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Thermal diversity of North American ant communities: Cold tolerance but not heat tolerance tracks ecosystem temperature

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Abstract

Aim: In ectotherms, gradients of environmental temperature can regulate metabolism, development and ultimately fitness. The thermal adaptation hypothesis assumes that thermoregulation is costly and predicts that more thermally variable environments favour organisms with wider thermal ranges and thermal limits (i.e., critical thermal minima and maxima, CT_{min} and CT_{max}) which track environmental temperatures. We test the thermal adaptation hypothesis at two biological levels of organization, the community and species level.

Location: Continental USA.

Time period: May–August 2016 and May–August 2017.

Major taxa studied: Ants (Hymenoptera:Formicidae).

Methods: We used ramping assays to measure CT_{max} and CT_{min} for 132 species of North American ants across 31 communities spanning 15.7° of latitude.

Results: Ants were cold tolerant in cooler environments particularly at the community level where CT_{min} was positively correlated with the maximum monthly temperature ($CT_{min} = 0.24CT_{max} - 0.4$; $R^2 = .39$, $p < .001$). In contrast, most ant communities included some highly thermophilic species, with the result that CT_{max} did not covary with environmental temperature means or extremes. Consequently, we found no evidence that thermally variable environments supported ant communities with broader thermal ranges. We found a strong phylogenetic signal in CT_{max} but not CT_{min} . Species level responses paralleled community data, where maximum monthly temperatures positively correlated with species CT_{min} but not CT_{max} , which was significantly lower in subterranean species. **Main conclusions:** Our results suggest a large fraction of continental trait diversity in CT_{max} and CT_{min} can be found in a given ant community, with species with high CT_{max} widely distributed regardless of environmental temperature. Species level analyses found the importance of local microclimate and seasonality in explaining thermal tolerances. Frequent invariance in CT_{max} of insects at a large scale might be caused by (a) local adaptations to a site's microclimates and (b) species acclimation potential, both of which cannot be accounted for with mean annual temperatures.

KEYWORDS

climate change, heat stress, insects, MAT, subterranean, thermal adaptation, thermal limits, thermal performance

1 | INTRODUCTION

Temperature governs the behaviour, physiology and fitness of organisms (Angilletta, 2009) and consequently drives species distributions and diversity patterns. Ectotherms are particularly sensitive to environmental temperature fluctuations as their body temperature depends on the thermal environment, which, in turn, directly affects their metabolism and activity (Buckley, Hurlbert, & Jetz, 2012; Huey & Kingsolver, 1989). Temperate zone ectotherms better withstand changes in thermal regimes than their tropical counterparts (Huey et al., 2009), and different evolutionary forces are predicted to act on upper and lower thermal tolerance (Grigg & Buckley, 2013). Thermal adaptations and temperature-dependent species distributions of ectotherms are particularly important in the context of recent increases in global temperature (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008; Deutsch et al., 2008; Huey et al., 2009; Sunday et al., 2014).

One key model from thermal ecology, the thermal adaptation hypothesis, predicts that (a) more thermally variable environments will generate organisms with broader thermal ranges (Janzen, 1967) and (b) an ectotherm's thermal limits will positively correlate with the maximum and minimum temperature of its environment. Although initially proposed, and tested, using species data collected from meta-analyses (Addo-Bediako, Chown, & Gaston, 2000), predictions from the thermal adaptation hypothesis can be tested at different biological levels of organization, each relevant to predicting the effects of climate change on ecological systems.

By far the most common level of organization used to test the thermal adaptation hypothesis is that of the species (Addo-Bediako et al., 2000; Blackburn, Gaston, & Loder, 1999; Diamond & Chick, 2018; Sheldon & Tewksbury, 2014). Species are often easily recognized across their geographic range, and strong covariance of species traits with environmental temperatures may arise if there is little inter-population variability. In closely related species, similar thermal traits present across a gradient of thermal regimes could suggest these traits are phylogenetically constrained and allow less opportunity for local adaptation. Strong phylogenetic signal of heat tolerance in terrestrial ectotherms, in this view, represents one such constraint to thermal adaptation (Hoffmann, Chown, & Clusella-Trullas, 2013; Kellermann et al., 2012). In contrast, cold tolerance of insects often shows greater geographic variability and lower phylogenetic signal than heat tolerance (Addo-Bediako et al., 2000; Chown, 2001; Diamond & Chick, 2018; Sunday, Bates, & Dulvy, 2012).

