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SYMPOSIUM

Heat tolerance predicts the importance of species interaction effects as the climate changes

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Synopsis Few studies have quantified the relative importance of direct effects of climate change on communities versus indirect effects that are mediated through species interactions, and the limited evidence is conflicting. Trait-based approaches have been popular in studies of climate change, but can they be used to estimate direct versus indirect effects? At the species level, thermal tolerance is a trait that is often used to predict winners and losers under scenarios of climate change. But thermal tolerance might also inform when species interactions are likely to be important because only subsets of species will be able to exploit the available warmer climatic niche space, and competition may intensify in the remaining, compressed cooler climatic niche space. Here, we explore the relative roles of the direct effects of temperature change and indirect effects of species interactions on forest ant communities that were heated as part of a large-scale climate manipulation at high- and low-latitude sites in eastern North America. Overall, we found mixed support for the importance of negative species interactions (competition), but found that the magnitude of these interaction effects was predictable based on the heat tolerance of the focal species. Forager abundance and nest site occupancy of heat-intolerant species were more often influenced by negative interactions with other species than by direct effects of temperature. Our findings suggest that measures of species-specific heat tolerance may roughly predict when species interactions will influence responses to global climate change.

Introduction

Ecologists have widely acknowledged the importance of incorporating species interactions into forecasts of responses to climate change (Tylianakis et al. 2008; Walther 2010), but there are few published studies that actually succeed in this because empirical data are rare and modeling tools are limited (Cahill et al. 2012; Angert et al. 2013). Empirical support for the role of species interactions in shaping population persistence and growth under climate change is mixed: some studies find a stronger role for direct effects of changes in climate on individual species (Chu et al. 2016), but others find a stronger role

for species interactions (Suttle et al. 2007). On the surface, it may appear that species interactions simply introduce noise into ecological forecasts owing to the inherent variability of interactions over space and time, and that the magnitude of these effects can vary across different systems. But recent work suggests that the magnitude of species interaction effects under climate change may be predictable based on species traits that are proxies for physiological performance and habitat use (Urban et al. 2012). For example, in grassland plant communities, the indirect effects of climate change, i.e.,

those mediated through species interactions, are strongest for species showing weak niche differentiation (Chu et al. 2016).

Such trait-based approaches have met with considerable success in forecasting the relative performance of species—the winners and losers—under the direct effects of climate change (see Pacifici et al. 2017 for a recent data-driven review; see also for trait-based forecasting frameworks: Suding et al. 2008; Chown 2012; Foden et al. 2013). Of the many traits that have been used, thermal tolerance has been an especially strong predictor of responses in a warming world. For example, in forest ant communities, greater heat tolerance is positively correlated with ant abundance and activity under experimental warming (Diamond et al. 2012, 2013; Stuble et al. 2013) and historical changes in abundance related to long-term patterns of climate change in the field (Resasco et al. 2014). But again, these approaches lack an explicit consideration of indirect effects of temperature change via altered species interactions. As temperatures rise, species that have limited tolerance of high temperatures may experience more density-dependent (competitive) interactions with other species as suitable thermal niche space for their foraging and other activities decreases. In contrast, the subset of species in the community with high heat tolerance may be subject to fewer density-dependent interactions because they have broader ranges of suitable thermal niche space along which they can differentiate relative to other members of the community under future warmed conditions; there is also some evidence that heat-tolerant species may gain competitive advantages in warmer conditions (Urban et al. 2012). A key question then is whether heat tolerance can predict the importance of competitive species interactions under warming.

Using ant forager abundance and nest occupancy of forest ants in field-based climate warming arrays, we tested whether the relative importance of competition, inferred from negative species interaction effects, was greater for heat-intolerant species compared with heat-tolerant species. In many habitats, competition among ant species for limited food and nest resources is intense (Herbers 1989; Cerdá et al. 1997), and heat-tolerant species may gain competitive advantages in warmed environments (Diamond et al. 2016). Within the experimental warming arrays, the forest floor was heated for 5 years at sites located in the northern and southern regions of the eastern USA, and ant foraging activity and nest occupancy were monitored approximately monthly during the growing season at each site. If the available thermal

niche space for heat-intolerant species shrinks in warmed habitats with concomitant increases in competition for limited food and nest resources (Fig. 1), we predict a negative relationship between species-specific heat tolerance and the importance of negative species interaction effects on forager abundance and nest occupancy.

