Geographic differences in effects of experimental warming on ant species diversity and community composition

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Abstract. Ecological communities are being reshaped by climatic change. Losses and gains of species will alter community composition and diversity but these effects are likely to vary geographically and may be hard to predict from uncontrolled "natural experiments". In this study, we used open-top warming chambers to simulate a range of warming scenarios for ground-nesting ant communities at a northern (Harvard Forest, MA) and southern (Duke Forest, NC) study site in the eastern US. After 2.5 years of experimental warming, we found no significant effects of accumulated growing degree days or soil moisture on ant diversity or community composition at the northern site, but a decrease in asymptotic species richness and changes in community composition at the southern site. However, fewer than 10% of the species at either site responded significantly to the warming treatments. Our results contrast with those of a comparable natural experiment conducted along a nearby elevational gradient, in which species richness and composition responded strongly to changes in temperature and other correlated variables. Together, our findings provide some support for the prediction that warming will have a larger negative effect on ecological communities in warmer locales at lower latitudes and suggest that predicted responses to warming may differ between controlled field experiments and unmanipulated thermal gradients.

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INTRODUCTION

The responses of ecological communities to climatic change depend both on environmental conditions at specific geographic locations and on the composition of and interactions between

co-occurring species (Tylianakis et al. 2008, Gilman et al. 2010, Singer and Parmesan 2010, Pelini et al. 2012). Populations and species occupying different locations may vary in their tolerances for abiotic changes (Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009, Andrew et al. 2013, Kingsolver et al. 2013). Additionally, the indirect effects of climate change mediated by species interactions can strengthen or reverse the effects of abiotic change (Suttle et al. 2007, Rouifed et al. 2010, Pelini et al. 2011a). As a consequence, it is difficult to predict how climatic change will shape the composition and diversity of local communities at small spatial scales.

However, at coarser grains of observation, such as latitudinal and elevational gradients, climatic differences may lead to predictable shifts in composition and diversity. In the simplest scenario, the poleward expansion of species geographic ranges may lead to an increase in diversity at higher latitudes, even though some species may disappear locally because they cannot tolerate warmer conditions. Net gains in species richness may arise because warming is unlikely to push many species above their thermal limits (Addo-Bediako et al. 2000, Deutsch et al. 2008, Tewksbury et al. 2008, Kingsolver et al. 2013). Conversely, at lower latitudes, sites should be more likely to lose species with increases in temperature because some species will exceed their critical thermal limits (Addo-Bediako et al. 2000, Deutsch et al. 2008, Tewksbury et al. 2008, Kingsolver et al. 2013) or experience too few days and hours within their range of optimal foraging temperatures.

Experiments that compare the effects of warming on communities near high- and low latitudinal range boundaries can test predictions about geographic patterns of warming effects on ecological communities. All other things being equal, "natural experiments" along elevational and latitudinal climate gradients can also predict which species can and will persist in particular climates (Ibanez et al. 2013). Differences in the response of species to natural thermal gradients and to controlled warming experiments might reflect dispersal limitation, historical effects, confounded gradients in natural experiments (Gotelli and Ellison 2012), or small-scale artifacts or design constraints in controlled field experiments (Wolkovich et al. 2012).

In this study, we examined community-level responses of forest ants to ongoing experimental warming in open-top chambers at a northern (Harvard Forest, Massachusetts) and a southern (Duke Forest, North Carolina) site in the eastern USA. These two sites represent the northern and southern boundaries of eastern US forests: Harvard Forest lies at the northern end of the Eastern Temperate Forests (Mixed Wood Plains) and the southern edge of the Northern Forests (Atlantic Highlands), whereas Duke Forest, within the Eastern Temperate Forests, is at the boundary between the Southeastern USA Plains and the Mississippi Alluvial and Southeast Coastal Plains (CEC 1997). Previous work in this system has demonstrated strong geographic differences in the responses of individual species to experimental warming: at the warmer southern site, ant species with higher thermal tolerances had higher worker densities and greater foraging activity in warmer chambers than did ants species with lower thermal tolerances (Diamond et al. 2012a, Stuble et al. 2013). At the cooler northern site, however, worker density of all species, regardless of their thermal tolerances, was highest in the warmer chambers. Similar responses have been observed in the soil microbial community, with larger shifts in both structure and function observed at the southern site (Cregger et al. 2014).

