narrowest range (929 m, CI: 630–1230). All taxonomic groups were observed at all elevations. Thermal tolerance range, CT_{max} – CT_{min} differed significantly among groups (thermal tolerance range: $F = 10.69$, $p < 0.001$; CT_{max}: $F = 11.92$, $p < 0.001$; CT_{min}: $F = 2.78$, $p < 0.05$, Figure S2) and grasshoppers had significantly larger thermal tolerance ranges, higher CT_{max} and lower CT_{min} than spiders, ants, or beetles (Figure S2). The critical temperatures of species observed at five or more elevations displayed a mixed pattern, with some populations exhibiting increasing values, others displaying decreasing values, and some showing no change with increasing elevation (see Figure S3). We observed a positive correlation between number of individuals measured and the thermal tolerance breadth and the elevational range across all taxonomic groups, except in grasshoppers (see Figure S4).

Our results are in accordance with the predictions of the climatic variability hypothesis. Overall, there was a significantly positive relationship between elevational range and thermal tolerance breadth as well as between temperature range and thermal tolerance breadth (elevational range: $p < 0.001$, $R^2 = 0.29$; temperature range: $p = 0.006$, $R^2 = 0.40$; Table 1, Figure 2a,d, Figure S5). Elevational ranges for species were similar across the two transects (Welch's t-test: $p = 0.63$, Table 1). The interactions of thermal tolerance breadth with transect was not significant (elevational range: transect $p = 0.53$; temperature range: transect $p = 0.23$, Table 1), indicating that the relationship between thermal tolerance and elevational range or temperature range did not differ between the two transects. The relationship between elevational range or temperature range and thermal tolerance breadth became even stronger when we combined the data for the two transects and calculated the total elevational range and the total temperature range for each species and relating this to the total thermal tolerance (Table S3). We found few differences when analysing the data separately for each of the four studied taxa (Figure 3). Thermal tolerance breadth was a strong predictor of elevational range at the taxon level, except for beetles (Table 2, Figure 2). The effects of transect and of the interaction between thermal tolerance and transect were not significant except for grasshoppers (Table 2). However, there was less predictive power shown by the thermal tolerance breadth in predicting temperature range for ants and beetles (Table 2). Again, the results of the taxon-specific analyses became even stronger after combining the data for the two transects as explained above (Table S4, Figure 2).

Our results also support the predictions of the climatic extreme hypothesis. Warm tolerance (CT_{max}) was a strong predictor of the minimum elevational limit as well as maximum temperatures

TABLE 1 Overall influence of thermal traits on elevational distributions, based on ordinary least squares models. The response variables elevational range, maximum elevational limit, minimum elevational limit, temperature range, minimum temperature and maximum temperature were separately modelled as function of the predictor variables body size, thermal trait (thermal range, CT_{max} or CT_{min}, the latter calculated as the mean of the 5 most extreme values, respectively), taxon, and transects. Body size (representing the mean of the 5 individuals for which CT_{max} and CT_{min} were calculated, respectively) and thermal traits were added as continuous variables, whereas transect and taxa were added as categorical variables to account for the differences due to different transect and different taxa. We also added interaction terms between thermal traits and transect as well as between thermal traits and taxa. R^2 values represent adjusted R^2 values for the entire model.

Overall (species = 116)

