Thermal traits predict the winners and losers under climate change: an example from North American ant communities

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Abstract. Across the globe, temperatures are predicted to increase with consequences for many taxonomic groups. Arthropods are particularly at risk as temperature imposes physiological constraints on growth, survival, and reproduction. Given that arthropods may be disproportionately affected in a warmer climate—the question becomes which taxa are vulnerable and can we predict the supposed winners and losers of climate change? To address this question, we resurveyed 33 ant communities, quantifying 20-yr differences in the incidence of 28 genera. Each North American ant community was surveyed with 30 1-m^2 plots, and the incidence of each genus across the 30 plots was used to estimate change. From the original surveys in 1994–1997 to the resurveys in 2016–2017, temperature increased on average 1°C (range, −0.4°C to 2.5°C) and ~64% of ant genera increased in more than half of the sampled communities. To test Thermal Performance Theory's prediction that genera with higher average thermal limits will tend to accumulate at the expense of those with lower limits, we quantified critical thermal maxima (CT$_{max}$: the high temperatures at which they lose muscle control) and minima (CT$_{min}$: the low temperatures at which ants first become inactive) for common genera at each site. Consistent with prediction, we found a positive decelerating relationship between CT$_{max}$ and the proportion of sites in which a genus had increased. CT$_{min}$, by contrast, was not a useful predictor of change. There was a strong positive correlation ($r = 0.85$) between the proportion of sites where a genus was found with higher incidence after 20 yr and the average difference in number of plots occupied per site, suggesting genera with high CT$_{max}$ values tended to occupy more plots at more sites after 20 yr. Thermal functional traits like CT$_{max}$ have thus proved useful in predicting patterns of long-term community change in a dominant, diverse insect taxon.

Key words: ants; climate change; incidence; insects; macrophysiology; temperature; thermal performance; thermal tolerance; traits.

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INTRODUCTION

As global temperatures increase, it is essential to build functional models that predict the responses of populations, communities, and ecosystems (Walther et al. 2002, Parmesan and Yohe 2003, Deutsch et al. 2008, Hellmann et al. 2008, IPCC 2014). Ectotherms are often a focus of such efforts, given the clear link between temperature and the growth, survival, and reproduction of organisms whose body temperatures track that of their environment (Chown and Nicolson

2004, Calosi et al. 2008, Colinet et al. 2015). Arthropods are (mostly) ectotherms that comprise ~46% of Earth's animal biomass (Bar-On et al. 2018) and may represent up to 5–10 million of Earth's species (Ødegaard 2000). Yet declines in arthropod abundance and species richness are already being documented with subsequent effects on ecosystem stability and the structure of food webs (Resasco et al. 2014, Diamond et al. 2016, Hallmann et al. 2017, Valtonen et al. 2017, van Klink et al. 2020, Welti et al. 2020). The ability to predict which arthropod taxa increase and which decrease—the "winners and losers"—is a crucial test for any theory predicting biotic responses to climate change.

Thermal Performance Theory posits the performance of an ectotherm should increase with temperature along a left-skewed curve up to an optimum before a quick decrease, after which the ectotherm ultimately loses muscle control and dies (Kingsolver and Huey 2008, Angilletta 2009, Sinclair et al. 2016). Two of the variables from a thermal performance curve—the critical minimum temperature (CT_{min}) at which an organism loses mobility and the critical maximum temperature (CT_{max}) at which it loses muscle control—hold considerable promise for predicting the responses of taxa to warming since both vary geographically (Deutsch et al. 2008) and within ecological communities (Kaspari et al. 2015). If, for example, populations that increase as environmental temperatures rise also have higher CT_{max}s, then these variables should have predictive value that may be scaled up to and across communities. Surprisingly, while we have long known that small temperature changes can increase generalist butterfly populations and lead to asymmetric range expansions (Parmesan et al. 1999, Warren et al. 2001, Chen et al. 2011), we know of little data on how the thermal limits of co-occurring populations in a warming environment predict which populations will increase and decrease (Stuble et al. 2013).