Based on these previous findings, we predicted that community composition and diversity would respond differently to warming at the northern and southern sites. Specifically, because most northern species rarely experience temperatures near their upper thermal limits, their performance and abundance should not be depressed by warming (Diamond et al. 2012a). If other ant species from warmer microhabitats such as forest gaps are able to colonize the chambers, ant community composition would change and diversity would increase in the warmer chambers at Harvard Forest. In contrast, at Duke Forest we predicted that ant diversity would decrease and community composition would change because many resident species experience temperatures that exceed their thermal tolerances. Within sites, we expected closely related species to respond to warming in similar ways due to shared evolutionary histories (Dia-

mond et al. 2012b).

Because both experiments and large-scale geographic patterns of diversity and species composition are used to forecast future responses to climatic change (Parry and IPCC 2007), assessing congruence between responses to experimental warming and natural warming is important. We compared the patterns in diversity and composition of ants under experimental warming with those along an elevational gradient in the Great Smoky Mountains. The elevational gradient shares many species with and spans a gradient of temperature increase similar to that generated by the warming treatments (Sanders et al. 2007).

METHODS

Study system.—Ants are the numerically dominant macroinvertebrates in eastern forests (King et al. 2013), contribute to important ecosystem services such as seed dispersal and nutrient cycling, and respond predictably to a variety of environmental conditions (reviewed in Del Toro et al. 2012), making them an ideal system for the study of community-level effects of warming. Other studies have demonstrated that air temperature can potentially influence ant community structure (Arnan et al. 2007, Wittman et al. 2010, Lessard et al. 2011), diversity (Kaspari et al. 2000, Sanders et al. 2007, Dunn et al. 2009, Pelini et al. 2011a), colony survival (Pelini et al. 2012), worker density (Pelini et al. 2011a, Diamond et al. 2012a), foraging behavior (Ruano et al. 2000, Pelini et al. 2011a, Stuble et al. 2013), and competitive interactions (Cerda et al. 1997, 1998).

Open-top warming chambers.—We used an open-top warming experiment at Harvard Forest, Massachusetts and Duke Forest, North Carolina, USA (design details in Pelini et al. 2011b). The warming array at each site consists of 12 5-m diameter (~22 m^3) open-top chambers in a regression design (Cottingham et al. 2005) that are held at ambient air temperatures (three control chambers) or are heated to one of the 0.5°C intervals between 1.5° and 5.5°C, inclusive, above ambient air temperature (one experimental chamber for each temperature set-point). The bottoms of the chamber walls are elevated 2–3 cm above the ground so that movement of ants and other arthropods into and out of the chambers is not restricted. These chambers have been operating continuously since January 2010. Four permanent pitfall traps (5 cm diameter) are located in each chamber. Each month, pitfall traps were opened and filled with 60–80 mL of 95% EtOH or glycol and left uncovered for 48 hours during rain-free conditions. Ants were then extracted and identified to species using regional keys (e.g., Ellison et al. 2012); identifications were confirmed at the Harvard University Museum of Comparative Zoology (Cambridge, Massachusetts). In this study, we compared ant species occurrences in the different warming scenarios using monthly pitfall data collected from January 2010 through July 2012.

Environmental variables.—Each chamber is fitted with environmental sensors that are linked to a data logger; environmental data are collected continuously at 1-minute intervals (Pelini et al. 2011b). We calculated the mean, minimum and maximum air temperature, and soil temperature at 2 and 6 cm, mean soil moisture, and growing degree days ($T_{base} = 15$°C; "GDD") for each chamber during January 2010–July 2012. Growing degree-days were summed across all time periods, but all the other metrics were averaged over sampling periods.

