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A physiological trait-based approach to predicting the responses of species to experimental climate warming

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Abstract. Physiological tolerance of environmental conditions can influence species-level responses to climate change. Here, we used species-specific thermal tolerances to predict the community responses of ant species to experimental forest-floor warming at the northern and southern boundaries of temperate hardwood forests in eastern North America. We then compared the predictive ability of thermal tolerance vs. correlative species distribution models (SDMs) which are popular forecasting tools for modeling the effects of climate change. Thermal tolerances predicted the responses of 19 ant species to experimental climate warming at the southern site, where environmental conditions are relatively close to the ants' upper thermal limits. In contrast, thermal tolerances did not predict the responses of the six species in the northern site, where environmental conditions are relatively far from the ants' upper thermal limits. Correlative SDMs were not predictive at either site. Our results suggest that, in environments close to a species' physiological limits, physiological trait-based measurements can successfully forecast the responses of species to future conditions. Although correlative SDMs may predict large-scale responses, such models may not be accurate for predicting site-level responses.

Key words: critical thermal maximum; Duke Forest, North Carolina, USA; ectotherm responses to global warming; Formicidae; global change; Harvard Forest, Massachusetts, USA; maximum entropy; physiology; species distribution model; temperate hardwood forests, eastern North America; thermal tolerance.

INTRODUCTION

Predicting biological responses to climate change is critical (Araújo et al. 2005), but a number of researchers have begun to emphasize the potential unpredictability of species' responses to climate change (e.g., Hill et al. 2002, McGeoch et al. 2006, Pelini et al. 2009, Doak and Morris 2010). If species-specific traits covary with their responses to climate change, such traits can be used to predict community change (Diamond et al. 2011, Angert et al. 2011). Physiological traits have been especially

successful in predicting responses of individual species to climate change (Chown et al. 2004, Helmuth et al. 2005, Buckley 2008, Deutsch et al. 2008, Pörtner and Farrell 2008, Huey et al. 2009, Kearney and Porter 2009, Sinervo et al. 2010, Diamond et al. 2012). However, these predictions have only been evaluated through simple correlations with historical, current, or projected future conditions (reviewed in Rowland et al. [2011]). Experimental manipulations provide a unique, but relatively underused, approach for evaluating the degree to which physiological traits may inform the responses of species to climate change.

Here, we used results from a pair of large-scale experimental climate warming arrays, positioned near the northern (Harvard Forest; Petersham, Massachusetts, USA; ~42° N latitude) and southern (Duke

Forest; Hillsborough, North Carolina, USA; ~36° N latitude) boundaries of temperate hardwood forests in eastern North America to test the ability of physiological thermal tolerance to predict responses of ant species to warming. In the extensive literature on ecological effects of global climate change, such experiments are rare because they are expensive and time-consuming. Temperature-induced changes in community composition (Walker et al. 2006), nutrient cycling (Rustad et al. 2001), and phenology (Wolkovich et al. 2012) have been previously documented in such experimental warming arrays, although ours is the first study to incorporate independent measures of physiological tolerance. We manipulated temperatures among experimental open-top chambers in a regression design that boosted air temperature in each chamber from 1.5 to 5.5°C above ambient. This range of temperatures encompasses a variety of future warming scenarios (IPCC 2007), and induced a wide range of species-specific responses in ant activity density. The key question we address here is: What is the best predictor of changes in ant activity density in the experimental chambers: measured physiological tolerances of individual species or the species-specific predictions of MaxEnt, a popular species distribution model (SDM; reviewed in Elith and Leathwick [2009])?

Although SDMs are typically used to predict distributions at large spatial scales, effects of the changing climate on species geographic ranges ultimately reflect population dynamics and the activity of individuals at local scales. By comparing three independent sources of data (activity responses to warming in a climate change field experiment, measurements of physiological tolerance of individual species, and MaxEnt predictions) at two locations (Harvard Forest and Duke Forest), we have a unique chance to evaluate MaxEnt predictions.

Ants are a good choice for this kind of comparison because they are ecologically important thermophiles in eastern deciduous forests (Sanders et al. 2007, Ellison et al. 2012), appear commonly in the warming chambers at both sites, and their geographic ranges are relatively well known (Fitzpatrick et al. 2011). For each of the ant species recorded in the experimental chambers, we independently measured their thermal tolerance (critical thermal maximum, CT_{max}) and quantified their projected changes in probability of occurrence under several climate change scenarios using correlative SDMs based on thermal indices of the environment.