Methods

Warming chambers

We explored foraging and nest-use of ant communities in response to climate warming in a pair of field-based experimental warming arrays. The arrays were established in comparable ecotypes (deciduous forest) at two sites: a warm, southern site (Duke Forest, located in the Piedmont region of North Carolina, USA) and a cool, northern site (Harvard Forest, located in the New England upland region of Massachusetts, USA). This extensive gradient spanned 6.5 degrees of latitude, yielding a mean annual temperature difference of 5.8 °C.

The arrays encompassed a total of 30 open-top chambers (15 per site). At each of the two sites, nine chambers experienced different levels of warming in increments of 0.5 °C from 1.5 °C to 5.5 °C above ambient temperature; each chamber remained at a constant level of warming amount above ambient temperature for the 5-year duration of the experiment. The chambers, each 5 m in diameter, warmed the forest floor year-round with thermostat-controlled forced air passed over hydronic heaters. At each of the two sites, six additional chambers experienced ambient temperature conditions; three of these chambers had forced air at ambient temperature, and three had no forced air infrastructure (Pelini et al. 2011). The range of temperatures spanned by the warming treatments encompasses climate projections of increased mean annual temperature from 1 °C to >5 °C over the next century (Intergovernmental Panel on Climate Change 2014) and represents a continuous experimental gradient of increasing temperature between sites where the unheated control chambers at the southern Duke Forest site had similar temperatures to the warmest heated chambers at the northern Harvard Forest site. The open-top chambers were also open at the bottom to allow free access to ants and other invertebrates, though most ants tended to remain within the chambers. More than 98% of foraging activity observed in the chambers involved workers originating from nests within the chambers (Stuble et al. 2013).

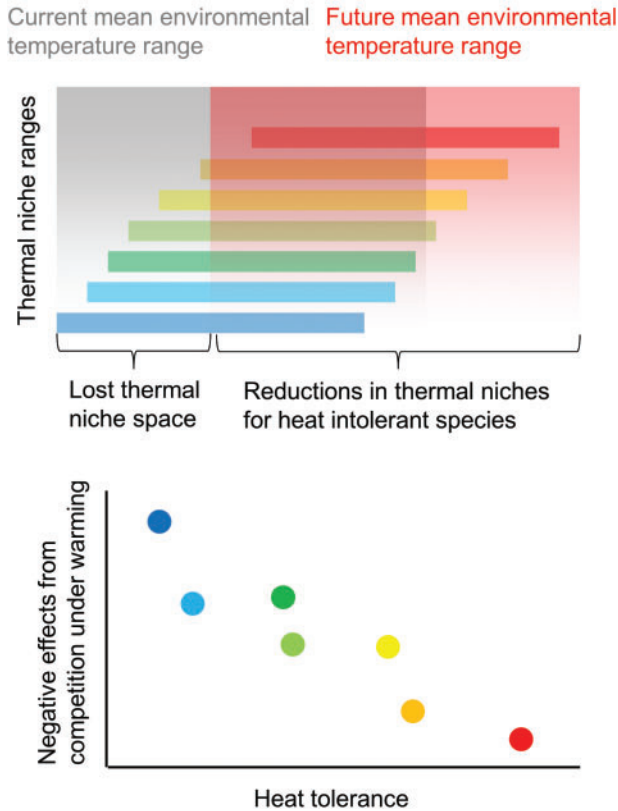


Fig. 1 Conceptual diagram of how temperature rise may predictably influence the availability of thermal niche space and the importance of competitive interactions based on heat tolerance. In the top panel, bars represent the thermal niche ranges of different species, with more heat-tolerant species represented in warmer colors. The gray shading indicates the current range of mean environmental temperatures and the red shading indicates the future range of mean environmental temperatures. The non-overlapping gray shading indicates the thermal niche space being lost with climate change, and the non-overlapping red shading indicates the thermal niche space being gained with climate change. In general, heat-intolerant species tend to lose thermal niche space with climate change. The bottom panel shows how the negative effects of competition may intensify for heat-intolerant species as they lose thermal niche space under climate change.

