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

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Running title: Predicting ant responses to warming

Abstract

Physiological tolerance of environmental conditions can influence species-level responses to climatic 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 versus correlative species distribution models (SDMs) which are popular forecasting tools for modeling the effects of climatic change. Thermal tolerances predicted the responses of 19 ant species to experimental climatic 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 6 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.

Keywords: critical thermal maximum, global change, Formicidae, physiology, species distribution model, thermal tolerance

Introduction

Predicting biological responses to climatic change is critical (Araújo et al. 2005), but a number of researchers have begun to emphasize the potential unpredictability of species' responses to climatic 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 climatic 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 climatic 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 under-used approach for evaluating the degree to which physiological traits may inform the responses of species to climatic change.

Here, we used results from a pair of large-scale experimental climatic warming arrays, positioned near the northern (Harvard Forest; Petersham, Massachusetts; ≈42° N lat.) and southern (Duke Forest; Hillsborough, North Carolina, USA; ≈36° N lat.) 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 reflects population dynamics and the activity of individuals at local scales. By comparing 3 independent sources of data (activity responses to warming in a climatic 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 (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 climatic 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 climatic 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 approximately 5 cm off of the ground to allow ants to move unrestricted) in the forest understory (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 non-lethal 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 minutes starting at 36 °C. At the end of every 10 minute interval, individual ants were checked for the loss of muscular coordination (Appendix B).

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

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 climatic change (Fitzpatrick et al. 2008). Here, we restricted our consideration of MaxEnt-derived changes in probability of occurrence to the approximately 1 km^2 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 responses 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 (Appendix B,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 climatic warming. The slope of the linear relationship between ln(cumulative worker density across all sampling events) and Δ_c was considered the response (Appendix B,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 – current, such that positive values indicate increased probability of occurrence under climatic warming) were considered continuous fixed effects. The calculation of the thermal accumulation slope was not possible for a small fraction (< 1%) of ant species which 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 one (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 (Appendix B,G).

Results and Discussion

Predictive ability of thermal tolerance. At the low-latitude site (Duke Forest), responses of ant species to experimental warming (1.5 to 5.5 °C above ambient temperature) 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), responses of ants to experimental warming were poorly predicted by individual CT_{max} (Fig. 1C). ANOVA revealed non-significant 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 6 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 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 climatic 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 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 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 (based on current climatic 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 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; Appendix C,D,E). ANOVAs of thermal accumulation slopes revealed significant effects of CT_{max}, but non-significant 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 non-significant 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 (Appendix C,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 climatic 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 climatic 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 climatic 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 ants, 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 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 climatic 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 climatic 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. Relationships between environmental temperature, warming chamber temperature manipulations and hypothesized ant thermal performance curves at the high latitude (Harvard Forest) and low latitude (Duke Forest) sites.

Appendix B. Methodological and analytical details on the construction and evaluation of models of ant responses to climate warming.

Appendix C. Model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative GCMs.

Appendix D. Thermal indices of current and future climates at Duke and Harvard Forests.

Appendix E. Model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative thermal indices.

Appendix F. Sample calculations of thermal accumulation slope.

Appendix G. Phylogenetic model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions.

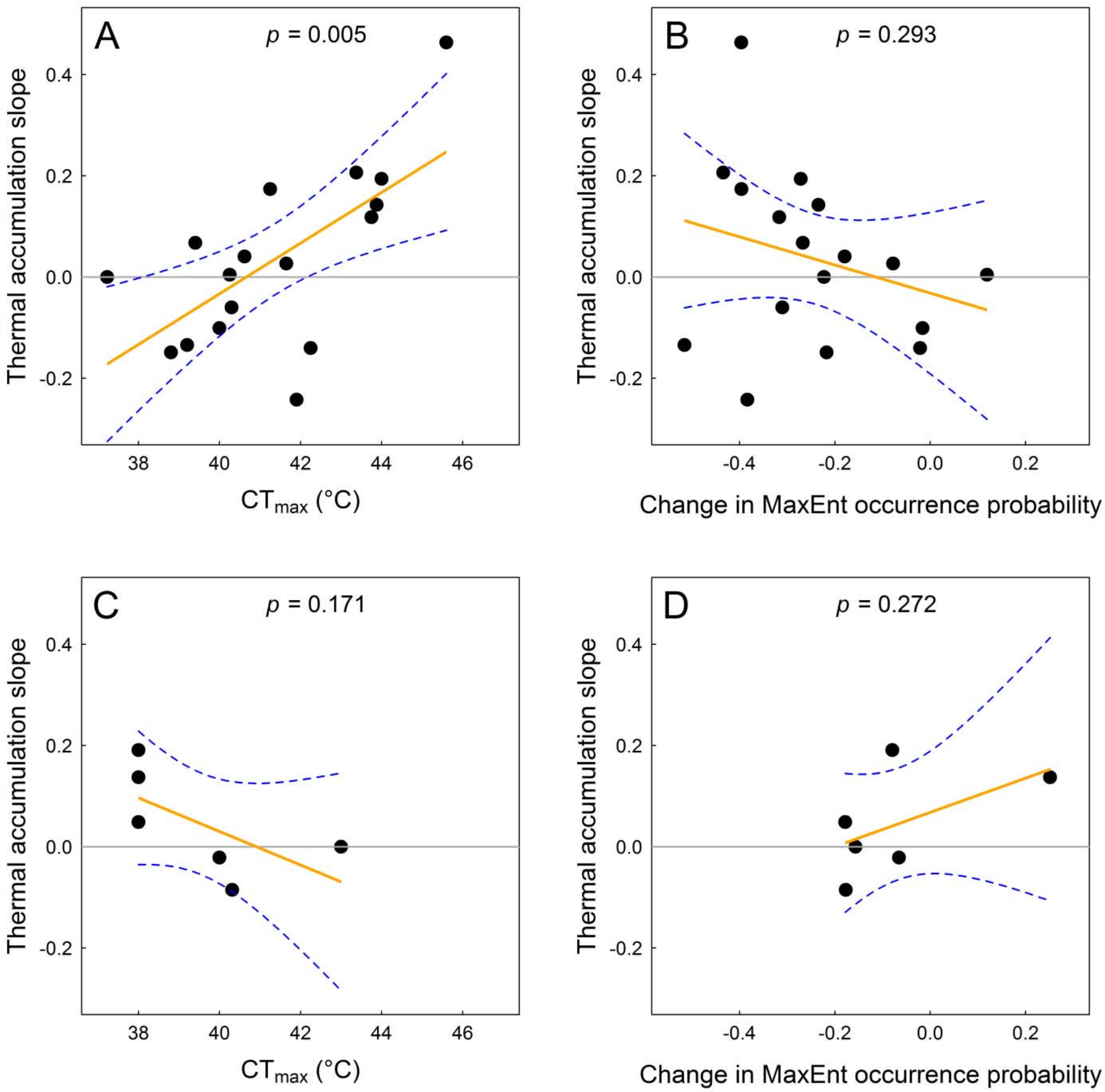
Appendix H. Ant worker density as a function of warming treatment at Harvard Forest.