We predicted that: (1) species with higher thermal tolerances would increase in abundance with experimental warming, owing to the widespread pattern among ectotherms of positive correlations between CT_{max} and the temperature at which optimal performance is reached (T_{opt}) (Huey and Kingsolver 1993); (2) species with greater probabilities of occurrence under projected climate warming according to correlative SDMs would become more abundant as experimental temperatures increased; and (3) CT_{max} would be a better predictor of

responses to warming for ants at the southern forest boundary (Duke Forest) than at the northern forest boundary (Harvard Forest). This final prediction is based on recent studies suggesting that ectothermic species at lower latitudes are relatively more sensitive to changes in temperature because of their narrow thermal performance curves, and because environmental temperatures are relatively closer to their upper thermal limits. By comparison, species at higher latitudes tend to be more tolerant of changes in temperature because of their broader thermal performance curves and because environmental temperatures at high latitudes are relatively far below their upper thermal limits (Appendix A; see especially fig. 1 in Tewksbury et al. [2008]; see also Deutsch et al. 2008, Dillon et al. 2010). In general, performance begins to decline sharply when T_{opt} is exceeded, which imposes strong limitations on occupying thermal environments that overlap the range of temperatures between T_{opt} and CT_{max}.

Materials and Methods

Warming chambers and ant collections

Both the Harvard Forest and Duke Forest sites include 12 open-top experimental plots (5 m in diameter, and raised ~5 cm off of the ground to allow ants to move unrestricted) in the forest understory (see Plate 1; details in Pelini et al. [2011]). Nine chambers are heated (by the addition of warmed air) according to a regression design of 0.5°C increasing intervals from 1.5 to 5.5°C above ambient air temperature (hereafter referred to as Δ_c), and three chambers are unheated controls ($\Delta_c = 0$). We used pitfall sampling to estimate ant activity density (Appendix B): monthly pitfall samples were conducted at Duke and Harvard Forest (April 2010–September 2011).

Thermal tolerance and species distribution models

We defined the *critical thermal maximum* (CT_{max}) as the temperature at which muscle coordination was lost (Lutterschmidt and Hutchison 1997), an ecologically relevant measure of CT_{max} as the temperature at which an individual could not escape to a nonlethal thermal environment (Lighton and Turner 2004). Ant workers of different species were collected in the forest adjacent to the chambers, and their thermal tolerances were tested individually (minimum 8 individuals per species at each site) in a heat block that generated a 2°C temperature increase 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 (Appendix B).

For species distribution models (SDMs), current climate data were obtained from WorldClim (Hijmans et al. 2005), and projected future climate data (for the year 2080 based on the CCCMA-CGCM2 model) from the International Centre for Tropical Agriculture (CIAT) (Ramirez and Jarvis 2008; Appendices B–E). North American occurrence data (presence only) for

PLATE 1.   A single chamber within the experimental climate warming array at Duke Forest, Hillsborough, North Carolina, USA (~36°). Photo credit: L. M. Nichols.

each of the ant species present in the pitfall traps at Duke and Harvard Forests were obtained from the primary literature and museum records (Fitzpatrick et al. 2011).

Analyses

We collected 24 and 11 species in pitfall traps at Duke and Harvard Forest respectively (excluding the non-ground-foraging ant species *Neivamyrmex texanus* and *Camponotus obliquus*; Appendix B). Of these species, we were able to obtain corresponding physiological and distribution data for 19 and 6 species, respectively. Average CT_{max} values were calculated for each species and used as a predictor variable in regression models of ant activity density responses in the experimental chambers. All analyses were performed in R (version 2.13.1; R Development Core Team 2011).

Physiological models

We used ANOVA to test whether physiological tolerance to high temperatures influences ant abundance (effectively, worker activity density, given comparable sampling areas in our study; Longino and Colwell 2011) in response to experimentally simulated climate warming. Cumulative worker density across sampling events was considered the response variable, and CT_{max}, Δ_c, and the interaction of CT_{max} with Δ_c, were considered as continuous fixed-effect predictor variables. All assumptions of ANOVA were met.