Because we were interested in the influence of the effect of warming among the chambers on ant communities rather than the specific temperature at the time of pitfall trapping or nest box observations, we computed the mean annual temperature (MAT) for each of the chambers with forced air (nine heated and three control chambers). The MAT of the chamberless control plots was computed for the single set of sensors located outside the warming chambers, and this average temperature was assigned as the MAT for all three of the chamberless control plots. Raw temperature data were recorded at hourly intervals throughout the year via a ground-based sensor network of thermistors in the chambers; MAT is the

mean of all hourly temperatures for the years in which the nest box censuses occurred.

Ant censuses using pitfall trapping and artificial nest boxes

At the start of the experiment in 2010, we placed four pitfall traps and four artificial nest boxes into each of the 30 chambers; midway through the experiment, we added another four nest boxes (Diamond et al. 2016). The pitfall traps (90 mL volume) contained 30 mL of propylene glycol (Prestone, LowTox) at Duke Forest or ethanol at Harvard Forest and were set flush with the soil surface in each chamber (Pelini et al. 2011; Diamond et al. 2012). During each sampling event, traps were left out for a 48-h sampling period. At the end of the 48-h sampling period, ants recovered in the pitfall traps were removed 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. Each nest box was constructed from balsa wood and a wood block of untreated pine ($14 \times 15 \times 2$ cm). We routed a zig-zag pattern into the top of the block, and cut an entryway in the side of the block. The nest box was covered on top with Plexiglas and a ceramic tile. The tiles were lifted to census the ant colony visible through the Plexiglas top; this observation technique provided minimal disturbance to the resident ant colony. Multiple occupancy of nest boxes was never observed: at each census, nest boxes were either occupied by a single colony or were empty.

Censuses of pitfall traps and nest boxes occurred approximately monthly during the growing season at each site over a span of over 5 years of experimental warming, from January 2010 to May 2015. This sampling scheme yielded 60 pitfall samples and 41 nest box observations at Duke Forest, and 37 pitfall samples and 19 nest box observations at Harvard Forest. Fewer censuses occurred at Harvard Forest because the snow-free growing season is much shorter there than at Duke Forest; ants generally were not collected in pitfall traps at Harvard Forest between November and March. Although we were able to identify all individuals from the pitfall traps to species, the taxonomic resolution of the nest box data was coarser. Because we did not disturb the nest boxes by collecting individual workers, we used ant genera as our taxonomic unit in several cases. At Duke Forest, the nest box taxa were identified as *Aphaenogaster* spp., *Brachyponera chinensis*, *Crematogaster lineolata*, and *Temnothorax curvispinosus*; at Harvard Forest, *Aphaenogaster* spp.,

Camponotus spp., *Myrmica* spp., and *Temnothorax longispinosus*. At Duke Forest, the pitfall species included *Aphaenogaster carolinensis*, *Aphaenogaster fulva*, *Aphaenogaster lamellidens*, *Aphaenogaster rudis*, *Brachyponera chinensis*, *Camponotus castaneus*, *Camponotus pennsylvanicus*, *Crematogaster lineolata*, *Formica pallidefulva*, *Formica subsericea*, *Myrmecina americana*, *Nylanderia faisonensis*, *Ponera pennsylvanica*, *Solenopsis invicta*, *Solenopsis molesta*, *Stenamma impar*, and *Temnothorax curvispinosus*; at Harvard Forest, *Aphaenogaster fulva*, *Aphaenogaster picea*, *Aphaenogaster rudis*, *Camponotus pennsylvanicus*, *Formica subsericea*, *Lasius alienus*, *Myrmica punctiventris*, *Stenamma impar*, *Temnothorax longispinosus*. For each species or species group, we used five separate occurrences in two separate warming chambers as the inclusion criteria for our analyses, which yielded 4 species or species groups from the nest box data at each site, and 17 species at Duke Forest and 9 species at Harvard Forest from the pitfall data.