Measures of diversity.—Most biodiversity measurements are sensitive to sampling effort and to the abundance per sampling unit (Gotelli and Chao 2013). Measuring biodiversity in climate-change experiments is especially challenging because warming treatments will alter the activity and movement of many poikilotherms, even without changing population size or community structure (Moise and Henry 2010). Thus, simultaneous decreases in abundances but increases in detection probability with warming could mask important treatment effects. Moreover, counting the number of ant workers in a trap is usually not valid statistically because the workers caught in a single trap often originated from the same colony (Gotelli et al. 2011). To ameliorate these effects, we used only the incidence of each species (presence or absence) in a chamber during a monthly sampling period (Longino et al. 2002, Kaspari et al. 2003, Gotelli et al. 2011). In each chamber at both sites, the sampling effort was equivalent: every chamber

Table 1. Range of values across experimental chambers for selected microclimate variables at the two study sites.

Environmental variable	Southern site	Northern site
Latitude (decimal degrees)	35.9	42.5
Elevation (m above sea level)	130	300
Mean air temperature (°C)	15.6–20.6	12.1–17.1
Minimum air temperature (°C)	3.3–7.6	0.90–5.2
Maximum air temperature (°C)	29.8–34.4	26.4–35.7
Soil temperature at 2 cm depth (°C)	14.9–16.5	10.6–12.8
Soil moisture (VWC)	0.098–0.26	0.10–0.19
Growing degree days (GDD)	17×10^3–30×10^3	5.4×10^3–14×10^3

Notes: Temperature and soil moisture values are based on conditions during 48-hour pitfall sampling periods across the 30-month study period. In contrast, growing degree days are accumulated across the 30-month study period ($T_{base} = 15$°C). The "Southern site" is Duke Forest (North Carolina, USA); the "Northern site" is Harvard Forest (Massachusetts, USA).

was sampled each month with pitfall traps open for 48 hours.

For each chamber, the resulting data were organized as an incidence matrix in which each row is a species, each column is a sampling period, and the entries indicated incidence (0 or 1) of each species at each sampling period. In addition to calculating the number of species per sampling unit ("species density" sensu Gotelli and Colwell 2001), we also calculated indices that are unbiased by sample size: PIE—the probability of an interspecific encounter, or the chance that two randomly drawn incidences represent two different species (Hurlbert 1971)—the first two Hill numbers (Hill 1973), and the asymptotic species diversity that would be found with maximum sampling effort (the Chao2 index; Chao 1987). Hill numbers are modified measures of species richness that take into account relative abundance. The first Hill number is equivalent to the exponent of the Shannon index, and it weights all species equally. The second Hill number is the inverse of the Simpson index, and is related to PIE. This index places more weight on common species.

Data analyses.—For each site, we examined correlations among environmental variables in the chambers (see Table 1 for ranges of values). All measures of air and soil temperature were strongly correlated with each other ($R^2 > 0.80$ for all comparisons) and with GDD, but were not correlated with soil moisture ($R^2 < 0.35$ for all comparisons). Given these findings, we used GDD and soil moisture as independent predictor variables in all subsequent analyses.

To examine the effects of environmental variables on diversity, we used linear regressions to determine if species density, Chao2, PIE, Hill.1, or Hill.2 were significantly associated with Site, GDD, soil moisture. We also included Site × GDD and Site ×soil moisture interaction terms in these models to determine if the diversity-climate relationships differed between sites. To yield more precise parameter estimates, we used a weighted linear regression model for Chao2, with the weights being proportional to the inverse of the estimated variance for Chao2. Because some extrapolations of species richness can have a very large estimated variance, this procedure down-weights those highly uncertain estimates in the regression models.

To determine if species composition varied with GDD at either site, we modified the bootstrap method presented in Gotelli et al. (2010) and used it to detect thermal trends. This method fits a trend line for exponential growth to each species, and then calculates the variance in these trend lines among species. A large variance among species indicates that some species are strongly increasing while others are decreasing. The variance in the trend lines is compared statistically to the expected variance based on random sampling of the pooled community. For this analysis, we analyzed the thermal trend lines for each species by fitting linear regression models of incidence counts of species (both untransformed and square root transformed) versus GDD at each study site. This approach controls for differences in overall incidence among chambers.

