



## SYMPOSIUM

# Using Physiology to Predict the Responses of Ants to Climatic Warming

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**Synopsis** Physiological intolerance of high temperatures places limits on organismal responses to the temperature increases associated with global climatic change. Because ants are geographically widespread, ecologically diverse, and thermophilic, they are an ideal system for exploring the extent to which physiological tolerance can predict responses to environmental change. Here, we expand on simple models that use thermal tolerance to predict the responses of ants to climatic warming. We investigated the degree to which changes in the abundance of ants under warming reflect reductions in the thermal niche space for their foraging. In an eastern deciduous forest system in the United States with approximately 40 ant species, we found that for some species, the loss of thermal niche space for foraging was related to decreases in abundance with increasing experimental climatic warming. However, many ant species exhibited no loss of thermal niche space. For one well-studied species, *Temnothorax curvispinosus*, we examined both survival of workers and growth of colonies (a correlate of reproductive output) as functions of temperature in the laboratory, and found that the range of thermal tolerances for colony growth was much narrower than for survival of workers. We evaluated these functions in the context of experimental climatic warming and found that the difference in the responses of these two attributes to temperature generates differences in the means and especially the variances of expected fitness under warming. The expected mean growth of colonies was optimized at intermediate levels of warming (2–4°C above ambient); yet, the expected variance monotonically increased with warming. In contrast, the expected mean and variance of the survival of workers decreased when warming exceeded 4°C above ambient. Together, these results for *T. curvispinosus* emphasize the importance of measuring reproduction (colony growth) in the context of climatic change: indeed, our examination of the loss of thermal niche space with the larger species pool could be missing much of the warming impact due to these analyses being based on survival rather than reproduction. We suggest that while physiological tolerance of temperature can be a useful predictive tool for modeling responses to climatic change, future efforts should be devoted to understanding the causes and consequences of variability in models of tolerance calibrated with different metrics of performance and fitness.

## Introduction

Global changes in land-use and climate ensure that species are increasingly likely to encounter novel environments (Grimm et al. 2008). This places a renewed urgency on understanding biological responses to environmental novelty. However, because these changes are occurring at a global scale

with potential impacts on millions of species, it is challenging to develop predictions for how each species might respond. To add to the issue, recent models of global biodiversity suggest that conservation planning based on the patterns of global diversity of well-studied vertebrate taxa, including birds, mammals, and amphibians, may not cover the

diversity of less-studied invertebrate taxa (Jenkins et al. 2013; see also Lawton et al. 1998 for similar findings at the regional scale). Together, these limits on conservation planning demand a predictive framework that reduces the dimensionality of this task by identifying key characteristics of those taxa and regions that are most vulnerable to climatic change. A number of frameworks have been proposed for accomplishing this task (Williams et al. 2008; Huey et al. 2012). Here, we focus on a promising component of these frameworks: the predictive ability of physiological tolerance of extreme temperatures. We use ants as a model system because they are geographically widespread, ecologically diverse, and have the potential to mediate numerous functions of ecosystems (Dunn et al. 2010; Wardle et al. 2011; Zelikova et al. 2011).

We build upon previous global-scale analyses showing that despite the greater increases in temperature anticipated at higher latitudes, ants inhabiting lower latitudes tend to be the most vulnerable to climatic change because environmental temperatures are close to their upper thermal tolerances (Diamond et al. 2012a). A pattern similar to the global pattern was recapitulated between two large-scale experimental-warming arrays, positioned at the northern and southern boundaries of temperate hardwood forests in eastern North America (Pelini et al. 2011); these chambers mimic the range of warming anticipated by the end of the century, from 1.5 to 5.5°C above ambient temperatures (IPCC 2007). We found that thermal tolerance predicted the responses of ants at the low-latitude site, where temperatures routinely exceed the upper thermal tolerances of ants—that is, ants with low thermal tolerances experienced declines in worker abundance and foraging intensity—but not at the high-latitude site, where temperatures remain below the upper thermal tolerances of ants (Diamond et al. 2012b; Stuble et al. 2013).

Temperature can have both indirect and direct impacts on fitness. In ants, increases in temperature can limit the amount of time available for foraging if temperatures approach or exceed the thermal tolerances of workers, with subsequent limits on colony growth. In contrast, temperature can directly impact colony growth through physiological constraints on the production of brood and the lifespan of workers (Porter 1988; Calabi and Porter 1989; Asano and Cassill 2011). Theory suggests that colony growth should be a strong correlate of fitness in ants (Oster and Wilson 1979), and this has been borne out empirically, as larger colonies maintain larger territories (Adams 1990; Tschinkel et al. 1995), deploy more foragers (Tschinkel 2011), and have a

higher probability of producing reproductives (Tschinkel 1993; Cole and Wiernasz 2000).

