
Article

The Janus of macrophysiology: stronger effects of evolutionary history, but weaker effects of climate on upper thermal limits are reversed for lower thermal limits in ants

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Handling editor: Rüdiger Riesch

Received on 26 June 2017; accepted on 22 November 2017

Abstract

Species may exhibit similar traits via different mechanisms: environmental filtering and local adaptation (geography) and shared evolutionary history (phylogeny) can each contribute to the resemblance of traits among species. Parsing trait variation into geographic and phylogenetic sources is important, as each suggests different constraints on trait evolution. Here, we explore how phylogenetic distance, geographic distance, and geographic variation in climate shape physiological tolerance of high and low temperatures using a global dataset of ant thermal tolerances. We found generally strong roles for evolutionary history and geographic variation in temperature, but essentially no detectable effects of spatial proximity *per se* on either upper or lower thermal tolerance. When we compared the relative importance of the factors shaping upper and lower tolerances, we found a much stronger role for evolutionary history in shaping upper versus lower tolerance, and a moderately weaker role for geographic variation in temperature in shaping upper tolerance when compared with lower tolerance. Our results demonstrate how geographic variation in climate and evolutionary history may have differential effects on the upper and lower endpoints of physiological tolerance. This Janus effect, where the relative contributions of geographic variation in climate and evolutionary history are reversed for lower versus upper physiological tolerances, has gained some support in the literature, and our results for ant physiological tolerances provide further evidence of this pattern. As the climate continues to change, the high phylogenetic conservatism of upper tolerance may suggest potential constraints on the evolution of tolerance of high temperatures.

Key words: biogeography, evolutionary history, latitudinal cline, macrophysiology, temperature, thermal tolerance.

It should come as no surprise that climate shapes variation among species in their physiological climatic tolerances, and indeed, evidence has been steadily accumulating in support of this relationship (Chown et al. 2004; Gaston et al. 2009; Chown and Gaston 2016). Such macrophysiological investigations of the relationship between climate and physiological tolerance across large regional to global scales have been carried out in a diversity of taxa ranging from plants to insects to mammals (e.g., Addo-Bediako et al. 2000;

Atkin and Tjoelker 2003; Sunday et al. 2011; Buckley et al. 2012; Araújo et al. 2013). But genetic or developmental constraints shared by closely related species can also shape tolerance trait values (Losos 2008; Revell et al. 2008). Phylogenetic signal, or the tendency of closely related species to resemble one another with respect to their trait values, can sometimes be quite high for physiological traits (Kellermann et al. 2012; Grigg and Buckley 2013). Quantifying the contribution of shared evolutionary history relative to geographic

variation in climate is therefore key to understanding the past evolution of physiological tolerances, and the potential for tolerances to evolve under rapid contemporary changes in climate.

Biogeographic patterns of physiological tolerances of temperature suggest that lower and upper tolerances may be differentially influenced by geographic variation in climate, reflecting environmental filtering and local adaptation, and evolutionary history, reflecting shared underlying genetic or developmental constraints due to common ancestry. For many ectothermic species, lower thermal tolerances appear to track latitudinal variation in climate more strongly than upper thermal tolerances (Sunday et al. 2011), and upper tolerances are frequently characterized by high levels of phylogenetic conservatism (Diamond et al. 2012; Kellermann et al. 2012). In a general sense, the culmination of these patterns suggest a 2-sided effect in the macrophysiology of thermal tolerances, wherein evolutionary history and geographic variation in climate have contrasting roles across lower and upper physiological tolerances. These 2-sided effects recall the Roman god Janus bearing one face looking forward and one backward, typically in context of the passage of time. Here, we have the backward-looking face of evolutionary history (phylogeny), and the forward-looking face of climate.

Although the consensus of the currently available data suggests lower thermal tolerances are more strongly influenced by geographic variation in climate, and upper thermal tolerances by evolutionary history, there is an overwhelming focus in the literature on upper thermal tolerances (Sunday et al. 2011), making it difficult to fully evaluate the generality of this pattern without more data on lower thermal tolerances. Beyond gaining a clearer understanding of extant biogeographic patterns in thermal tolerances, quantifying the differential effects of geographic variation in climate and evolutionary history on upper and lower tolerances has important implications for organismal responses to global climate change. If tolerances are more strongly influenced by shared evolutionary history, then we may expect that this phylogenetic conservatism would lead to a reduced ability to respond to future changes in climate; however, if tolerances are more strongly influenced by geographic variation in climate, then we may expect greater lability in the response to environmental change.