Appendix I. Regressions of maximal accumulation temperature as functions of thermal tolerance and MaxEnt predictions.

Appendix J. Regressions of thermal accumulation slope (including standard errors) as functions of thermal tolerance and MaxEnt predictions.

Figure legends

Figure 1. The predictive ability of thermal tolerance versus species distribution models in ant responses to warming at high and low latitudes: thermal accumulation slope (the slope, β, 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 change in probability of occurrence across MaxEnt models based on current and future (2080) climate as defined by mean annual temperature) at (A,B) the low latitude site (Duke Forest), and (C,D) the high latitude site (Harvard Forest). Each point represents a single species; 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.


A
p = 0.005
B
p = 0.293
C
p = 0.171
D
p = 0.272
Thermal accumulation slope
0.4
0.2
0.0
-0.2
38
40
42
44
46
CTmax (°C)
-0.4
-0.2
0.0
0.2
Change in MaxEnt occurrence probability

473

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APPENDIX A. Relationships between environmental temperature, warming chamber temperature manipulations and hypothesized ant thermal performance curves at the high latitude (Harvard Forest) and low latitude (Duke Forest) sites.

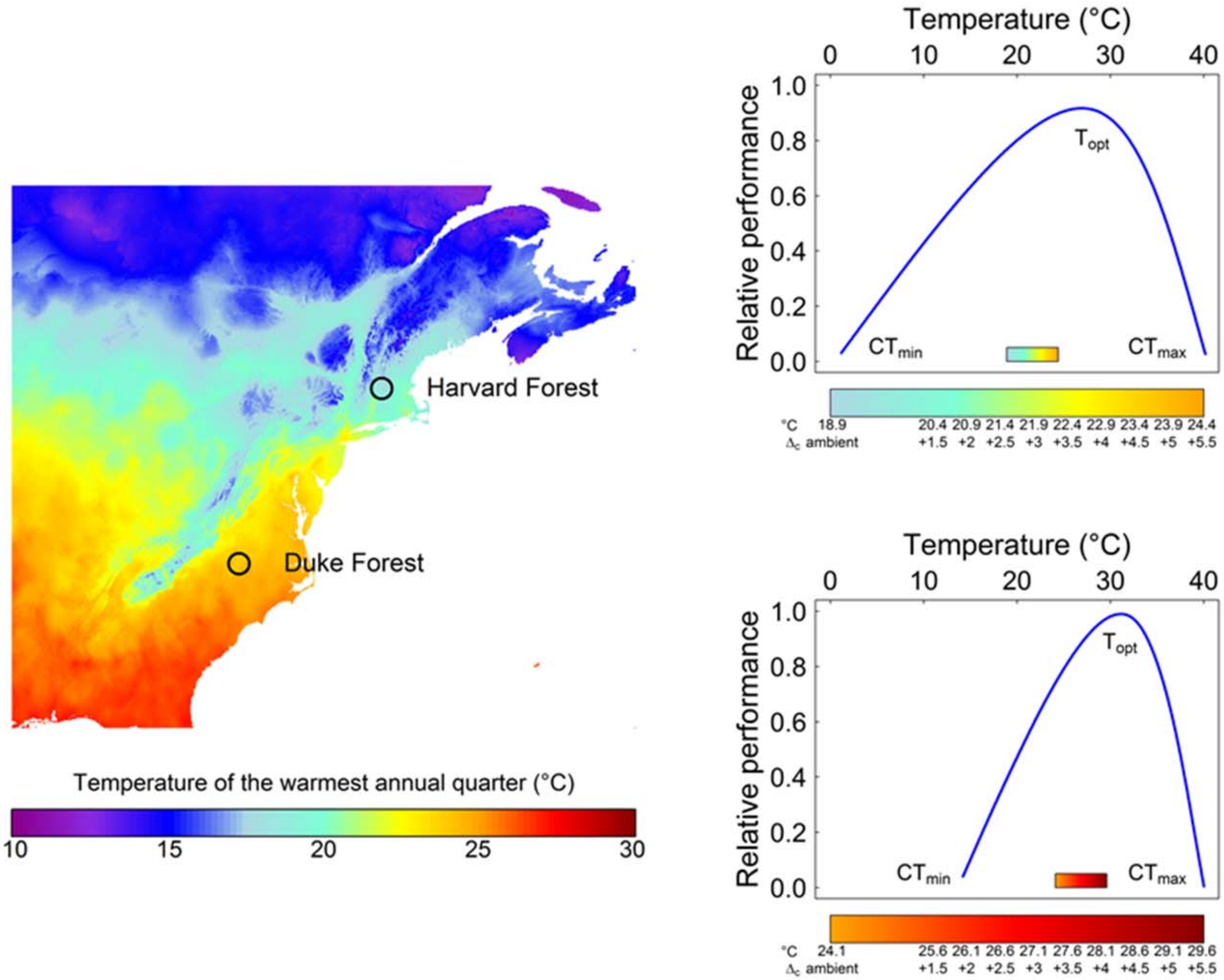

FIG. A1. Relationships between environmental temperature, warming chamber temperature manipulations and hypothesized ant thermal performance curves at the high latitude (Harvard Forest) and low latitude (Duke Forest) sites. The left panel depicts the current temperature of the warmest annual quarter (°C) derived from WorldClim. The two rightmost panels depict hypothesized thermal performance curves (blue lines), with relative performance as a function of temperature at the high latitude (top panel) and low latitude (bottom panel) sites. The color gradients correspond with the current temperature of the warmest annual quarter (ambient temperature) at each site, and temperatures of the warmest annual quarter after applying the warming chamber treatments (1.5 to 5.5 °C above ambient temperature). Note that environmental temperatures in the warming chambers are much closer to the thermal optimum (T_{opt}) and critical thermal maximum (CT_{max}) at the low latitude site compared with the high latitude site.

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APPENDIX B. Methodological and analytical details on the construction and evaluation of models of ant responses to climate warming.

Methodological details

Pitfall collections

To sample ants, we placed four pitfall traps (90 mL volume) containing propylene glycol (30 mL; Prestone, LowTox) flush with the soil surface in each chamber. During each sampling event, traps were left out for a 48-hour sampling period (performed monthly; see below). At the end of the 48-hour sampling period, individual ants recovered in the pitfall traps were removed from the propylene glycol and preserved in 95% ethanol. All ants were identified to the species level; pinned voucher specimens are retained at North Carolina State University, and at Harvard Forest.