MaxEnt models

We fit maximum entropy (MaxEnt) correlative species distribution models (SDMs) for each species with standard settings for the maxent function from the dismo package in R (Hijmans et al. 2011). Three sets of MaxEnt models were developed based on current and future (2080) environmental variables most relevant to manipulated aspects of the experimental arrays (i.e., thermal indices): (1) mean annual temperature, (2) mean temperature during the warmest annual quarter, and (3) maximum temperature during the warmest annual quarter. We used these thermal indices to develop models to predict the probability of occurrence within North America, and then extracted the probability-of-occurrence values for each species at each site under current and future climates. Typically, projected changes in probability of occurrence across a species' entire range are used to infer species' responses to climate change (Fitzpatrick et al. 2008). Here, we restricted our consideration of MaxEnt-derived changes in probability of occurrence to the ~1-km² areas containing the Duke and Harvard Forest experimental warming sites. In this way, the spatial scales were comparable for comparisons of thermal tolerances, MaxEnt predictions, and respons-

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es to experimental warming. MaxEnt usually performs more poorly when it is underparameterized than it does when it is overparameterized (Warren and Seifert 2011); to address this issue, we used expanded sets of MaxEnt models fit with all 19 bioclim variables (Appendices B and C). These results were qualitatively similar to the thermal index-only models. Therefore, we present the MaxEnt models based on just the thermal indices (Hijmans and Graham 2006).

Model comparisons

We used ANOVA to test the ability of physiological thermal tolerance and correlative SDMs to predict the responses of ants to experimentally simulated climate warming. The slope of the linear relationship between ln (cumulative worker density across all sampling events) and Δ_c was considered the response (Appendices B and F), and CT_{max} and the difference in the probability of occurrence of a particular ant species based on current and future (2080) climate derived from MaxEnt models (future minus current, such that positive values indicate increased probability of occurrence under climate warming) were considered continuous fixed effects. The calculation of the thermal accumulation slope was not possible for a small fraction (<1%) of ant species that only occurred within a single chamber across all sampling events (Appendix B). Therefore, we also examined a complementary response variable, the maximal accumulation temperature (positively correlated with thermal accumulation slope; $r = 0.78$), which allowed us to include these species in our analyses. The maximal accumulation temperature was defined as the mean of the chamber deltas (Δ_c) in which a given species occurred, where the contribution of each Δ_c was weighted by cumulative worker density (across all sampling events) for that given species in that given chamber. Cumulative worker densities were normalized to sum to 1 (for a given species among all the chambers in which it occurred) prior to this calculation.

For simplicity, hereafter we explicitly use "CT_{max}" to refer to the critical thermal maximum, "Δ_c" to refer to the degrees Celsius above ambient for each experimental warming chamber, and "MaxEnt prediction" to refer to the change in probability of occurrence between current and future climates; similarly, we refer to the response variables as "thermal accumulation slope" (slope of the linear relationship between ln (cumulative worker density) and Δ_c) and "maximal accumulation temperature" (mean Δ_c weighted by cumulative worker density). In all of these analyses, it is the different species, not the experimental chamber or the site, that represent the replicate observations.

Phylogenetic autocorrelation

To account for the potential influence of phylogenetic autocorrelation on our results, we re-ran our models of ant responses to warming using phylogenetic generalized least squares (PGLS from the CAIC package; Orme et al. 2009) under an assumption of trait evolution by Brownian motion. For each model, the maximum-likelihood estimate of λ was used to scale the model covariance (Appendices B and G).