Here, we further explore the mechanisms underlying the responses of ants to climatic warming. Specifically, we examine (1) how reductions in foraging time (the amount of thermal niche space for foraging that exceeds the upper thermal tolerance of an ant species) correspond with changes in the abundance of ants under experimental warming and (2) how estimates of vulnerability of particular species under climatic change are altered by the choice of performance or component of fitness employed, that is, the survival of workers versus a more comprehensive metric of fitness, colony growth.

## Materials and methods

### Warming chambers

The details of our warming chambers are presented elsewhere (Pelini et al. 2011), but briefly, the high-latitude (42° N) site at Harvard Forest and the relatively low-latitude (36° N) site at Duke Forest each contain 12 open-top experimental plots (5 m in diameter). At each site, nine chambers are heated by the addition of warmed air in a regression design of 0.5°C increasing intervals from 1.5 to 5.5°C above ambient air temperature, and three chambers are unheated controls. The chambers add a fixed amount of heat (according to the target amount of warming), such that increases in mean temperature are achieved (target and actual differences between chamber temperatures and ambient chambers are on average within 0.3°C) without alterations to the variance in temperature. Because previous work in this system showed that ants are more vulnerable to climatic change (and exhibit much stronger responses to warming) at the low-latitude site (Duke Forest) than at the high-latitude one (Harvard Forest), we focus exclusively on Duke Forest in the analyses presented here. The chambers at Duke Forest have been heated continuously since January 2010; we present data through January 2013, representing three full years of warming and its impact on the performance of ants.

### Loss of thermal niche space under warming

We first estimated the thermal niche using kernel density distributions of air temperatures in the chambers during peak activity periods for foraging (hours 10 through 18 during the reproductive season when colonies are growing; May through September). Given that we are focusing on peak periods for foraging, it is likely that these temperature distributions estimate the available thermal niches for

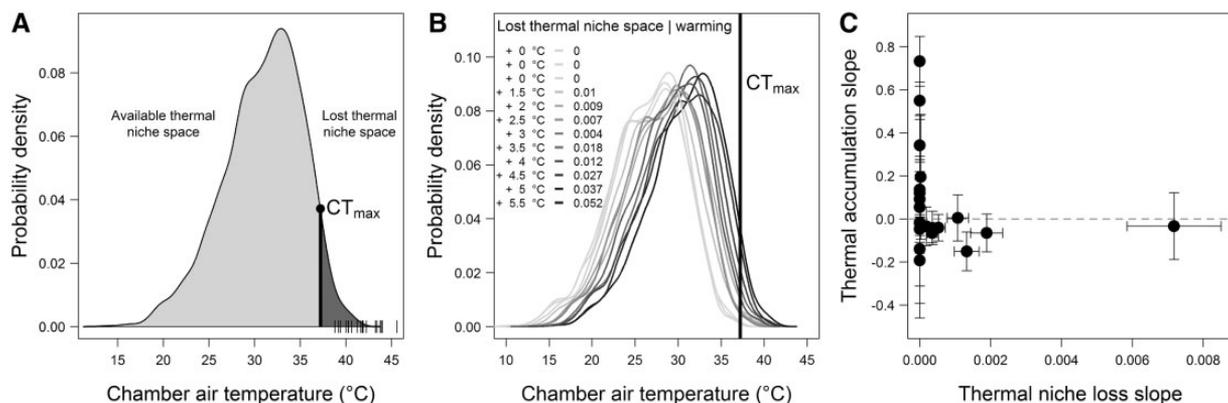
ants foraging in the chambers. It is possible that ants are not actively foraging during this entire period; therefore, we focus our analyses and interpretations on alterations to the time available for foraging, rather than on the time of active foraging. We then calculated how much of the thermal niche was lost, specifically how much of the thermal niche (computed using kernel density estimation, which disperses the mass of the empirical cumulative density function over a regular grid, on the air temperatures of the warming chambers) (Silverman 1986) exceeded the upper thermal tolerance of a given ant species (critical thermal maximum,  $CT_{max}$ , defined as the temperature at which muscular coordination is lost; see Diamond et al. 2012b for original data and methods for estimating  $CT_{max}$ ) (Fig. 1A). Because air temperatures in the different warming chambers were recorded at the same times and on the same scale (hourly over the course of 3 years), the total areas under the kernel density curves are the same, ensuring that the loss of thermal niche space can be directly compared among chambers. In general, our thermal-niche-loss models assume that temperature is the major driver of the activity of ants, and do not include the impacts of other abiotic and biotic variables.

