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Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants

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Abstract

Effects of climate warming on wild populations of organisms are expected to be greatest at higher latitudes, paralleling greater anticipated increases in temperature in these regions. Yet, these expectations assume that populations in different regions are equally susceptible to the effects of warming. This is unlikely to be the case. Here, we develop a series of predictive models for physiological thermal tolerances in ants based on current and future climates. We found that tropical ants have lower warming tolerances, a metric of susceptibility to climate warming, than temperate ants despite greater increases in temperature at higher latitudes. Using climatic, ecological and phylogenetic data, we refine our predictions of which ants (across all regions) were most susceptible to climate warming. We found that ants occupying warmer and more mesic forested habitats at lower elevations are the most physiologically susceptible to deleterious effects of climate warming. Phylogenetic history was also a strong indicator of physiological susceptibility. In short, we find that ants that live in the canopies of hot, tropical forest are the most at risk, globally, from climate warming. Unfortunately this is where many, perhaps most, ant and other species on Earth live.

Keywords: biodiversity, Formicidae, global warming, insect, physiology, temperature

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Introduction

Global climate change has already altered the conditions nearly every terrestrial organism on Earth faces (IPCC, 2007). A key question becomes how the responses of organisms to such change are likely to vary across taxa and regions. Biological responses to global climate change in general, and climate warming in particular, are inevitably an outcome of an organism's physiology (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey *et al.*, 2009), behavior (Kearney *et al.*, 2009), ecology (Thomas *et al.*, 2004; Parmesan, 2006), and evolutionary history (Etterson & Shaw, 2001; Willis *et al.*, 2008; Davis *et al.*, 2010). A challenge has been to unite these components into a single framework that might allow us to evaluate their relative contributions, and ultimately, to develop general predictive models for some of the millions of species on Earth, many of which are insects.

Early biogeographic work suggested the general hypothesis that organisms inhabiting lower latitudes may have narrower tolerances of environmental conditions than those living elsewhere (Janzen, 1967). A rich body of work considered how such biogeographic patterns, for example in the latitudinal extents of species, may be influenced by physiological tolerance (e.g. Rapoport, 1982; Stevens, 1989, 1992; Letcher & Harvey, 1994; Gaston *et al.*, 1998; Addo-Bediako *et al.*, 2000; Fernandez & Vrba, 2005; reviewed in Ghalambor *et al.*, 2006). Only recently have such macrophysiological analyses been considered in context of climate change, whether historic or modern (Chown & Gaston, 2008). One emerging pattern for ectotherm taxa studied to date is that organisms inhabiting lower latitudes may be more physiologically susceptible to climate warming than organisms at higher latitudes, despite the relatively greater increases in temperature anticipated at higher latitudes (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey *et al.*, 2009; Sunday *et al.*, 2011). This pattern results from tropical organisms inhabiting warm

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environments close to their upper physiological thermal tolerances compared with temperate organisms inhabiting relatively cool environments far from their upper thermal tolerances. The next step is to understand the generality of these results, particularly for organisms in natural habitats. In addition, it is necessary to put such variation in warming in a phylogenetic context if the relative influence of phylogenetic conservatism and local adaptation are to be understood (Huey *et al.*, 2009). Finally, we need to understand not just where organisms are at risk, but which groups are at risk. In other words, are there predictable attributes of organisms that make them particularly predisposed to extinction due to climate warming?

Here we take advantage of the wealth of physiological, ecological and phylogenetic data available for ants, that, combined with globally extensive fieldwork, allow us to explore how these factors combine with geographic variation in climatic conditions to determine responses to current and future climate warming. Most multicellular species on Earth are insects (Grimaldi & Engel, 2005) – ants in particular comprise perhaps as many as 20 000 species, inhabit nearly all major terrestrial habitats, and are ecologically critical in their roles as predators, scavengers and herbivores (Wilson, 1990). However, analyses of the spatial patterns in the responses of insects are few relative to other taxa (Thomas *et al.*, 2004), with the possible exception of work based on insect pests (Deutsch *et al.*, 2008) and disease vectors (Reiter, 2001; Ogden *et al.*, 2006).