We set out to examine the Janus effect in macrophysiology—the differential effects of evolutionary history and geographic variation in climate on upper and lower physiological tolerances—using ants as a model system and a global-scale dataset of their thermal tolerances. Ants are a ubiquitous feature of many habitats: given their abundance, distribution, and key roles in ecosystem function, their geographic ranges, and physiological tolerances of major environmental variables including temperature and aridity are well characterized (Del Toro et al. 2012; Diamond et al. 2012). We address the question of relative determinants of variation in tolerance by partitioning variance in physiological tolerance of high and low temperature into phylogenetic distance and geographic (spatial) distance, and, after these phylogenetic and spatial distances are accounted for, by examining the direct influence of geographic variation in climate on thermal tolerance traits (Freckleton and Jetz 2009). The expectations under this approach are that: more closely related species will exhibit more similar tolerance values; species that are in closer spatial proximity to one another will exhibit more similar tolerance values; and, after accounting for phylogenetic and spatial distance, geographic variation in climate will shape tolerances such that warmer, less thermally variable environments will yield the highest values of upper and lower tolerance (Sunday et al. 2011). Using this approach, we evaluate the evidence for the differential

effects of evolutionary history and geographic variation in climate on thermal tolerances, that is, that evolutionary history will be relatively more important for upper tolerance, and that geographic variation in climate will be relatively more important for lower tolerance.

Materials and Methods

Data sources

Ant thermal tolerance

We updated a global dataset of ant upper and lower thermal tolerances (Diamond et al. 2012) with new empirical data, and with 3 published studies that were not previously included in the dataset (Clusella-Trullas et al. 2010; Baudier et al. 2015; Verble-Pearson et al. 2015). All thermal tolerances were based on the critical temperatures (CTs) at which muscular coordination was lost, and were estimated on individuals using a biologically relevant dynamic temperature ramping protocol (Terblanche et al. 2011). For each species, we computed the mean upper and lower thermal tolerances (the critical thermal maximum, CT_{\max} , and the critical thermal minimum, CT_{\min} , respectively) from populations across the entire geographic range where possible, and otherwise used thermal tolerances from near the center of the geographic range. Although intraspecific variation in thermal tolerances across latitude is known for some ant species (Diamond et al. 2012), to be able to partition variance in tolerance into geographic and phylogenetic components, our analyses were necessarily focused at the species level. An ideal scenario for such an analysis would be one in which species had similar tolerance responses across latitude, such that species mean tolerances would be sufficient to capture the variation of interest. Achieving this scenario is challenging as species occupy different latitudinal ranges, and may exhibit different tolerance responses to latitude even over comparable latitudinal ranges. For our analyses, the situation we wished to avoid was one in which species mean tolerances are systematically correlated with the slope of the relationship between population tolerance and latitude. To evaluate this possibility, we examined the correlation between (phylogenetically corrected) ant species mean thermal tolerances and the slope of the relationship between tolerance and latitude. We found these variables to be uncorrelated, allowing us to focus on mean differences among species in their thermal tolerance (see the Supplementary Material).

Phylogenetic distance

To explore the role of evolutionary history in shaping ant thermal tolerances, we used a genus-level ant phylogeny (Moreau and Bell 2013), and interpolated unknown species relationships as terminal polytomies.

Geographic distance

To explore the role of geographic (spatial) distance in shaping ant thermal tolerances, we developed an occurrence dataset by combining the geographic coordinates of individual ant species occurrences from AntWeb records, the georeferenced occurrences from the updated global thermal tolerance dataset and a published dataset of ant occurrences (Fitzpatrick et al. 2011). We used a dynamic alpha hull method (Rabosky et al. 2016) to compute the geographic range of each species in the thermal tolerance dataset, and then obtained the centroids of each of these ranges. We used the range centroids to

compute the spatial distance between ant species ranges (following Jetz and Freckleton 2015; Cardillo and Skeels 2016).

Geographic variation in climate

To explore the role that geographic variation in climate plays in shaping thermal tolerance, we extracted 5 bioclimatic variables describing variation in temperature from WorldClim 2.0 (Fick and Hijmans 2017), at a 30 arc-s (~ 1 km) resolution, throughout the estimated range for each species. We then computed the average values, across the entire range, of mean annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature seasonality, and temperature isothermality. We selected these temperature variables on the basis that they cover climatic means, extremes, and variability in temperature, each of which can shape thermal tolerance in different ways and to different degrees (Angilletta 2009).