Finally, we compared the slope of the relationship between the fraction of thermal niche space lost and the degree of warming in the chambers (“thermal-niche-loss slope”) with the slope of the relationship between the abundance of ants (natural log transformed) and the degree of warming in the chambers (“thermal-accumulation slope”). Although the

thermal-accumulation slope and thermal-niche-loss slope share the degree of warming as denominators, we present these results as slopes to ensure equal representation among species. Qualitatively similar results were obtained when examining the abundance of ants (natural log transformed) as a function of the loss of thermal niche space as when examining the thermal-accumulation slope as a function of the thermal-niche-loss slope; furthermore, the similarity in results indicates that deviations from linearity of the abundance of ants as a function of the degree of warming do not strongly influence our results. Most species exhibit strong linear components in their responses to warming in the chambers (Appendix F of Diamond et al. 2012b, but see *T. curvispinosus*, described later), so we focus on linear rather than quadratic terms in models of abundance as a function of warming to be able to compare responses among ant species. Abundance data for 20 species were obtained from monthly pit-fall trapping from January 2010–2013 in the chambers (most observations occurred during the growing season), and represent the accumulation of individuals in each chamber since the beginning of heating the chambers in January 2010. We expected that species with greater loss of thermal niche space would have flat or negative relationships between abundance and the degree of warming in the chambers.

### Survival of workers and growth of colonies under warming

For one focal species, *T. curvispinosus*, we estimated the survival of workers and growth of colonies as



**Fig. 1.** The relationship between the degree of loss of the thermal niche space and the density of ant workers, each expressed as a function of the degree of warming of the chambers. **(A)** Conceptual diagram for the loss of thermal niche space when temperatures exceed  $CT_{max}$ ; the temperature profile in the warmest chamber (+5.5°C); and the  $CT_{max}$  of *Nylanderia faisonensis*, a species with one of the lowest  $CT_{max}$  values (37°C) that occurs in our warming chambers are shown; the remaining  $CT_{max}$  values (19 species) are indicated by hash marks along the x-axis; note that some species exhibit no loss of thermal niche space. **(B)** A sample calculation of the loss of thermal niche space as a function of the degree of warming in the chambers using *N. faisonensis*. **(C)** The thermal-accumulation slope ( $\pm 1$  SE) as a function of the thermal-niche-loss slope ( $\pm 1$  SE).

functions of temperature in the laboratory. We used Weibull functions, the best-fitting functions among Gaussian and quadratic functions that were also considered [Akaike's Information Criterion (AIC)] was the basis for comparing fits to the data; see Angilletta 2006); when the Weibull and Gaussian functions had comparable fits to the data, the Weibull was preferred owing to theoretical predictions of skew in curves describing performance as a function of temperature (Schoolfield et al. 1981). The *T. curvispinosus* colonies originated from North Carolina, USA, at sites near the Duke Forest experimental warming chambers. Colonies were maintained in growth chambers under diurnally fluctuating thermal regimes with mean temperatures of 21, 26, and 31°C for 2 months (each diurnal range was 10°C; 14:10 L:D;  $n = 12, 11,$  and 12 colonies per temperature treatment, respectively), after which time, we assessed both production of brood and survival of workers within each colony, which served as an estimate of colony growth (see Pelini et al. 2012 for original data and details on rearing ants; all colonies had queens). Both metrics were expressed relative to the initial size of the colony, and the ordinate of each function was determined by the maximum proportion of surviving workers or number of brood produced.

Although life-table analyses of ant colonies that would allow the computation of comprehensive measures of fitness, that is net reproductive rate ( $R_0$ ), are relatively nascent for this taxon (Ingram et al. 2013), the growth of an ant colony may serve as a useful proxy of the colony's fitness. The probability that a colony will produce reproductive tends to be higher for larger colonies than for smaller ones (Tschinkel 1993; Gordon and Wagner 1997; Cole and Wiernasz 2000). Additionally, larger colonies may provide a buffer against environmental uncertainty (Cassill 2002), and this could lead to higher lifetime fitness benefits. Regardless of the precise mechanism, growth of the colony is almost certainly a more comprehensive estimate of fitness than is the more often studied survival of workers.