As a metric of the susceptibility of species to climate warming, we employ the widely used 'warming tolerance', the difference between an organism's critical thermal maximum ($\mathrm{CT}_{\max}$) and a thermal index of its habitat (T_{habitat}) (Deutsch *et al.*, 2008; Angilletta, 2009; Jaramillo *et al.*, 2009). Warming tolerance provides an estimate of how much an organism can warm before reaching ecological death, i.e. the point at which an organism could not escape to a thermal refuge. To determine which ants are most susceptible to climate warming, we first examine broad patterns in warming tolerance as a function of latitude. We then refine our predictions of which ants are most susceptible to climate warming, using a model selection approach to develop a predictive model for warming tolerance which considers the contributions of climate variables, ecological traits and phylogenetic history.

Materials and methods

Definition of the critical thermal maximum

For all empirical tests and when possible for data obtained from primary literature sources (see below), the $\mathrm{CT}_{\max}$ was defined as the temperature at which muscle coordination is lost (Lutterschmidt & Hutchison, 1997). $\mathrm{CT}_{\max}$ is an ecologically relevant metric of tolerance, as it defines the temperature at which an individual could not escape to a non-lethal thermal environment (Lighton & Turner, 2004). Individual organisms can, of course, modulate their exposure to extreme temperatures behaviorally, such that for a given environment two organisms with the same $\mathrm{CT}_{\max}$ may differ in their probability of encountering lethal temperatures. Nonetheless, $\mathrm{CT}_{\max}$ is a useful starting point for understanding broad, macrophysiological patterns in thermal tolerance.

Definition of warming tolerance

We defined warming tolerance as the difference between an ant's $\mathrm{CT}_{\max}$ and a thermal index of its habitat. Several indices of environmental temperature (and thus warming tolerance) have been used previously (e.g. mean annual temperature as in Deutsch *et al.*, 2008; and mean maximum daytime temperature during the warmest 3 months of the year as in Huey *et al.*, 2009). Although these various indices are sufficient to examine qualitative differences in warming tolerance (and vulnerability to climate warming) across large regional or global scales, the precise quantitative relationship between warming tolerance and latitude is likely to be contingent upon the choice of environmental temperature index. Here, for general models of latitudinal variation in warming tolerance we focus on warming tolerance defined by the difference between $\mathrm{CT}_{\max}$ and mean temperature during the warmest quarter of the year ($T_{\mathrm{qt\ mean}}$), given the importance of warm-season temperatures to biological responses to climate warming. However, for combined climate and ecological trait-based models (see below), we focus on warming tolerance based on mean annual temperature ($T_{\mathrm{an\ mean}}$) as a proxy of vulnerability to climate warming, given the superior performance of warming tolerance based on $T_{\mathrm{an\ mean}}$ (in terms of distribution, model convergence, and model diagnostics) compared with warming tolerance based on $T_{\mathrm{qt\ mean}}$.

All environmental temperature data were obtained from WorldClim (Hijmans *et al.*, 2005). $T_{\mathrm{an\ mean}}$ and $T_{\mathrm{qt\ mean}}$ were rescaled to units of degrees Celsius, such that warming tolerance is the degrees Celsius an individual can warm until reaching ecological death.

Data sources

Our analyses included 269 unique accessions (based on combinations of 156 species and 42 geographic locations) from 53 genera. Data on critical thermal maxima were in part obtained from the primary literature [28 studies; 72 species; 28 genera; 84 of 269 unique accessions (combinations of species × site); see Appendix S1 in Supporting Information], but the majority of our data came from empirical determinations of $\mathrm{CT}_{\max}$ for ants collected in the field by the authors of this study (data are available at the Harvard Forest Data Repository, http://harvardforest.fas.harvard.edu/data/archive.html). For all empirical tests, entire colonies or colony fragments of ants were collected from natural habitats. Ants were placed individually into 1.5 mL Eppendorf tubes which contained cotton in the lid cap to eliminate a potential thermal refuge. The tubes were transferred to a heating dry block (Thermal Lok USA Scientific, Ocala, FL, USA), and the temperature was increased by 2 °C every 10 min starting at 36 °C. At the end of every 10 min interval, individual ants were checked for the loss of muscular coordination, indicating CT_{max} (within a 2 °C resolution) was achieved (Appendix S1).