As described in Gotelli et al. (2010), we analyzed the model with and without detection errors. In the first model, we assumed there were no errors in detection and that all species present in each chamber were detected in pitfall catches. This analysis is based on the observed incidence

Table 2. ANOVA table for diversity metrics modeled as a function of site, growing degree days (GDD), soil moisture, and site-GDD and site-soil moisture interactions.

Diversity variable	Climate variable	df	F
Species density	GDD	1, 18	350***
	Soil moisture	1, 18	37.6***
	Site	1, 18	66.5***
	Site × GDD	1, 18	0.243
	Site × Soil moisture	1, 18	0.654
PIE	GDD	1, 18	23.7***
	Soil moisture	1, 18	0.266
	Site	1, 18	7.99*
	Site × GDD	1, 18	0.059
	Site × Soil moisture	1, 18	1.87
Hill.1	GDD	1, 18	186***
	Soil moisture	1, 18	13.4**
	Site	1, 18	34.5***
	Site × GDD	1, 18	0.483
	Site × Soil moisture	1, 18	1.085
Hill.2	GDD	1, 18	161***
	Soil moisture	1, 18	8.29**
	Site	1, 18	31.7***
	Site × GDD	1, 18	0.000
	Site × Soil moisture	1, 18	1.05
Chao2	GDD	1, 18	116***
	Soil moisture	1, 18	0.589
	Site	1, 18	43.2***
	Site × GDD	1, 18	10.3**
	Site × Soil moisture	1, 18	0.334

Notes: We used a weighted linear regression model for Chao2, with the weights being proportional to the inverse of the estimated variance for Chao2. Because some extrapolations of species richness can have a very large estimated variance, this procedure down weights those highly uncertain estimates in the regression models. Sites are as in Table 1.
$*P < 0.05; ** P < 0.01; *** P < 0.001.$

matrix. In the second variation, we assumed there were detection errors and that some rare species were present that were not detected in any of the pitfall traps. For this analysis, we estimated the number of missing species with the Chao2 estimator. We added additional rows to represent these additional rare species in the analysis, and assigned relative abundances to be less than one half of the relative abundance of the rarest species in each community (see Gotelli et al. 2010 for details).

To determine if closely related species responded similarly to the temperature manipulation, we used the phylosig function from the R library *phytools* (Revell 2012) to estimate Blomberg's K (Blomberg et al. 2003) for the coefficients from regression models of species-incidence counts versus GDD. Phylogenetic sampling error was incorporated using the methods described in Ives et al. (2007). The phylogeny of Moreau and Bell

(2013) was used in analyses for both study sites; but because this phylogeny is resolved only to genus, we treated unknown species relationships as terminal polytomies.

Finally, we used linear regression to compare the relationships between ant species richness and temperature in our two experimental sites to those that occur along an observational gradient in the Smoky Mountains that span a comparable temperature range (~5°C) along an elevational gradient (Sanders et al. 2007).

Data availability.—All raw data are available on the Harvard Forest data archive (Ellison et al. 2009).

RESULTS

With the exception of PIE, diversity increased with GDD and soil moisture and was higher at the southern study site (Table 2). PIE increased significantly with GDD and also was higher at the southern site. The relationship between diversity and climate between sites (i.e., site × GDD) was statistically significant for Choa2, which increased significantly with GDD at the southern site but was not significantly associated with GDD at the northern site (Table 2). At the southern site, asymptotic species richness (Chao2) decreased significantly with warming at a loss rate of one species per 2,400 GDD (~1°C) (Fig. 1). Species density (the number of species per unit area), PIE, and other diversity indices did not respond significantly to warming or to changes in soil moisture at either study site (Table 2). Species composition at the southern site differed more with temperature than expected by chance (Fig. 2A), although the significance of this effect depended on the data transformation and the inclusion of undetected species in the model (untransformed: $P = 0.020$ and 0.020; square root-transformed: $P = 0.143$ and 0.193 for undetected species included or excluded, respectively).

In contrast, at the northern site, there were no significant effects of temperature on asymptotic species richness, species density, PIE (Table 2, Fig. 1B), or species composition (Fig. 2B). Fewer than 10% of the species at either site responded significantly to warming, and the number of increasing and decreasing species were similar at both sites (Fig. 3).