RESULTS AND DISCUSSION

Predictive ability of thermal tolerance

At the low-latitude site (Duke Forest, North Carolina, USA), responses of ant species to experimental warming (1.5 to 5.5°C above ambient temperature, in 0.5° increasing intervals, Δ_c) were well-predicted by physiological tolerance of the ants to high temperatures (critical thermal maximum, CT_{max}). ANOVA revealed a significant interaction effect between CT_{max} and Δ_c on post-treatment cumulative worker density ($F_{1,174} = 6.33$, $P = 0.0128$; the main effects of CT_{max}, $F_{1,174} = 0.491$, $P = 0.485$, and Δ_c, $F_{1,174} = 0.290$, $P = 0.591$, were not significant), indicating the relationship between worker density and the degree of experimental warming was contingent upon the ants' thermal tolerance. Specifically, species with higher thermal tolerance had greater worker densities under warmer conditions (Fig. 1A). In contrast, at the high latitude site (Harvard Forest, Massachusetts, USA), responses of ants to experimental warming were poorly predicted by individual CT_{max} (Fig. 1C). ANOVA revealed nonsignificant effects of CT_{max} ($F_{1,43} = 0.127$, $P = 0.723$, Δ_c, $F_{1,43} = 1.51$, $P = 0.226$, and their interaction, $F_{1,43} = 1.40$, $P = 0.243$). Instead, worker densities were greatest in the warmest experimental treatments: regardless of CT_{max}, all six species achieved their maximum densities in warming treatments of 3.5°C above ambient or greater (Appendix H). At the high-latitude site, maximum daily temperatures never exceeded 38°C (the lowest CT_{max} of species at Harvard Forest) in any of the warming chambers. As a consequence, there was little risk of any species exceeding its CT_{max}, and ant performance may improve under the warmest treatments as ants approach their optimal-performance temperature, T_{opt}. However, at the low-latitude site, maximum daily temperatures exceeded 37°C (the lowest CT_{max} of species at Duke Forest) during 9% of the year (based on mean hourly temperatures) among all of the warming chambers. As a consequence some species are likely to have experienced temperatures in excess of their CT_{max} in the warmest treatments, resulting in the differential representation of worker densities among species in the warming treatments.

Collectively, these results suggest that CT_{max} may be a useful predictor of species' responses to climate warming in regions with relatively warm baseline temperatures where species are close to their upper thermal limits. CT_{max} may not be a good predictor in regions with relatively cool baseline temperatures where species are
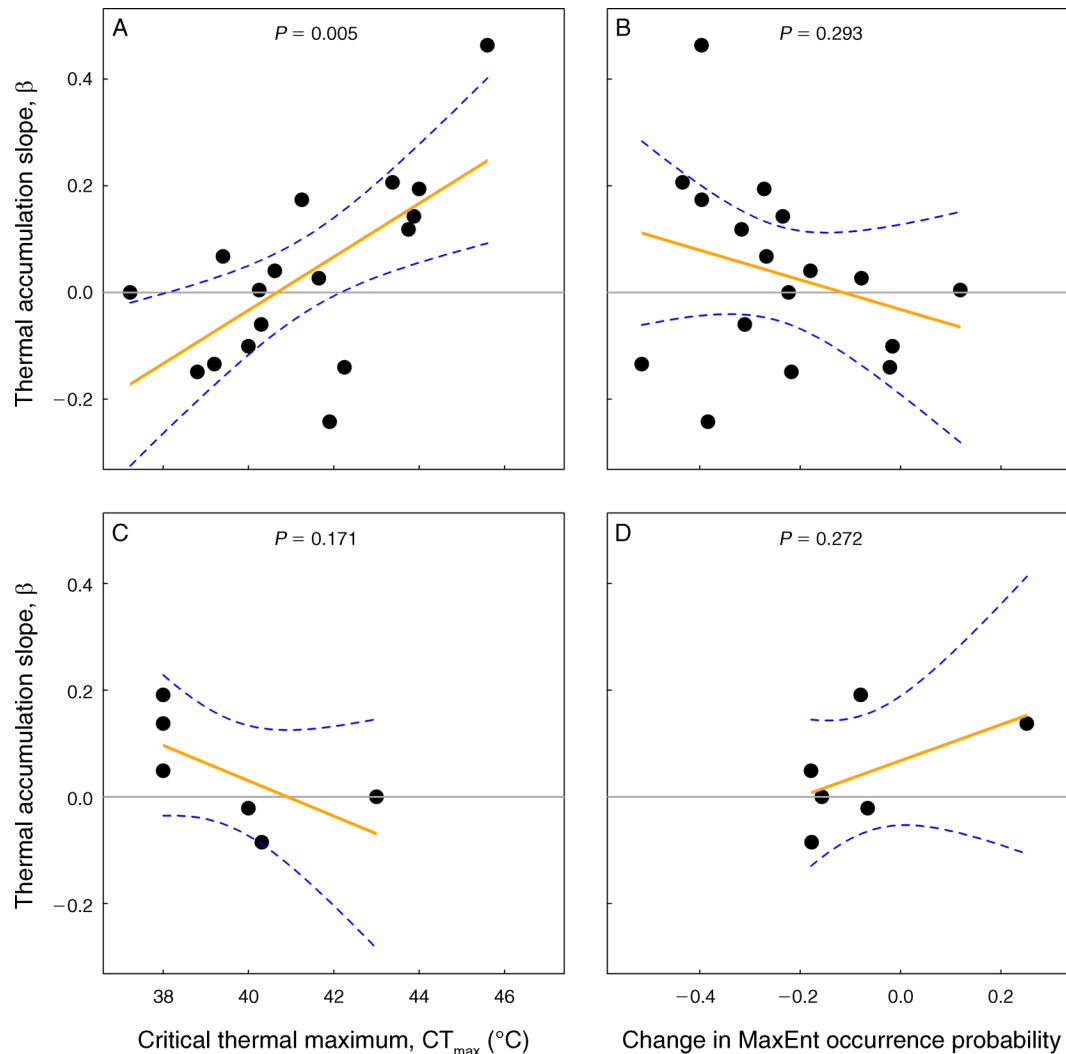
FIG. 1. The predictive ability of thermal tolerance vs. species distribution models in ant responses to warming at high and low latitudes. The thermal accumulation slope (β) is the slope of the linear relationship between ln(cumulative worker density) and chamber delta (Δ_c, °C) as a function of (A, C) the critical thermal maximum (CT_{max}, °C), and (B, D) MaxEnt prediction. The MaxEnt prediction is the change in probability of occurrence across MaxEnt species distribution models based on current and future (2080) climate as defined by mean annual temperature) at (A, B) the low-latitude site (Duke Forest, North Carolina, USA), and (C, D) the high-latitude site (Harvard Forest, Massachusetts, USA). Each point represents a single species; the solid orange lines represent simple linear regressions (P values indicate whether the slope is significantly different from zero), and dashed blue lines represent 95% confidence intervals.