Ants (Hymenoptera: Formicidae) are an abundant, ecologically important group of insects (Hölldobler and Wilson 1990, Del Toro et al. 2012) with peak thermal maxima higher than many other model ectotherm taxa like flies and lizards (Huey et al. 2009, Kellermann et al. 2012, Diamond and Chick 2018). Moreover, changes in ant abundance likely ramify through ecosystems given their roles in biological control, nutrient cycling, seed dispersal, and soil aeration (Philpott and Armbrecht 2006, Lengyel et al. 2010, Griffiths et al. 2018, Swanson et al. 2019) while often acting as important bioindicators of disturbance and change (Andersen and Majer 2004, Parr et al. 2004, Del Toro et al. 2010). Here, we present two sets of data—an initial survey in the mid-1990s and a resurvey approximately 20 yr later using the same methods—from 33 North American ant communities. Our goal was to quantify changes in local incidence of 28 common genera. At each site, we also measured CT_{min} and CT_{max} of common species. We combine these two datasets to test the prediction that a 20-yr warming trend has favored genera with higher thermal maxima and minima, as predicted by Thermal Performance Theory.

MATERIALS AND METHODS

Study sites and their temperature

In 2016–2017, ants were resampled from May to August across North America at 33 sites previously sampled in 1994–1997 (Fig. 1; Kaspari et al. 2000, Kaspari et al. 2019). These sites spanned 15.7° in latitude and 51.6° in longitude from warm southwestern deserts in California to cool northeastern deciduous forests in Massachusetts. Many of these sites occur at Long-Term Ecological Research (LTER) stations, National Ecological Observatory Network (NEON) field sites, or within protected areas such as national or state parks and forests (Appendix S1: Table S1).

Monthly temperature data from 1993 to 2017 were extracted from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) datasets at Oregon State University. These values were derived at a 4-km spatial resolution from the grid cell overlapping each of the 33 sampling sites. For each site, we calculated the average mean annual temperature (hereafter MAT) and the change in temperature between the two surveys' mean annual temperatures measured from June to May of the preceding year (hereafter ΔTemp). We then created average MAT and ΔTemp values for each ant genus from the sites where that genus occurred.

Sampling ants at each site

At each site, we used identical sampling methods from the original survey by setting out 30 1-
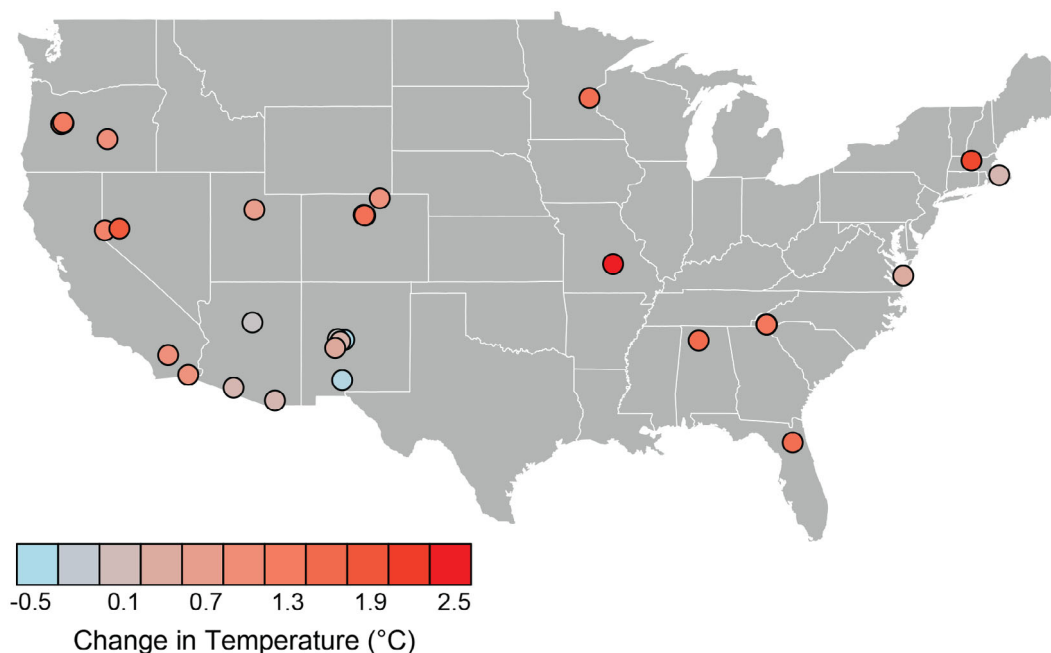
Fig. 1. Geographic distribution of sampled ant communities at 33 sites that have increased in temperature by an average of 1°C after 20 yr. The color of each point is scaled along a gradient from light blue, indicating a slight decrease in temperature, to bright red, indicating an increase in temperature.

