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Shannon L. Pelini
Harvard Forest

Mark Boudreau
NC State University

Neil McCoy
NC State University

Aaron M. Ellison
Harvard Forest

Nicholas J. Gotelli
University of Vermont

See next page for additional authors

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Authors

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Shannon L. Pelini,[1],† Mark Boudreau,[2],[5] Neil McCoy,[2] Aaron M. Ellison,[1] Nicholas J. Gotelli,[3] Nathan J. Sanders,[4] and Robert R. Dunn[2]

[1]Harvard Forest, Harvard University, Petersham, Massachusetts 01366 USA
[2]Department of Biology, North Carolina State University, Raleigh, North Carolina 27695 USA
[3]Department of Biology, University of Vermont, Burlington, Vermont 05405 USA
[4]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996 and Center for Macroecology,
Evolution and Climate, Department of Biology, University of Copenhagen, Denmark

Abstract. Climatic change is expected to have differential effects on ecological communities in different geographic areas. However, few studies have experimentally demonstrated the effects of warming on communities simultaneously at different locales. We manipulated air temperature with in situ passive warming and cooling chambers and quantified effects of temperature on ant abundance, diversity, and foraging activities (predation, scavenging, seed dispersal, nectivory, granivory) in two deciduous forests at 35° and 43° N latitude in the eastern U.S. In the southern site, the most abundant species, *Crematogaster lineolata*, increased while species evenness, most ant foraging activities, and abundance of several other ant species declined with increasing temperature. In the northern site, species evenness was highest at intermediate temperatures, but no other metrics of diversity or foraging activity changed with temperature. Regardless of temperature, ant abundance and foraging activities at the northern site were several orders of magnitude lower than those in the southern site.

Key words: climate change; community composition; foraging; Formicidae; warming experiment.

[5] Present address: Department of Biological and Agricultural Engineering, University of Georgia, Griffin, Georgia 30223 USA.
† E-mail: spelini@fas.harvard.edu

INTRODUCTION

The ecological impacts of projected climatic change are likely to have a strong geographic signal. For species that have geographic ranges constrained by temperature, warming may facilitate population increases and range expansions at high latitudes while simultaneously decreasing population sizes and contracting ranges at low latitudes (Parmesan and Yohe 2003). Other studies suggest that the consequences of warming will be more severe at lower latitudes, where organisms may be more sensitive to fluctuating temperatures (Deutsch et al. 2008, Tewksbury et al. 2008, Dillon et al. 2010). Differential responses of populations to warming at high versus low latitudes also can be accompanied by community-level changes such as increases in species diversity at high latitudes and decreases in species diversity at low latitudes (Menendez et al. 2006, Wilson et al. 2007).

Other factors may obscure, or even ameliorate, the geographic signal of climate change on ecological communities. For example, temperature increases are expected to be more pronounced at high latitudes (Solomon et al. 2007).

Local adaptation to historical climates, and corresponding maladaptation to new climates, also may be more pronounced at high latitudes (Pelini et al. 2009). Although individual organisms at low latitudes may be more sensitive to climatic change than those at high latitudes, ecological communities at low latitudes could be more resilient to environmental change because they are generally more diverse (Wittebolle et al. 2009). Yet, because most experimental studies of the effects of warming have been conducted at single sites (but see Doak and Morris 2010), it is unclear whether warming will have differential effects on the structure and function of similar communities and ecosystems across latitude and diversity gradients. Here, we report the results of a temperature manipulation experiment on ant community composition and foraging activity in deciduous forests that was conducted simultaneously at two sites, separated by 8 degrees of latitude (~1000 km), in the eastern United States.

We focused on ants because they are numerically dominant in many terrestrial ecosystems, and their foraging activities, including seed dispersal, nectivory, granivory, predation, and scavenging, cut across many trophic levels and can affect ecosystem processes such as nutrient cycling (cf. Hölldobler and Wilson 1990, Folgarait 1998). We experimentally manipulated a key component of climatic change—atmospheric warming—because temperature is correlated with patterns of ant diversity and abundance (Kaspari et al. 2003, Sanders et al. 2007, Dunn et al. 2009), seasonal patterns of activity (Dunn et al. 2007), foraging behavior (Ruano et al. 2000), and the outcomes of interactions between species (Cerdá et al. 1997, Holway et al. 2002). We hypothesized that changes in air temperature would have different effects on ant abundance, species richness, species evenness, and foraging activities at the two sites. We expected that ant abundance, diversity and foraging activities would increase in the northern site, where cooler temperatures may be limiting, while ant abundance, diversity and foraging may decrease at the southern site, where many ant species are already exposed to temperatures near their thermal limits.