far from their upper thermal limits (Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009).

Predictive ability of correlative species distribution models

The MaxEnt species distribution models based on mean annual temperature, mean temperature during the warmest quarter, and maximum temperature during the warmest quarter for current and future (2080) climates were themselves statistically well supported: species occurrences were significantly correlated with these thermal variables, and AUC_{test} values (area under the curve, based on current climate conditions) were >0.8 in

all cases (to obtain AUC_{test} values, 20% of the data were withheld for testing using k-fold partitioning). We emphasize, however, that our primary interest was in relative differences among species in the change in probability of occurrence from current to future conditions, and how these differences potentially relate to species' responses to experimental warming, rather than in the precision of individual SDMs.

In this respect, correlative species distribution models (SDMs) were poor predictors compared with CT_{max} at the southern site, and equally poor predictors as CT_{max} at the northern site (Fig. 1B, D; Appendices C–E).

ANOVAs of thermal accumulation slopes revealed significant effects of CT_{max}, but nonsignificant effects of MaxEnt predictions (calibrated with mean temperature during the warmest quarter) at the southern site: CT_{max}, $F_{1,14} = 10.3$, $P = 0.00639$; MaxEnt, $F_{1,14} = 0.560$, $P = 0.467$. ANOVAs of thermal accumulation slopes revealed nonsignificant effects of both CT_{max} and MaxEnt predictions (calibrated with mean temperature during the warmest quarter) at the northern site: CT_{max} ($F_{1,3} = 0.159$, $P = 0.717$; MaxEnt, $F_{1,3} = 1.84$, $P = 0.268$). Results for ANOVAs of maximal accumulation temperature were qualitatively similar (Appendix I). These results do not reflect our particular choices of thermal index or future climate models, and were robust to many alternative calibrations of the MaxEnt models (Appendices C and E).