m^2 plots, 10 m apart in a 330-m transect. Within each plot, ants were collected by hand while sifting through litter, debris, and vegetation. Each plot was then baited for 30 min with Keebler Sandies Pecan Shortbread cookies, a commonly used ant bait, and all ant strays were collected. As plots were 10 m apart, we caveat our collection methods as workers could not be assigned to unique colonies and the lack of colony identity was an unavoidable limitation. Specimens were identified to genus using taxonomic keys (e.g., Fisher and Cover 2007) and then compared to a reference collection maintained at the University of Oklahoma by the senior author from the original sampling event.

We quantified the change in incidence for each genus that occurred at 3 or more sample sites. We excluded genera that only occurred at one or two sites as these taxa were rare and usually only collected in the 2016–2017 resurvey (e.g., *Neivamyrmex* army ants occurring in one plot total). For both the original and resurvey, we calculated the incidence of each genus as the number of plots (out of 30) at each site where it was

recorded. Our measure of change was determined as:

$$\Delta = \left(\frac{N_{new}}{N_{new} + N_{original}}\right)$$

where N_{new} represents the number of sites where a genus' incidence was higher in the new survey and $N_{original}$ represents the number of sites where a genus' incidence was higher in the original survey. We did not include sites where no change occurred (i.e., static sites) as these made up a small portion of the total number of genus by site comparisons (nine out of 337, 2.7%) and measures of change with and without these nine genus by site combinations were highly correlated (Pearson correlation, $t = 45.41$, $r = 0.99$, $P < 0.001$). Our measure of change is thus the proportion of sites (0.0–1.0), excluding static sites, where a genus' incidence had increased in 2016–2017 compared to 1994–1997. As an example, if a genus had a value of 0.2 that would indicate that incidence in the new survey was higher at only 20% of the sites where that genus

occurred while at the other 80% of sites, incidence was lower.

Thermal tolerance and phylogenetic signal

We measured the critical thermal minima (CT_{min}) and maxima (CT_{max}) of ants using a ramping protocol commonly used to measure thermal tolerance (Kaspari et al. 2015, Bujan et al. 2020*a*). For most of the common species at each site, we collected at least ten live workers and placed individual workers into 1.5-mL microcentrifuge tubes that had been modified with modeling clay to remove a thermal refuge in the cap (Roeder et al. 2018*a*). For CT_{max}, we placed five vials with ants into a Thermal-Lok 2-position dry heat bath (USA Scientific, Orlando, Florida, USA; advertised accuracy $\pm$ 0.2°C) prewarmed to 36°C. Every 10 min, ants were checked to see whether they had reached their critical thermal limit by rotating the vials and looking for a righting response. The temperature was then increased to 2°C, and the process was repeated until all ants had lost muscle control. Similarly, for CT_{min}, we placed five ants into an EchoTherm IC20 chilling/heating dry bath (Torrey Pines Scientific, Carlsbad, California, USA; advertised accuracy $\pm$ 1°C) precooled to 20°C and followed the methods above except we decreased the temperature 2°C every 10 min. We averaged species values within a genus to create genus-level CT_{max} and CT_{min} values (Appendix S1: Table S2). We found little within-genus variation in CT_{max} and CT_{min}, especially compared to cross-genus variation (see Appendix S1: Table S2). Standard error values within a genus were on average around 0.7°C for CT_{max} and 1.2°C for CT_{min} while the range in average CT values across genera was 14.4°C for CT_{max} and 11.0°C for CT_{min}. Because of these differences and others who have used genus-level CT values (Boyle et al. 2021, Guo et al. 2020), we believe our response variables are justified.