We evaluated the worker-survival and colony-growth functions with the air temperature data from the experimental warming chambers during the growing season (May through September), available at a temporal resolution of 1 h over the course of 3 years since heating began in the chambers. The resulting distributions of expected survival of workers and growth of colonies were transformed (log-inverse and square root, respectively) to meet normality assumptions for estimating means and standard deviations; we present summary statistics

that were back-transformed to the original scale of the data. The natural history of *Temnothorax* spp. ensures that air temperatures are likely to be particularly relevant for this group's physiological performance because *Temnothorax* spp. lives in fallen acorns, walnuts, and twigs, and is intimately tied to its nest, such that the ability of these ants to behaviorally thermoregulate and avoid stressful air temperatures is limited (Mitrus 2013).

## Results and discussion

### Global and regional responses to warming

Ants and several other ectothermic taxa are likely to be more vulnerable to climatic change in the tropics compared with more temperate regions (Deutsch et al. 2008; Huey et al. 2009; Diamond et al. 2012a; but see Walters et al. 2012). These findings are contrary to previous expectations that ectotherms inhabiting higher latitudes would be more vulnerable owing to the greater amounts of warming anticipated in these regions. The basis of increased tropical vulnerability appears to be related to biogeographic patterns in thermal adaptation; tropical ectotherms have evolved in thermally invariant environments and tend to exhibit narrower ranges of thermal tolerance compared with temperate and higher-latitude ectotherms (Janzen 1967; Brattstrom 1968, 1970). Because tropical ectotherms experience environmental conditions already close to their thermal optima and upper thermal tolerances, even small increases in environmental temperature can lead to population decline or extirpation (Deutsch et al. 2008).

Interestingly, this global pattern of increased vulnerability of species living closer to the equator appears to hold even among sites at higher and lower latitudes within the temperate zone. The responses of ants to experimental climatic warming suggest that those from lower temperate latitudes are more vulnerable to warming compared with those from higher temperate latitudes. At our low-latitude site, the  $CT_{max}$  (an ecologically relevant metric of thermal tolerance based on the survival of workers in our study) predicted both general activity (Diamond et al. 2012b) and foraging activity (Stuble et al. 2013), such that species with lower  $CT_{max}$  values were less abundant and exhibited reduced foraging activity in the warmest experimental chambers. Air temperatures in the warmest experimental chambers can exceed the  $CT_{max}$  values of some ant species, but the question arises as to how much of the thermal niche space is lost for the species inhabiting the chambers, and whether this relates to changes in their abundance when subjected to warming.

### Loss of thermal niche space under warming

Here, we quantified the relationship between the degree of the thermal niche space lost (i.e., how much of the temperature distributions of the chambers exceeded the  $CT_{\max}$  of a particular ant species) and the changes in abundance of ant species under the experimental manipulations of temperature (Fig. 1B and C). Our models of thermal niche loss are a measure of the reduction of the time available for foraging. Reductions in available foraging time could contribute to reductions in the colony's performance by reducing the quantity or quality of food retrieved. Reductions in thermal niche space might also lead to an increase in competition since there is less thermal space in which organisms can distribute their activity (Urban et al. forthcoming). Interestingly, even with  $5.5^{\circ}\text{C}$  of warming, we found that the majority of 20 species we examined experienced no loss of thermal niche space. However, of the 35% of species that exhibited significant losses of thermal niche space, 71% exhibited significant or trending declines in abundance with experimental warming (Fig. 1C). Thus, for some species with low thermal tolerances, the loss of thermal niche space can be sufficient to drive reductions in foraging and potentially in colony size. It is important to note that these models were constructed with survival-based  $CT_{\max}$ , and temperature can have differential impacts via different components of performance and fitness. How warming impacts not only survival but also other components of fitness, particularly reproduction, is an important, but open, question in many systems.

### Impacts of warming via different components of fitness

Estimates of tolerance frequently are based on proxies or components of fitness such as survival, body size, or development time. Few estimates of tolerance are based on more comprehensive metrics such as net reproductive rate ( $R_0$ ) and intrinsic rate of increase ( $r$ ), largely owing to the practical limits of obtaining these data (Ingram et al. 2013). For example, ideally our models of thermal niche loss would be calibrated with more comprehensive metrics of fitness rather than the survival of workers, but only data on survival are presently available to cover the diversity of ant species present in the experimental warming chambers. Yet importantly, in some cases, these more comprehensive metrics of tolerance can have narrower ranges compared with other metrics such as survival (reviewed by Angilletta 2009; Kingsolver et al. 2011). Because many estimates of

vulnerability to climatic change are based on survival, we may be misestimating potential impacts: survival functions can determine conditions that are immediately lethal, but populations may stop growing before lethality is reached (i.e., when  $R_0 < 1$  or  $r < 0$ ), which over time can contribute to local extirpation.