Correlative SDMs offer many advantages for ecologists: they are easy to develop and can successfully predict range shifts in some species (Kearney et al. 2010). The relative ease of developing correlative SDMs results in part from the simplification of the biological world inherent in their use (Fitzpatrick et al. 2007). The application of correlative SDMs in climate change impact assessment has been criticized (Dormann 2007, Fitzpatrick and Hargrove 2009), largely on the basis that correlative SDMs ignore evolution and complex interactions between species, which may themselves change as the climate changes (Schmitz et al. 2003). We are careful here to note that our correlative SDMs based on environmental thermal indices are relatively simplistic, and that more sophisticated methods for generating species distribution models can be applied when more detailed data are available. For example, SDMs have incorporated additional variables such as land use (Heikkinen et al. 2006), and mechanistic versions of SDMs are capable of incorporating effects of physiology and demography (Buckley 2008, Kearney and Porter 2009). However, such methods trade off predictive power with greater investment in data collection and analysis. Although more sophisticated modeling techniques are always possible, the results of our study suggest physiological traits alone can be important predictors of responses of individual species to climate warming in regions where species are close to their physiological limits. In such cases, physiological-based models outperform relatively simple forms of correlative SDMs, at least with respect to experimental climate warming at the site level. Perhaps SDMs perform better only at the large spatial scales at which they are typically used (Heikkinen et al. 2006). On the other hand, if they are to be of practical use, they should have some relevance to changes at individual sites. The fact that simple laboratory measures of thermal tolerance (CT_{max}) are good predictors of activity density responses in experimental warming arrays suggests that additional measurements of behavioral and physiological responses to warming may be more productive than continued refinements of correlative SDMs.

What else is needed for improved predictive ability?

Depending on the metric used to quantify responses to warming, thermal tolerance (CT_{max}) alone explained a sizable fraction of the variation (38 to 42%) among species at the warm site. Although indirect responses (including indirect species effects and interactions mediated by temperature) may play an important role, direct effects of temperature on performance are critical for understanding the responses of ant—and probably many other ectotherms—to global warming. The unexplained variation in our analyses can be partly understood by focusing on the biology of the outlier species. For example, at the warm site, *Camponotus americanus* and *C. pennsylvanicus* tended to occupy relatively cool chambers despite their intermediate CT_{max} values; at a global scale, such forest specialist species tend to be relatively intolerant of warming (Diamond et al. 2012). In addition, two other *Camponotus* species (*C. chromaiodes* and *C. castaneus*), tended to occupy moderately heated chambers—chambers below or at the level predicted by the regression of ant responses to warming against CT_{max}. Such phylogenetic clustering suggests the possible presence of shared developmental or genetic constraints on thermal tolerance. We did indeed detect non-zero levels of phylogenetic signal in the model, but CT_{max} was still a significant predictor of responses to warming at the low-latitude site (Appendix G).

Our results suggest that the subset of the species in the regional species pool in the southeastern United States that will become more abundant with climate warming will be those with high thermal tolerances. Although our study focused on those species already present at the study sites, the same trends might also hold more generally within the larger regional species pool. We speculate that species with high thermal tolerances from distant southern sites might be among the first to colonize the new climate environments generated by regional warming. Similarly, if one considers the global species pool of ants being transported/introduced around the world (e.g., Suarez et al. 2005), those with high thermal tolerances are good candidates for successful establishment in novel environments that have experienced warming.

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SUPPLEMENTAL MATERIAL

Appendix A

A figure depicting relationships among environmental temperature, warming-chamber temperature manipulations, and hypothesized ant thermal performance curves at the high-latitude (Harvard Forest) and low-latitude (Duke Forest) sites (*Ecological Archives* E093-216-A1).

Appendix B

Methodological and analytical details on the construction and evaluation of models of ant responses to climate warming (*Ecological Archives* E093-216-A2).

Appendix C

A table summarizing ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative global climate change models (*Ecological Archives* E093-216-A3).

Appendix D

A table presenting thermal indices of current and future climates at Duke and Harvard Forests (*Ecological Archives* E093-216-A4).

Appendix E

A table presenting model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative thermal indices (*Ecological Archives* E093-216-A5).

Appendix F

A figure presenting sample calculations of thermal accumulation slope (*Ecological Archives* E093-216-A6).

Appendix G

A table presenting phylogenetic model summaries, by site, of ant responses to climate warming based on thermal tolerance and MaxEnt predictions (*Ecological Archives* E093-216-A7).

Appendix H

A figure presenting ant worker density as a function of warming treatment at Harvard Forest (*Ecological Archives* E093-216-A8).

Appendix I

A figure presenting regressions of maximal accumulation temperature as functions of thermal tolerance and MaxEnt predictions (*Ecological Archives* E093-216-A9).

Appendix J

A figure showing regressions of thermal accumulation slope (including standard errors) as functions of thermal tolerance and MaxEnt predictions (*Ecological Archives* E093-216-A10).