We tested for phylogenetic signal in ant thermal traits by calculating Pagel's λ using an ant phylogeny (Moreau and Bell 2013) pruned to include the genera for which we measured thermal tolerance. We added one genus that was not present in the original tree, *Ponera*, as a sister group to *Hypoponera* and ran separate analyses for CT_{max} and CT_{min} as we did not measure CT_{min} for the genus *Stigmatomma*. Pagel's λ considers how traits that are distributed on a phylogeny compare to those expected from Brownian motion by transforming the original tree using the parameter λ, which ranges from zero to one (Pagel 1999). As λ approaches one, traits show greater phylogenetic signal.

Statistical analyses

All analyses were run in R, version 3.5.1. We used an information theoretic approach to rank multiple generalized linear regressions (GLM) with binomial error distributions that compared thermal traits (CT_{max} and CT_{min}) and environmental variables (MAT and ΔTemp) to our measure of change. We tested CT_{max} and CT_{min} separately as we had additional data for the CT_{max} of the genus *Stigmatomma*. Pagel's λ was calculated to check thermal traits for a phylogenetic signal in the ape and phylosignal packages.

Regression models were ranked by Akaike's information criterion (AIC), and ΔAIC values for each model were calculated from the difference of the AIC of ith model and the model with the lowest AIC value. Akaike weights (w_i) were then calculated and represent a weight of evidence that model i was the best fit (Burnham and Anderson 2002). Regressions were visually inspected for non-linear relationships (i.e., quadratic and cubic relationships) and compared to their linear counterparts using AIC. Cragg and Uhler pseudo-r^2 values were determined using the pscl package. For multiple regression models, predictor variables were checked for multicollinearity using a variance inflation factor (VIF) cutoff = 3 in the car package. We also calculated Pearson correlation coefficients between (1) CT_{max} and CT_{min} to check for a trade-off in thermal traits, (2) a genus' ΔTemp and MAT to examine if genera occurring in warm locales were experiencing greater changes in temperature, and (3) a genus' proportional change in incidence and the magnitude of that change (i.e., average change in number of plots occupied) to check whether genera increasing at more sites were also increasing at more plots within those sites.

RESULTS

Mean annual temperatures of our study sites ranged 24.2°C, from a cold Alpine tundra in Colorado (MAT = -1.0°C) to a warm desert in

southern California (MAT = 23.2°C). The mean increase across sites was 1.0°C (±0.1 SE) between the two sampling events (range, −0.4°C in a New Mexico high desert to +2.5°C in a Missouri mixed hardwood forest; Fig. 1). We collected 28 ant genera at three or more of the 33 sites. Of these genera, 18 (64%) had higher incidence in 2016–2017 than in the original sample 20 yr prior.

Ant incidence change increased with CT_{max}

CT_{max}s varied 14.4°C from a low of 38.8°C in *Brachymyrmex* to a high of 53.2°C in *Forelius*. CT_{min}s ranged less, from 0.2°C in *Prenolepis* to 11.2°C in *Brachymyrmex*. A genus' CT_{max} and CT_{min} were not correlated (Pearson correlation, $t = -0.89$, $r = -0.17$, $P = 0.383$). We also found no phylogenetic signal that would account for the variation in CT_{max} ($\lambda = 0.37$, $P = 0.665$) or CT_{min} ($\lambda < 0.01$, $P = 1$) across these common genera.

While the ΔTemp experienced was correlated with MAT (Pearson correlation, $t = -2.71$, $r = -0.47$, $P = 0.012$), variance inflation factors suggest little collinearity between CT_{max} (VIF = 1.4), MAT (VIF = 1.6) and ΔTemp (VIF = 2.1). We tested these correlated, but not colinear, predictors and found that as a genus' CT_{max} value increased so did the proportion of communities in which its incidence—the number of plots occupied—likewise increased 20 yr hence (Fig. 2 a; Table 1). Moreover, CT_{max} was the only parameter in each model within two AIC of the top model, accounting for 17.2% of the variation in the proportion of sites where genera increased (Table 1; GLM, $y = 0.06x - 2.66$, AIC = 105.89, $w_i = 0.35$).