Monthly pitfall samples were conducted at Duke and Harvard Forest (April 2010 - September 2011). Pitfall data also were collected for each chamber following chamber construction, but prior to the setting of experimental temperature treatments (September - November 2009). We examined such 'pre-treatment' data for potential preexisting biases in species abundance across chambers. A gap exists between the pre- and post-treatment data because we restrict our analyses of post-treatment data to those data collected after the stabilization of Δ_cs in experimental chambers which required approximately 4 months. We restricted our analyses to those ground-foraging ant species which were sampled in the pitfall traps at Duke and Harvard Forests, and excluded data on a primarily subterranean, exceptionally rare species that does not nest in the chambers (*Neivamyrmex texanus*), and a canopy specialist species (*Camponotus obliquus*).

Thermal tolerance

Colony fragments of ants (workers only) were collected from open and forested areas adjacent to the Duke and Harvard Forest warming sites, and comparable habitats within Wake Co. (North Carolina, USA) and Worcester Co. (Massachusetts, USA). Colony fragments were maintained with continuous access to food and water at a non-stressful temperature of 25 °C, ensuring ants were in good condition prior to thermal testing (testing occurred within 24 hours of collection). Ants were placed individually into 1.5mL 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), and the temperature was increased by 2 °C every 10 minutes starting at 36 °C until the loss of ant muscular coordination which indicated CT_{max} was reached.

Species distribution models

Current climatic data were obtained from WorldClim at a 30 arc-second (1 km) resolution (Hijmans et al. 2005). Statistically downscaled global climate change models (GCM) based on the third IPCC Assessment Report were obtained from the International Centre for Tropical Agriculture (CIAT) (Ramirez and Jarvis 2008), and used to derive predicted future climate data for 2080. We examined a range of different GCMs (CCCMA-CGCM2, CSIRO-MK2, and HCCPR-HADCM3 at a 30 arc-second resolution); because results were similar across different climate models, we focus on results from the CCCMA-CGCM2 model (Appendix C,D). This model predicts a 4.6 °C increase in temperature at Duke Forest, and 4.8 °C increase at Harvard Forest by the year 2080.

North American occurrence data (presence-only) for 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). The median number of records was 111 species^{-1} and ranged from 13 to 471 for the Duke and Harvard Forest species examined in our study.

Phylogenetic autocorrelation

We fit phylogenetic generalized least squares (PGLS) models where the degree of phylogenetic autocorrelation (Pagel's λ) was simultaneously co-estimated. Lambda is a measure of phylogenetic inertia, or how closely the structure in the model residuals resembles the structure of the phylogeny, with greater values indicating greater phylogenetic structure. Phylogenetic associations among ant genera were based on the phylogeny of Moreau et al. (2006). Unknown relationships among species were interpolated as polytomies.