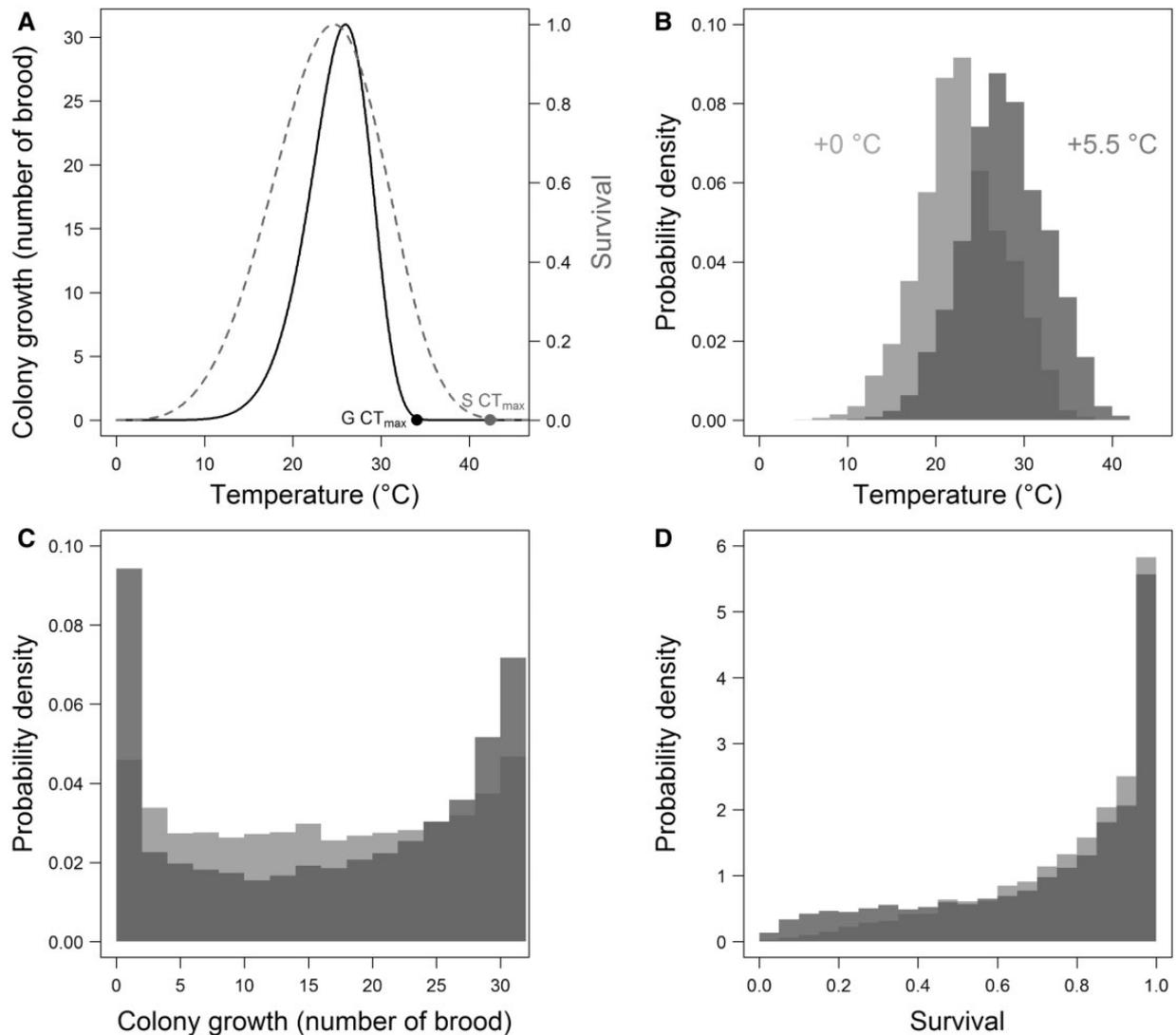
We used the acorn ant, *T. curvispinosus*, to illustrate how estimates of vulnerability to climatic change might be altered by the choice of tolerance metric used in the context of a colonial ectotherm. *Temnothorax curvispinosus* is a relatively heat-tolerant ant, with a mean  $CT_{\max}$  of  $43.4^{\circ}\text{C}$  (using a dynamic-temperature ramping method of assessing thermal tolerance) (Diamond et al. 2012b). As a consequence, this species experienced no reductions in thermal niche space under experimental climatic warming (Fig. 1B). From ant colonies reared in the laboratory under different thermal treatments (Pelini et al. 2012), we were able to estimate the survival of workers and the growth of colonies, a more comprehensive metric of fitness related to  $R_0$  (discussed earlier), as functions of temperature. We found that the worker-survival function lies outside the function that describes the growth of colonies; indeed, on the warm end of the function, the upper tolerances of these two attributes differed by  $8.3^{\circ}\text{C}$  (colony growth  $CT_{\max} = 34.1^{\circ}\text{C}$ ; survival  $CT_{\max} = 42.4^{\circ}\text{C}$ , an estimate that is relatively close to that using the dynamic-temperature method presented earlier; Fig. 2A). *Temnothorax curvispinosus* thus appears to survive much higher temperatures than those that colony growth of colonies.