As the relationship with CT_{max} appeared non-linear, we further tested and found that a quadratic and cubic fit were better than the linear model, accounting for an additional 13–15% of the variation for increasing incidence (Table 2). In the quadratic model, which had the lowest AIC value, incidence peaked and then slightly decreased for thermally tolerant ant genera with CT_{max} values above the average of 46.1°C (Fig. 2 a). In contrast, a genus' CT_{min} was unrelated to its 20-yr change in incidence with CT_{min} values clustering around the genera mean of 5.7°C (Fig. 2b; Table 1). There was also a strong, positive correlation between a genus' change in
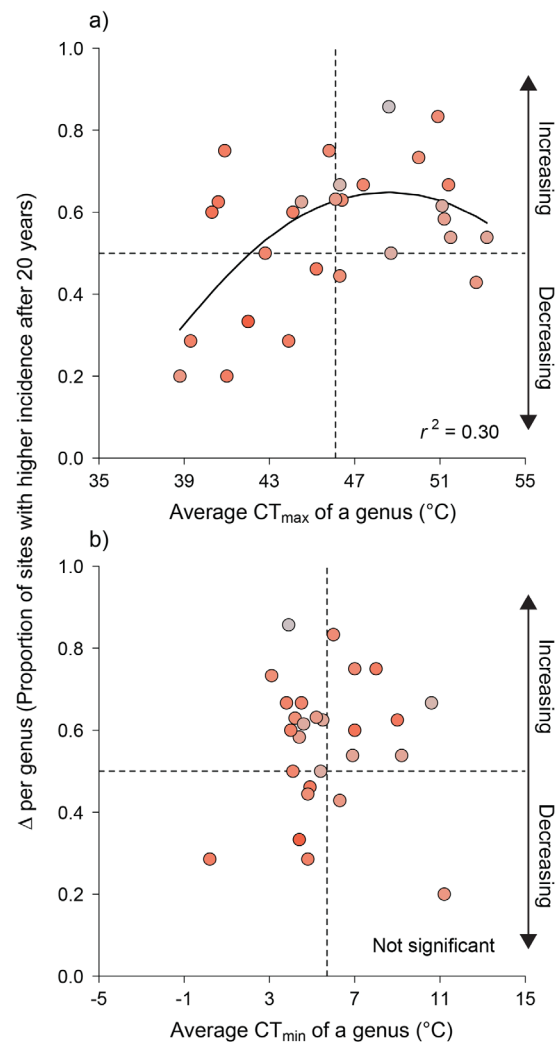

Fig. 2. Relationship between ant thermal traits and the proportion of sites where that genus was found with higher incidence after 20 yr (i.e., Δ per genus). Panel (a) depicts CT_{max} and panel (b) depicts CT_{min}. Each point is a genus. The color of each point ranges from light blue to bright red indicating decreasing to increasing average temperature change, respectively, at sites where that genus was found (see Fig. 1 for more details). Vertical dashed lines represent average CT_{max} or CT_{min} across all genera. Genus values that are above the horizontal dashed line represent an overall increase in the new survey while genus values below this line represent a decrease.

incidence and the magnitude of that change (Fig 3; Pearson correlation, $t = 8.37$, $r = 0.85$, $P < 0.001$). In other words, genera with high

Table 1. AIC scores and weights of multiple linear regression models testing how thermal traits (CT_{max} or CT_{min}), mean annual temperature (MAT), and the change in temperature between the two surveys (ΔTemp) affected the proportion of sites where genera have increased in incidence.