Supporting analyses and results

Potential for pre-existing patterns in ant activity density

Prior to chamber deltas being set at Duke and Harvard Forest, we found little evidence of systematic variation in the worker density of ants among different chambers (ANOVA revealed a non-significant effect of chamber on pre-treatment cumulative worker density at Duke Forest: $F_{11,74} = 0.317$, $P = 0.980$, and at Harvard Forest: $F_{11,8} = 0.581$, $P = 0.802$), indicating our post-treatment results of CT_{max} being predictive of ant activity density do not simply reflect pre-existing patterns of warming chamber colonization.

ANOVA models based on thermal accumulation slope

For ANOVA models in which the slope of the linear relationship between ln(cumulative worker density) and Δ_c was considered the response, and CT_{max} and the difference in MaxEnt probability of occurrence between current and future climate were considered continuous fixed effects, two species (*Amblyopone pallipes* and *Temnothorax pergandei*) from Duke Forest were excluded from this analysis owing to their occurrence in only a single temperature treatment (slopes relating ln(cumulative worker density) and Δ_c could not be estimated).

We additionally performed ANOVAs of thermal accumulation slope as functions of CT_{max} and MaxEnt predictions with the residuals weighted by 1/(SE of the thermal accumulation slope). The results were qualitatively similar to our unweighted analyses. We focus on the unweighted analyses, as weighted analyses introduce some degree of systematic bias in which species that naturally occur at low frequency, but nonetheless respond to warming treatments, are necessarily weighted less than more frequently occurring species with comparable responses to the warming treatments (Appendix J).

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APPENDIX C. Model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative GCMs.

TABLE C1. Model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative GCMs.

GCM[*]	**Site**	**Response**	**Predictor**	***F***[†]	***P***
CCCMA-CGCM2	Duke Forest	maximal accumulation temperature	CT_{max}	9.80	0.00646
			MaxEnt	0.166	0.689
		thermal accumulation slope	CT_{max}	11.4	0.00450
			MaxEnt	0.993	0.336
	Harvard Forest	maximal accumulation temperature	CT_{max}	0.0884	0.786
			MaxEnt	0.0739	0.803
		thermal accumulation slope	CT_{max}	0.577	0.503
			MaxEnt	0.0899	0.784
CSIRO-MK2	Duke Forest	maximal accumulation temperature	CT_{max}	9.87	0.00630
			MaxEnt	0.0196	0.890
		thermal accumulation slope	CT_{max}	10.5	0.00589
			MaxEnt	3.04	0.103
	Harvard Forest	maximal accumulation temperature	CT_{max}	0.0843	0.790
			MaxEnt	0.342	0.600
		thermal accumulation slope	CT_{max}	1.43	0.318
			MaxEnt	0.0367	0.860
HCCPR-HADCM3	Duke Forest	maximal accumulation temperature	CT_{max}	12.0	0.00316
			MaxEnt	1.69	0.212
		thermal accumulation slope	CT_{max}	12.0	0.00385
			MaxEnt	1.18	0.296
	Harvard Forest	maximal accumulation temperature	CT_{max}	2.09	0.244
			MaxEnt	0.0002	0.990
		thermal accumulation slope	CT_{max}	0.0206	0.895
			MaxEnt	0.462	0.546

[*]MaxEnt models are constructed using all 19 bioclim variables (L-1 regularization using the default settings was employed) to facilitate overall comparisons among different climate models; similar results were obtained using thermal indices (mean annual temperature, mean temperature during the warmest quarter, and maximum temperature during the warmest quarter) as individual predictors.

[†](Numerator degrees of freedom, denominator degrees of freedom) for predictors: Duke Forest maximal accumulation temperature = (1, 16); Duke Forest thermal accumulation slope = (1, 14); Harvard Forest maximal accumulation temperature and thermal accumulation slope = (1, 3).

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APPENDIX D. Thermal indices of current and future climates at Duke and Harvard Forests.

TABLE D1. Thermal indices of current and projected future climates based on three climate change models at Duke and Harvard Forests.

Site	Thermal index	Temperature (°C; current WorldClim, 2080 CCCMA-CGCM2, CSIRO-MK2, HCCPR-HADCM3)
Duke Forest	Mean annual temperature	14.5, 19.1, 19.6, 19.4
	Mean temperature warmest quarter	24.1, 29.3, 29.2, 30.8
	Maximum temperature warmest quarter	31.4, 38.8, 36.4, 39.3
Harvard Forest	Mean annual temperature	7.3, 12.1, 14.2, 12.1
	Mean temperature warmest quarter	18.9, 23.7, 24.8, 25.1
	Maximum temperature warmest quarter	27.1, 31.7, 33.0, 34.1

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APPENDIX E. Model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative thermal indices.

TABLE E1. Model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions developed with alternative thermal indices.