A second level of organization at which to test the thermal adaptation hypothesis is the community—the suite of potentially interacting species in a given area. Species interact with other species, and their thermal traits within a suite of traits may shape the outcomes of biotic interactions. For example, species may occupy different thermal niches within a community representing different times of day (Kaspari & Weiser, 2000) or different microclimates (Stark, Adams, Fredley, & Yanoviak, 2017); each offering exclusive access to resources at those temperatures. Behaviourally dominant ants tend

to occupy the common, less extreme portions of the thermal envelope, while subdominant ants are active in extreme temperatures (Cerdá, Retana, & Cros, 1998; Roeder, Roeder, & Kaspari, 2018). A community focus allows us to explore the central tendency of traits across communities that may positively correlate with habitat temperatures as predicted by the thermal adaptation hypothesis.

To test the thermal adaptation hypothesis, we used ants—one of the most abundant, widespread, and ecologically important insect taxa. Most ants are thermophilic, with their abundance and diversity positively associated with temperature (Dunn et al., 2009; Kaspari, Yuan, & Alonso, 2003). However, there is only mixed evidence that ant thermal limits positively correlate with the temperature means in different habitats. Across four communities arrayed along mountainsides between 1,500 and 3,000 m, critical thermal maximum (CT_{max}) failed to vary with mean temperature, while critical thermal minimum (CT_{min}) was lower at higher elevation (Bishop, Robertson, Van Rensburg, & Parr, 2017). The same lack of variability in CT_{max} occurred in communities along a lower elevational gradient (Nowrouzi, Andersen, Bishop, & Robson, 2018). In contrast, a species level meta-analysis found on average higher CT_{max} in home ranges with higher maximum temperatures, and lower CT_{min} in home ranges that had lower minimum temperatures (Diamond & Chick, 2018). Critical thermal minimum in this meta-analysis also showed a much stronger correlation with environmental means than CT_{max} .

Here we combine the strengths of both approaches to test the relationship of thermal limits and environmental temperatures at a continental scale using a nested approach: testing the predictions of the thermal adaptation hypothesis across 31 North American ant communities and 132 species. Our communities span 15.7° of latitude within North America across a variety of ecosystems, including warm deserts, alpine tundra, and hard wood forests. We use a genus level phylogeny to identify phylogenetic signal in thermal limits and identify genera that are less likely to have a competitive advantage in a warmer future world.

2 | METHODS

2.1 | Sampling sites

We collected and tested ant species across 31 sites in North America from May to August in 2016 and 2017 (Supporting Information Figure S1, Table S1). At each of the sites we used foragers of the most common species for our experiments, totalling 3,898 individual ants from 132 species. The foragers were collected in the vicinity of their nest, usually when exiting to forage, so we were certain of the colony identity. We predominantly sampled diurnal species, except in the desert where some of the species we measured were nocturnal. Total number of species depended on the total species richness of the site (for details on richness see Kaspari, Bujan, Roeder, de Beurs, & Weiser, 2019). At low diversity sites we sampled all the species while at sites with high richness (> 15 species) we tested the proportion of total richness using the most commonly occurring species.

The number of species tested ranged from 1 in alpine tundra to 17 in a mixed deciduous forest. These sites spanned 15.7° in latitude from 29.7° in Florida to 45.4° in Minnesota (Supporting Information Figure S1). Elevation ranged from 1 to 3,737 metres above sea level.