Elevation range	Slope	SE	R^2	p-value	df	Temperature range	Slope	SE	R^2	p-value	df
Thermal range	**106**	**±29**	**0.29**	**<0.001**	**123**	**Temperature range**	**0.416**	**±0.3**	**0.40**	**0.006**	**123**
Body size	−0.586	±18		0.97		Body size	0.059	±0.09		0.51	
Transect	849	±1783		0.63		Transect	−9.75	±8.9		0.28	
Transect: Thermal range	−22	±35		0.53		Transect: Thermal range	0.21	±0.17		0.238	
Beetles	509	±3025		0.86		Beetles	8.18	±15.26		0.59	
Grasshoppers	−4094	±2220		0.06		Grasshoppers	−17.93	±11.20		0.11	
Spiders	518	±1698		0.76		Spiders	4.66	±8.56		0.58	
Beetles: Thermal range	−3.35	±61		0.95		Beetles: Thermal range	−0.15	±0.31		0.61	
Grasshoppers: Thermal range	75	±42		0.07		Grasshoppers: Thermal range	0.29	0.21		1.39	
Spiders: Thermal range	1.85	±33		0.95		Spiders: Thermal range	−0.06	0.17		0.70	
Minimum elevation						**Maximum temperature**					
CT_{max}	**−80**	**±25**	**0.36**	**0.002**	**123**	**CT_{max}**	**0.31**	**0.13**	**0.64**	**0.017**	**129**
Body size	−3.5	±14.37		0.80		Body size	0.01	0.05		0.84	
Transect	−2275	±1584		0.15		Transect	7.10	8.07	0	0.38	
Transect: CT_{max}	37	±30		0.22		Transect: CT_{max}	−0.04	0.15		0.79	
Beetles	−2316	±2735		0.39		Beetles	9.86	14.1		0.48	
Grasshoppers	2960	±1730		0.08		Grasshoppers	−13.5	8.91		0.13	
Spiders	−510	±1365		0.70		Spiders	1.68	6.96		0.80	
Beetles: CT_{max}	42	±55		0.44		Beetles: CT_{max}	−0.17	0.28		0.53	
Grasshoppers: CT_{max}	−52	±32		0.10		Grasshoppers: CT_{max}	0.23	0.16		0.16	
Spiders: CT_{max}	3.37	±26		0.89		Spiders: CT_{max}	−0.003	0.13		0.98	
Maximum elevation						**Minimum temperature**					
CT_{min}	**−234**	**±54**	**0.31**	**<0.001**	**123**	**CT_{min}**	0.61	0.34	0.27	0.07	123

(Continues)

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TABLE 1 (Continued)

Overall (species =116)

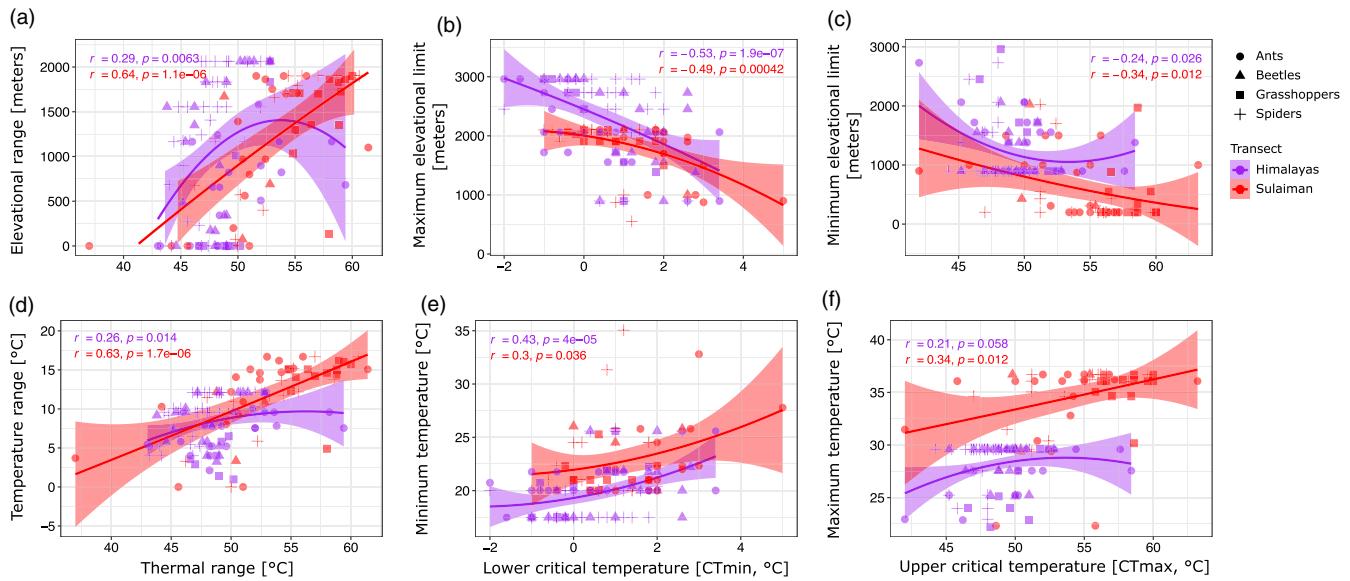|	Elevation range					Temperature range				
	Slope	SE	R^2	p-value	df	Slope	SE	R^2	p-value	df
Body size	26.41	±15		0.09		−0.06	0.08		0.41	
Transect	**−464**	**±127**		**<0.001**		**2.70**	**0.69**		**<0.001**	
Transect: CT_{min}	134	±83		0.10		0.03	0.45		0.94	
Beetles	283	±178		0.11		−0.01	0.97		0.98	
Grasshoppers	−73	±238		0.75		0.08	1.25		0.94	
Spiders	**257**	**±129**		**0.04**		−0.35	0.70		0.61	
Beetles: CT_{min}	−169	±111		0.12		0.30	0.59		0.61	
Grasshoppers: CT_{min}	**−365**	**±157**		**0.02**		0.57	0.83		0.49	
Spiders: CT_{min}	−24	±92		0.79		0.54	0.50		0.27	