Methods

Study sites

The warming experiment was conducted simultaneously at two sites, Harvard Forest ("northern site") and Duke Forest ("southern site"). Harvard Forest is in central Massachusetts in the northern hardwood hemlock-white pine transition zone (42°31′48″ N, 72°11′24″ W, 300 m elevation above sea level (a.s.l.)). The mean annual temperature at Harvard Forest is 7.1°C and the mean annual precipitation is 1066 mm. Our experimental site at Harvard Forest is in an ~70-yr-old oak-maple stand in the Prospect Hill Tract. Duke Forest is near Hillsborough, North Carolina (35°52′0″ N, 79°59′45″ W, 130 m a.s.l.), in the Piedmont region. The mean annual temperature at Duke Forest is 15.5°C and mean annual precipitation is 1140 mm. Our experimental site at Duke Forest is in an ~80-yr-old oak-hickory stand within the Eno River Unit.

Harvard Forest and Duke Forest share more than 30 ant species but they differ substantially in ant diversity and abundance (Pelini et al. 2011). An additional 65 species have been recorded at Duke Forest but not at Harvard Forest, and an additional 12 species have been recorded at Harvard Forest but not at Duke Forest. Ants are active at Harvard Forest April through November while those at Duke Forest are active year-round, but peak abundance occurs May–August at both sites. In our experimental chambers during the six months of this experiment, we captured 16,000 individuals from 28 species at Duke Forest and fewer than 1000 individuals from 9 species at Harvard Forest. Only one species, *Aphaenogaster rudis*, occurred in the experimental chambers at both sites.

Minichamber design and deployment

We altered air temperatures in the forest understory near the forest floor by using passively heated and cooled minichambers (Lessard et al. 2010, Wittman et al. 2010). Each minichamber was a table-shaped frame of 1.3-cm-diameter PVC pipe that supported a 1 × 1 m open-top frame 57 cm above the ground. Previous work on ant communities has documented ant responses to both abiotic and biotic changes caused by these treatments in similar sized plots (e.g., Kaspari et al. 2003, Sanders et al. 2007, McGlynn

et al. 2009). A common ant at both sites, *Aphaenogaster rudis*, has foraging and nest emigration distances shorter than 1 m (Smallwood 1982). To reduce temperatures, we covered the top frame of 10 of the minichambers at each site with a 1 × 1 m piece of shade cloth mesh that reduced solar gain by 80% but allowed for rain penetration to the soil surface. To raise temperatures in 10 of the minichambers at each site, we attached clear polyethylene sheeting to the top and along each side down to a height of 9 cm above the soil. We punched 25 6-mm-diameter holes in a uniform pattern in the top polyethylene to allow for rain penetration. We also established 10 control minichambers, which were PVC frames only. We secured the legs of the minichambers to the ground with iron rods.

Under the forest canopy at both sites, we arranged the 30 minichambers in a completely randomized design, with neighboring minichambers being separated by at least five meters. We deployed the minichambers in April 2009, when many ant species actively move their nests (Smallwood 1982). We left the minichambers in place until the experiment was ended in September 2009.

Temperature

We recorded air and soil temperatures in all of the northern minichambers with thermistors connected to a Campbell Scientific data logger (CR100, Logan, Utah). At the southern site, we measured air temperature in seven randomly-chosen minichambers of each treatment (i.e., 21 out of the 30 minichambers) using iButton® electronic temperature sensors (Dallas Semiconductors, Dallas, Texas). We shielded all air temperature sensors from direct sun and rain and placed them 5 cm above the litter layer beneath the minichambers.

Though the minichamber treatments were implemented as one-factor ANOVA design with three treatment levels (cooling, warming, control), there was substantial variation in temperature within treatment groups due to microhabitat and other variables not manipulated in this study. Thus, we treated the temperature manipulation as a continuous variable and used regression to determine the effects of variation in temperature on ant assemblage composition and foraging activities (Inouye

2001, Cottingham et al. 2005). We note that both regression and ANOVA are linear models of identical mathematical form, and unlike ANOVA, regression analysis can identify potential nonlinearities in associations between temperature and ant response variables (Cottingham et al. 2005, Meyers et al. 2009).

Though variation in soil temperature is also an important determinant of ant community structure and foraging activities, we used air temperature data in analyses of temperature effects on ant composition and activity because soil temperature was not measured at the southern site. Soil temperatures did track air temperatures similarly in the three minichamber treatments (i.e., the differences between average soil and air temperatures were the same in the three treatments) at Harvard Forest (ANOVA: $F_{2,37} = 1.6$, P = 0.21; Fig. 1). We are confident that the associations we report between air temperature and ant community structure and foraging activities reflect real responses to temperature change. Finally, we also calculated the average daily range of temperatures by subtracting the daily minimum from the maximum for each minichamber and used this variable to test whether or not diurnal variation in temperature affected the ant communities that we studied.