MaxEnt calibrating variable[*]	**Site**	**Response**	**Predictor**	***F***[†]	***P***
$\mathbf{T_{an}}$	Duke Forest	maximal accumulation temperature	CT_{max}	8.65	0.00960
			MaxEnt	1.46	0.244
		thermal accumulation slope	CT_{max}	8.91	0.00983
			MaxEnt	0.460	0.509
	Harvard Forest	maximal accumulation temperature	CT_{max}	0.0188	0.900
			MaxEnt	0.0005	0.983
		thermal accumulation slope	CT_{max}	1.23	0.348
			MaxEnt	0.507	0.528
$\mathbf{T_{qt}}$	Duke Forest	maximal accumulation temperature	CT_{max}	9.51	0.00712
			MaxEnt	0.287	0.599
		thermal accumulation slope	CT_{max}	10.3	0.00639
			MaxEnt	0.560	0.467
	Harvard Forest	maximal accumulation temperature	CT_{max}	0.228	0.666
			MaxEnt	0.290	0.628
		thermal accumulation slope	CT_{max}	0.159	0.717
			MaxEnt	1.84	0.268
$\mathbf{T_{max}}$	Duke Forest	maximal accumulation temperature	CT_{max}	10.7	0.00481
			MaxEnt	1.89	0.188
		thermal accumulation slope	CT_{max}	12.2	0.00357
			MaxEnt	2.00	0.179
	Harvard Forest	maximal accumulation temperature	CT_{max}	0.398	0.573
			MaxEnt	0.881	0.417
		thermal accumulation slope	CT_{max}	0.570	0.505
			MaxEnt	0.0407	0.853

[*]MaxEnt calibrating variable abbreviations: T_{an} = mean annual temperature; T_{qt} = mean temperature during the warmest annual quarter; T_{max} = maximum annual temperature. Projected future distributions were developed using the CCCMA-CGCM2 climate model.

[†](Numerator degrees of freedom, denominator degrees of freedom) for predictors: Duke Forest maximal accumulation temperature = (1, 16); Duke Forest thermal accumulation slope = (1, 14); Harvard Forest maximal accumulation temperature and thermal accumulation slope = (1, 3).

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APPENDIX F. Sample calculations of thermal accumulation slope.