Heat tolerance

Our measure of heat tolerance was the critical thermal maximum (CT_{\max}), defined here as the temperature at which muscle coordination of an individual forager was lost in a controlled laboratory heating experiment. This metric provides an ecologically relevant measure of heat tolerance because it represents 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 from forests near the warming sites; mean heat tolerance for each species was computed separately for each of the two sites. Although the focal ant species are relatively abundant and widespread throughout North America, and our experimental warming sites are positioned within the range boundaries of these species (Lach et al. 2010; Gibb et al. 2017), we used site-specific heat tolerances to account for potential local adaptation throughout the geographic ranges of the ant species in our analyses (e.g., Warren and Chick 2013). Heat tolerances were tested individually (minimum 8 individuals per species at each site) in a heat block for which the temperature was increased at a slow ramping rate of $0.2\text{ }^{\circ}\text{C min}^{-1}$ starting at $36\text{ }^{\circ}\text{C}$. Because the rate of experimental temperature increase can influence the estimate of thermal tolerance (Terblanche et al. 2011), we refit all of our statistical models using an alternative measure of CT_{\max} based on a fast-ramp temperature increase of $1\text{ }^{\circ}\text{C min}^{-1}$ starting at $36\text{ }^{\circ}\text{C}$. Our models that used CT_{\max}

assessed with the fast ramp yielded qualitatively similar results to those assessed with the slow ramp; we present the results only from the slow-ramp experiment for which we were able to obtain measurements for more species.

Statistical analyses for the species interactions and temperature models

To explore the influence of species interactions (specifically, negative interactions; see below) and temperature on nest site occupancy, we used the nest box data and constructed generalized linear models with a binomial error structure, in which the proportion of nest boxes occupied was the response variable, and chamber temperature and the proportion of nest boxes occupied by a single non-focal species were separately considered as predictor variables. We used AIC to determine whether models with temperature or non-focal species nest box occupancy were better predictors of focal species nest box occupancy. To quantify the importance of temperature relative to negative species interactions, we developed a binomial response variable in which we assigned a score of 0 when models with temperature as a predictor were more important, i.e., they had the lowest AIC value by 2 or more units, and we assigned a score of 1 when models with the non-focal species as a predictor were more important, again having the lowest AIC value by 2 or more units. In cases where the difference in AIC between temperature and negative species interaction models was less than two, we assigned a score of 0.5. For each focal species, we computed the mean proportion of times the species interaction models were selected as the best-fitting models, i.e., as an indicator of the overall importance of species interactions versus temperature.

Of course ants engage in many types of species interactions from competition to predation to mutualism and involve both other ant species and non-ant species (Lach et al. 2010). As competition among ant species for limited food and nest resources is a major driver of ant performance and distribution (Cerda et al. 2013), we focus on competitive species interactions among ants in our experimental warming arrays. We infer competitive interactions from negative effects of non-focal species on focal species, and as a consequence, we do not distinguish between specific mechanisms of competition (e.g., more contact-based interactions such as aggression or nest defense versus more diffuse interactions such as exploitative competition over shared food resources; see Diamond et al. 2016 for a full discussion of this issue). Hereafter we refer to negative species

interaction effects, as these were the effects we were able to quantify with our experiments, and intend these effects as a proxy for general competitive interactions among ant species within our warming arrays. Because we were specifically testing the hypothesis that competition intensifies for heat-intolerant species in warmed environments, for models that indicated species interactions were more important, we restricted further consideration of these models to those where the effect of the non-focal species on the focal species was negative. For models that indicated temperature effects were more important, we did not restrict our models based on the sign of the effect. We also performed comparable analyses in which the sign of the species interaction coefficient was not restricted to be negative and found qualitatively similar results to our focal analyses, so we present only those analyses with the negative species interaction coefficient for consistency with our hypothesis. We then explored whether heat tolerance explained the importance of negative species interactions using a generalized linear model with a quasi-binomial error structure. We used *F*-tests to assess the statistical significance of chamber temperature, because these tests are most appropriate for models in which dispersion is estimated by the method of moments (Crawley 2007).