Composition of the complete dataset

The final dataset of phylogenetic distance, geographic distance, and climate covariates included 148 species for CT_{\max} and 59 for CT_{\min} . We had CT_{\max} values for 32 tropical ($0\text{--}23.5^\circ$ absolute latitude), 41 subtropical ($23.5\text{--}35^\circ$ absolute latitude), and 75 temperate ($35\text{--}66.5^\circ$ absolute latitude) species (based on the latitudinal position of the range centroid). Likewise, we had CT_{\min} values for 8 tropical, 19 subtropical, and 32 temperate species. Although we had many species for which we had CT_{\max} but no CT_{\min} (Figure 1), we had no species with CT_{\min} values but no corresponding CT_{\max} . Given these biases toward upper thermal tolerance and temperate species, we re-analyzed our dataset excluding less well-replicated tropical species and species for which we only had CT_{\max} and no corresponding CT_{\min} values (see the Supplementary Material; Table 1). Our final dataset included mostly native species, though we did also include the following introduced species for which we had tolerance, phylogenetic, and geographic data: *Anoplolepis gracilipes*, *Brachyponera chinensis*, *Linepithema humile*, *Monomorium floridana*, *Monomorium pharaonis*, *Pheidole pallidula*, *Solenopsis geminata*, *Solenopsis invicta*, *Tetramorium bicarinatum*, and *Tetramorium caespitum*. We used all available thermal tolerance data for these species, without regard for native or introduced range location. Similarly, we computed the indices of geographic variation in temperature throughout their native and introduced range. The dynamic alpha hull range estimation method we used allows for disjoint range components, a scenario that frequently arises for introduced species (the range centroid in these cases was estimated from the largest range component). Because of this ambiguity in geographic and climatic parameters for introduced species, we re-analyzed our data using only native species (see the Supplementary Material). All statistical analyses were performed using R (R Core Team 2016).

Relative contributions of phylogenetic distance, geographic (spatial) distance, and geographic variation in climate to interspecific variation in ant thermal tolerances

To explore the relative contributions of geographic distance and phylogenetic distance to variation in ant thermal tolerance, we used a statistical variance partitioning method (Freckleton and Jetz 2009). In this method, there are 3 parameters— φ is the proportion of the trait variance attributable to space, $\gamma = (1-\lambda)(1-\varphi)$ is the proportion of the trait variance independent of phylogeny or space,

and $\lambda' = \lambda(1-\varphi)$ is the proportion of the trait variance attributable to phylogeny. The parameters γ , λ' , and φ always sum to 1, and are estimated using maximum likelihood. V is a variance–covariance matrix describing the expectation, and is a function of φ and λ ; Σ is a variance–covariance matrix of the phylogenetic distances among species, b is a vector of the heights of the tips from the phylogeny, and W is a variance–covariance matrix of the spatial distances among species.

$$V(\phi, \lambda) = \gamma b + \lambda' \Sigma + \varphi W.$$

We used the *regress* function and library to partition variance components following Cardillo and Skeels (2016). We performed this method separately for upper thermal tolerance (CT_{\max}) and lower thermal tolerance (CT_{\min}).

Initially, we performed a visual exploration of ant thermal tolerances along temperature and precipitation climatic gradients using Whittaker biomes (Whittaker 1962). The biome plots suggested substantial effects of climate on some components of thermal tolerance, with the axis describing variation in mean annual temperature exhibiting the strongest association. We therefore focused our subsequent analyses of geographic variation in climate on indices of environmental temperature. We included geographic variation in climate—mean annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature seasonality, and temperature isothermality—as covariates in our variance partitioning models of upper and lower thermal tolerance. To avoid multicollinearity, driven by strong correlations among temperature climate variables, we considered each predictor separately.

Because correlations among traits could also drive patterns of phenotypic variation beyond the influence of evolutionary history and geographic variation in climate alone (Hoffmann 2010), we performed a complementary analysis of correlated evolution of upper and lower thermal tolerance. To accomplish this task, we performed correlation analysis on the phylogenetically independent contrasts of both CT_{\max} and CT_{\min} (Felsenstein 1985).

Results

Models that partitioned variance in thermal tolerance into phylogenetic and geographic components detected a moderate to large role for phylogenetic distance (Figure 1), but a very small role for geographic (spatial) distance (Figure 2). These results indicate that shared evolutionary history is overall more important for explaining variation in thermal tolerances compared with spatial proximity. Critically, however, we found the strength of the role of evolutionary history to depend on the tolerance trait under consideration: the role of evolutionary history was quite strong for upper thermal tolerance, CT_{\max} , but considerably weaker for lower thermal tolerance, CT_{\min} (Table 1). This result for CT_{\min} appears unlikely to reflect sampling bias owing to fewer lower tolerance values compared with upper tolerance values (see the Supplementary Material).