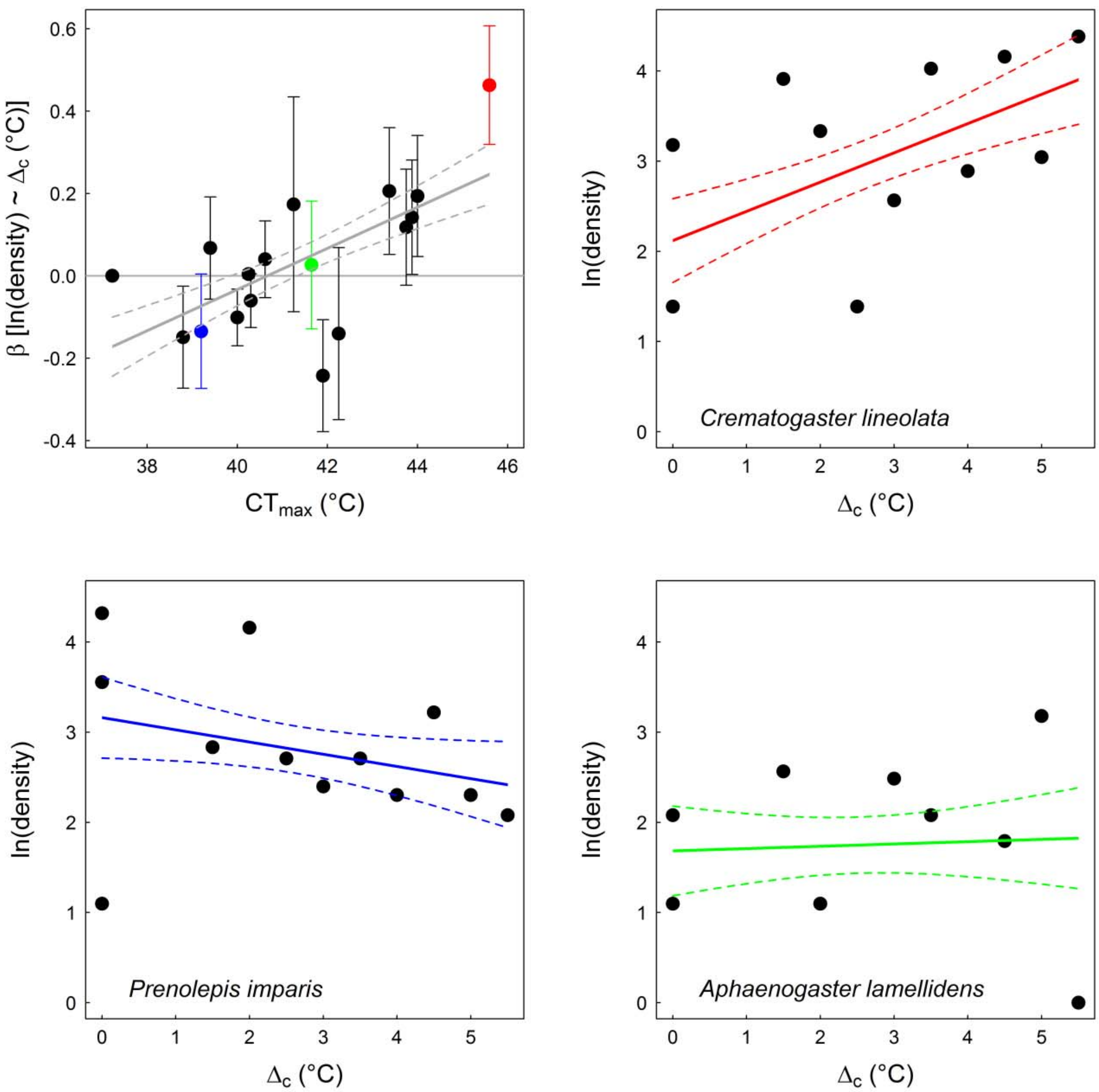

FIG. F1. Sample calculations of thermal accumulation slope. The top left panel presents the thermal accumulation slope (± 1 SE) as a function of CT_{max} for the 19 species at Duke Forest; the solid grey line indicates the slope of this regression, and the dashed grey lines indicate the standard errors of the predicted values. The remaining panels present examples of the calculation of the thermal accumulation slope (the natural log of worker density as a function of the °C above ambient among the different warming chambers). Three species with different functional responses to warming are presented: a heat tolerant species (*Crematogaster lineolata*; red lines), a heat intolerant species (*Prenolepis impairs*; blue lines), and a heat insensitive species (*Aphaenogaster lamellidens*; green lines). The solid line is the thermal accumulation slope for each of these species, and the dashed lines indicate the standard errors of predicted values; these lines correspond with the point estimates (slope ± 1 SE) presented in the top left panel.

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APPENDIX G. Phylogenetic model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions.

TABLE G1. Phylogenetic model summaries of ant responses to climate warming based on thermal tolerance and MaxEnt predictions.

Site	Response	Predictor*	*F*	*P*	λ
Duke Forest	maximal accumulation temperature	CT_{max}	9.29	0.00869	0.348
		MaxEnt (T_{an})	0.893	0.361	
	thermal accumulation slope	CT_{max}	11.2	0.00485	0.136
		MaxEnt (T_{an})	0.297	0.594	
	maximal accumulation temperature	CT_{max}	9.28	0.00871	0.359
		MaxEnt (T_{qt})	0.878	0.365	
	thermal accumulation slope	CT_{max}	11.2	0.00482	0.282
		MaxEnt (T_{qt})	0.767	0.396	
	maximal accumulation temperature	CT_{max}	10.6	0.00583	0.358
		MaxEnt (T_{max})	2.91	0.110	
	thermal accumulation slope	CT_{max}	12.2	0.00362	0.274
		MaxEnt (T_{max})	2.04	0.175	
Harvard Forest	maximal accumulation temperature	CT_{max}	0.00718	0.940	<0.0001
		MaxEnt (T_{an})	0.0002	0.990	
	thermal accumulation slope	CT_{max}	8.47	0.101	<0.0001
		MaxEnt (T_{an})	0.348	0.615	
	maximal accumulation temperature	CT_{max}	0.00776	0.938	<0.0001
		MaxEnt (T_{qt})	0.162	0.726	
	thermal accumulation slope	CT_{max}	11.7	0.0758	<0.0001
		MaxEnt (T_{qt})	1.25	0.380	

	maximal accumulation temperature	CT_{max}	0.305	0.636	<0.0001
		MaxEnt (T_{max})	4.07	0.181	
	thermal accumulation slope	CT_{max}	5.73	0.139	<0.0001
		MaxEnt (T_{max})	0.865	0.450	

[*]MaxEnt predictors: T_{an} denotes mean annual temperature, T_{qt} denotes mean temperature during the warmest quarter, and T_{max} denotes maximum temperature during the warmest quarter.

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APPENDIX H. Ant worker density as a function of warming treatment at Harvard Forest.