Model	Intercept	Trait	MAT	ΔTemp	AIC	ΔAIC	w_i	Pseudo-r^2
Critical thermal maxima								
CT_{max}	−2.66*	0.06*	—	—	105.89	0.00	0.35	0.17
CT_{max} + MAT	−2.45	0.07*	−0.05	—	106.74	0.85	0.23	0.21
CT_{max} + ΔTemp	−2.76	0.07	—	0.03	107.88	1.99	0.13	0.17
CT_{max} + MAT + ΔTemp	−1.44	0.06	−0.07	−0.32	108.34	2.45	0.10	0.22
Null	0.33*	—	—	—	109.05	3.16	0.07	—
ΔTemp	0.69*	—	—	−0.39	109.76	3.87	0.05	0.05
MAT + ΔTemp	2.00*	—	−0.08	−0.76	109.87	3.98	0.05	0.11
MAT	0.55	—	−0.02	—	110.89	5.00	0.03	0.01
Critical thermal minima								
Null	0.36*	—	—	—	104.15	0.00	0.31	—
ΔTemp	0.65	—	—	−0.32	105.31	1.16	0.17	0.03
MAT + ΔTemp	1.75	—	−0.06	−0.64	106.02	1.87	0.12	0.08
MAT	0.53	—	−0.01	—	106.06	1.91	0.12	<0.01
CT_{min}	0.37	<−0.01	—	—	106.15	2.00	0.11	<0.01
CT_{min} + ΔTemp	0.74	−0.01	—	−0.34	107.26	3.11	0.07	0.03
CT_{min} + MAT + ΔTemp	1.75	0.02	−0.07	−0.65	107.95	3.80	0.05	0.08
CT_{min} + MAT	0.52	0.01	−0.02	—	108.05	3.90	0.04	<0.01

Note: Models are ordered by the lowest ΔAIC. w_i values are rounded to two decimal places and may not sum to 1. Values in boldface and accompanied by an asterisk (*) indicate a significant coefficient at $P < 0.05$.

Table 2. Linear, quadratic, and cubic regression models testing relationships between ant genera critical thermal maxima (CT_{max}) and the proportion of sites where genera increased in incidence.

Model	Intercept	x	x^2	x^3	AIC	ΔAIC	w_i	Pseudo-r^2
Quadratic	−33.88*	1.42*	−0.01*	—	103.50	0.00	0.50	0.30
Cubic	164.35	−11.62	0.27	<−0.01	104.47	0.97	0.31	0.32
Linear	−2.66*	0.06*	—	—	105.89	2.39	0.15	0.17
Null	0.33*	—	—	—	109.05	5.55	0.03	—

Note: Models are ordered by the lowest ΔAIC. w_i values are rounded to two decimal places and may not sum to 1. Values in boldface and accompanied by an asterisk (*) indicate a significant coefficient at $P < 0.05$.

CT_{max} values tended to occupy more plots at more sites after 20 yr.

DISCUSSION

Thermal performance curves are bracketed by two functional traits—CT_{min} and CT_{max}—of great potential utility for predicting changes in an ectotherm's performance, and hence its abundance, in a warming world. Here, we realize that utility—predicting genera that are increasing or decreasing—by combining a new regional dataset on 20-yr changes with a dataset on the thermal tolerances of common ant genera. To our knowledge, this is the first study to successfully combine long-term community-level changes and thermal traits to predict the winners and losers under climate change in a common and ecologically important arthropod group.

Genera with high CT_{max} are more likely to increase

A key focus of research in global change biology is the identification of functional traits—aspects of the phenotype linked to fitness (McGill et al. 2006, Kraft and Ackerly 2010, Soudzilovskaia et al. 2013, Wong et al. 2019)—that predict population responses to warming. We used a
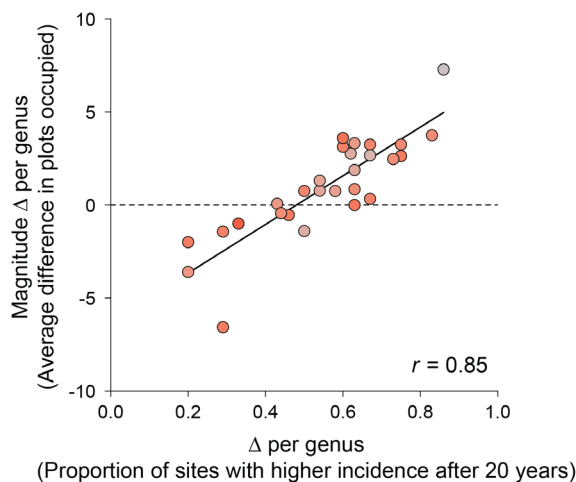
Fig. 3. Correlation between the proportion of sites where a genus was found with higher incidence after 20 yr (i.e., Δ per genus) and the average difference in number of plots occupied per site (i.e., magnitude Δ per genus). The color of each point ranges from light blue to bright red indicating decreasing to increasing average temperature change, respectively, at sites where that genus was found (see Fig. 1 for more details). The horizontal dashed line represents a magnitude Δ = 0.