Ecological data for nest site location, habitat type, and foraging underground were obtained from the primary literature and confirmed with expert opinion. Nest site locations were quantified by assigning a number on the scale of 1–4 corresponding with the vertical location of the nest site: 1 = on/in ground, leaf litter; 2 = logs, herbaceous or small woody plants (understorey); 3 = trunks of trees (subcanopy); 4 = tops of trees, arboreal (canopy). Habitat cover was quantified by relative differences in the degree of cover: 1 = open; 2 = forest edges or species which regularly occupy both open and/or forested habitats; 3 = forested. Foraging underground was treated as a binomial variable (whether or not a given species forages underground). Elevation and climate data were obtained using GIS: seasonality (standard deviation of annual temperatures) and indices of environmental temperature were calculated from WorldClim (Hijmans *et al*., 2005), and aridity was calculated from climate and solar radiation data (Trabucco & Zomer, 2009). We are careful here to note that remotely sensed environmental data may not necessarily reflect the conditions experienced by ants, although at a minimum these data are sufficient to examine relative differences in risk from climate warming. Geographic coordinates for the climate data were taken directly from GPS for empirical estimates or extracted from primary literature sources reporting CT_{max}; when precise coordinates were not available, the center latitude and longitude of the county (US only) or region (outside of the US) in which ants were collected was used.

Phylogenetic associations among ant genera were based on the phylogeny of Moreau *et al.* (2006), obtained from TreeBase http://www.treebase.org. Genera represented in the trait dataset, but not in the phylogeny, were assigned to the most closely related genus represented in the phylogeny.

Statistical analyses

All statistical analyses were performed using R (version 2.11.1; R Development Core Team, 2010). To evaluate the ability of climate and ecological traits to predict warming tolerance while accounting for shared phylogenetic history, we performed phylogenetic generalized least squares models (PGLS from the CAIC package; Orme *et al*., 2009) under an assumption of trait evolution by Brownian motion. We used an information-theoretic approach to select the most likely model for predicting warming tolerance in ants, given the available data (Burnham & Anderson, 2002). The initial pool of models included warming tolerance ($CT_{max}-T_{an\ mean}$) as the response variable, and all combinations of the following terms (including an intercept-only model; see Appendix S1 for details): habitat cover, nest site nested within degree of habitat cover (denoted as habitat cover/nest site; hierarchical nesting was necessary as ants that maintained nests in open habitats tended to occupy nest sites closer to the ground), foraging underground, maximum annual temperature, aridity, seasonality and elevation.

For each model, the maximum likelihood estimate of λ was used to scale the model covariance. The best-fitting models were selected on the basis of AIC [Akaike's information criterion; given the large number of samples, model fit assessed using AIC corrected for small sample sizes (AICc), was comparable to AIC]. The best-fitting model subset was defined as those models with ΔAIC's <4 (ΔAIC being defined as the difference between the AIC of the current model and the minimum AIC in the entire pool of models). After identifying the best-fitting models, ΔAIC's were recalculated based on this subset; corresponding Akaike weights (the probability that a given model, m_i, out of i alternative models is the best model given the data; see Burnham & Anderson, 2002) are therefore based on recalculated ΔAIC's. We accounted for uncertainty in the models in the best-fitting model subset, by performing model averaging: estimates of each parameter were averaged across the best-fitting models (means were weighted by the Akaike weight of a given model). Unconditional standard errors were also computed for model averaged estimates (Buckland *et al*., 1997; Burnham & Anderson, 2002).

Results

Physiological responses to climate warming across latitude

Compared with latitudinal variation in environmental temperature, variation in the CT_{max} was quite small (Fig. S1), although CT_{max} decreased with distance from the equator (i.e. absolute latitude, hereafter defined as |latitude|; $\beta \pm SE = -0.0527 \pm 0.0166$, $t = -3.17$, df = 267, $P = 0.002$; we also examined a model of CT_{max} with linear and quadratic terms for |latitude|, and found that the quadratic term was marginally significant, $t = -1.87$, df = 266, $P = 0.0623$, suggesting CT_{max} may be highest at mid-latitude desert regions, though more data are needed to fully evaluate this pattern). In general, species at relatively low latitudes (typically hotter environments) tended to be more tolerant of high temperatures.