2.2 | Thermal tolerance measurements

Critical thermal limits are temperatures at which animals lose voluntary muscle control (Lutterschmidt & Hutchison, 1997). We used five workers (mean \pm SE: 4.8 ± 0.05) to measure heat tolerance—critical thermal maximum (CT_{max}), and five workers (4.7 ± 0.05) to measure cold tolerance—critical thermal minimum (CT_{min}). Thus, we used 10 workers from a single colony, and we tested several colonies per species depending on species abundance [$N_{(colonies\ CT_{max})} = 1.7 \pm 0.06$; $N_{(colonies\ CT_{min})} = 1.5 \pm 0.05$]. We tested the ants immediately after field collections. To avoid acclimation, we did not keep the colonies in the lab overnight. To measure CT_{max} we used a digital dry bath (USA Scientific Thermal-Lok 2-position dry heat bath, Ocala, Florida; advertised accuracy $\pm 0.2^\circ\text{C}$). We placed each worker in a 1.5 ml microcentrifuge tube and filled the cap with modelling clay to prevent the ants from hiding inside the cap above the heating block. We used an established protocol for measuring ant CT_{max} (Diamond et al., 2012; Kaspari, Clay, Lucas, Yanoviak, & Kay, 2015) in which the workers are inspected every 10 min for movement, and the temperature is raised 2°C , starting at 36°C . Upon inspection, each vial was shaken to see if the ants had lost their righting response and, if they did, that temperature was recorded as their CT_{max} . The CT_{min} for each worker was determined in the same way, after lowering the temperature at the same rate as for CT_{max} , except the trials started at 20°C . To measure CT_{min} we used a chilling/heating dry bath (Torrey Pines Scientific EchoTherm™ IC20, Carlsbad, California; advertised accuracy $\pm 1^\circ\text{C}$). In total we measured CT_{max} of 2,113 workers from 422 colonies, and CT_{min} of 1,785 workers from 374 colonies. Using this method where workers are individually heated up in microcentrifuge tubes, Kaspari et al. (2015) found no correlation between body size and critical thermal limits of different ant species. But when thermal limits of the same ant species were measured on a hot plate, body size was highly correlated with thermal tolerance, and large ants were able to heat up and cool down more slowly. In a study of several highly polymorphic tropical genera, body size was a significant predictor of thermal tolerances (Baudier, D'Amelio, Malhotra, O'Connor, & O'Donnell, 2018; Baudier, Mudd, Erickson, & O'Donnell, 2015). However, we found no correlation of CT_{max} and body size across almost 200 workers from 14 monomorphic ant species in a North American ant community from southern Oklahoma (Bujan & Roeder unpublished data).

2.3 | Environmental temperature measurements

Temperature data from 1995 through 2015 were extracted from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) datasets created by the PRISM Climate Group at Oregon

State University (www.prism.oregonstate.edu; downloaded winter 2017). We used the monthly datasets covering the conterminous USA with a 4-km spatial resolution. The temperature dataset was developed by applying the PRISM model to point station data. PRISM data have been proven to be well suited to regions with mountainous terrain because they incorporate a conceptual framework that addresses the spatial scale and pattern of orographic processes (Daly et al., 2008, 2015). We downloaded all monthly gridded observations for temperature between January 1995 through December 2015. We then derived the grid cell values for the 31 point locations by extracting the information for the grid cell overlapping the point location. After examining the relationship of ant thermal limits and thermal ranges with mean annual temperature (MAT), means of the hottest month of each year (mean monthly maximum temperature) and coldest month of each year (mean monthly minimum temperature), we then tested if ant thermal ranges increase with increase in environmental temperature ranges—the difference between mean monthly maximum temperature and mean monthly minimum temperature.

2.4 | Data analyses

We performed all analyses in R version 3.3.2 (R Core Team, 2016). For each species at each site we calculated mean CT_{max} , CT_{min} , and thermal range—the difference between CT_{max} and CT_{min} (Huey & Stevenson, 1979). To test how CT_{max} , CT_{min} and thermal range vary with environmental temperature means at the community level we used generalized linear models (GLMs; *glm* function in R). For community level analyses we calculated the median value of thermal limits across all species at a site to represent the central tendency of the community thermal limits. To control for potential seasonal differences, which might affect thermal limits (Bujan, Roeder, Yanoviak, & Kaspari, 2020), we used the sampling month as one of the predictors in both community and species level analyses. Thus, our full GLM model testing variation in thermal traits included one of the environmental temperatures (MAT, maximum temperature or minimum temperature) and the sampling month. To select the optimal model, we used an information theoretic approach (Burnham & Anderson, 2002). After constructing our models, we ran a model comparison based on the difference in Akaike's information criterion (ΔAIC) values—the difference of the AIC of the *i*th model and the model with the lowest AIC value. To test if autocorrelation was present in the residuals of our community level GLMs, we used a Durbin-Watson test (*dwtest* function in R) from the *lmtest* package (Zeileis & Hothorn, 2002). As we did not find autocorrelated residuals across the models we did not include geographic distance in our models.

