SYMPOSIUM

U g P g P ed c e Re e f A C a c Wa g

Sarah E. Diamond,[1,*] Clint A. Penick,[*] Shannon L. Pelini,[†] Aaron M. Ellison,[‡] Nicholas J. Gotelli,[§] Nathan J. Sanders[¶] and Robert R. Dunn[*]

[*]Department of Biology, North Carolina State University, Raleigh, NC 27695, USA; [†]Department of Biology, Bowling Green State University, Bowling Green, OH 43403, USA; [‡]Harvard Forest, Petersham, MA 01366, USA; [§]Department of Biology, University of Vermont, Burlington, VT 05405, USA; [¶]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

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[1]E-mail: sarah_diamond@ncsu.edu

Synopsis

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 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

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°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°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°C (colony growth $CT_{max} = 34.1°C$; survival $CT_{max} = 42.4°$

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 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 ecotherms, 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—influenced 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 demographical data for ectothermic species inhabiting the topics and lower temperate zone where the impacts of warming may be the greatest, and for which we have the fewest data.

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