To examine broad patterns in physiological responses to climate warming, we first modeled warming tolerance ($CT_{max}-T_{qt\ mean}$) as a function of latitude. Warming tolerance increased with |latitude| ($\beta \pm SE = 0.147 \pm 0.0271$, $t = 5.41$, df = 267, $P < 0.0001$; Fig. 1). Phylogenetically corrected analyses (phylogenetic generalized least squares, PGLS, models) of warming tolerance as a function of |latitude| were very

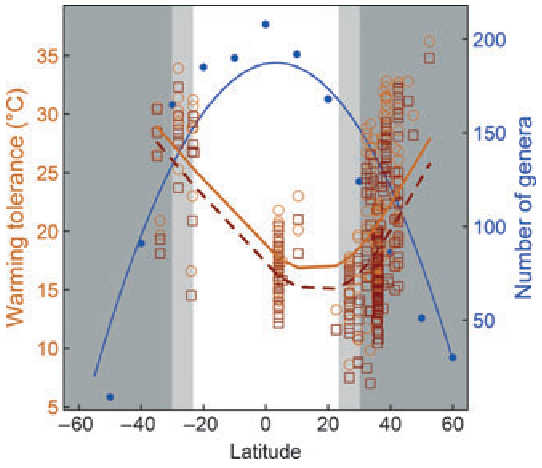

Fig. 1 Warming tolerance ($\mathrm{CT}_{\max}-T_{\mathrm{qt\ mean}}$ in °C; left axis) and the number of ant genera (right axis) as a function of latitude (in decimal degrees). For warming tolerance, each point (open symbols) is the warming tolerance for a single species from a given geographic location. For the number of genera (blue filled circles), each point is the cumulative number of unique genera in 10° latitudinal bins starting with 0 ± 5°, and moving away from the equator in either direction. Curved lines for warming tolerance are based on smoothing splines, each with smoothing parameter = 1.45. Data based on the current climate (orange open circles, solid line) and climate projections for the year 2050 (red open squares, dashed line) are shown. The curved line for the number of genera is based on the quadratic regression against latitude. Light gray shaded areas extending from > |23.5|° to ≤ |30|° indicate subtropical regions, dark gray shaded areas extending > |30|° indicate temperate regions, and the center white area extending ≤ |23.5|° indicates tropical regions.

similar to the uncorrected model ($\beta \pm \mathrm{SE} = 0.130 \pm 0.0254$, $t = 5.14$, df = 267, $P < 0.0001$). In all subsequent models of warming tolerance as a function of |latitude| (see below), the results of phylogenetic analyses were comparable to non-phylogenetic analyses, so we present the results of phylogenetic analyses. In addition, we re-performed the analysis of warming tolerance on a dataset which excluded the tropical data (for which we had comparatively less geographic replication), and found that the significant positive relationship between warming tolerance and |latitude| strongly held for this subset ($\beta \pm \mathrm{SE} = 0.598 \pm 0.0773$, $t = 7.74$, df = 204, $P < 0.0001$).

To understand the concordance of warming tolerance (or intolerance) and ant diversity, we simultaneously examined the relationships of warming tolerance and ant biodiversity (based on the number of genera, which is a strong correlate of species diversity, Dunn *et al.*, 2010; see Guénard *et al.*, 2010 for ant diversity data) as a function of latitude (Fig. 1). Warming tolerance is the lowest where ant diversity is the highest. The vast majority of ant genera (and implicitly species) fall within the region where warming tolerance is the lowest.

We used three climate warming projections for the year 2050 (Ramirez & Jarvis, 2008; climate scenario SRES A2a, models CGCM3.1-T47, BCCR-BCM 2, and GISS-AOM) to examine the consequences of both mean increases in temperature and spatial heterogeneity in temperature increases for warming tolerance. Because our models of warming tolerance under each of the different warming scenarios were remarkably similar, we present the results for the GISS-AOM model as representative. In general, warming tolerance decreased with projected climate warming between 2010 and 2050, as environmental temperatures approached species' thermal maxima. For two of 269 ant populations, the 2050 projected maximum annual temperature of the habitat exceeded their current $\mathrm{CT}_{\max}$ (Fig. 2), indicating potential extinction of such populations in the absence of dispersal and other mitigating factors. Importantly, the greater projected increases in temperature at higher latitudes were insufficient to alter the current pattern of lower warming tolerance in the tropics (warming tolerance as a function of |latitude|, 2050: $\beta \pm \mathrm{SE} = 0.112 \pm 0.0249$, $t = 4.50$, df = 267, $P < 0.0001$; Figs 1 and 2).