Although spatial proximity was not a strong predictor of variation in thermal tolerance (even when restricting our analyses to range centroids occurring at positive latitudes; see the Supplementary Material, Table S1), we found that geographic variation in temperature was a highly significant predictor of variation in both CT_{\max} and CT_{\min} . However, opposite to the general patterns we observed for the role of evolutionary history, we found stronger effects (the magnitude of the effect relative to the standard error) of

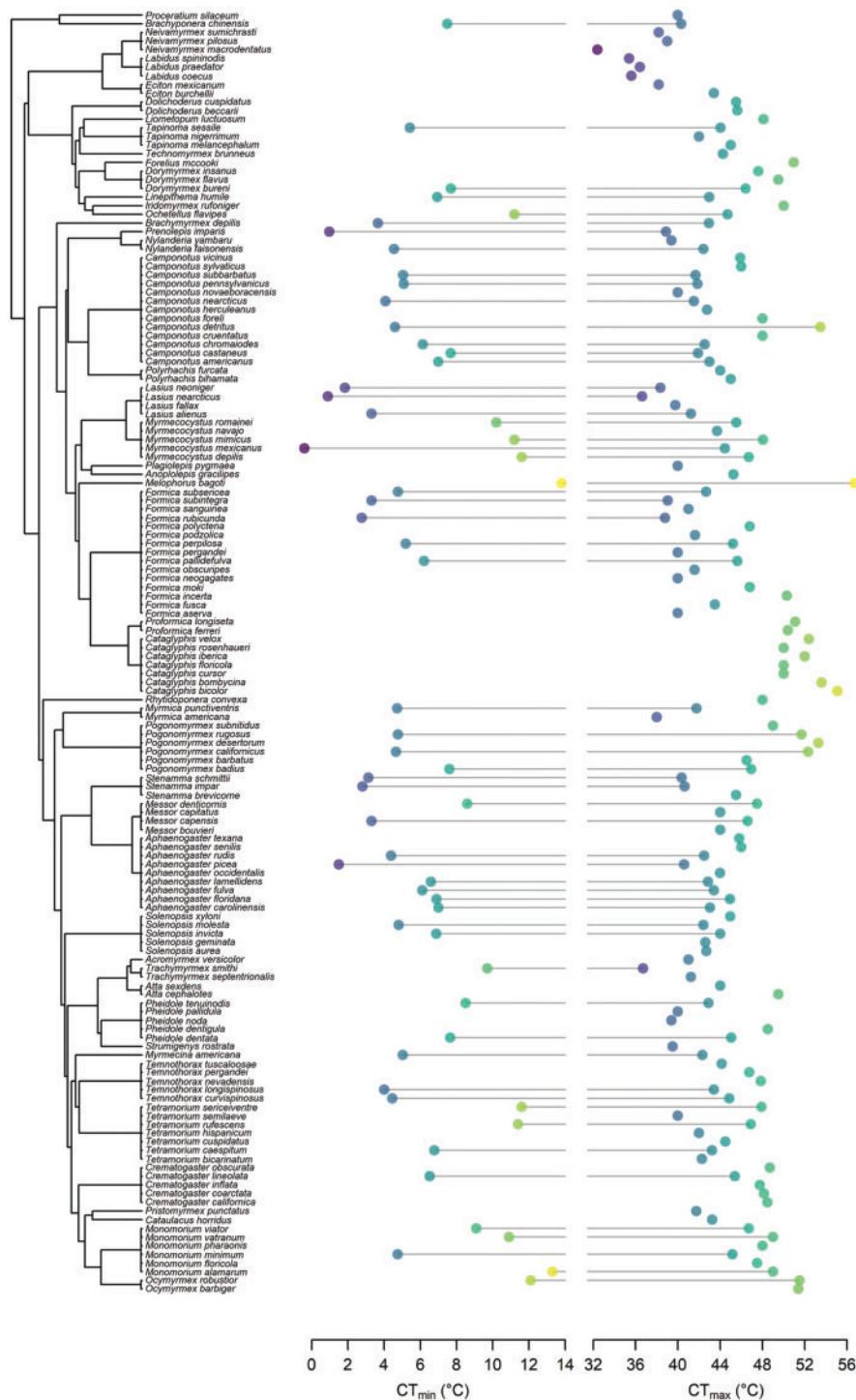


Figure 1. Upper and lower thermal tolerances of ant species in a phylogenetic context. Color shading corresponds with the magnitude of thermal tolerance: within each tolerance type, lower values are represented by purple symbols, and higher values are represented by yellow symbols. For lower thermal tolerance (CT_{min}), this means that more cold tolerant ants have purple symbols; for upper thermal tolerance (CT_{max}), this means that more heat tolerant ants have yellow symbols. Note that while each species has an upper thermal tolerance, not all species have a lower thermal tolerance.

temperature on CT_{min} compared with CT_{max} (Figures 3 and 4 and Table 1). For both CT_{max} and CT_{min} , we found that tolerance values increased with rising environmental temperature means and extremes (mean annual temperature, and maximum temperature of the warmest month and minimum temperature of the coolest month,

respectively). Specifically, ant species were more heat tolerant when the temperature profiles throughout their geographic range had higher average maximum temperatures, and ant species were less cold tolerant when temperature profiles throughout their geographic range had higher average minimum temperatures.