To explore the influence of negative species interactions and temperature on forager abundance, we used the pitfall data and constructed a second series of generalized linear models with a Poisson error structure, in which the number of foragers (workers) was considered the response variable, and chamber temperature and a single non-focal species abundance were separately considered as predictor variables. We again used the AIC-based model selection approach to compute the overall importance of negative species interactions and examined its relationship with heat tolerance.

Results

At both the northern and southern sites, and for both the pitfalls and nest boxes, forager abundance and nest box occupancy were negatively related to the heat tolerance of individual species (Figs. 2 and 3). Heat tolerance was a significant predictor of the importance of negative species interactions on forager abundance (pitfall data) ($F=8.72$, $P=0.00735$, $df=1$), and there were no effects of site ($F=0.0263$, $P=0.873$, $df=1$) or an interaction between site and CT_{max} ($F=0.105$, $P=0.749$, $df=1$), indicating that this relationship was consistent between sites.

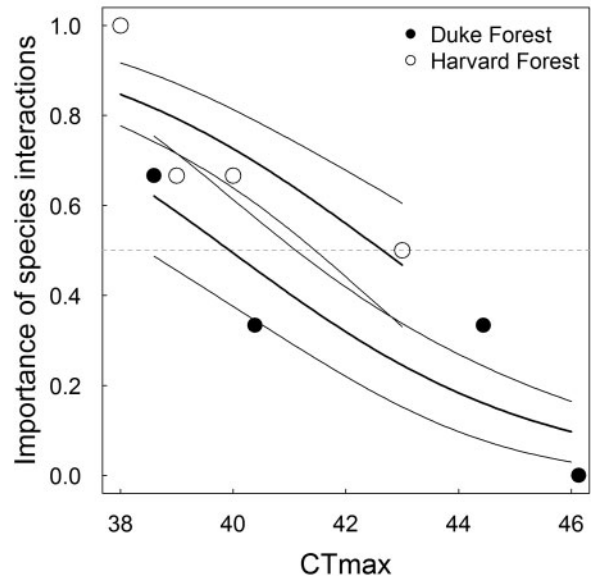


Fig. 2 The importance of negative species interactions in determining nest site occupancy as a function of heat tolerance. Importance is calculated as the mean proportion of models where species interactions were more important than temperature (by 2 AIC units) in determining nest site occupancy. Above the dashed line at 0.5, species interactions are more important; below the line, temperature is more important for nest site occupancy. Predicted values and their standard errors from a model with heat tolerance and site as explanatory variables are shown in solid lines.

Heat tolerance also predicted effects of negative species interactions on nest site occupancy (nest box data) ($F=9.19$, $P=0.0291$, $df=1$), and there was a significant effect of site ($F=8.29$, $P=0.0346$, $df=1$), but not of the interaction between site and CT_{max} ($F=0.0224$, $P=0.888$, $df=1$). Specifically, negative species interactions were overall more important at the high-latitude site than at the low-latitude site.

In each of the four response-type-by-site datasets, the total number of observations of each species during the course of the warming experiment was uncorrelated with CT_{max} , which suggests that sampling bias was not responsible for the relationships between CT_{max} and negative species interaction effects that were observed (Duke Forest pitfall: $r=0.113$, $P=0.665$, $df=15$; Duke Forest nest box: $r=0.382$, $P=0.618$, $df=2$; Harvard Forest pitfall: $r=-0.469$, $P=0.202$, $df=7$; Harvard Forest nest box: $r=-0.906$, $P=0.0939$, $df=2$).