Ant community composition

In September 2009, we terminated the experiment and collected all of the leaf litter within each minichamber to sample ants. We extracted, identified and counted ants from all organic matter and loose surface soil in the 1 m² area using Winkler extractors (Fisher 1998). We used general linear models with Poisson error distributions to examine relationships between total ant abundance and species richness with average temperature and diurnal variation in temperature at both sites. We estimated species evenness using Hurlbert's PIE (probability of an interspecific encounter; Hurlbert 1971) for each minichamber. This diversity index is equivalent to the slope of an individual-based rarefaction curve measured at its base (Olsweski 2004). We used general linear models to examine the relationship between PIE and temperature in the southern site, but because of strong departures from normality in data from the northern site, we examined these latter data using locally weighted
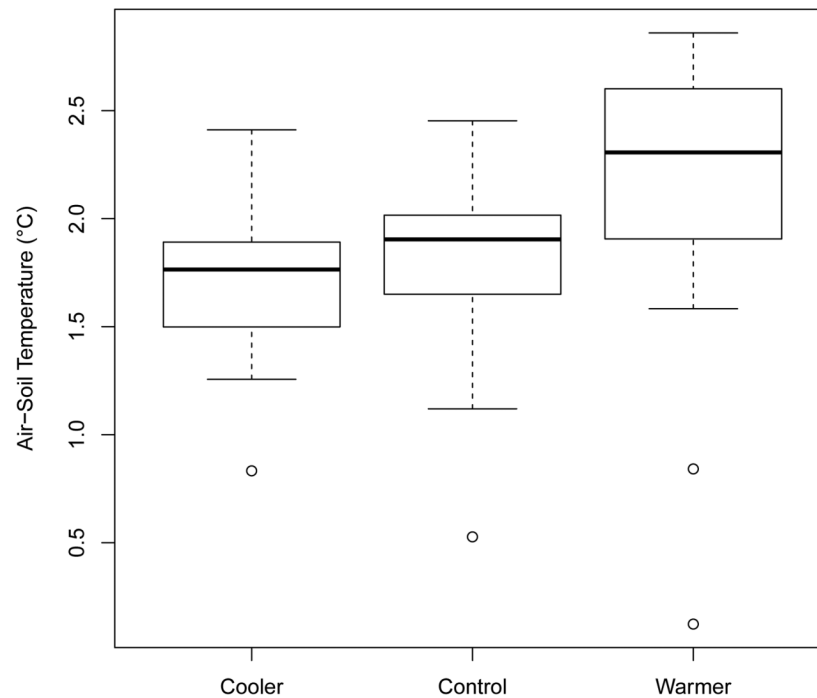
Fig. 1. Average difference between air and soil temperature June–August in the northern minichambers. "Cooler" minichambers represent PVC frames covered with shade cloth, "Control" minichambers are PVC frames only, and "Warmer" minichambers have PVC frames covered with plastic.

scatterplot smoothing.

Foraging activities

We recorded the rate at which ants removed different kinds of baits to assess effects of temperature on foraging activities. We used Demerara sugar grains (Signature Brands, Ocala, Florida) to estimate nectivory rates, live adult termites (*Reticulatermes flavipes*) to estimate predation rates (Wilson 1971), dead adults of *R. flavipes* or *Tenebrio molitor* (mealworms) to estimate scavenging rates (Jeanne 1979), and milled oat grain (*Avena sativa*) to estimate granivory rates (Valone and Kaspari 2005). We also measured rates of removal of seeds of wild ginger (*Asarum canadense*), a native forest understory species that occurs at both sites and that has seeds with eliasomes that are commonly dispersed by ants in the eastern U.S. (Hölldobler and Wilson 1990).

We conducted the bait removal experiments at both sites in August through early September 2009. On each census day, we used only one bait type. In each minichamber, we placed one 55-cm-diameter plastic petri dish with ten units of bait and recorded the number of bait units remaining at 30-minute intervals for two hours. We quantified removal of bait as the area under the curve of the number of baits removed versus time. This measure of activity integrates time to discovery, number of foragers, and rate of removal. To adjust for outliers, we used robust regression to examine the relationship between foraging activities and temperature at both sites.

All statistical analyses were performed in R (version 2.9.0, R Development Core Team 2007) or EcoSim (Version 7.0, Gotelli and Entsminger 2011).