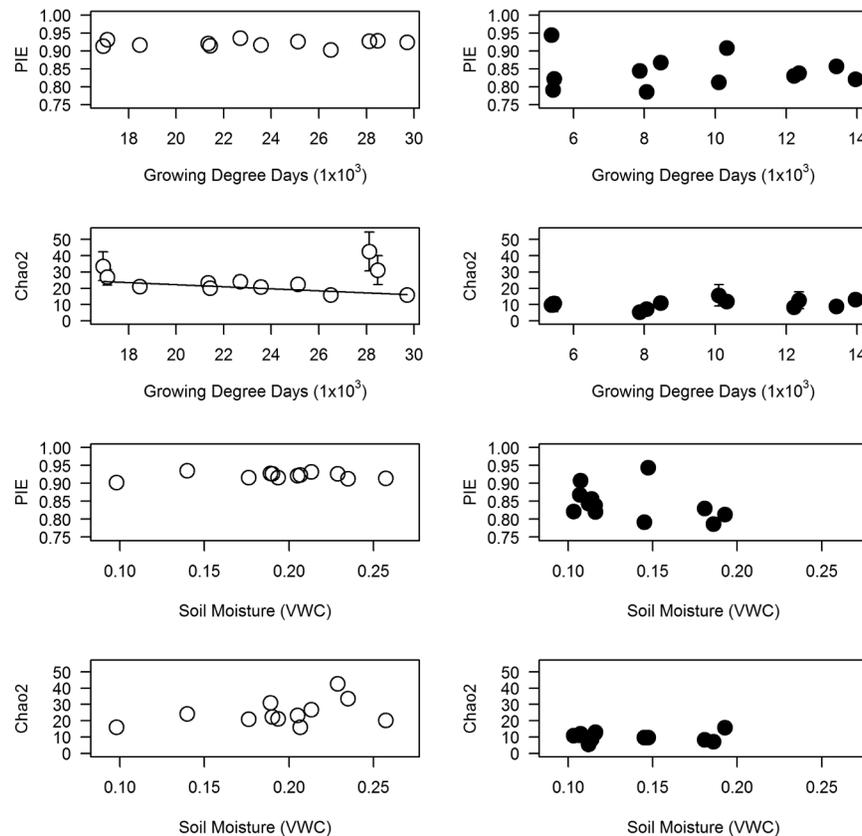With increasing GDD at the southern site,

Fig. 1. Regression plots for Chao2 and PIE (mean ± SE) as a function of the number of growing degree days (GDD) and soil moisture at the southern (open circles) and northern (filled circles) study sites. The "Southern Site" is Duke Forest (North Carolina, USA); the "Northern Site" is Harvard Forest (Massachusetts, USA). We found only one statistically significant relationship ($P < 0.05$): Chao2 estimates of diversity decreased significantly with GDD at the southern site. We used a weighted linear regression model for Chao2, with the weights being proportional to the inverse of the estimated variance for Chao2. Because some extrapolations of species richness can have a very large estimated variance, this procedure down-weights those highly uncertain estimates in the regression models. The line of best fit for Chao2 is based on this weighted linear regression model. Growing degree days were summed across all time periods.

Aphaenogaster rudis decreased in incidence, whereas *Crematogaster lineolata* and *Crematogaster vermiculata* increased in incidence (see Fig. 3A for linear regression coefficients and significance levels). With increasing GDD at the northern site, *Camponotus herculeanus* decreased significantly in incidence, whereas *Myrmica pinetorum* marginally increased in incidence with increasing temperature (Fig. 3B).

Closely related species did not experience statistically similar incidence responses to warming. At the southern site, the statistical dependence among species' incidence owing to their phylogenetic history ('phylogentic signal') was moderate (Bloomberg's $K = 0.448$). Phylogenetic signal in incidence at the southern site also was less than the expectation from a model of Brownian trait evolution ($K = 1$), and not significantly different from that predicted by a simple tip-shuffling randomization ($P = 0.618$). At the northern site, phylogenetic signal was higher ($K = 0.904$; $P = 0.050$).