Discussion

Although the direct effects of climate change on communities have been studied in some detail, the indirect effects of climate change, while being

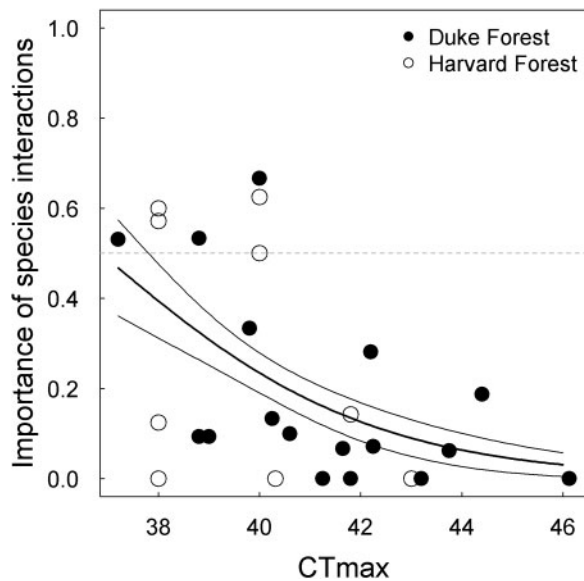


Fig. 3 The importance of negative species interactions in determining forager abundance as a function of heat tolerance. Importance is calculated as the mean proportion of models where species interactions were more important than temperature (by 2 AIC units) in determining forager abundance. Above the dashed line at 0.5, species interactions are more important; below the line, temperature is more important for nest site occupancy. Predicted values and their standard errors from a model with heat tolerance as an explanatory variable are shown in solid lines.

discussed as potentially important, are largely understudied (Buckley 2013; Urban et al. 2016). There are few tests of the importance of indirect effects of climate change via altered species interactions, and even fewer that examine whether these outcomes are predictable based on species traits (Moritz and Agudo 2013; Ockendon et al. 2014). In this study, experimental warming of forest ant communities at high and low latitude sites within the eastern USA revealed that the importance of negative species interactions in determining forager abundance and nest site occupancy was predictable from measures of heat tolerance: heat-intolerant species were more strongly driven by negative species interactions compared with more heat-tolerant species. Together, these results suggest a variable, but predictable, role for altered species interactions in shaping community responses to climate change.

Recent work in grassland plant communities has linked climatic niche differentiation between interacting species to the magnitude of species interaction effects, such that species with more climatically similar niches exhibited greater species interaction effects (Chu et al. 2016). However, the main finding of Chu and colleagues—that the direct effects of climate are much stronger than indirect effects of species

interactions—contrasts with a number of plant and animal studies showing a stronger role for species interactions (Suttle et al. 2007; Ockendon et al. 2014). In terms of whether the direct effects of temperature versus species interactions are more important in shaping ant community forager abundance and nest site occupancy, our results reveal mixed support, because we found cases where temperature was more important and cases where negative species interactions were more important (Figs. 2 and 3). Uniquely however, our study shows how this variation can be explained by heat tolerance of the focal species alone, with heat-intolerant species exhibiting higher values of the importance of negative species interaction effects.

Biogeographers have long been interested in this question of species interactions and whether they are predictable across latitude. Although historically the assumption has been that biotic interactions are more important (often quantified as the intensity of interactions or the degree of specialization between interaction species) at lower latitudes, recent work has revealed mixed support for this hypothesis (Schemske et al. 2009; Moles et al. 2011; Ollerton 2012). Our results partially challenge the species interaction-latitude hypothesis, because the nest box data revealed overall greater importance of negative species interactions at the higher latitude site compared with the lower latitude site (Fig. 2). However, we did not detect a site effect in models of negative species interactions using pitfall trap data. It is possible that negative species interactions are more difficult to detect with pitfall data than with nest box data, where competition for nest sites and resources near nest sites is based on interference and direct species interactions rather than use of shared resources by foragers; alternatively, the sample sizes were smaller for the nest box data, so perhaps the site effect is an artifact of limited sampling. Future tests of the species interaction-latitude hypothesis may be facilitated by the rapid accumulation of thermal tolerance datasets (Sunday et al. 2014; Gunderson and Stillman 2015) and species interaction data (Vázquez et al. 2007).