RESULTS

Temperature

Average temperatures during the experiment at the southern and northern sites were 22.8 ± 0.3°C and 17.5 ± 0.4°C across treatments, respectively. Warming and cooling minichamber treatments increased and decreased average temperatures ~0.3°C relative to controls at both
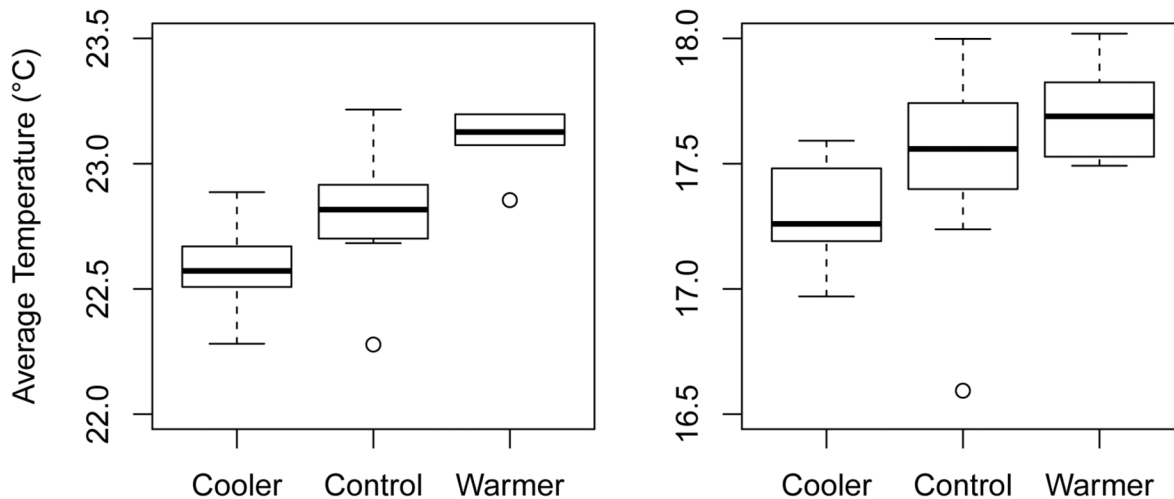
Fig. 2. Average temperatures June–August in the southern (left) and northern (right) minichambers. "Cooler" minichambers represent PVC frames covered with shade cloth, "Control" minichambers are PVC frames only, and "Warmer" minichambers have PVC frames covered with plastic. Temperatures were recorded in only 21 out of the 30 minichambers at the southern site.

sites (Fig. 2). In addition, diurnal variation in air temperature (i.e., difference between daily minimums and maximums) did not differ across minichamber treatments (southern site ANOVA: $F_{2,17} = 1.7$, $P = 0.22$; northern site ANOVA: $F_{2,27} = 2.9$, $P = 0.07$).

Ant community composition

We collected a total of 16,421 individuals and 28 ant species at the southern site and 780 individuals and 9 ant species at the northern site. *Crematogaster lineolata* was the most abundant ant species in the southern site, and *Aphaenogaster rudis* was the most abundant ant species in the northern site. Overall, ant abundance (i.e., number of individuals across all ant species), species richness, and evenness (PIE) were significantly higher at the southern site than at the northern site (abundance: $F_{1,43} = 62$, $P < 0.001$; richness: $F_{1,43} = 194$, $P < 0.001$; evenness: $F_{1,43} = 119$, $P < 0.001$).

Total abundance of ants increased by 240% for every 1°C increase in temperature at the southern site ($\chi^2 = 2800$; $P < 0.001$), but was not associated with average temperature at the northern site (Fig. 3, upper panels). Species evenness decreased by 60% with 1°C increase in average temperature in the southern site ($\chi^2 = 6.9$; $P = 0.009$) and was highest at intermediate temper-

atures in the northern site (Fig. 3, middle panels). Species richness was not associated with average temperature at either site (Fig. 3, lower panels). Species evenness also was highest at intermediate levels of diurnal variation in temperature in the northern site, but no other metrics of ant community composition were associated with diurnal variation in temperature (Fig. 4). The abundance of *C. lineolata*, the most abundant ant species at the southern site, increased by 190% with temperature ($\chi^2 = 5700$; $P < 0.001$) while the abundance of *Aphaenogaster rudis*, the most common ant at the northern site did not vary with temperature ($\chi^2 = 1.7$; $P = 0.19$).

Foraging activities

Across temperatures, foraging activities were higher at the southern site (seed dispersal: 700%; nectivory: 130%; granivory: 1000%; predation: 200%; scavenging: 650%). However, when foraging activity was standardized to account for differences in abundance at the two sites, per capita foraging activities were substantially higher at the northern site (seed dispersal: 200%; nectivory: 700%; granivory:16%; predation: 700%; scavenging: 300% higher at the northern site).