We analysed species level variation in mean CT_{max} , CT_{min} , and thermal range with generalized linear mixed effect models (GLMMs) using the *lmer* function in the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017). We used one of the environmental temperatures, month of sampling, and habitat as fixed effects in the models. We accounted for habitat differences,

as species specialized for one type of habitat may never experience the conditions present in other habitats. Thus we added habitat in species level analyses and we used three categories: subterranean, ground, canopy. We were conservative with our habitat classification and considered species to be canopy ants only if they nest and forage in the canopy, and as subterranean if they both nest and forage underground. Our largest category included ground nesting ants, which forage in the litter, understory, or in the canopy and experience the broadest range of temperatures. Habitat use was assigned using personal observations and recorded biology of North American ants [http://antweb.org (accessed 10 November 2019); Ellison, Gotelli, Farnsworth, & Alpert, 2012; Klotz, Hansen, Pospischil, & Rust, 2008; Mackay & Mackay, 2002; Seifert, 2018]. We included sampling site as a categorical random factor to account for the multiple measurements performed at one locality. Additionally, we included species as a categorical random factor because some species occurred at multiple locations. We used the same model selection based on AIC criterion, as for the community level analysis. We calculated the R^2 of the optimal GLMMs using function *r.squaredGLMM* in the *MuMIn* package (Barton & Barton, 2019). We report both marginal- R_m^2 , which takes into consideration only variance explained by the fixed factors, and the conditional- R_c^2 , which includes the effect of the random factors. We examined autocorrelation plots of the optimal GLMMs to test if their residuals show significant autocorrelation; as we did not find any we did not include geographic distance in our species level models.

To test for phylogenetic signal in thermal limits and thermal range we used an ultrametric ant phylogeny by Moreau and Bell (2013) pruned to 36 branches, which corresponds to the number of genera for which we measured both CT_{max} and CT_{min} . Two of our genera (*Novomessor* and *Veromessor*) were recently split from the genus *Aphaenogaster* (Demarco & Cognato, 2015) and were not present in the phylogeny. We added these two genera as sister genera to genus *Aphaenogaster*. We did the same for genus *Nylanderia*, which we added as a sister genus to the most closely related genus *Paratrechina* (LaPolla, Brady, & Shattuck, 2011). We calculated the total of 39 genus level averages for each of the traits in question. Then, we used Blomberg's K (Blomberg, Garland, & Ives, 2003) and Pagel's λ (Pagel, 1999) to inspect for phylogenetic signal. We performed all phylogenetic analysis using packages *ape* (Paradis, Claude, & Strimmer, 2004) and *phylosignal* (Keck, Rimet, Bouchez, & Franc, 2016). The data that support the findings of this study are openly available in *figshare*: <https://doi.org/10.6084/m9.figshare.11866386>.

3 | RESULTS

In total we tested thermal limits of 132 ant species, from 40 genera and 8 subfamilies. The measured thermal maxima ranged from 38.8°C (*Brachymyrmex depilis*, scrub oak forest, MA) to 57.0°C (*Forelius pruinosus*, desert, NM), and thermal minima from -1.0°C

(*Formica subnitens*, xeric scrub, NM) to 15.7°C (*Tetramorium nevadensis*, shrubland, UT). Ant thermal ranges ($CT_{max} - CT_{min}$) varied from 24.6 to 52.0°C.

The first most striking pattern was how, regardless of the temperature of the ecosystem, co-occurring ant species varied widely in their thermal traits. Across the 31 communities, the median range of CT_{max} within a community was 9.3°C—52% of the total range we recorded for species in North America. Likewise, the median range of CT_{min} within communities was 5°C—31% of the total range we recorded for species in North America. Thus, the average ant community supported populations that spanned 1/3 to 1/2 of the variation in CT_{min} and CT_{max} recorded for 132 species at the continental scale.