When we used these functions to examine the distribution of survival of workers and of growth of colonies in the context of the environmental temperatures in our experimental warming chambers, we found that while expected mean survival began to decline sharply in only those warming chambers that were  $>4^{\circ}\text{C}$  above ambient conditions (Fig. 3A), expected mean growth of colonies exhibited a somewhat different pattern, with chambers having moderate amounts of warming ( $2\text{--}4^{\circ}\text{C}$ ) yielding the highest growth, and very cool and very warm chambers yielding the lowest growths (Fig. 3B). Because the absolute range of temperatures during the growing season across all chambers ( $5.9\text{--}41.5^{\circ}\text{C}$ ) falls within the limits of the survival function ( $3.8\text{--}42.4^{\circ}\text{C}$ ), the decrease in expected mean survival would appear to result from the skewness of the function, that is, that survival declines more rapidly on the warm end of the curve above the optimal temperature for survival than on the cool end (Fig. 2A). For expected mean growth, both skewness

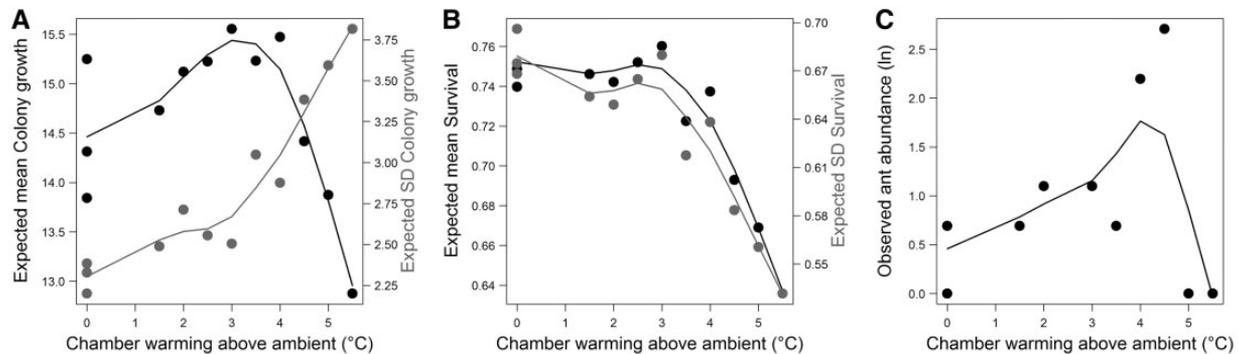
(again, decreasing more steeply at temperatures higher than the optimum) and breadth—optimal temperatures not being frequently reached in the cool chambers (minimum temperature for colony growth was estimated at 11.6°C) or being frequently exceeded in the warm chambers (maximum temperature for colony growth was estimated at 34.1°C)—appear to result in moderate amounts of warming leading to the greatest growth.