At the southern site, per degree of warming, seed dispersal, nectivory, and granivory de-
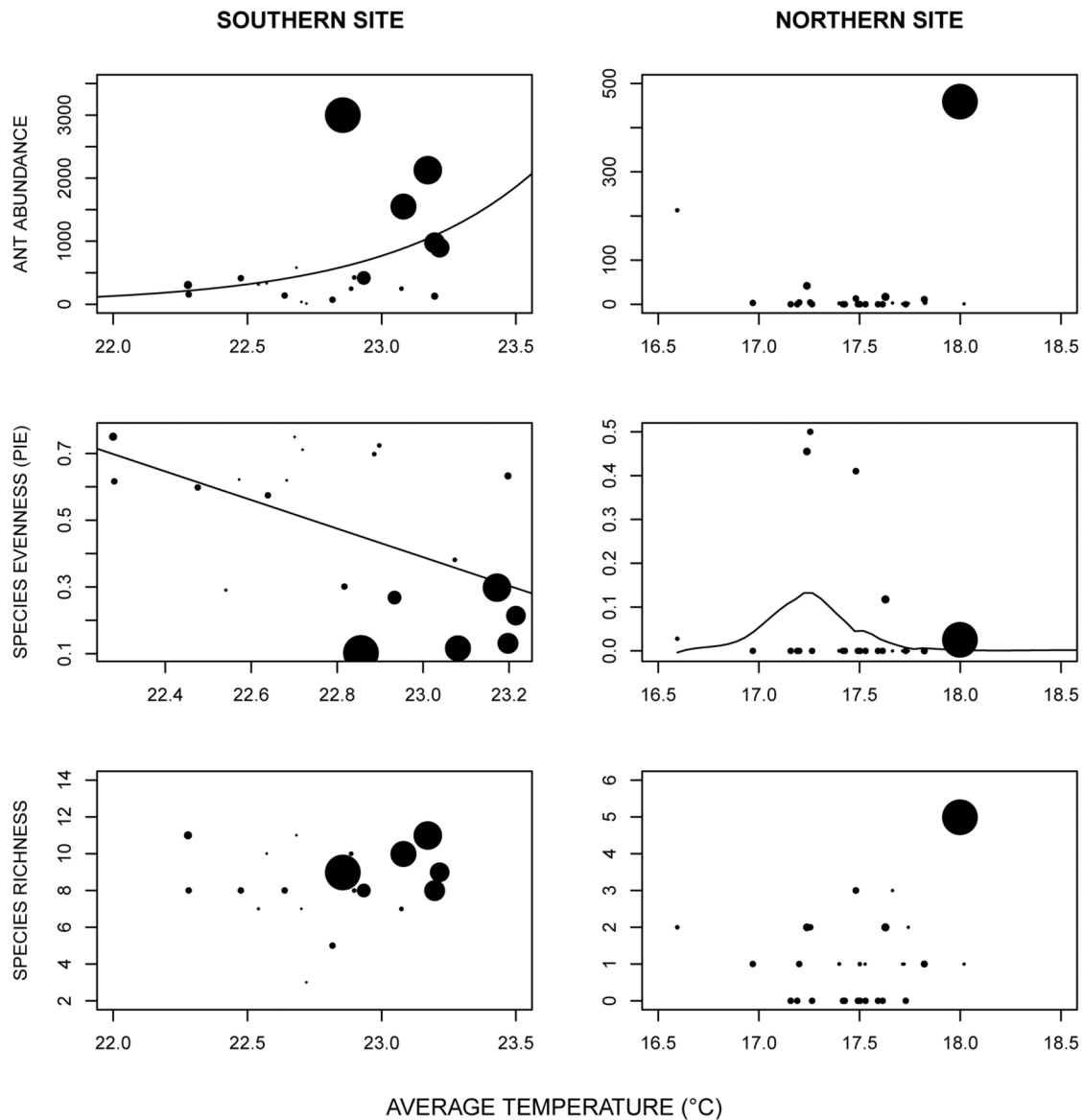
Fig. 3. Scatterplots of ant diversity measures (total ant abundance, species evenness (Hurlbert's PIE), species richness) against average temperature at the southern (left panels) and northern (right panels) study sites. Symbol sizes for each replicate are proportional to the square root of abundance of the most common species at each site (*Crematogaster lineolata* at the southern study site and *Aphaenogaster rudis* at the northern study site).

creased approximately 50% from the site averages for these activities (Fig. 5, left panels). At the northern site, none of the foraging activities were altered substantially by temperature (Fig. 5, right panels). Diurnal variation in temperature was negatively associated with nectivory and granivory at the southern site and weakly positively associated with scavenging at the northern site

(Fig. 6).