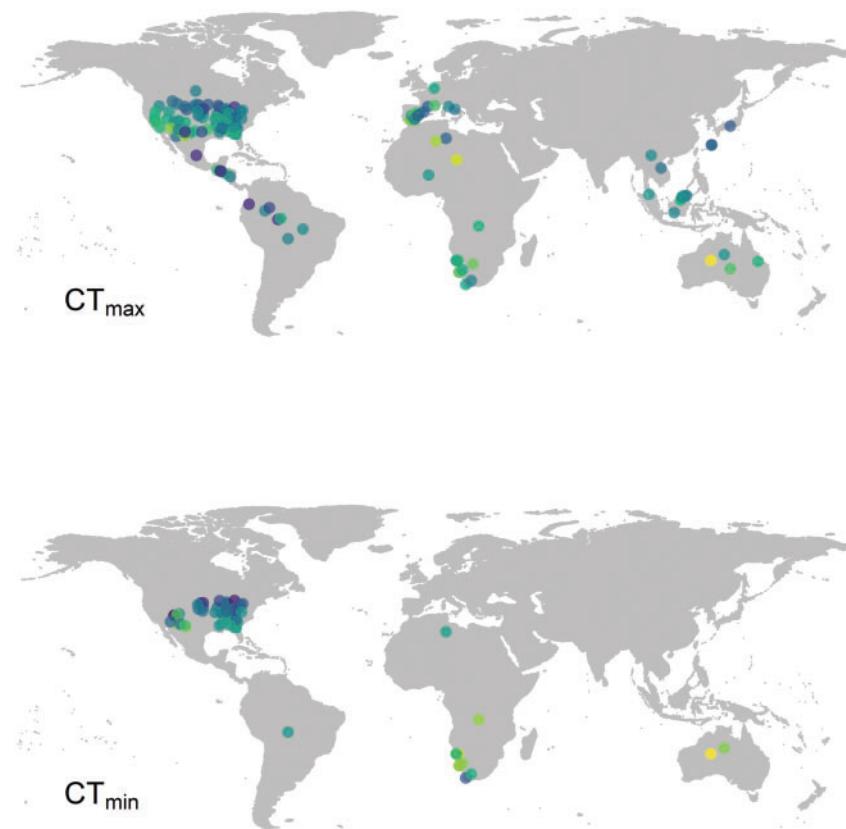


Figure 2. Upper and lower thermal tolerances of ant species in a geographic context. The top panel represents upper thermal tolerance (CT_{\max}), and the lower panel represents lower thermal tolerance (CT_{\min}). Color shading corresponds with the magnitude of thermal tolerance: lower values are represented by purple symbols and higher values are represented by yellow symbols. The location of points corresponds with the geographic position of the range centroid for a given species.

Table 1. Model results partitioning variance into phylogenetic distance, geographic distance, and climatic variables (1 = intercept-only model, mean annual temperature = MAT, maximum annual temperature = T_{\max} , isothermality = T_{iso} , temperature seasonality = T_{sea})

Response	Predictor	Number param.	AIC	Intercept	β	SE	γ	λ'	φ	t	P	P_{adj}
CT_{\max} (all)	1	4	515	43.2	—	—	0.24	0.76	7.42E-11	—	—	—
	MAT	5	483	37.3	0.0332	0.00558	0.214	0.786	1.40E-09	5.96	9.07E-09	3.63E-08
	T_{\max}	5	486	25.8	0.0543	0.00962	0.264	0.736	9.67E-11	5.65	4.04E-08	1.21E-07
	T_{iso}	5	499	38.6	0.0932	0.0227	0.212	0.788	7.32E-11	4.1	3.36E-05	3.36E-05
	T_{sea}	5	495	46.4	-0.00056	0.000125	0.213	0.787	7.52E-11	-4.52	6.26E-06	1.25E-05
CT_{\max} (subset)	1	4	221	43.7	—	—	0.319	0.681	1.10E-10	—	—	—
	MAT	5	182	34	0.0594	0.0079	0.186	0.814	1.13E-10	7.52	2.14E-10	8.56E-10
	T_{\max}	5	192	13.4	0.0918	0.0149	0.177	0.823	9.91E-11	6.17	3.72E-08	3.72E-08
	T_{iso}	5	188	31.8	0.282	0.0421	0.222	0.778	1.12E-10	6.7	5.00E-09	1.50E-08
	T_{sea}	5	190	52.9	-0.00131	0.000205	0.247	0.753	1.16E-10	-6.38	1.68E-08	3.37E-08
CT_{\min}	1	4	199	6.55	—	—	0.667	0.333	1.72E-10	—	—	—
	MAT	5	164	-0.931	0.0494	0.00709	0.83	0.17	5.90E-10	6.96	1.86E-09	4.31E-09
	T_{\min}	5	165	7.28	0.0344	0.0049	0.941	0.0591	1.67E-05	7.03	1.44E-09	4.31E-09
	T_{iso}	5	164	-3.68	0.243	0.0336	1	2.13E-09	3.55E-06	7.24	6.34E-10	2.54E-09
	T_{sea}	5	167	14.4	-0.00111	0.000162	1	8.13E-08	3.39E-10	-6.85	2.83E-09	4.31E-09