functional trait approach to dissect how diversity within the ants—for example, CT_{max} varying 14.4°C across 28 common genera—informs how their community occurrence has shifted after 20 yr. Our results reveal that CT_{max} is necessary, but not sufficient to predict winners and losers. An inspection of Figure 2a reveals that genera that are increasing (i.e., occupying more plots in their respective communities) occur across almost the entire range of CT_{max}; those that are decreasing are heavily biased toward low thermal tolerance (i.e., $CT_{max} < 46$°C). Some of these genera (e.g., *Brachymyrmex* and *Stigmatomma*) declined 80% from the mid-1990s samples and were found in forests with relatively high degrees of warming (+1.6°C).

The resulting nonlinearity suggests a few working hypotheses. The first proposes the reasonable notion that more than one trait determines trends in an ant genus' incidence. In this case, some aspect of natural history allows low CT_{max} genera like *Myrmecina*, *Ponera*, and *Strumigenys* to increase while co-occurring

Brachymyrmex and *Stenamma* decrease. At the same time, some of the most thermophilic genera like *Monomorium* and *Forelius* ($CT_{max} = 53$°C) that are active at the hottest parts of the day have incidence levels that are relatively stable compared to large colony dominants like *Crematogaster*, *Formica*, and *Solenopsis* ($CT_{max} = 46$°–51°C). Here, we suggest that more modest increases in temperature, especially in the already hottest desert ecosystems, may provide no advantage to the thermophiles while increasing the competitive ability of the dominant genera that forage in these communities for most hours of the day, including night when warming is most prevalent (Cerdá et al. 1998, Alward et al. 1999, Barton and Schmitz 2018, Roeder et al. 2018a). Both of these hypotheses are likely informed by trade-offs in thermal and other functional traits (Bujan et al. 2016, Penick et al. 2017).

Resistance to climate change in ecological communities

The relationship between thermal tolerance and abiotic conditions has been mixed for arthropods: Meta-analyses have generally shown a weak-to-nonexistent relationship between a population's CT_{max} and the mean annual temperature of the habitat or geographic range (Addo-Bediako et al. 2000, Sunday et al. 2011, Hoffmann et al. 2013, Bujan et al. 2020a). Instead, upper thermal limits are often more phylogenetically constrained by evolutionary history, a result that has been documented for ants (Diamond et al. 2012) but one we did not observe in our analyses. We posit the lack of signal is partially due to reduced sample size—28 genera compared to 40 genera in Bujan et al. (2020a) and 156 species in Diamond et al. (2012)—which parallels a similar result observed in communities of montane ants in southern Africa (Bishop et al. 2017). More specifically, we only used data from ants that occurred in three or more sites and thus genera like *Atta*, *Acromyrmex*, and *Cyphomyrmrex*, all of which are fungus gardeners with low thermal tolerance, were not included. If these groups were included, a phylogenetic signal in heat tolerance may have been observed. But why do analyses of population data fail to find CT_{max}s tracking environmental temperature?

One possible answer is the diversity of CT_{max}s in any given ecological community potentially

promotes the coexistence of some suite of species. For example, a moderately diverse grassland community may support a low CT_{max} *Prenolepis* winter ant, the nocturnal and crepuscular low CT_{max} *Lasius*, two dominant *Crematogaster* and *Solenopsis* species that maintain large colonies and forage most hours of the day, and thermophile specialists like *Forelius* and *Monomorium* that emerge for a few superheated hours daily (Prather et al. 2018, Roeder et al. 2018*a*). As microclimate is increasingly found to be an important abiotic factor structuring communities (Potter et al. 2013, Storlie et al. 2014, Kaspari et al. 2015, Woods et al. 2015), our measure of temperature—MAT—may underestimate the available thermal niche space in many temperate North America locations. Yet certain tropical species like army ants (Baudier et al. 2015, Baudier et al. 2018) may be less resistant to moderate increases in temperature, if the more uniform temperatures in the tropics promote thermal specialization. If this scenario is true, we should expect community-level comparisons of thermal tolerance across tropical sites to show better matches between environmental temperature and CT_{max}. This, indeed, seems to be the case in a Panama rainforest, where the CT_{max}s of ants from the tropical canopy are consistently higher than those from the cooler shaded understory 30 m below (Kaspari et al. 2015). However, an alternative explanation could be that tropical ectotherms operate within a narrow range of temperatures because the tropics are simply hotter (Payne and Smith 2017).