DISCUSSION

Climatic change is expected to have differential effects on ecological communities in different geographic areas, but forecasts of climatic change based on global or even large-scale regional
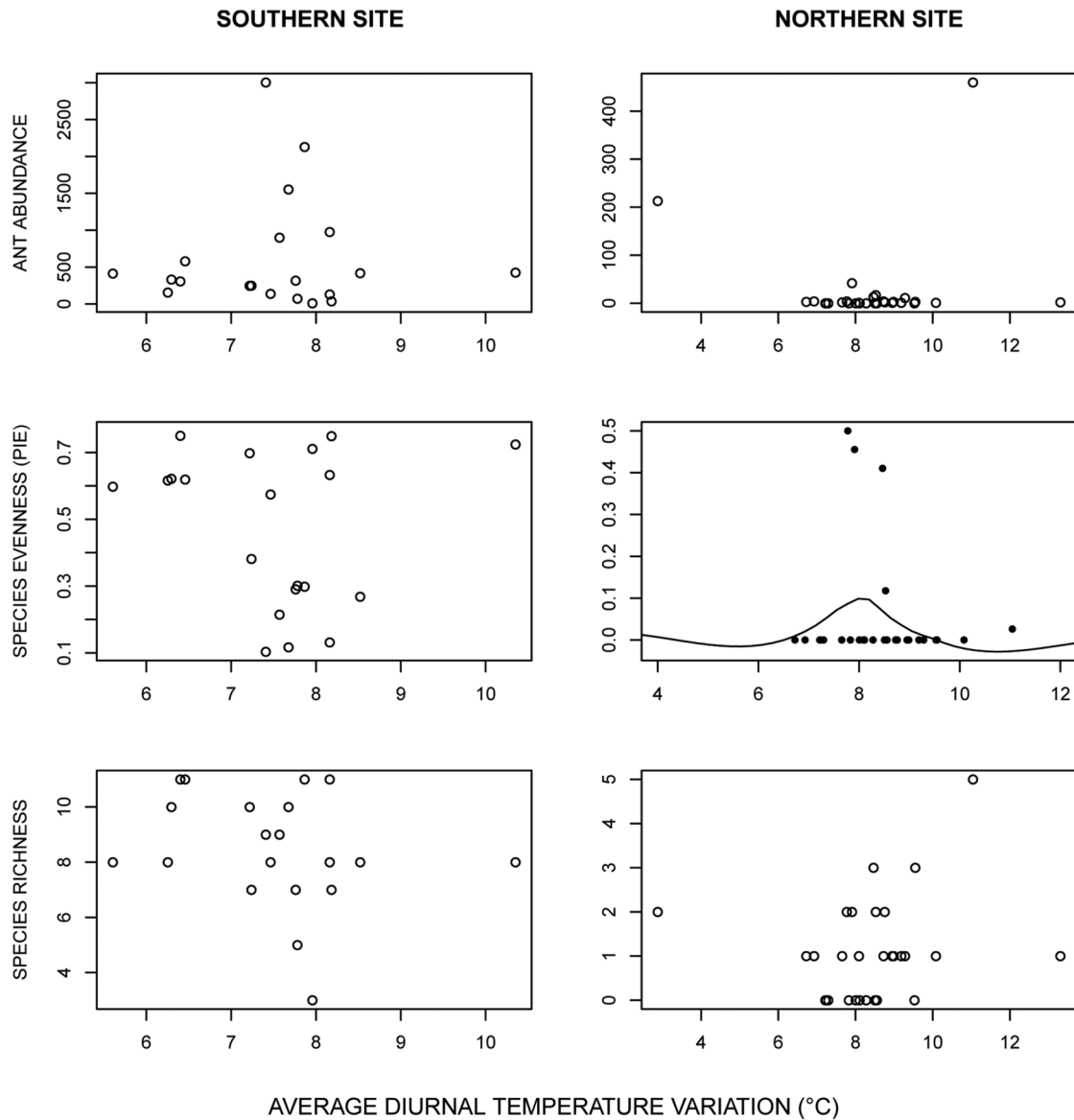
SOUTHERN SITE **NORTHERN SITE**

AVERAGE DIURNAL TEMPERATURE VARIATION (°C)

Fig. 4. Scatterplots of ant diversity measures (total ant abundance, species evenness (Hurlbert's PIE), species richness) plotted against average diurnal variation in temperature (daily maximum − daily minimum temperature) at the southern (left panels) and northern (right panels) study sites.