All bold values are statistiaclly significant.

(minimum elevational limit: $p=0.002$, $R^2=0.36$; maximum temperature: $p=0.017$, $R^2=0.64$ Table 1, Figure 2c,f). The two transects did not vary in terms of the effect of CT_{max} on minimum elevational limits and maximum temperatures (minimum elevational limit: $p=0.22$; maximum temperature: $p=0.15$ Table 1, Figure 2c). As was CT_{max} for the minimum elevational limit, at both transects CT_{min} was a strong predictor of maximum elevational limit but not of minimum temperature (maximum elevation limit: $p<0.001$, $R^2=0.31$; minimum temperature: $p=0.07$, $R^2=0.27$, Table 1, Figure 2b); in other words, species with lower CT_{min} values occurred at higher elevations both at the Sulaiman and the Himalaya transect. When repeating the analyses for each taxon separately, the results for the relationship between maximum elevation/minimum temperature and CT_{min} remained robust (Table 2). However, for CT_{max} the pattern was less consistent across taxa: in beetles, CT_{max} was not a strong predictor of the minimum elevational limits of species and also CT_{max} was not a strong predictor of the maximum temperature experienced by the species belonging to ants, beetles and spiders (Table 2). However, when combining the data for both transects, CT_{min} and CT_{max} were strong predictors of minimum temperatures and maximum temperatures experienced by the species for all taxonomic groups, except for the beetles (Table S4). We found strong relationship between elevational limits and temperature limits (Figure S6).

4 | DISCUSSION

In one of the largest field campaigns of its kind, we found that eco-physiological traits predicted species distributions for 116 species across four taxonomic groups across two elevational transects. In line with the predictions of the climatic variability hypothesis, we found that species with broader thermal tolerance breadths, on average, occupy larger elevational ranges or temperature ranges compared to species with narrower thermal tolerance breadths. The positive relationship of thermal tolerance breadth and elevational range or temperature range was consistent across taxa, with the exception of beetles. Our results are also in line with the climatic extremes hypothesis: critical thermal limits (CT_{max} and CT_{min}) predict lower and upper elevational limits as well as maximum and minimum temperatures. These relationships between thermal and elevational/temperature limits were consistent among the four taxa studied.

Ectothermic species depend upon temperature to function in the environment (Angilletta, 2009; Angilletta Jr & Dunham, 2003). Such temperature dependence suggests that ectotherms should need broader thermal tolerances to occur along extensive environmental gradients. Our results confirm this assumption in four arthropod taxa along two different elevational gradients in central and northern Pakistan. Although these transects differ considerably in their climatic conditions and vegetation, the relationship between thermal traits and distributional ranges are largely congruent between them, indicating that thermal physiology plays a similar role despite differences between transects. The positive correlation between