Notes: β and SE describe properties of the estimated slope for climatic predictors (presented on the original data scale from WorldClim 2), and t , P , and P_{adj} (adjusted P -values for multiple comparisons across different predictors of thermal tolerance) describe the significance tests for climatic predictors. γ , λ' , and φ describe the estimated variance components for independent, phylogenetic, and spatial components. For CT_{\max} , 2 sets of results are shown: one using the full dataset, and one using a reduced dataset that only includes records for which CT_{\min} values are also available. Sample sizes: $CT_{\min} n = 59$, $CT_{\max} n = 148$.

We observed similar relationships between mean annual temperature and upper and lower thermal tolerance, with ants having higher CT_{\max} and CT_{\min} being associated with higher mean annual temperature environments (Table 1). Ant species were also more heat

tolerant and less cold tolerant when the average isothermality of the temperature throughout their geographic range was greater (i.e., when temperature profiles were more homogenous), and when the average seasonality was lower (Table 1).

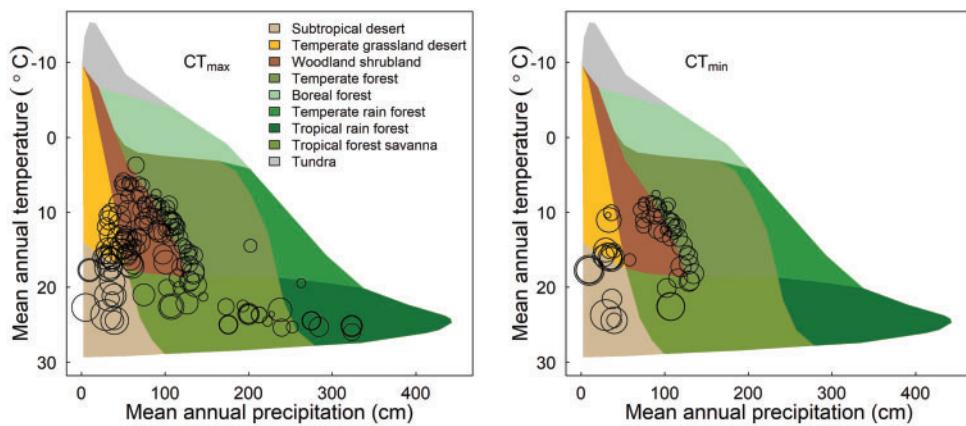


Figure 3. Upper and lower thermal tolerances of ant species in context of Whittaker biomes. Increasing circle size corresponds with greater CT_{\min} values (less cold tolerant) and greater CT_{\max} values (more heat tolerant).