3.1 | Community level thermal tolerance

Across the 31 communities, only CT_{min} —not CT_{max} or thermal range—varied as predicted by the thermal adaptation hypothesis (i.e., we found ants with lower CT_{min} in cooler ecosystems). Critical thermal minimum significantly increased with maximum monthly temperature while MAT or minimum monthly temperature were not good predictors of CT_{min} (Figure 1a, Supporting Information Table S2, $R^2 = .39$, $p = .001$). In contrast, CT_{max} failed to increase with any of these three measures of environmental temperature (Figure 1a, Supporting Information Table S2) and thermal range did not covary with environmental temperatures or temperature ranges (Supporting Information Figure S2, Table S2). In both cases the optimal regression models could not be distinguished from the null model.

3.2 | Species level thermal tolerance

Cooler areas contained species with lower CT_{min} as we observed a significant decrease of CT_{min} at lower mean maximum temperatures (Figure 1b). Species CT_{min} was significantly predicted by maximum temperature, sampling month and habitat (Supporting Information Table S3; $R_m^2 = .21$, $R_c^2 = .76$). The optimal models for predicting species CT_{max} contained habitat and month of sampling, but none of the temperature variables (Supporting Information Table S3). The only significant predictor of ant CT_{max} was habitat, as subterranean ants had significantly lower CT_{max} (Figure 2; $R_m^2 = .20$, $R_c^2 = .85$). Ant thermal ranges were negatively correlated with temperatures (MAT and maximum temperature, Supporting Information Figure S2) once sampling month and habitat were included in the model ($R_m^2 = .20$, $R_c^2 = .81$). However, environmental thermal ranges were not good predictors of ant thermal range (Supporting Information Table S3).

3.3 | Phylogenetic signal in thermal limits

To test for phylogenetic signal of thermal limits we used genus level averages of upper and lower thermal tolerances. We found a strong

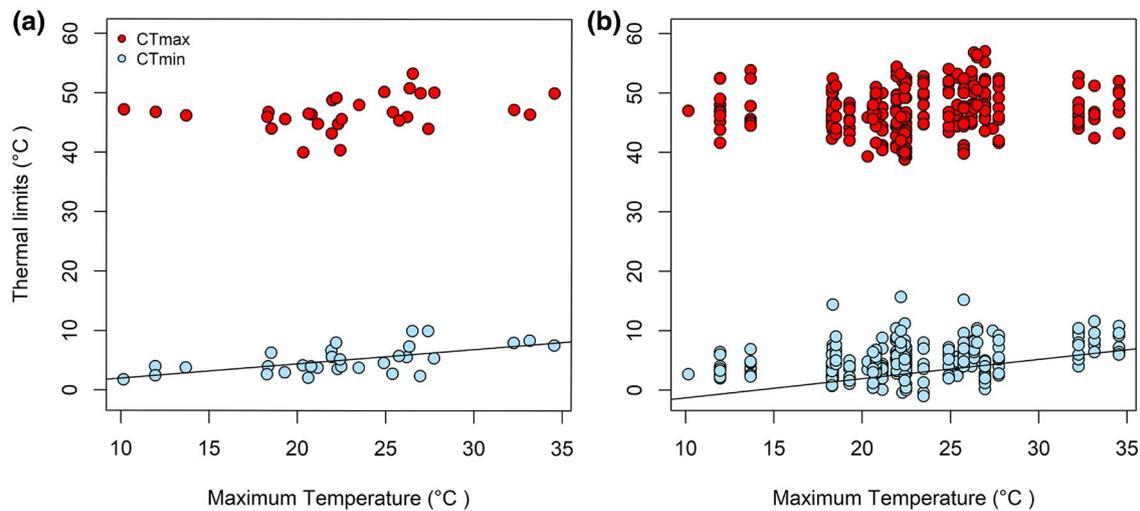


FIGURE 1 Relationship between upper and lower thermal limits and mean maximum temperature at the: (a) community level, (b) species level. Critical thermal maximum (CT_{max}) in red, and critical thermal minimum (CT_{min}) in blue. Only significant relationships with temperature are shown.

