

SYMPOSIUM

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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

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 ef-



Fig. 1

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 *A. a.*, *a.* spp., *B. a.*, *a.*, *C. m.*, *a.*, *a.*, and *T. m.*; at Harvard Forest, *A. a.*, *a.* spp.,

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

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

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, *P. ruginervis*, 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

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