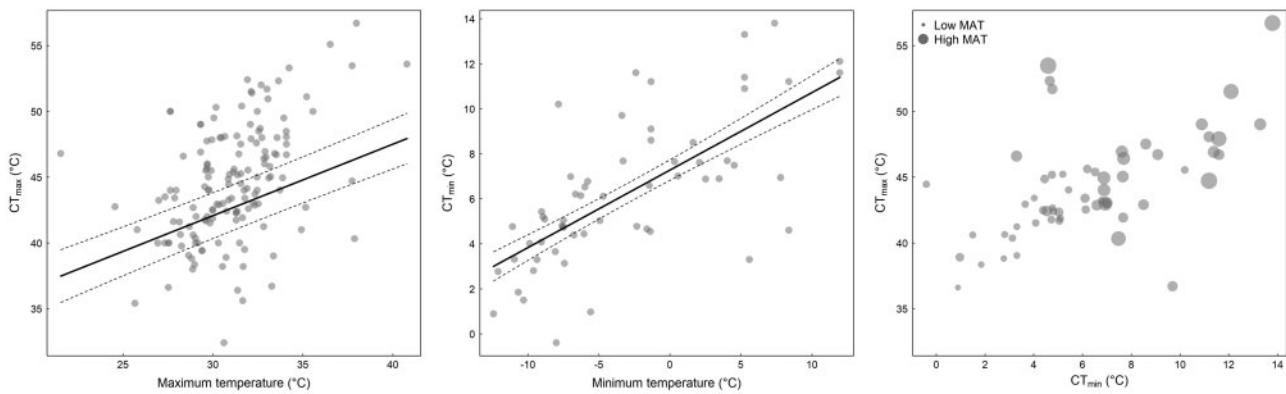


Figure 4. Relationships between ant species upper and lower thermal limits and bioclimatic variables. Upper thermal tolerance (CT_{\max}) is expressed as a function of maximum temperature of the warmest month ($^{\circ}\text{C}$) (left panel); lower thermal tolerance (CT_{\min}) is expressed as a function of minimum temperature of the coldest month ($^{\circ}\text{C}$) (middle panel); and the relationship between upper and lower thermal tolerance and how these covary with mean annual temperature (right panel). Each temperature index is expressed as the mean throughout an individual species range. Predicted values (solid lines) and standard errors (dashed lines) are shown for upper and lower thermal tolerances modeled as functions of environmental temperature variables (see the text for model descriptions).

When we evaluated the possibility of correlated evolution among CT_{\max} and CT_{\min} (i.e., a separate test of evolutionary constraint on tolerance compared with the variance-partitioning models described above), we found a moderate, but statistically significant positive correlation between these tolerance traits ($r = 0.331$, 95% CI = [0.0793, 0.543], $t = 2.62$, $P = 0.0112$, $df = 56$). To account for non-independence among species, the correlation analysis was based on the phylogenetically independent contrasts of CT_{\min} and CT_{\max} . This result indicates that while upper and lower tolerances are correlated, the strength of the association is on the weaker side, allowing upper and lower thermal tolerances to be differentially (albeit, not entirely independently) shaped by evolutionary history and geographic variation in climate.

Discussion

Variation in physiological traits is common among species and across geographic clines (Angilletta 2009), but what forces drive this variation? Specifically, what are the relative contributions of geography, through environmental filtering and local adaptation, and evolutionary history, through shared underlying genetic or developmental constraints due to common ancestry, to the resemblance (or lack of resemblance) among species in terms of their

physiological traits? Although the individual components of this question have been addressed in some detail (Blomberg et al. 2003; Chown et al. 2004), fewer studies have examined the relative influence of geography and phylogeny (Freckleton and Jetz 2009). In this study, we asked whether the upper and lower physiological tolerances of temperature for ant species considered at a global scale are more strongly conserved across evolutionary history or geography, both in terms of spatial distance and bioclimatic clines in temperature. We found that while upper thermal tolerances of ants are highly conserved phylogenetically, lower thermal tolerances are considerably less conserved phylogenetically and, to some degree, are more strongly influenced by geographic variation in temperature relative to upper thermal tolerances. Our results underscore the importance not only of partitioning variation in traits along geographic and phylogenetic axes, but also the importance of assessing the entire range of thermal tolerance, as upper and lower tolerances can operate under different constraints.

The role of evolutionary history in shaping physiological tolerances appears to be highly variable across diverse taxonomic groups and types of physiological traits. In this study, we found a relatively high phylogenetic signal in upper thermal tolerances, CT_{\max} , of ants ($\lambda = 0.76$ – 0.82 depending on the specific model under consideration, see Table 1; λ ranges from 0 to 1, with 0 representing a star

phylogeny, or no phylogenetic signal, and 1 representing congruence with a Brownian model of trait evolution, or high phylogenetic signal; see the [Supplementary Material](#) for results from an alternative model of trait evolution). Similarly, previous work has shown a high phylogenetic signal ($\lambda=0.9$) in the thermal niches (difference between CT_{\max} and habitat temperature) of ants globally (Diamond et al. 2012). *Drosophila* and amphibians likewise show high phylogenetic signal in CT_{\max} (Kellermann et al. 2012) and thermal niches (Hof et al. 2010), respectively. Rolled-leaf beetles are an exception to this pattern, exhibiting little role for evolutionary history in shaping CT_{\max} (García-Robledo et al. 2016). Likewise, mammals are also an exception, exhibiting little role for evolutionary history in shaping their thermal niche, with a much larger role for geographic variation in climate (Cooper et al. 2011). Indeed, the pattern for mammals is more representative of our results for the lower thermal tolerances, CT_{\min} , of ants, which exhibited a weak role for evolutionary history but a strong role for geographic variation in climate.