FIGURE 2 Relationships between thermal traits and elevational distributions or experienced temperatures, with (a, d) the relationship between thermal tolerance range and elevational range or temperature range, (b, e) the relationship between CT_{min} with maximum elevational limit and minimum temperature experienced, and (c, f) the relationship between CT_{max} and minimum elevational limit and maximum temperature experienced. Points (with each point indicating a species) and regression lines for the Himalaya transect are indicated in purple, points and lines for the Sulaiman transect are shown in pink; different point symbols indicate different arthropod taxa. We applied linear models with a quadratic term to model elevational range as a function of thermal range and temperature range.
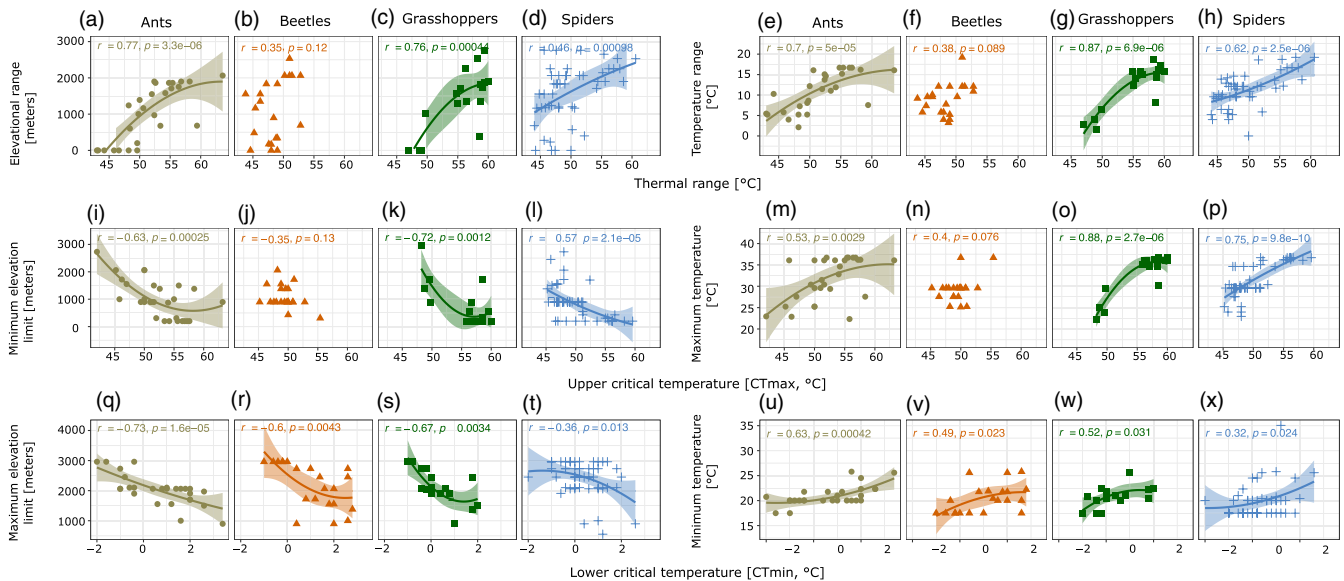
FIGURE 3 Relationships of thermal traits with the geographical distributions and experienced temperatures combine at two transects. Panels (a–h) show the relationships of thermal tolerance range with elevational ranges or temperature ranges; panels (i–p) show the relationships of upper critical temperatures (CT_{max}) with minimum elevation limits or maximum temperatures experienced: panels (q–x) show the relationships of lower critical temperatures (CT_{min}) with maximum elevation limits or maximum temperatures experienced. Regression lines are not added for the relationships that were not statistically significant.

thermal tolerance breadth and elevational range or temperature range was consistent even when conducting the analyses separately for the four different taxonomic groups, with beetles being the only exception. However, with only three beetle species being part of the dataset collected at the Sulaiman transect in central Pakistan and about 20 species in samples from the Himalaya transect in northern

Pakistan, the species set of this taxon is rather imbalanced, especially given that beetles are the most speciose insect taxon. Studies conducted in North America and Europe have demonstrated a significant correlation between the thermal tolerance range and elevational range of ectothermic species. However, this relationship has not been observed to the same extent in endothermic species,

TABLE 2 Influence of thermal traits on elevational distributions of ants, beetles, grasshoppers and spiders, based on ordinary least squares models. The response variables elevational range, maximum elevational limit, minimum elevational limit, temperature range, minimum temperature and maximum temperature were separately modelled as function of the predictor variables body size, thermal trait (thermal range, CT_{max} or CT_{min}, the later calculated as the mean of the 5 most extreme values respectively), and transects. Body size (representing the mean of the 5 individuals for which CT_{max} and CT_{min} were calculated, respectively) and thermal traits were added as continuous variables and transect was added as categorical variable to account for the differences due to different transect. We also added interaction terms between thermal traits and transect. R^2 values for the entire model.