We recorded a total of 72 species in the Great Smoky Mountains dataset and in the chambers at the two study sites. The Smoky Mountain dataset shared 18% and 10% of this species list with the
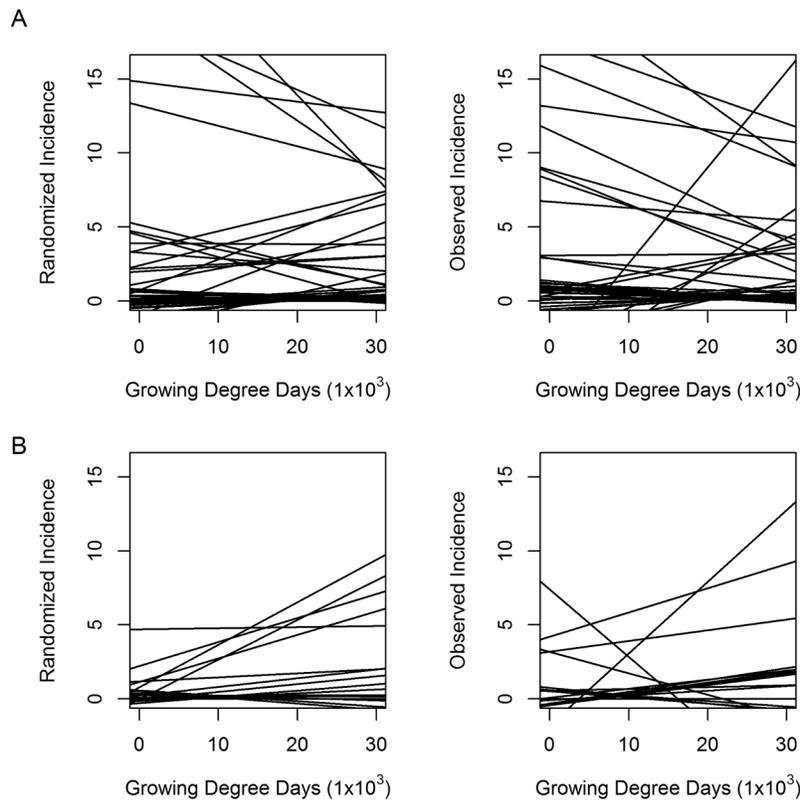
A

B

Fig. 2. Thermal trends in community composition at (A) the southern site and (B) the northern site. Sites are as in Fig. 1. For each site, we used bootstrapping and hierarchical modeling (modified from Gotelli et al. 2010) to estimate the slope of incidence as a function of GDD (pooled across the entire study period) for each species. Here we show the linear trends for all species plotted against GDD for both the observed and one randomized community.

southern and northern sites, respectively. Approximately 7% of the species were shared by all three sites; 30% were found only at the southern site, 19% only in the Great Smoky Mountains, and 11% only at the northern study site. Species density significantly increased with temperature in the Great Smoky Mountains ($F_{1,27} = 40$; $P < 0.001$; Fig. 4).

DISCUSSION

We found that community composition and diversity of northeastern US forest ants responded differently to increasing temperatures in experimental manipulations at northern (Harvard Forest, MA) and southern (Duke Forest, NC) sites and across a nearby natural temperature gradient (Smoky Mountains National Park, TN). Our results show weak support for the prediction that warming will have a larger negative effect on ecological communities in warmer locales at lower latitudes (Deutsch et al. 2008, Tewksbury et al. 2008, Kingsolver et al. 2013). Within the experimental sites, individual species responded variably to warming (Figs. 2 and 3), potentially complicating our ability to make precise predictions regarding community-level responses to climate change. These idiosyncratic responses may be attributed to variation in the abiotic tolerances of different species occupying the same locale and of geographically separated populations within species (Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009, Andrew et al. 2013, Kingsolver et al. 2013).