Refining predictions of physiological responses to climate warming

To refine our predictions of physiological responses to climate warming, we used a model selection approach to examine how climatic and ecological variables influence warming tolerance while accounting for (and considering) the influence of shared evolutionary history. During the model selection process, five models of warming tolerance were found to have strong levels of empirical support ($\Delta\mathrm{AIC} < 4$; Table S1; see also Tables S2 and S3); hereafter we refer to these models as the best-fitting model subset. The amount of total variation in warming tolerance explained by the models was substantial, around 75% for models comprising the best-fitting model subset. There was a strong consensus among models regarding the importance of climatic variables, phylogenetic history, and to a lesser degree, ecological traits: the magnitude and direction of these effects were similar across models in the best-fitting model subset (see Table 1 for model averaged coefficients). Models based on warming tolerance from the 2050 climate projections yielded qualitatively similar results to models based on the current climate, indicating climatic variables, ecological traits and evolutionary history may be useful predictors of both current and future responses to climate change.

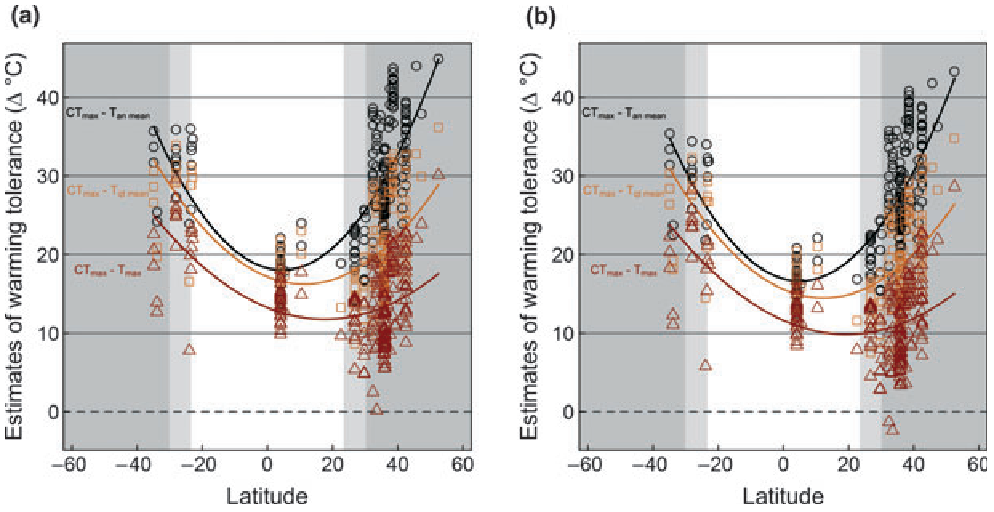

Fig. 2 Warming tolerance (°C) as a function of latitude (in decimal degrees) based on our primary definition of warming tolerance as the difference between the critical thermal maximum and mean annual temperature ($\mathrm{CT_{max}}-T_{\mathrm{an\ mean}}$; black circles), and complementary definitions as the difference between the critical thermal maximum and mean temperature during the warmest quarter of the year ($\mathrm{CT_{max}}-T_{\mathrm{qt\ mean}}$; orange squares), and difference between the critical thermal maximum and maximum annual temperature ($\mathrm{CT_{max}}-T_{\mathrm{max}}$; red triangles). Quadratic regressions for $\mathrm{CT_{max}}-T_{\mathrm{an\ mean}}$ (current, $y = 18.3–0.106x + 0.0117x^2$; 2050 projected, $y = 16.9–0.114x + 0.0114x^2$; black lines), $\mathrm{CT_{max}}-T_{\mathrm{qt\ mean}}$ (current, $y = 17.2–0.170x + 0.00743x^2$; 2050 projected, $y = 15.6–0.180x + 0.00735x^2$; orange lines), and $\mathrm{CT_{max}}-T_{\mathrm{max}}$ (current, $y = 13.3–0.168x + 0.00476x^2$; 2050 projected, $y = 11.6–0.183x + 0.00473x^2$; red lines) are presented for visualization. Each point is the warming tolerance for a single species from a given geographic location. Light gray shaded areas extending from >|23.5|° to ≤ |30|° indicate subtropical regions, dark gray shaded areas extending >|30|° indicate temperate regions, and the center white area extending ≤ |23.5|° indicates tropical regions. Data based on (a) current climate and (b) climate projections for the year 2050 are shown.