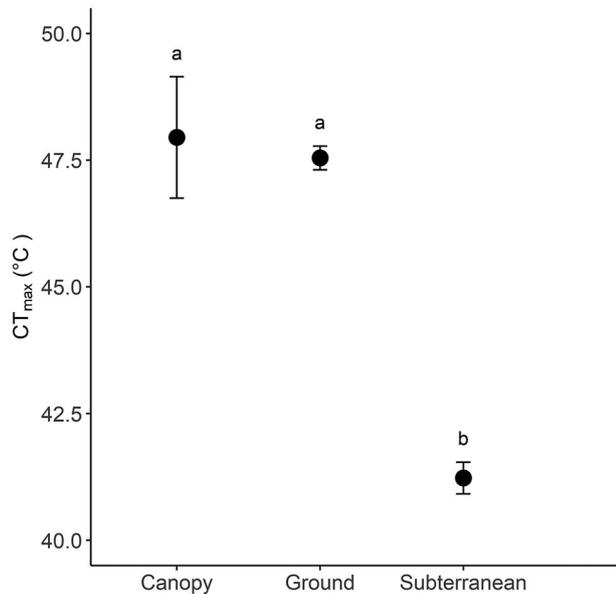


FIGURE 2 Mean critical thermal maximum (CT_{max}) across three tested habitats. Error bars represent standard errors. Pairwise comparisons were calculated from the optimal generalized linear mixed effect model (GLMM). Habitats with significantly different means ($\alpha = 0.05$) are marked with different letters.

phylogenetic signal in CT_{max} : Blomberg's $K = 0.71$, was significantly different from $K = 0$ ($p = .006$). Pagel's λ was significantly different from $\lambda = 0$, confirming a strong phylogenetic signal in CT_{max} ($\lambda = 0.94$, $p = .019$). Conversely, CT_{min} showed no phylogenetic signal suggesting that the evolution of this trait is not different from random with respect to phylogeny (Figure 3; $K = 0.36$, $p = .69$; $\lambda = 0.00007$, $p = 1$). Thermal ranges also showed phylogenetic signal, but not as pronounced as CT_{max} (Supporting Information Figure S3; $K = 0.58$, $p = .049$; $\lambda = 0.68$, $p = .070$).

4 | DISCUSSION

The thermal adaptation hypothesis is a cornerstone of mechanistic approaches to global change biology. By combining community level analyses across the continental USA, we show that CT_{min} s of North American ant communities follow climatic gradients. However, environmental temperatures did not predict ant CT_{max} or thermal ranges at the community level. The same was true for our species level analyses, until we accounted for adaptation to sources of localized temperature variation (i.e., habitat, month). We found that the best predictor of CT_{max} is species habitat, while thermal ranges were wider in cooler habitats. However, the key element of the thermal adaptation hypothesis—that variable environments favour broader thermal ranges—was not supported at the species level, even after accounting for the microclimatic differences. Since the optimal models for all thermal traits included both month and habitat microclimate, this suggests that factors such as local adaptation or acclimatization to different microclimates (Baudier et al., 2018; Esch, Jimenez, Peretz, Uno, & O'Donnell, 2017), differences in resource availability (Bujan & Kaspari, 2017), or seasonal plasticity of thermal limits (Bujan et al., 2020; Kay & Whitford, 1978) could be maintaining local niche variation in key thermal traits. This acclimation or adaptation potential could be tested by acclimation experiments and studies examining intraspecific variation in thermal limits.