climatic patterns are unlikely to provide accurate assessments of short-term, small-scale changes in temperature, which ultimately regulates local ant abundance, richness, and foraging activities (Wehner et al. 1992, Cerdá et al. 1997, Azcarate et al. 2007, Chong and Lee 2009). Furthermore, few studies have experimentally demonstrated the effects of warming on communities simultaneously at different locales (but see Doak and Morris 2010). Our experimental results suggest that even modestly warmer average daytime temperatures can have large impacts, some mediated disproportionately by abundant species, on ant communities at lower latitudes. However, at higher latitudes, observed responses were much weaker and in general they may be slower than observed in other studies (cf. Parmesan and Yohe 2003).
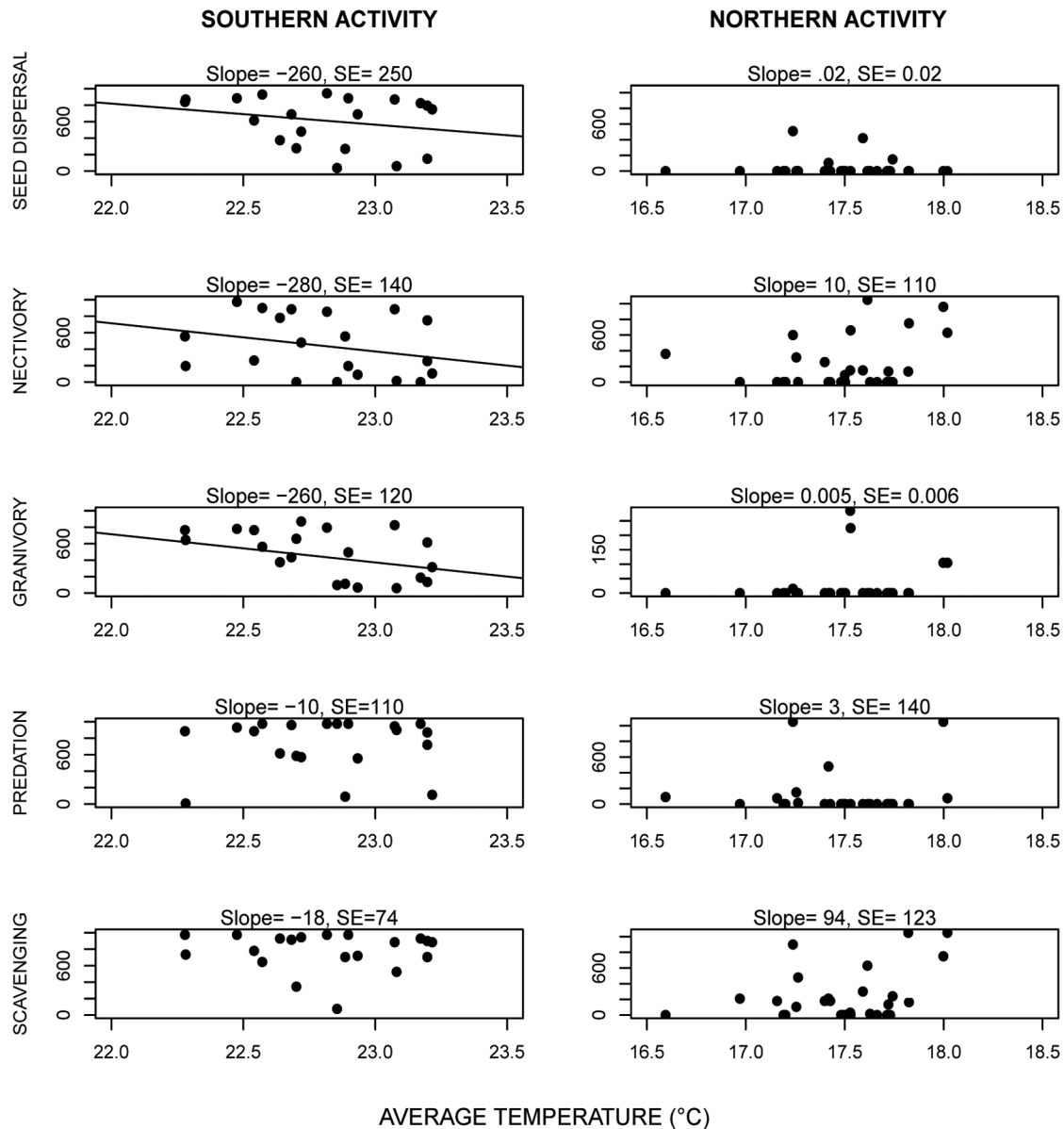
Fig. 5. Scatterplots of ant foraging activities ((bait units removed) × minutes) against average temperature at the southern (left panels) and northern (right panels) study sites. This measure of activity integrates time to discovery, number of foragers, and rate of removal. Slopes and standard errors of the regression lines are shown. Best-fit lines are presented for activities where the slope ± SE of temperature versus bait units removed × minutes did not cross zero.