Table 1 Model averaged parameter estimates and regression statistics based on the best-fitting model subset

Parameter[*]	β_{MA}	$\mathrm{SE_{MA}}$	t_{global}[†]	$P > t_{\mathrm{global}}$
Intercept	48.8	3.12	15.0	<0.001
T_{max}	−0.0794	0.00697	−11.2	<0.001
Seasonality	0.000724	0.000101	6.34	<0.001
Aridity	−0.000305	0.0000418	−6.07	<0.001
Elevation	0.00120	0.000357	3.54	0.000489
Habitat cover	0.300	0.390	1.09	0.278
Habitat cover/ nest site	−0.279	0.131	−2.14	0.0331
Forage underground[‡]	−1.01	1.12	−0.911	0.363

[*] For each parameter, model averaged coefficients (β_{MA}) and standard errors ($\mathrm{SE_{MA}}$) were based on weighted means from the best-fitting models [weighted by the Akaike weight (w_i) for each model, i, in which the term occurs]; see Table S1 for Akaike model weights (see Burnham & Anderson, 2002 for the details of model averaging).

[†] Regression statistics are based on a global PGLS model containing all of the terms identified as part of the best-fitting model subset.

[‡] The directionality of the binomial variable, foraging underground, was assigned such that positive incidences of foraging underground = 1, and negative incidences of foraging underground = 0.

Climate variables

The climate variables of maximum annual temperature, seasonality, and aridity were the strongest predictors of warming tolerance, as each variable was present in all of the models in the best-fitting model subset (indicated by relative importance values of 1; Table S1). Ants occupying habitats characterized by a lower degree of seasonality and greater maximum annual temperatures had significantly lower warming tolerance (Table 1; Fig. S2a,b). In addition, ants occupying more arid habitats had significantly greater warming tolerance (Table 1; Fig. S2c). This pattern may, in part, be driven by desert specialist ant taxa, such as *Cataglyphis* and *Ocymyrmex* (from the Sahara and Namib deserts, respectively), which have some of the greatest absolute values of $\mathrm{CT_{max}}$, documented for any animal and therefore relatively great warming tolerance despite their living in relatively warm environments. However, we found similar negative relationships between the aridity of their habitat and warming tolerance for several non-desert specialist taxa, suggesting the generality of this pattern. Elevation explained a significant amount of residual variation not explained by climate variables considered in the strict sense (maximum temperature, seasonality, and aridity), with species at lower elevations tending to have lower warming tolerance (Table 1; Fig. S2d).

Phylogenetic history

In general, we found a high degree of phylogenetic inertia in models of warming tolerance, with values of λ around 0.9 (Table S1; Fig. S3). Outside of the modeling framework, there was considerable variability in the degree of phylogenetic signal present in the ecological traits and CT_{max} themselves (Table S2). Habitat cover, nest site and CT_{max} had low, but significant, phylogenetic signal. Related species were more dissimilar than expected under Brownian evolution [not an uncommon result for ecological and physiological traits, and may or may not indicate some degree of evolutionary lability in these traits, when considered individually; see (Blomberg *et al.*, 2003) for details on interpreting phylogenetic signal]. In contrast, foraging underground had a high degree of phylogenetic signal. Species were at least as similar in their foraging habits as expected under Brownian evolution, and trended toward being more conserved than expected (Table S2; Fig. S3).

Ecological traits

Despite the substantial contributions of climate and phylogenetic history to warming tolerance, ecological traits were identified as components of the best-fitting model subset. Nest site hierarchically nested within the degree of habitat cover and whether species foraged underground had modest relative importance values during the model selection process (Table S1), so we interpret these results with caution. Nest site, given the degree of habitat cover, was significantly and negatively related to warming tolerance. Ants that occupy more arboreal nesting sites in more forested habitats tended to have lower warming tolerance (Table 1; Fig. S2e). Foraging underground was non-significant in the PGLS analysis of the global model, although ants that forage underground tended to have lower warming tolerance (Table 1; Fig. S2f). Because foraging underground tended to be phylogenetically conserved (see above), the predictive value of this trait may be indistinguishable from that of phylogenetic history.