Another prediction, that thermal limits positively correlate with environmental temperatures, accounts for 39% of the variation in community median CT_{min} but failed to predict variation in CT_{max} . This is likely due to the strong phylogenetic signal that we found in CT_{max} but not CT_{min} . Species level analysis revealed the importance of local adaptation, as variation in CT_{max} was best explained by the habitat. Combined, our community and species level analyses suggest that both CTs might be more plastic than previously thought, and this

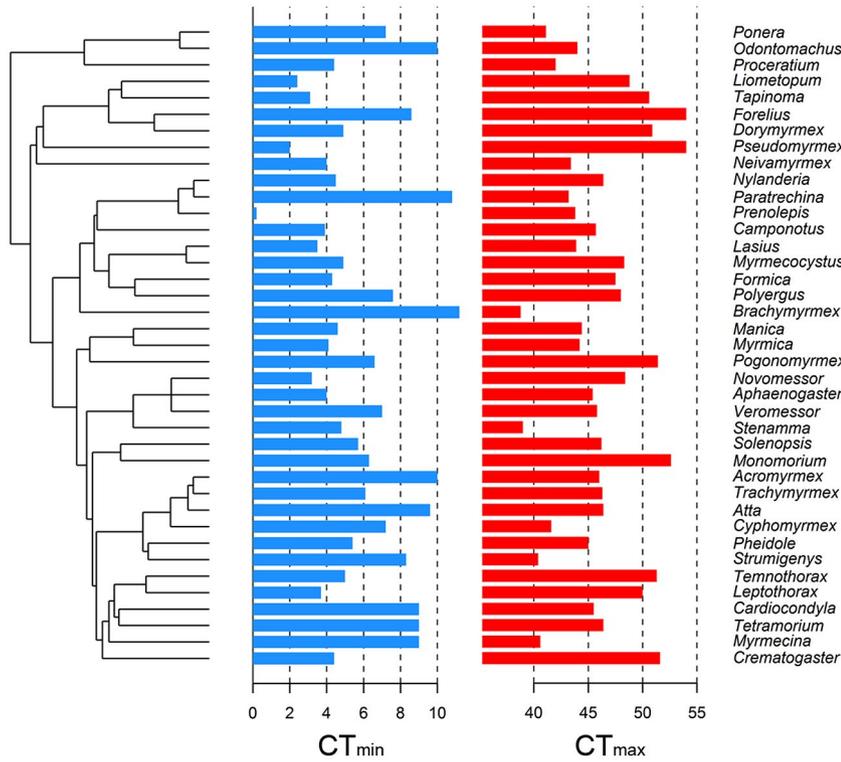


FIGURE 3 Relatedness of the 39 genera tested and genus level means of their thermal limits: critical thermal minimum (CT_{min}) in blue, and critical thermal maximum (CT_{max}) in red.

could be another reason, in addition to phylogeny, why CT_{max} of insects is often poorly predicted by environmental temperatures.

4.1 | Thermal adaptation hypothesis is sensitive to spatio-temporal scale

Our results support a growing literature suggesting that lower thermal limits of insects follow environmental temperatures unlike upper thermal limits, which do not change in a predictive fashion across latitudes (Addo-Bediako et al., 2000; Klok & Chown, 2003). Ants respond similarly as, at both community and species level, we found a strong effect of maximum temperature on CT_{min} , but not CT_{max} (Figure 1). Two regional studies of ant communities (Bishop et al., 2017; Nowrouzi et al., 2018) concur that CT_{max} fails to positively correlate to environmental temperature, while a global meta-analysis found a strong positive correlation of both CT_{max} and CT_{min} with environmental temperatures: MAT, maximum temperature, minimum temperature (Diamond & Chick, 2018). Not all environmental temperatures follow the same latitudinal pattern at a global scale. Generally, minimum air temperatures have a linear relationship with latitude, while maximum air temperatures increase slightly at mid-latitudes and then decrease towards the poles (Sunday et al., 2014). Despite this latitudinal pattern of thermal extremes, both our study and Diamond and Chick (2018) found a linear relationship of maximum air temperature and ant CT_{min} at the species level. In our case only maximum temperature was a good predictor of CT_{min} after we accounted for habitat and season.

This suggests that ants can locally adapt or acclimate to local spatial and temporal temperature gradients, which is key to

understanding community change in a warming world. As Lancaster (2016) suggests, insect thermal tolerance can depend on their expansion range, and insects with expanding ranges show invariant CT_{max} across latitudes, while CT_{max} of non-range expanding species follow latitudinal clines being lower at lower MAT at higher latitudes. In our study environmental temperatures were not good predictors of CT_{max} , which could suggest that we sampled primarily range expanding species that have plastic thermal ranges.