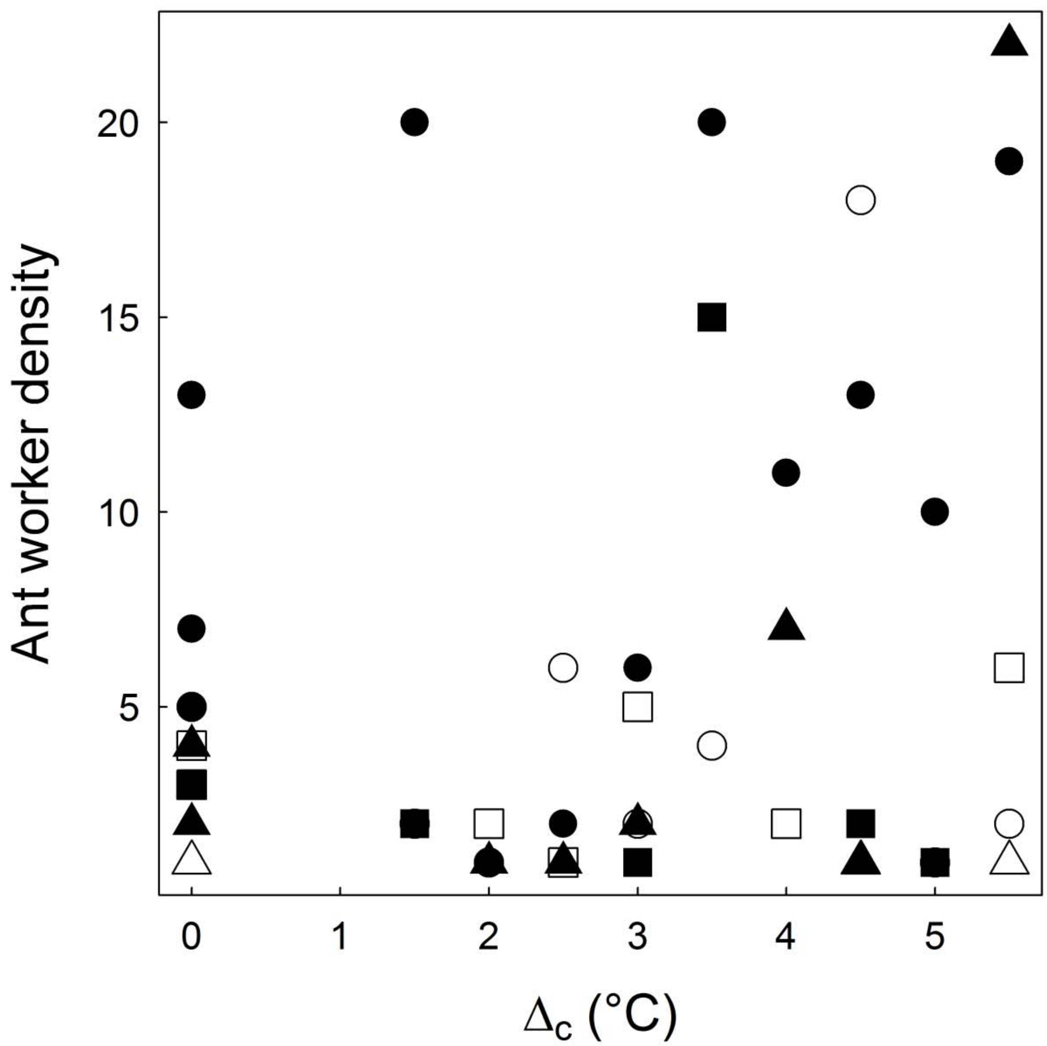

FIG. H1. Ant worker density as a function of chamber delta (°C) at Harvard Forest. Symbols correspond with species identity: *Aphaenogaster rudis* (filled circles), *Camponotus pennsylvanicus* (open circles), *Formica subsericea* (filled squares), *Lasius alienus* (open squares), *Myrmica punctiventris* (filled triangles), *Temnothorax longispinosus* (open triangles).

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APPENDIX I. Regressions of maximal accumulation temperature as functions of thermal tolerance and MaxEnt predictions.

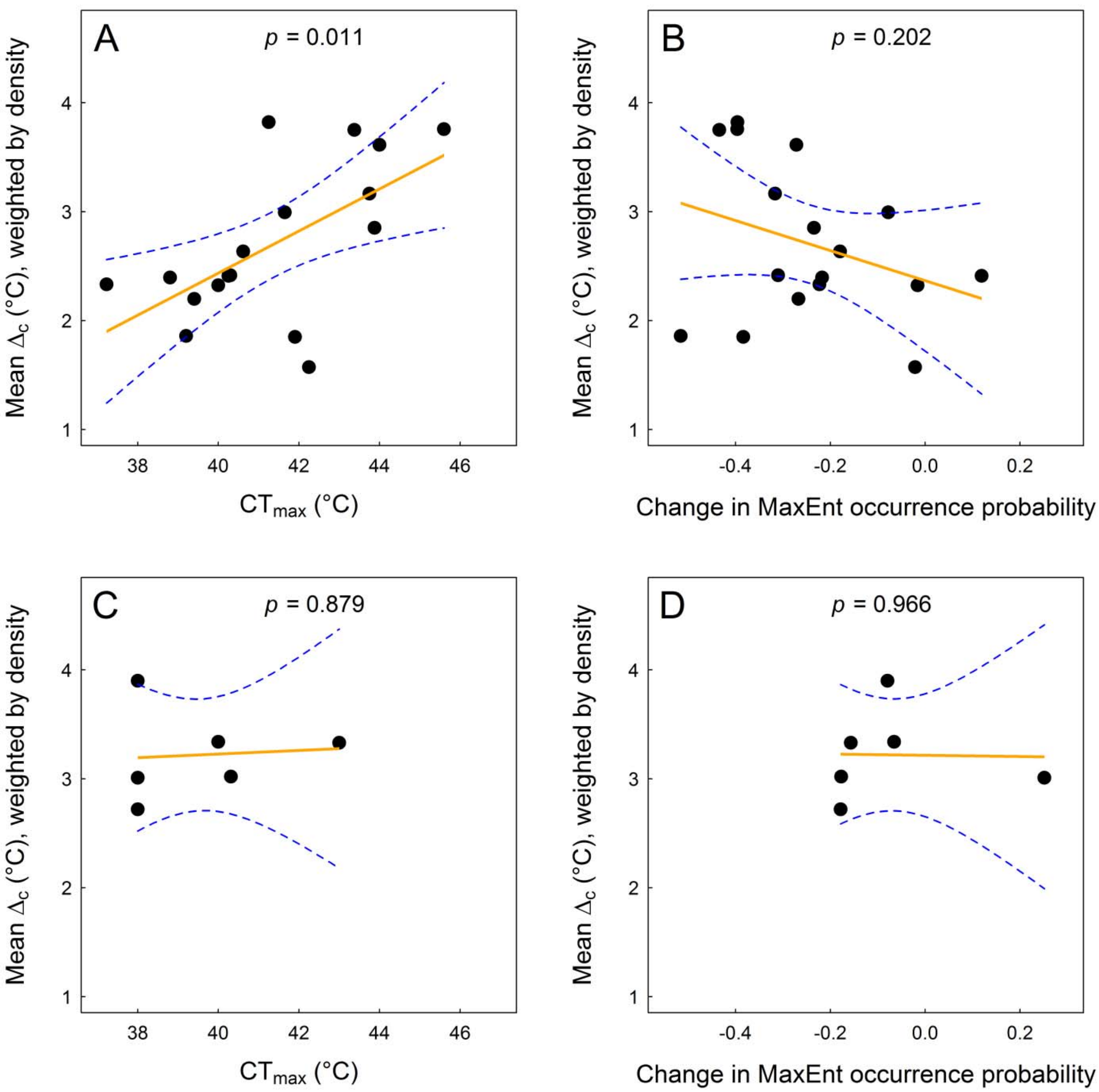

FIG. I1. The predictive ability of thermal tolerance versus species distribution models in ant responses to warming at high and low latitudes: thermal accumulation slope (the slope, β, of the linear relationship between ln(cumulative worker density) and Δ_c) as a function of (A,C) the critical thermal maximum (CT_{max}), and (B,D) MaxEnt prediction (the change in probability of occurrence across MaxEnt models based on current and future (2080) climate as defined by mean annual temperature) at (A,B) the low latitude site (Duke Forest), and (C,D) the high latitude site (Harvard Forest). Each point represents a single species; 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.