Elevation range	Slope	SE	R^2	p-value	df	(Temperature response)	Slope	SE	R^2	p-value	df
Ants (species = 30)						Temperature range					
Thermal range	**76**	**±30**	**0.35**	**0.01**	**34**	Thermal range	0.26	0.17	0.49	0.13	34
Body	22	45		0.63		Body	−0.041	0.26		0.8	
Transect	−544	2122		0.79		Transect	−17.07	12.21		0.17	
Transect: Thermal range	15	42		0.70		Transect: Thermal range	0.41	0.24		0.09	
Minimum elevation						**Maximum temperature**					
CT_{max}	**−77**	**±30**	**0.35**	**0.01**	**36**	CT_{max}	0.31	0.21	0.45	0.14	36
Body	5.24	39		0.89		Body	−0.14	0.27		0.60	
Transect	−2612	±2168		0.23		Transect	6.8	15.23		0.65	
Transect: CT_{max}	41	42		0.33		Transect: CT_{max}	−0.02	0.29		0.92	
Maximum elevation						**Minimum temperature**					
CT_{min}	**−248**	**±57**	**44**	**<0.001**	**34**	**CT_{min}**	**0.67**	**0.33**	**0.35**	**0.049**	**34**
Body	40	30		0.19		Body	−0.008	0.17		0.96	
Transect	164	251		0.51		Transect	−1.91	1.44		0.19	
Transect: CT_{min}	−40	114		0.72		**Transect: CT_{min}**	**1.35**	**0.65**		**0.04**	
Beetles (species = 28)						Temperature range					
Thermal range	137	±77	0.02	0.09	28	Thermal range	0.38	0.3	<0.001	0.18	28
Body	−22	54		0.68		Body	−0.08	0.22		0.71	
Transect	14,263	16,237		0.39		Transect	11.48	69.11		0.87	
Transect: Thermal range	−292	322		0.37		Transect: Thermal range	−0.23	1.37		0.86	
Minimum elevation						**Maximum temperature**					
CT_{max}	−23	±58	0.03	0.69	28	CT_{max}	−0.007	0.26	0.50	0.97	28
Transect	9109	6321		0.16		Transect	−39.9	28.27		0.17	
Transect: CT_{max}	−181	123		0.16		Transect: CT_{max}	0.89	0.55		0.12	
Maximum elevation						**Minimum temperature**					

TABLE 2 (Continued)

Elevation range	Slope	SE	R^2	p-value	df	Temperature range	Slope	SE	R^2	p-value	df
CTmin	−369	±127	0.27	0.009			1.10	0.50	0.38	0.04	
Body	29	41		0.48			−0.14	0.16		0.39	
Transect	−349	565		0.54			6.5	2.21		0.008	
Transect: CTmin	−158	359		0.66	17		−0.722	1.4		0.61	17
Grasshoppers (species = 17)											
Thermal range	343	±82	0.60	<0.001		Maximum temperature	1.54	0.47	0.72	0.004	17
Body	12	20		0.55			0.15	0.11		0.19	
Transect	13,906	6020		0.03			68.89	34.73		0.06	
Transect: Thermal range	−274	112		0.02	61		−1.28	0.64		0.06	
Minimum elevation						**Minimum temperature**					
CTmax	−301	±102	0.81	0.008			1.05	0.41	0.83	0.02	
Transect	−17,118	7882		0.04			60.51	32.37		0.07	
Transect: CTmax	320	145		0.04			−1.03	0.59		0.10	
Maximum elevation						**Maximum temperature**					
CTmin	−777	±83	0.36	<0.001			2.38	0.59	0.42	<0.001	
Body	15	11		0.19			−0.17	0.08		0.04	
Transect	−352	118		0.008			1.81	0.84		0.04	
Transect: CTmin	530	128		<0.001			−0.99	0.91		0.29	
Spiders (species = 48)											
Thermal range	183	±42	0.36	<0.001			0.72	0.19	0.43	<0.001	45
Body	9.173	65		0.88			0.04	0.30		0.87	
Transect	1284	2854		0.65			−10.8	13.29		0.41	
Transect: Thermal range	−46	56		0.42	45		0.15	0.26		0.56	
Minimum elevation						**Maximum temperature**					
CTmax	−80	±54	0.31	0.14			0.35	0.21	0.73	0.10	
Body	−46	48		0.34			0.15	0.19		0.43	
Transect	−1111	3217		0.73			2.52	12.86		0.84	
Transect: CTmax	18	64		0.77			0.03	0.25		0.90	