Discussion

Here we found tropical species to be more vulnerable to climate warming than temperate species, both in general and when we accounted for other factors, such as phylogenetic history and ecological traits. This result is perhaps surprising given the focus of most work on climate warming has been on those far northern and southern ecosystems where the relative increase in temperature will or has already been greatest (Root *et al.*, 2003). Yet, fitting with earlier work (e.g. Deutsch *et al.*, 2008), the results of our global analysis of ant warming tolerance are unambiguous in their indication that tropical species are more susceptible to climate warming owing to their relatively low warming tolerance, despite the anticipated greater rate of temperature increase at higher latitudes (IPCC, 2007). In particular, we found warming tolerance, or the amount an individual can warm before reaching ecological death, declines sharply approaching the equator. Ants at lower latitudes have a much smaller 'thermal buffer', making them more susceptible to deleterious effects of climate warming. From a conservation standpoint, the apparent generality of this relationship is far from ideal, as warming tolerance is lowest in the tropics, where biodiversity is the greatest (Fig. 1; see also Deutsch *et al.*, 2008; Huey *et al.*, 2009; Tewksbury *et al.*, 2008; Dillon *et al.*, 2010; for a different perspective, see Sinervo *et al.*, 2010, who suggest relatively widespread vulnerability to warming).

This pattern of increased susceptibility to climate warming in the tropics has been found in several groups of herpetofauna (Tewksbury *et al.*, 2008; Huey *et al.*, 2009; but see Sinervo *et al.*, 2010) and for agricultural pests and other relatively widespread insect species (Deutsch *et al.*, 2008). Importantly, here we were able to sample many species using consistent methods in the field, across independent biogeographic regions. In addition, we were able to take advantage of the well-supported phylogenetic hypotheses to disentangle the pattern of decreased warming tolerance in the tropics from both shared evolutionary history and taxon-specific idiosyncratic responses. Our results support and extend results from earlier studies, but with important caveats.

Why are tropical species more at risk from climate warming? An ant's ability to withstand climate warming, or its warming tolerance, is an outcome of its physiological thermal tolerance and the temperature of its environment. Relative to the variation among regions in environmental temperature, the variation in upper thermal tolerance is minimal for the ants considered in our study (assessed by the CT_{max}), and for many other ectotherms (assessed by CT_{max} and other similar metrics such as the upper lethal thermal limit; Addo-Bediako *et al.*, 2000; Deutsch *et al.*, 2008; Huey *et al.*, 2009; Sunday *et al.*, 2011; but see Brett, 1971; who found considerable latitudinal variation in CT_{max} of fishes). If upper thermal tolerances remain relatively invariant across latitude for other taxa, warming tolerance should increase with distance from the equator ($|\text{latitude}|$) for nearly all or perhaps even all taxa. In essence, the only way for a given taxon to fail to show a latitudinal gradient in warming tolerance would be for the upper thermal tolerances to increase as rapidly with decreases in latitude as do environmental temperatures themselves. For example, in the ants considered here, this would require tropical species to have a median $\mathrm{CT}_{\max}$ of 56.1 °C (based on warming tolerance defined by $\mathrm{CT}_{\max}-T_{\mathrm{an\ mean}}$), a value similar to the highest reported for any species of any taxon (56.8 °C for the Australian desert specialist ant, *Melophorus bagoti*; Christian & Morton, 1992), and 5.81 °C above the top 5% of ant $\mathrm{CT}_{\max}$ values. Alternatively, the pattern might fail to exist if temperate species had much lower $\mathrm{CT}_{\max}$ values than they actually do, but this too is unlikely. Again for ants, this would require temperate species to have a median $\mathrm{CT}_{\max}$ of 32.4 °C, a value 2.4 °C below the bottom 5% of ant $\mathrm{CT}_{\max}$ values. In short, the reduced warming tolerance of tropical species appears very likely to generalize across taxa. Because the latitudinal gradient in diversity also tends to generalize (e.g. more species in the tropics), the conclusion that the vast majority of species at risk from climate change are in the tropics is unavoidable (see also Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey *et al.*, 2009).

Although there is substantial variation in upper thermal tolerances across taxa (Sunday *et al.*, 2011), the fact remains that given the high thermal tolerance of ants (the median $\mathrm{CT}_{\max}$ of ants in our study was 43.3 °C), climate warming may be non-lethal for most populations of ants, at least based on physiological thermal limits. Most of the species and populations we examined are unlikely to experience lethal temperatures soon, however, they are still likely to be influenced by warming. Tropical species below their warming tolerance may still experience days or weeks above their warming tolerance. Conversely, temperate species, which are much farther below their warming tolerance may actually benefit from climate warming. Fire ants (*Solenopsis invicta*) in eastern North America, for example, experience maximal colony growth at 32 °C (Porter & Tschinkel, 1993), yet ambient temperatures in their invaded range are typically below this temperature. Climate warming may benefit fire ants in their North American invaded range, as all else being equal, we would expect increasing temperatures to push these ants closer to their maximal performance (see also Huey *et al.*, 2009).