4.2 | Phylogenetic signal is pronounced in upper thermal limits

After controlling for phylogeny, we did not find a correlation between CT_{max} and CT_{min} (Supporting Information Figure S4). This decoupling of thermal limits is assumed to be caused by lower spatial variability in environmental temperature maxima than environmental minima at the global scale (Chown, 2001; Gaston & Chown, 1999). While there is support for this decoupling in lizards (Huey & Kingsolver, 1993) and across different insect taxa (Addo-Bediako et al., 2000; Chown, 2001; Kellermann et al., 2012; Klok & Chown, 2003) previous examination of ant species showed a positive correlation of these two traits (Diamond & Chick, 2018). Decoupling of CT_{max} and CT_{min} is likely caused by differential effects of evolutionary history on these two traits where one is more constrained, and the other more plastic. Cold tolerance in insects is frequently more plastic (Klok & Chown, 2003; Terblanche, Klok, Krafusur, & Chown, 2006), but the physiological mechanisms responsible for plasticity of insect CT_{min} are still poorly understood (MacMillan & Sinclair, 2011). Upper thermal limits often show phylogenetic signal

in ectotherms, and the lack of correlation between upper thermal limits and climatic gradients is sometimes coupled with the variation in lower thermal limits (García-Robledo, Kuprewicz, Staines, Erwin, & Kress, 2016; Hoffmann et al., 2013). In accordance with these findings, we recorded a strong phylogenetic signal in ant CT_{max} but not in CT_{min} . The genera that consistently exhibited low and less variable CT_{max} (40–44°C), but highly variable CT_{mins} are the most early-diverging genera: *Ponera*, *Odontomachus* and *Proceratium*.

Ants, however, might be using other traits to aid with heat tolerance. Behavioural thermoregulation can enable them to avoid detrimental temperatures, but they might have to compete with other species occupying the same thermal niche (Roeder et al., 2018). Higher melanization of ants is present in cooler environments (Bishop et al., 2016), so altering cuticle colour might enable ants to withstand prolonged radiation. These and other traits, such as diet rich in sugary secretions (Bujan & Kaspari, 2017) or high phosphorus availability, which both can increase CT_{max} (Kaspari et al., 2016), require more attention in future studies examining thermal limits in ants.

Additionally, small cursorial ectotherms like ants experience the temperature of the boundary layer—the air layer next to the surface, which can average up to 10°C warmer than air temperature (Kaspari et al., 2015; Oke, 1978; Stark et al., 2017). Thus, the environmental temperature means might not be appropriate for measuring biologically meaningful responses of cursorial insects and instead temperature variation (Sheldon & Tewksbury, 2014) or daily fluxes (Paaijmans et al., 2013) should be used. Nevertheless, global change models of animal responses rely almost exclusively on air temperatures, including prior research on ants, so knowing their relationship to physiological adaptations is increasingly important. We show that part of this variability can be accounted for with microclimatic differences between habitats and sampling months. This suggests two working hypotheses. First, local adaptations to spatial diversity in microclimate (e.g., soil, shade, surface, canopy) and temporal acclimatization across the seasons (winter through summer) are likely key to making informed predictions about future changes in North American ant communities. Moreover, behavioural adaptations within a community allow coexisting ant populations to take advantages of thermal slices of the environment to discover, recruit, and defend resources (Cerdá et al., 1998; Roeder et al., 2018). Second, thermal stability in CT_{max} suggests that taxonomic membership may be informative in global change biology, predicting which genera increase and decrease, at a continental scale, in a warming world.

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AUTHOR CONTRIBUTIONS

JB, KAR, MDW, and MK conceived the ideas and designed the methodology. JB, KAR, MDW, and MK conducted fieldwork and collected the data on thermal limits. KdB assembled the temperature data. JB analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare <https://doi.org/10.6084/m9.figshare.11866386>.

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BIOSKETCH

Jelena Bujan is a postdoctoral researcher at the University of Lausanne interested in physiological adaptations and their role in structuring insect communities and distributions. Her current research explores physiological and behavioural plasticity of ants in thermally stressful environments.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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