TABLE 2 (Continued)

Elevation range	Slope	SE	R²	p-value	df	Temperature range	Slope	SE	R²	p-value	df
Maximum elevation						Minimum temperature					
CTmin	−243	±193	0.31	**0.01**		CTmin	0.91	0.552	0.38	0.08	
Body	−83	62		0.19		Body	0.23	0.34		0.49	
Transect	−656	193		**0.001**		Transect	4.03	1.05		**<0.001**	
Transect: CTmin	83	182		0.64		Transect: CTmin	0.83	0.98		0.40	

All bold values are statistiacly significant.

likely due to the greater physiological reliance of endotherms on internal temperature regulation as compared to ectotherms, which are more reliant on their external environment (Arnan et al., 2015; Calosi et al., 2008; Chick et al., 2020; Freeman, 2016; Khaliq et al., 2017).

We have noted a strong correlation between CT_{max} and maximum temperatures, with the lower elevational limits of species also influenced by their CT_{max}. The limited evolutionary potential of ectotherm species in response to rising temperatures puts them at risk, as they may be unable to adapt to increasing temperatures (Diamond et al., 2012; Hoffmann et al., 2013; Hoffmann & Sgrò, 2011). In such cases, species may shift their distributional ranges to higher elevations to better suit their thermal preferences, assuming no evolution occurs. However, such a shift may not be possible for high-elevation species due to the lack of suitable habitat at even higher elevations. Our findings indicate that species have a safety margin between 9 and 33°C based on air temperatures calculated as the difference between CT_{max} and ambient temperature, suggesting that they are not currently under significant stress to track their thermal preferences. However, during April, we observed ground temperatures of up to 60°C along the Sulaiman transect, where the majority of species are ground-dwelling. This suggests that many species in this area are already at risk of being exposed to temperatures beyond their tolerance limits during summer months, with safety margins ranging from −18 to 3.2°C. The situation is different along the Himalaya transect, where the ground is covered with vegetation, meaning that species may not be exposed to temperatures that are close to their tolerance limits.

Different populations inhabiting different elevations may be adapted to local conditions and may show differences. The populations of the four taxonomic groups under study exhibit diverse patterns in their critical temperatures with respect to elevation. For most critical temperature values decreased as elevation increased, but a few species of ants and grasshoppers exhibited an increase in critical temperature values. For several species of all four taxa yet, critical temperature values did not vary systematically with elevation. Previously contradictory patterns of thermal tolerance breadth along elevational gradients similar to the gradients in our study have been reported (Bishop et al., 2017; Chick et al., 2020; Nowrouzi et al., 2018). As temperatures continue to rise, species with strong local adaptations may be at risk of local extirpation if their populations are unable to evolve in response. The highly variable responses of different species within ecological communities make it difficult to accurately predict how certain taxonomic groups will respond to climate change in a general sense, posing a significant challenge for researchers and conservationists alike.

Our study is unique on two accounts. First, we test predictions of two macrophysiological hypotheses across four taxa that have been exposed to similar environmental conditions. By doing so, we believe that a lot of potentially confounding factors such as methodological differences, that have been shown to be able to cause between 6% and 82% of variation in the data (Lenoir et al., 2020; Terblanche et al., 2007) as well as temporal or geographical differences have been accounted for. Our results are in line with other

studies that found similar influence of thermal tolerance on elevational distribution of different ectotherm taxa (Calosi et al., 2008; Chick et al., 2020; Gaston & Chown, 1999; Gaston & Spicer, 2001). Secondly, we report on ectotherm diversity from a region where very few empirical, hypothesis-driven studies have been conducted so far (Hussain, 2017; Sial et al., 2012; Umar et al., 2018). Therefore, our data will contribute to drawing a more complete picture regarding global thermal tolerance distribution (Bennett et al., 2018) and thereby to a better representation of global biodiversity data (Meyer et al., 2015).