For any particular species, a variety of factors, including acclimation, adaptive evolutionary responses, dispersal and behavioral responses, may mitigate physiological sensitivity to climate warming. While some taxa, such as lizards, exhibit limited acclimation responses (Ghalambor *et al.*, 2006), in ants, acclimation can lead to substantial variation in $\mathrm{CT}_{\max}$ (on the order of several °C; Kay & Whitford, 1978) but this is not universal (Jumbam *et al.*, 2008), and even if biased systematically by several °C – which seems very unlikely – our general results would remain unaltered. Similarly, although rapid evolutionary responses to temperature have been widely documented in invertebrates (e.g. Santos *et al.*, 2005), such responses are likely to be greatest in species with short generation times. Queens (and hence colonies) of many ant species can live years, sometimes tens of years, such that rapid evolutionary responses in ants seem unlikely to be the rule. In terms of their longevity, ants are far more like perennial plants or even vertebrates such as lizards than they are like solitary insects. In this regard, it is noteworthy that recent work from Sinervo *et al.* (2010) on Mexican lizards suggests that these lizards cannot evolve rapidly enough to track current climate change as a result of constraints imposed by the genetic architecture of thermal preference. More to the point, our models of warming tolerance exhibited substantial phylogenetic autocorrelation, which may indicate underlying shared developmental, genetic or architectural constraints on responses to climate warming in ants.

In theory, species that experience conditions too warm for survival can move to track suitable climate (Parmesan *et al.*, 1999; Parmesan, 2006). In practice, this may prove difficult for many species. Tropical species encounter very little change in temperature per unit of distance along latitudinal gradients compared with temperate species (Colwell *et al.*, 2008). It should be easier for tropical species to track suitable habitat conditions along the relatively steeper gradients in climate with elevation (Bush & Hooghiemstra, 2005). However, recent work in tropical ants along the Barva elevational transect in Costa Rica suggests the majority of those ant species will encounter large gaps between current and projected elevational ranges with climate warming, which may make long-distance dispersal necessary for tracking suitable habitat (Colwell *et al.*, 2008). Another possibility is that organisms may be able to track suitable thermal habitats at small scales via behavioral regulation. Ants, for example, can move their nest sites, either horizontally or vertically to track favorable conditions (Jones & Oldroyd, 2007). If all species have similar levels of such flexibility, the curve for warming tolerance simply shifts up. A more likely scenario is that some life histories are more conducive to behavioral plasticity (such as soil nesting). It is possible such behavioral plasticity will be a pre-adaptation for responses to future climate change. In a practical sense, variation in species' ecologies and may prove an effective predictor of responses to climate warming when adequately documented, rather than simply introducing noise into data.

Indeed, using a full complement of climatic, ecological and phylogenetic tools, we were able to build a strong predictive model for warming tolerance in ants, allowing us to refine our predictions of just which types of species are most likely to be at risk. After accounting for additional climatic and ecological variables and shared evolutionary history among ants, seasonality remained a strong predictor of warming tolerance. This confirms that ants in more seasonal environments (i.e. temperate regions at higher latitudes) have greater warming tolerance compared with ants in more aseasonal environments (i.e. tropical regions at lower latitudes), an outcome expected based on theory (Janzen, 1967; Deutsch *et al*., 2008; Huey *et al*., 2009). In addition, our results suggest ants were more at risk if they occupied warmer, wetter forests, or, to a lesser degree, those that foraged underground. Previous work has found similar patterns for smaller subsets of ants, in which ants occupying moist, lowland areas are physiologically susceptible (Colwell *et al*., 2008) – our results suggest the global generality of this pattern.

In short, we find that ants that live in the canopies of hot, tropical forest are the most at risk, globally, from climate warming. Unfortunately this is where many, perhaps most, ant and other species on Earth live. The sustained development of integrative models, which incorporate climatic, ecological and evolutionary components, will provide critical predictive insight into species' responses and susceptibility to climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details on physiological and phylogenetic methods.
Figure S1. Critical thermal maxima as a function of latitude.
Figure S2. Added variable plots for all terms identified as part of the best-fitting warming tolerance models.
Figure S3. Critical thermal maxima and ecological traits mapped on to the phylogeny of ant genera.
Table S1. Summary of the best-fitting warming tolerance models.
Table S2. Phylogenetic signal present in ecological traits and critical thermal maxima.
Table S3. Correlations among climate variables.