Interestingly, the pattern for expected mean growth of colonies as a function of the degree of warming in the chambers was more functionally

similar (optimized at intermediate amounts of warming) to the pattern of observed abundances in the chambers (Fig. 3A and C) compared with expected mean survival, which decreased only at very high levels of warming (Fig. 3B). Principal components (PCs) analysis using different amounts of warming as “traits” and different types of performance curves as “replicates” revealed that the loadings on PC1 were all of the same sign when comparing the spline fits of colony growth and abundance as functions of warming, but the loadings on PC1 changed signs (both from low to



**Fig. 2.** Laboratory-estimated colony-growth and survival functions for *T. curvispinosus* in the context of air temperatures from the warming chambers. (A) Colony growth (solid line) and survival (dashed line) as functions of temperature (°C), with the estimated  $CT_{max}$  for each indicated as  $GCT_{max}$  and  $SCT_{max}$ , respectively. (B) Distributions (using kernel density estimation) of air temperatures of the +0°C and +5.5°C warming chambers. (C) Distributions (using kernel density estimation) of the colony-growth function evaluated using air temperatures of the chambers, with results from the +0°C (light gray bars) and +5.5°C (dark gray bars) chambers shown. (D) Distributions (using kernel density estimation) for the worker-survival function evaluated using air temperatures of the chambers, with results from the +0°C (light gray bars) and +5.5°C (dark gray bars) chambers shown.



**Fig. 3.** Expected colony growth and survival of *T. curvispinosus* under the temperatures measured in the experimental climatic-warming chambers and observed changes in abundance in the warming chambers. **(A)** Expected mean and standard deviation of colony growth, obtained by applying air temperatures of the chambers to the laboratory-estimated colony-growth function, expressed as a function of the degree of warming in the chambers. **(B)** Expected mean and standard deviation of survival, obtained by applying air temperatures of the chambers to the laboratory-estimated survival function, expressed as a function of the degree of chamber warming in the chambers. **(C)** The natural log of abundance of *T. curvispinosus* as a function of the degree of warming of the chambers. In each panel, smoothing splines are used to visualize the patterns of responses.

intermediate temperatures and from intermediate to high temperatures) when comparing the spline fits of survival and abundance as functions of warming, indicating more substantial differences in the shape of the curve in the latter case (see Izem and Kingsolver 2005 for details of the modeling approach). The similarity in colony growth and abundance patterns as functions of warming suggests that the pitfall trapping method of estimating performance may in fact capture more inclusive metrics of performance such as colony growth. This result is somewhat surprising given the inherent differences between our field and laboratory experiments on ants' responses to warming, particularly the differences in timescale (3 years of warming in the field vs. 2 months in the laboratory). The results from the field represent the impacts of warming throughout the colony-growth season and overwintering, whereas the results from the laboratory represent only the impacts throughout a portion of the colony-growth season. It is perhaps encouraging that results from the field and laboratory are in agreement for the responses of *T. curvispinosus* to warming; however, in general, more research is needed on the mechanisms underlying organismal responses to warming throughout ontogeny (Williams et al. 2012).

In contrast to the variance in expected survival, which decreased along with decreases in expected mean survival in the warming chambers, the variance in expected colony growth increased with greater warming (Fig. 3A and B). Indeed, while there are more frequent opportunities for achieving the highest levels of colony growth in the warmest (+5.5°C) chamber, *T. curvispinosus* is expected to even more frequently experience temperatures at which the

colony cannot grow, leading to an overall reduction in expected mean colony growth in the warmest chambers (Fig. 2C and D). Furthermore, because the experimental chambers alter the mean, but not the variance, of environmental temperature, the anticipated increases in temperature–variance with global climatic change (IPCC 2007) may exacerbate the current pattern of increased variance in expected fitness for *T. curvispinosus*, and possibly for other species.

*Temnothorax curvispinosus* and the many other species in the genus *Temnothorax* represent somewhat unique cases because their entire colonies are exposed to changes in surface temperature since they nest inside acorns, walnuts, or twigs on the forest floor. This constraint should also be present in ants that nest arboreally, but ground-nesting species generally have more depth to thermoregulate by transporting brood deeper underground to escape excessive temperatures at the surface (Penick and Tschinkel 2008). Although these species should be buffered from negative effects of warming outside their nests, thermophilic species may be able to take advantage of surface-warming by tracking higher temperatures inside their nests to produce brood earlier in the season or to expand the amount of time that optimal brood-rearing temperatures are present at some depth inside their nests. Future work is needed to determine how species with different nesting habits and different temperature preferences for rearing of brood may respond to warming.

One component currently missing from these analyses is how generation time varies as a function of temperature. For social ectotherms, generation

time may be related to both the age when reproductives are first produced (the ergonomic phase of colony growth, after Oster and Wilson 1979) and to the lifespan of the queen (Ingram et al., in press). Although individual workers might be relatively short lived, queens—the functional reproductive unit for social ectotherms—exhibit considerable variability in lifespan, extending from several months of age to nearly 30 years (Keller 1998). In addition, the rate of the colony's growth should affect the duration of the ergonomic phase; faster colony growth should correlate with decreases in the amount of time required before the first reproductives are produced. For ants, and perhaps for other social ectotherms, one way to cope with the large variance in generation time is to estimate the longevity of colonies based on other physiological and demographic parameters (Shik et al. 2012); however, these models still need to be expressed within a temperature-dependent framework.