Although it is useful to identify traits that predict the magnitude of direct versus indirect effects of temperature change on communities, ultimately we are interested in the consequences of these changes, i.e., whether these changes result in population increase, decrease, or even local extirpations. Simulation models have shown that heat-tolerant species are able to outcompete and even eradicate less heat-tolerant species under changing climates (Urban et al. 2012). Our results support this finding:

forager abundance and nest occupancy were driven more by direct effects of temperature than by negative interactions with other species (Figs. 2 and 3) and our previous work in this system has shown substantial advantages to warming for the most heat-tolerant species with respect to colony size and growth, forager abundance, and ability to hold nest sites (Diamond et al. 2012, 2013, 2016; Stuble et al. 2013). Indeed, recent laboratory work on the temperature-dependence of colony growth components in forest ants, showed that heat-tolerant species appear to be limited primarily by access to heat for brood production and development requirements (Penick et al. 2017).

Our findings appear to be robust, because we detected a negative relationship between heat tolerance and the importance of negative species interactions using both ant forager abundance and nest occupancy data each at two distinct locations. Despite this, there are some limitations and caveats with our analysis. With forager abundance data from pitfall trapping and occupancy data from nest box observations, we still lack direct evidence of each competitive interaction (inferred by negative effects of non-focal species on focal species abundance and nest occupancy) in the experiment. This criticism is perhaps most strongly levied against the ant forager abundance data obtained with pitfall trapping, where interactions are potentially more diffuse compared with the nest box occupancy data. In contrast, interactions are more direct for the nest box data as single colonies of different species compete directly for occupancy of nest sites. Of course our approach somewhat buffers against this possibility because we are directly competing models of forager abundance or nest box occupancy based on temperature change against those with the abundance or presence of a non-focal species as a predictor. The results from another experimental manipulation of temperature (in this case, using shading treatments) and its impacts on ant communities are also illuminating here. Species were spatially segregated at bait stations at low temperatures but not at high temperatures, and species with weak thermal niche differentiation segregated more frequently at baits than species with greater differentiation, collectively suggesting that species-specific thermal performance can drive the competitive landscape (Wittman et al. 2010).

Further, the restriction of our analyses to ant species that were active during the growing season enabled us to identify an exception that proves the rule. The winter ant, *Prenolepis imparis*, is a unique species in forest ant communities, because it is active during the cooler months when few other ant species are foraging,

but relatively inactive during the warm months when most other species are active (Dunn et al. 2007; Ellison et al. 2012). In our analyses, the winter ant had a low heat tolerance (39.6 °C) but was not strongly affected by negative species interactions (its mean importance value for negative species interactions, or the fraction of models where non-focal species responses were a better predictor than temperature, was <0.1). Such a result is what we would expect for a species with a winter-active phenotype and one which is unlikely to interact with many other ant species.

Our results suggest when species interactions may be important to consider in models of responses to climate change: negative species interactions tend to be more important for heat-intolerant species, consistent with a model in which warming reduces available thermal niche space and increases competitive interactions for species with lower heat tolerances (Fig. 1). However, it is necessary to explore the extent to which these patterns generalize over different types of interactions (for example, competition versus predation, parasitism, or mutualism), taxa, and geographic location. In terms of ecological forecasting and management implications, the key question is whether we can safely ignore species interactions, and develop forecasts based on single-species models calibrated with climatic variables (Chu et al. 2016). The evidence so far is decidedly mixed. Here we suggest a potential trait-based approach to this question, using heat tolerance as a general guide for when negative species interactions are more likely to influence responses to global climate change.

Data Availability

All data are available on the Harvard Forest Data Archive (<http://harvardforest.fas.harvard.edu/harvard-forest-data-archive>), dataset hf-113.

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