Our study investigated two distinct mountain regions with different habitats, providing a comprehensive evaluation of the long-standing inquiry regarding the influence of physiological tolerance on species distribution across four major ectothermic taxa (Khaliq et al., 2017; Slatyer et al., 2013; Stuart-Smith et al., 2017). The implications of our findings go beyond these particular taxa, assuming that ectotherms in general display similar reactions to environmental changes. Our study reveals a challenging future for species with limited thermal tolerance, as they may struggle to adapt to future shifts in temperature regimes (Warren & Chick, 2013). Based on our research, we propose that integrating knowledge of thermal tolerance into broader conservation efforts might enable proactive and adaptive approaches to mitigate the effects of climate change (Hof, 2021). By considering the thermal requirements and limitations of species, conservationists can develop strategies to safeguard habitats, facilitate species migration, and protect vulnerable populations (Hof, 2021). This contribution will enhance the long-term survival and resilience of ecosystems in a changing world. An integrative and holistic approach to studying the impacts of climate change on mountain biodiversity, encompassing a wider range of taxa and regions, can generate additional physiological data. Furthermore, incorporating other significant biological factors such as biotic interactions, dispersal limitations and energetic requirements can enhance predictions of species responses to a changing climate (Methorst et al., 2017).

4.1 | Caveats

We note that there are some caveats of our study. First, we sampled along two different transects and could not capture the differences in microclimatic conditions that individuals may experience, even though microclimatic variation is an important factor especially in mountainous areas (Scherrer & Körner, 2011) and thermal tolerances of insects may be strongly influenced by the climatic conditions they experience locally (Rodrigues & Beldade, 2020). Furthermore, sampling was done in different months at the two transects due to differences in temperatures: we had to avoid sampling during the months of May, June, July and August at the Sulaiman transect due to extremely high temperatures, whereas we sampled during these 4 months at the Himalaya transect as temperatures were mild during these months. Apart from these months, temperatures during nights were very low at the Himalaya transect. However, despite these temporal inconsistencies, our inferences should be robust, as the effect of transect on the observed relationships was low.

Second, our measurements of cold tolerance below 0°C were not done with automated equipment, but with ice containers. However, we kept the temperature constant and continuously monitored the temperatures using three different thermometers. Additionally, we repeated the measurements for different individuals belonging to the same population sampled during different months and found that values were very close to each other. Our relatively fast ramping speed of 1°C per minute may have contributed to high thermal tolerance (CT$_{max}$) values overall. Even though this should not influence the patterns observed in our study, as all measurements were made in a standardized manner, it needs to be borne in mind when comparing our results to other studies. Nevertheless, similarly high values have already been reported in the literature (Nascimento et al., 2022). We acknowledge that we did not allow much time for individuals to acclimatize and measured critical thermal limits as soon as we reached the laboratory (Slatyer et al., 2016). To test for the effect of acclimatization, we did measure critical thermal temperatures for some individuals after keeping them for 2–5 days in the laboratory. The values were very similar, and we did not include these individuals in our analysis to keep similar conditions for all individuals.

Third, we measured CT$_{min}$ and CT$_{max}$ on the same individual (CT$_{min}$ first and afterward CT$_{max}$). This procedure may have an effect on the measured values of upper critical temperatures due to the cold shock that individuals may have experienced (Sinclair et al., 2015). However, at the Sulaiman range in year 2017, we measured only CT$_{max}$, and not CT$_{min}$ values. As the CT$_{max}$ values are very similar across the three sampling years at the Sulaiman range, we assume that any potential effect of measuring critical temperatures on the same individual is negligible for the interpretation of our findings.