Second, the functional traits CT_{max} and CT_{min} are uncorrelated in our dataset ($P = 0.383$) suggesting they are not constrained by a trade-off, which allows for a diversity of thermal ranges (i.e., $CT_{range} = CT_{max} - CT_{min}$) to occur. Among the ants we studied, there are at least three reasons to evolve a broad thermal range. The first is to be an opportunistic generalist: *Tapinoma* is a cosmopolitan genus (Menke et al. 2010) which we collected from Massachusetts to New Mexico and maintains a thermal range from 3.1°C to 50.0°C; it also increased at 73% of our study sites. The second is to occupy a thermally variable nest site: The largely arboreal genus *Crematogaster* lives in twigs and branches that supercool in winter and superheat in summer; its thermal range averaged 4.4°–51.2°C and its incidence

increased at 58% of sites. Finally, genera common at high elevations also experience the greatest range of temperature: *Leptothorax*, which we primarily collected along elevational gradients in Colorado and Oregon, had a thermal range from 3.8° to 51.4°C and increased at 67% of its sites. These three genera—*Tapinoma*, *Crematogaster*, and *Leptothorax*—had among the lowest CT_{min}s but all increased in the 2016–2017 resurvey, likely in part due to their high CT_{max}s.

In contrast to CT_{max}, CT_{min} is unpredictive of genus-level change in North American ants. This is not for a lack of existing variation in CT_{min} which is similar (11.0°C) to CT_{max} (14.4°C). Yet this result is somewhat surprising as environmental temperatures can be important correlates of lower thermal tolerances in ants, at least across elevation and geography (Warren and Chick 2013, Bishop et al. 2017, Diamond and Chick 2018, Bujan et al. 2020*a*). Perhaps one reason for this discrepancy is the varying cost of a mismatch between the environmental temperature and either of the two thermal limits. Given the non-linear, accelerating nature of a thermal performance curve, small increases in temperature near the peak of the curve have a stronger effect on performance and, as a consequence, small discrepancies between the temperature at peak performance and CT_{max} potentially have a greater effect on an organism's performance—the rate it traverses the curve—compared to small changes in CT_{min}.

Caveats and next steps

The temporal dynamics of ecological communities arise from multiple factors acting at varying time scales (Schröder et al. 2005, Fukami and Nakajima 2011, Dornelas et al. 2014, Christensen et al. 2018, Roeder et al. 2018*b*). Here, we focused on large chunks of undisturbed habitat (reducing the potential effects of fragmentation) where relatively long-lived species frequently nest underground (and thus have a thermal refuge) while often collectively acting as dietary generalists (avoiding the complexities of ontogenetic niche shifts). The ants, by many lines of reasoning, are thermophilic ectotherms that should benefit from moderate warming.

Furthermore, given the importance of long-term data in understanding biotic change in the Anthropocene (Hallmann et al. 2017, Cardinale

et al. 2018, Eisenhauer et al. 2019), our dataset has both strengths and weakness. Strengths include using standardized methods to quantify 20-yr differences in incidence for all the common ant genera across 33 habitats ranging from desert to tundra and testing hypotheses from important theory using a new dataset on thermal tolerance. A weakness is that we examine two snapshots separated by 20 yr rather than a series of annual surveys. Thermal traits were also not quantified in the original surveys during the mid-90s, and thus, we cannot account for the potential of thermal traits plastically varying through time. Surely, documenting how CT_{max} and CT_{min} change daily, seasonally, and annually will be an important topic for future research (Nelson et al. 2018, Bujan et al. 2020*b*). That said, these 33 resurveys required two years and over three person-years to collect and analyze. Resurveys with short between sample intervals (e.g., monthly or yearly surveys as performed in studies of rodents [Ernest et al. 2016] and trees [Hubbell et al. 2014]) would unquestionably improve our ability to quantify patterns and causes of change in North American ant communities.

Acknowledgments

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