Because temperature affects the fitness metrics  $r$  (intrinsic rate of increase) and  $R_0$  (net reproductive rate) differently owing to generation time (Huey and Berrigan 2001), and because the incorporation of generation time into models of the vulnerability of ectotherms to climatic change has been suggested to produce qualitatively different results from models lacking this component (Walters et al. 2012), estimating generation time is especially important. Our analyses from ants, and others from ectotherms more generally, indicate greater vulnerability in the tropics (Deutsch et al. 2008; Huey et al. 2009; Diamond et al. 2012a). However, Walters et al. (2012) recently suggested that the increased turnover (i.e., shorter generation time) in warmer regions could recoup this increased vulnerability, particularly because shorter generation times could speed adaptive evolution, allowing tropical ectotherms to respond sufficiently rapidly to warming despite their thermal specialization and reduced genetic variation. From the perspective of conservation planning, the qualitative differences in predictions for large-scale regional vulnerability of ectotherms to climatic change is far from ideal, and points to the need to integrate ecological and evolutionary models.

## Conclusions

In this study, we expanded upon previous work in this system, which established a strong positive relationship between changes in the abundance of ants under warming and their upper thermal tolerances. Specifically, we examined the relationship between

temperature and performance both in context of alterations to the thermal niches for foraging under experimental climatic warming, and how the choice of tolerance metric—the survival of workers versus a more comprehensive fitness metric, colony growth—affected expected fitness under warming. Here, we provide results that suggest the loss of thermal niche space for foraging among 20 ant species at one site is somewhat related to decreases in abundance with experimental climatic warming, but that we may be underestimating the loss of niche space when calibrating models with the survival of workers rather than colony growth. In support of this idea, we found that for one well-studied species, the range of thermal tolerance for the survival of workers was much broader than for the growth of colonies. Furthermore, this difference in the range and shape of the relationship between fitness components and temperature-induced differences in expected means and variances of fitness under warming.

We suggest that understanding how physiological performance is influenced by current and anticipated changes in temperature can serve as a useful baseline model (the focus of our study), with additional effort directed at understanding how this relationship is moderated by physiological acclimation, adaptation, behavior, and alterations to the biotic background (see Table 1 for a summary of the components of thermal-tolerance models for the responses of ectothermic species to climatic warming). Indeed, the models that we explored in this study assume thermal tolerances to be fixed, yet tolerances can be altered via acclimation, adaptive evolutionary responses, or may fail to fully capture organismal vulnerability in the face of behavioral compensatory responses. Furthermore, our models are based on air temperatures rather than on body temperatures; yet, in some cases air temperatures may be poor indicators of environmental pressures, as body temperatures can differ substantially from air temperatures (Table 1). Improving estimates of relevant environmental parameters and of components of fitness along environmental gradients will often necessarily tradeoff with research effort and investment; however, to be able to assess the most useful predictors of the responses of species to climatic change, detailed estimates both of the environment and of organismal responses are critical. We concur with recent calls for increased physiological and demographic data for ectothermic species inhabiting the tropics and lower temperate zone where the impacts of warming may be the greatest, and for which we have the fewest data.

**Table 1** Components of predictive models of the responses of ectothermic species to climatic warming based on thermal tolerance

| Components of the model |   | References   |
|-------------------------|---|--|
| Thermal environment     | Spatio-temporal resolution of environmental temperature | Finer spatial and temporal resolution allows computation of variability of fitness   |
|                         | Air temperature versus body temperature                 | Body temperatures are often more reflective of organismal performance than are air temperatures  |
| Physiology              | Short-term versus long-term population dynamics         | Survival can allow estimation of immediate relative vulnerability across space, time, or species, but reproductive output and generation time are needed to understand long-term vulnerability |
| Moderators              | Phenotypic plasticity                                   | Warmer conditions can increase upper thermal tolerances (within generations)   |
|                         | Behavioral plasticity                                   | Behaviorally mediated thermoregulation can avoid body temperatures exceeding upper thermal tolerances  |
|                         | Adaptive evolutionary responses                         | Warmer conditions can select for increased upper thermal tolerances (across generations)   |
|                         | Biotic background                                       | Alterations to resources, competitors, predators, and pathogens can improve or exacerbate responses to warming   |

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