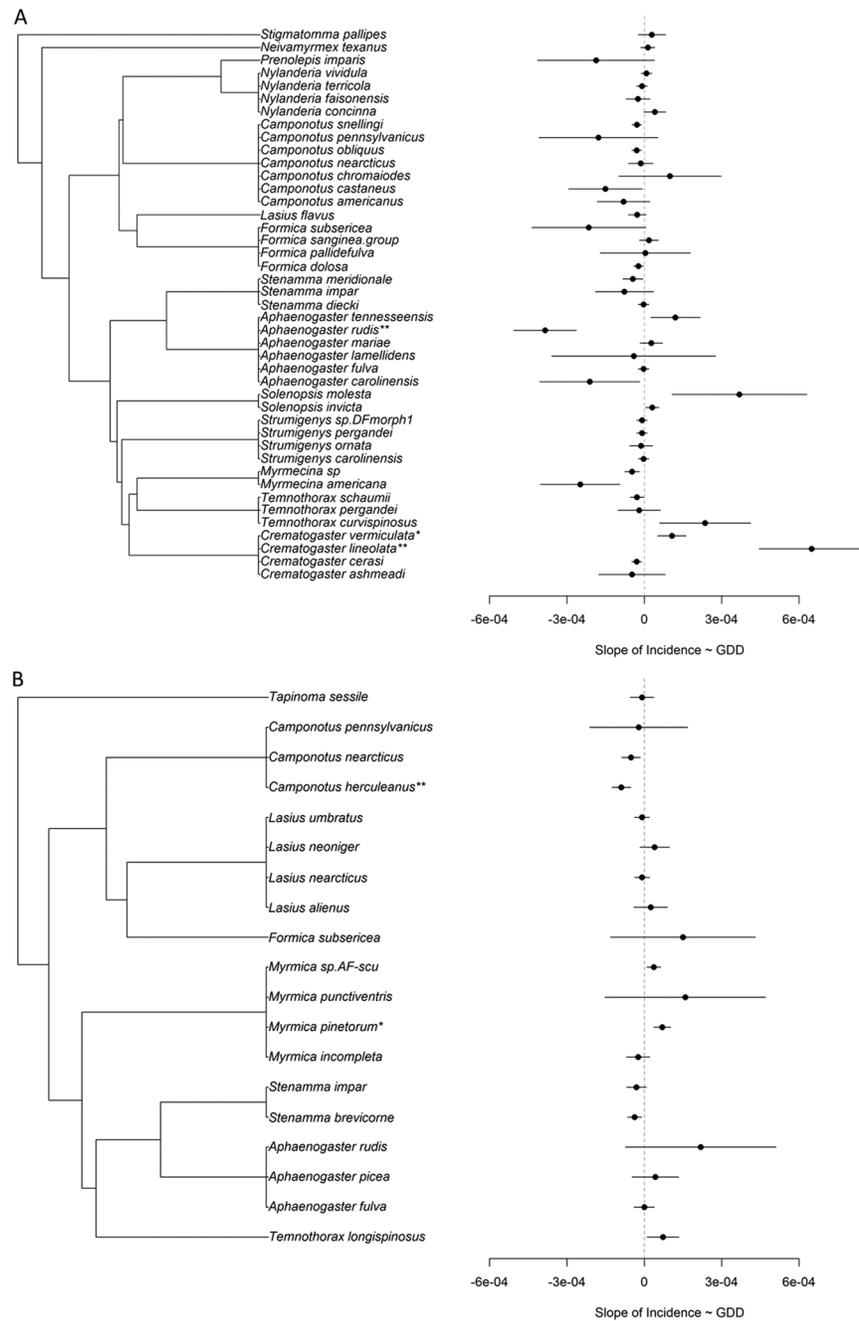Previous work in this study system suggests that the variable responses of these ant species