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APPENDIX J. Regressions of thermal accumulation slope (including standard errors) as functions of thermal tolerance and MaxEnt predictions.

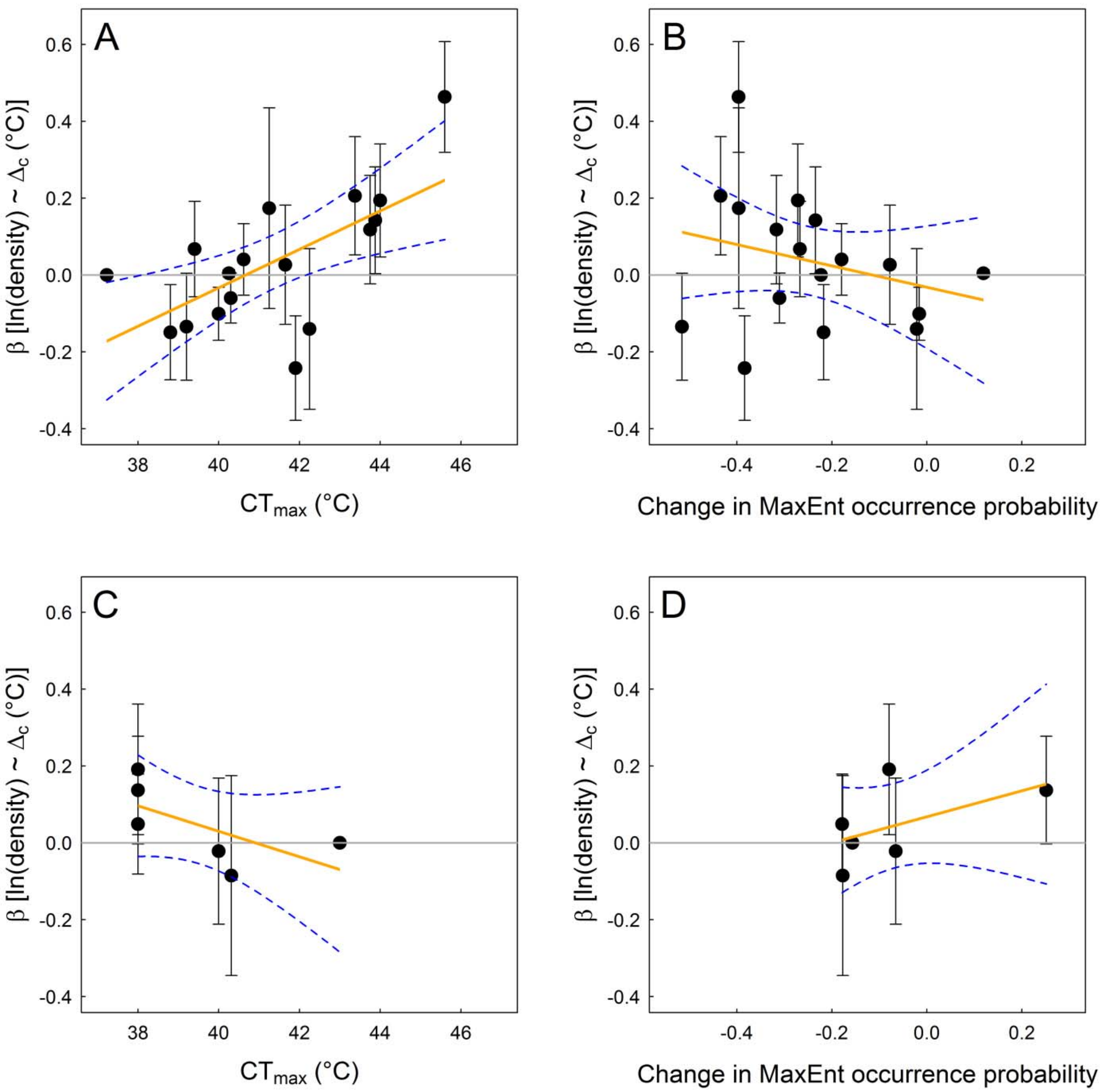

FIG. J1. The predictive ability of thermal tolerance versus species distribution models in ant responses to warming at high and low latitudes: thermal accumulation slope (the slope, β, of the linear relationship between ln(cumulative worker density) and Δ_c) as a function of (A,C) the critical thermal maximum (CT_{max}), and (B,D) MaxEnt prediction (the change in probability of occurrence across MaxEnt models based on current and future (2080) climate as defined by mean annual temperature) at (A,B) the low latitude site (Duke Forest), and (C,D) the high latitude site (Harvard Forest). Each point represents a single species; solid orange lines represent simple linear regressions, and dashed blue lines represent 95% confidence intervals.