Fourth, the number of individuals measured can affect the measurement of thermal tolerance breadth. Typically, large sample size yield greater trait variation, increasing the likelihood of observing a wider thermal tolerance range. Our findings confirmed this relationship, while also revealing a strong connection between the number of individuals measured and a species' elevational range. This suggests that we tended to sample more individuals from species with greater elevational ranges and the difference is not entirely driven by differences in the numbers of measured individuals per species but due to experienced climatic conditions. To ensure consistency in our sampling approach, we conducted our study using a standardized method and revisited the same site several times across all sampled year.

Fifth, it should be noted that we could not test for the relative amount of plasticity and adaptiveness in the variation of the physiological traits. Mixed evidence has so far been presented for limited seasonal plasticity, and adaptive capacities in different taxa have been reported (Andrew et al., 2013; Bujan et al., 2020). Assuming that plasticity in the thermal traits measured in our field work and experiments is limited, we might predict that the distributions of the studied species will also change in response to changes in temperature regimes. However, our results should be robust at least for the summer months, which is the most active season for ectotherms in

this region and most relevant in a context of rising temperatures due to ongoing and future climate change. Lastly, we acknowledge that there is a possibility of cryptic species or simply misidentifications in our data, and these may have different thermal tolerances that may influence our results (Paraskevopoulou et al., 2018). However, there are few congeneric species in our samples, therefore we are confident of the patterns reported in our study.

5 | CONCLUSIONS

Overall, we found consistent patterns across four distinct arthropod groups—ants, beetles, spiders, and grasshoppers—which highlight that the thermal physiology of ectotherms plays an important role in determining species distributions and limiting their ranges, at least across the two studied transects. Our findings are also relevant for a better understanding of the potential responses of species to a changing climate. Several recent studies have highlighted that species are on the move and tracking their preferred temperature regimes (Freeman et al., 2021; Pecl et al., 2017). A tight relationship of thermal traits with the range and temperature limits points toward a contraction of elevational ranges for the species studied if temperature increases at lower elevations (Colwell et al., 2008). In general, all four studied taxa appear to respond to spatial variation in climate in a similar manner. However, probably due to the unique life history of each arthropod lineage, we also noted a few differences. These differences may point toward the role of behavioural thermoregulation, a common strategy to avoid extreme climatic conditions, especially in ectotherms (Andrew et al., 2013; Sunday et al., 2014). If species' geographic limits are predominantly constrained by their physiology, they would be under pressure to tightly track their preferred thermal niches, unless they evolve, acclimate or migrate at different rates. If such species fail to do so due to competition with other species, to mismatches in species interactions (Schleuning et al., 2020) or due to geographic barriers (White, 2016), they may be facing dire situations in the future.

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SUPPORTING INFORMATION

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

Figure S1. Distribution of critical thermal minima and critical thermal maxima across three sampling years.

Figure S2. Analysis of variance of thermal tolerance range, upper critical temperatures and lower critical temperatures among four taxa. Statistically significant pairwise differences of means using Tukey's post-hoc test are shown as horizontal lines of each significant pairs with significance level is showing by the stars. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$ and $****p < 0.0001$.

Figure S3. The populations of species of four taxonomic groups under study exhibit diverse patterns in their critical temperatures with respect to elevation. Some groups show a decrease in critical temperature values as elevation increases, while others exhibit an increase in critical temperature values, or critical temperature values remain unchanged despite changes in elevation. Each colour dot represents a population, while the coloured regression lines correspond to individual species, with confidence intervals displayed in matching colour. Our analysis focused exclusively on species with data available for at least five populations.

Figure S4. Relationship between the number of individuals measured per species and the thermal tolerance breadths and elevational range occupied by each species.

Figure S5. Relationship between elevational range (measured as the difference between the maximum and minimum elevation occupied by each species) and experienced thermal range (measured as the standard deviation of temperatures experienced by each species across all sites occupied)

Figure S6. The relationship between the minimum temperature and maximum temperature, as measured in the field during sampling, is examined in relation to the maximum and minimum elevation of each species. Each data point represents a unique species.

Table S1. Uploaded on the Figshare.

Table S2. Physiological thermal tolerances, geographical range limits information at species level at two trasects.

Table S3. Overall influence of thermal traits on elevational distributions, based on ordinary least squares models.

Table S4. Influence of thermal traits on elevational distributions of ants, beetles, grasshoppers and spiders, based on ordinary least squares models.