In these examples however, it is difficult to disentangle the influence of the type of physiological trait under investigation from the influence of taxonomic group. Lizards provide a rare exception, as there are data on multiple physiological tolerance traits and the contributions of evolutionary history and geographic variation in climate to each. Earlier work found that models which incorporated phylogeny into examinations of CT_{\max} , CT_{\min} , and lizard body temperature, T_b , fit the data substantially better than models without phylogeny (Huey et al. 2009). More recent work confirmed that lizards have moderate-to-high conservatism of body temperature and thermal tolerance breadth, though interestingly CT_{\max} appears to be more strongly influenced by geographic variation in climate than evolutionary history, and CT_{\min} appears to be influenced little by either evolutionary history or geographic variation in climate (Grigg and Buckley 2013). Our results for ant CT_{\min} values are similar to those for lizards in that we saw little role for geographic distance and a relatively small role for evolutionary history (though we did observe substantial clines in CT_{\min} with mean and minimum annual temperatures and temperature variability); however, our results for CT_{\max} diverge from the patterns observed in lizards, as we found a weaker role for geographic variation in climate and a substantial role for evolutionary history in shaping the upper tolerances of ants. In general, there are relatively few comparative datasets for which both CT_{\min} and CT_{\max} are available for the same species leaving open the question of differential effects of evolutionary history and geographic variation in climate across different tolerance traits in other systems.

Macrophysiology—the study of physiological traits in context of environmental variation at broad spatial scales—of insects has consistently shown a stronger relationship between latitudinal variation in climate and CT_{\min} compared with CT_{\max} (Addo-Bediako et al. 2000; Sunday et al. 2011). This decoupling of CT_{\min} and CT_{\max} is a hallmark of terrestrial ectotherm systems (though marine systems appear to be an exception, Chown 2001) both from the perspective of macrophysiological investigations showing that CT_{\min} and CT_{\max} respond differently across latitudinal clines in temperature, and from intraspecific investigations showing similar decoupling of upper and lower tolerance traits among populations (reviewed in Chown and Nicolson 2004). Our analyses of ant thermal tolerances support this pattern of decoupling of tolerance traits, as we found CT_{\min} and CT_{\max} to be differentially shaped by climate and, importantly, we were able to further show decoupling through the differential influence of evolutionary history on upper and lower tolerances. We did detect a significant correlation between the phylogenetically independent contrasts for CT_{\min} and CT_{\max} in ants,

suggesting some evidence of correlated evolution and potential evolutionary constraint between these 2 traits, but the strength of this relationship was weak, supporting the idea of (partial) decoupling of thermal tolerance traits. In some systems, for example in lizards, CT_{\min} and CT_{\max} appear to be entirely uncorrelated (Grigg and Buckley 2013). Again, this variation in the importance of correlated evolution of tolerance traits among different systems indicates the need for more datasets where both upper and lower tolerances are available for the same species.

Because our analyses concern the lability or conservatism of thermal tolerances, our results have important implications for ant responses to ongoing and future changes in climate. Already there is an abundance of evidence pointing to greater susceptibility of tropical organisms to changing climatic conditions due to generally limited phenotypic plasticity in upper thermal tolerance (Gunderson and Stillman 2015), and particularly in the tropics, reduced thermal safety margins (Huey et al. 2012) and lower evolutionary potential in upper thermal tolerance (Diamond 2017). Our results additionally show high levels of phylogenetic conservatism in upper thermal tolerances of ants, suggesting potential constraints on evolutionary change in the ability to cope with increasingly warmer temperatures. As global temperatures rise, the constraints on performance imposed by CT_{\min} are likely to become less important at higher latitudes, and the constraints on performance imposed by CT_{\max} are likely to become more important at lower latitudes (Deutsch et al. 2008).

In conclusion, we developed a global dataset of ant species thermal tolerance traits and partitioned variance in tolerance according to phylogenetic distance, geographic (spatial) distance, and geographic variation in temperature. Our major finding was the differential effects of evolutionary history and geographic variation in climate on upper and lower thermal tolerances of ants, with upper tolerances being more evolutionarily conserved and lower tolerances being more evolutionarily labile (instead lower tolerances were shaped more by climatic variation in temperature). This finding and recent work from lizards and other systems suggest the Janus of macrophysiology—the differential effects of evolutionary history and geographic variation in climate on upper and lower tolerances—may be widespread. From the perspective of changing climatic regimes, this situation is less than ideal, as the ability to evolve increased upper tolerances in a warming world may be limited. Together, these results underscore the importance of assessing the entire range of thermal performance and drivers, both to understand historical influences on physiological traits, and to predict responses to ongoing changes in climate.

Author Contributions

S.E.D. conceived and performed the analysis and wrote the first draft. L.D.C. contributed thermal tolerance data, and both authors contributed to revisions of the manuscript.

Acknowledgment

We thank Rudy Riesch, David Bierbach, and Martin Plath for the opportunity to contribute to this special column, and 3 anonymous reviewers for helpful comments on a previous version of the manuscript.

Funding

This research was supported by start-up funding from Case Western Reserve University to S.E.D.

Conflict of Interest

The authors declare no conflicts of interest.

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