Fig. 3. Ant species responses to warming at (A) the southern site and (B) the northern site. Sites are as in Fig. 1. The slope of incidence as a function of growing degree days (GDD) is presented in context of ant phylogenetic history (Moreau and Bell 2013). The magnitudes and directions of the slopes of incidence as a function of GDD slopes indicated by distance from the zero line and positive/negative values, respectively); significance is indicated by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The slopes have been scaled, but not centered, such that shaded circles always correspond with positive slopes. Data for *Protomagnathus americanus* are not included in the figure because this species is not represented in Moreau's phylogeny; the results for this species are: slope = 2.3E–05, SE = 6.2E–05; $P = 0.72$.
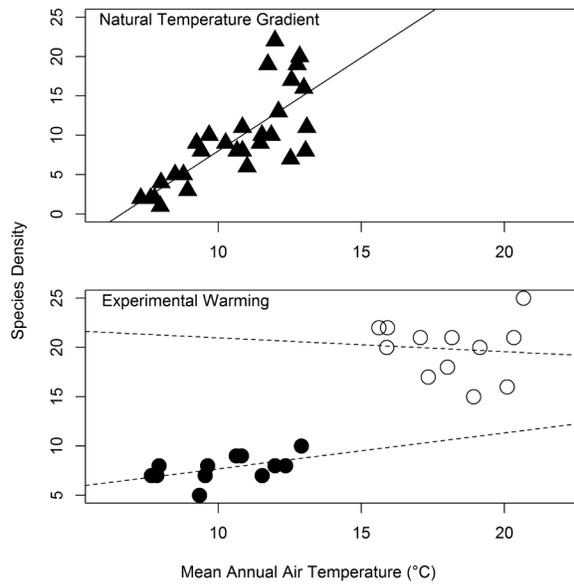
Fig. 4. Ant species richness as a function of mean air temperature at sites in the Smoky Mountains (triangles; upper panel) and southern (filled circles) and northern (open circles) experimental chambers (lower panel). Sites are as in Fig. 1. Solid lines represent statistically significant relationships ($P < 0.05$); dashed are non-significant.

may be predictable based on the thermal tolerance (CT_{max}) of these species (Diamond et al. 2012a, Stuble et al. 2013). Specifically, the relationships between experimental warming and ant worker densities and foraging were significantly associated with CT_{max}, but only for ants at the southern study site. Applying the same approach to this dataset of species incidence, we found that CT_{max} was not significantly associated with the incidence–GDD slope (see Figs. 2 and 3) ($F_{1,18} = .2.8$, $P = 0.11$). Although ants with higher CT_{max} may be more active in higher temperatures (Diamond et al. 2012a, Stuble et al. 2013), other processes such as thermoregulation (Sunday et al. 2014) or changes in nest architecture (Jones and Oldroyd 2007) may allow ant species to persist in the short run in environments that exceed their CT_{max}. In the long run, these acclimations may lead to a reduction in colony size and eventual extirpation (Sinervo 2010).

At our southern experimental field site, the incidence of several species in the genus *Crema-togaster* increased with warming. In previous studies, we found that worker density of *C. lineolata*, a species with one of the highest CT_{max} values of those collected in the warming chambers, increased 76% (Diamond et al. 2012a) and foraging increased 40% per degree of experimental warming (Stuble et al. 2013) at Duke Forest. Using a comparison of historical and current data, we also found that the abundance of *C. lineolata* doubled over a 35-year period with 2.7°C warming at a site in South Carolina, 450 km south of Duke Forest (Resasco et al. 2014). *Crematogaster lineolata* was not collected in chambers at the northern site, but it has been collected from open habitats nearby (Pelini et al. 2011b) and could, therefore, potentially affect higher-latitude ant communities if it were to invade warmer forested areas.

The experimental effects of increasing temperatures on ant diversity also did not match correlative patterns of increasing species richness with temperature along a natural thermal gradient (Fig. 4) (also see Menke et al. 2014). Differences in species composition along environmental gradients may be confounded by differences in habitat quality and other uncontrolled variables. Warming experiments may better capture the immediate effects of temperature change on activity and population dynamics of species occupying contemporary communities, but they can be sensitive to time lags and the spatial scale of the experiment (Sundqvist et al. 2013), depending on the relative rates of species losses due to local extinction and gains to due dispersal and evolution. Comparisons of experimental and natural gradients are needed because natural gradients likely reflect long-term effects of temperature change on species interactions, dispersal, and evolutionary change in communities while experiments can isolate the effects of temperature from other variables.

Our study suggests that ant community responses to warming in lower latitudes are more likely to experience decreases in diversity and changes in composition than those at higher latitudes (Colwell et al. 2008). Future research efforts should assess the consequences of abundance increases of thermophilic species, which could exert strong indirect effects of warming through species interactions.

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