At the more species-rich southern site, the abundance of *Crematogaster lineolata*, the most abundant species at that site, increased with temperature. Warming may have resulted in acceleration of successful brood production and development, or *C. lineolata* may have moved from cooler patches to the small islands of heat formed by the treatment (Moise and Henry 2010). Both effects are likely to occur as increases in mean temperatures create new thermal landscapes in which some, but not all, patches are warmer than current conditions. At the same
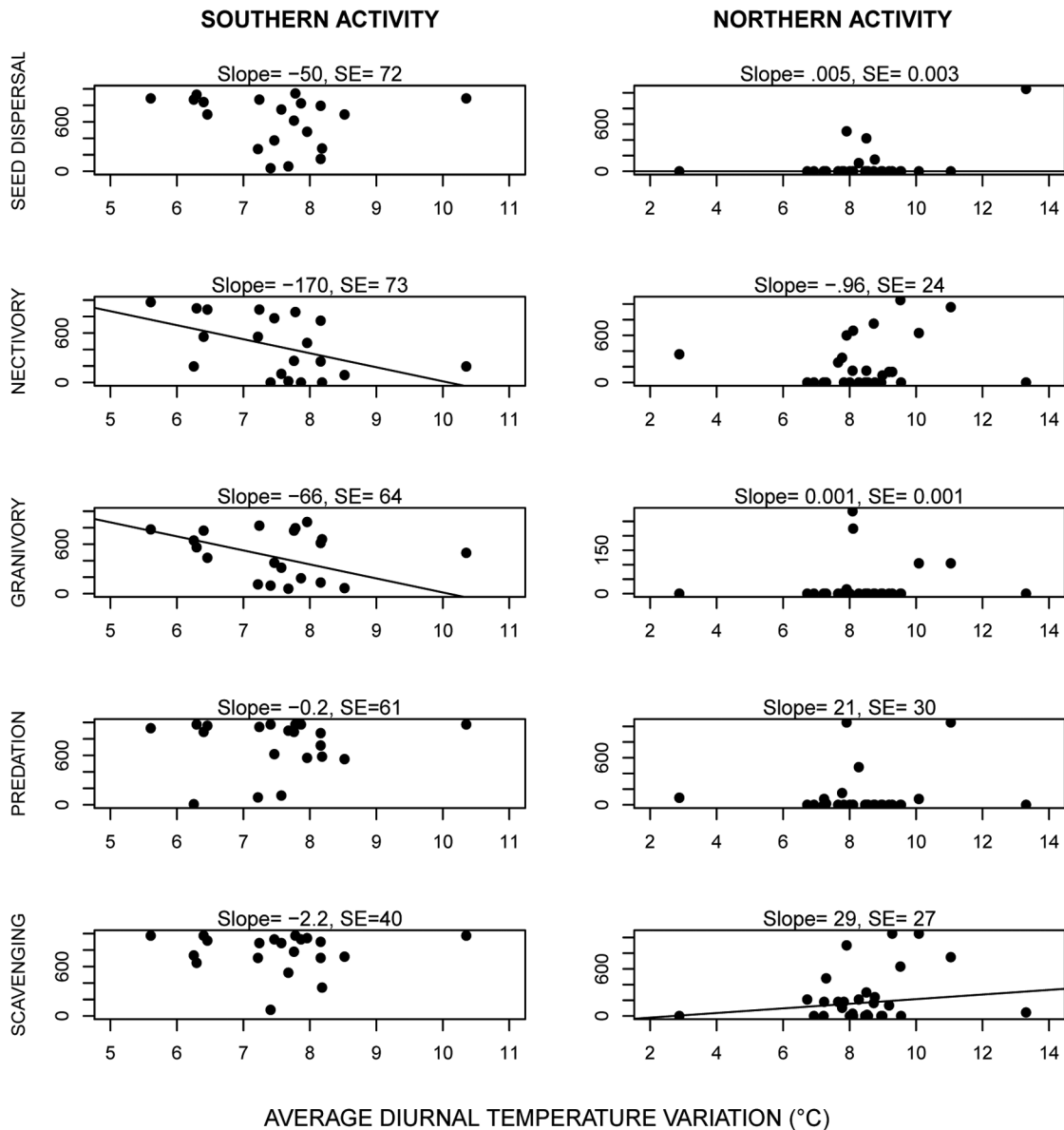
Fig. 6. Scatterplots of ant foraging activities ((bait units removed) × minutes) against average diurnal variation in temperature (daily maximum − daily minimum temperature) at the southern (left panels) and northern (right panels) study sites. This measure of activity integrates time to discovery, number of foragers, and rate of removal. Slopes and standard errors of the regression lines are shown. Best-fit lines are presented for activities where the slope ± SE of temperature versus bait units removed × minutes did not cross zero.

time that the abundance of *C. lineolata* increased, species evenness and overall ant foraging activities decreased with increasing temperature. We suggest that this result may be due to competitive displacement by *C. lineolata* of other species in the chambers. Altered dominance patterns

driven by climatic change have been shown in other systems and may be a common feature of the earliest responses of communities to warming (e.g., Kardol et al. 2010).

In contrast to the strong responses we observed at the southern site, we observed relative-

ly weak responses at the northern site, even though foraging of colonies at the northern site is likely to be limited by cold temperatures (cf. Hölldobler and Wilson 1990). Among community measures, only species evenness was associated with temperature, reaching highest values at intermediate temperatures. These responses were opposite of our initial predictions. It is possible that the overall low ant abundance at the northern site limits the ability to detect responses. Greater increases in temperature may be needed before the abundances of northern populations increase. Alternatively, it may be the case that the structure and dynamics of more temperate ant communities are not limited exclusively by temperature. Several studies now exist in which northern populations of insects do not experience changes in population sizes with warming (e.g., Adler et al. 2007, Pelini et al. 2009).

The different responses of ant communities to temperature at our two study sites also could be associated with other factors that co-vary with latitude. Although the two study sites do share many ant species and occur in similar deciduous forests, they differ dramatically in ant abundance, diversity and foraging activity. Furthermore, historical differences in climate, particularly temperature, and differences in seasonality may have been strong selective agents that constrain responses to temperature. For example, cold temperate species may have higher thermal maxima relative to ambient temperatures (Deutch et al.) such that species at higher latitudes have to be warmed more to experience fitness consequences.

By manipulating temperature only during spring and summer, we focused on the effects of warming on rates of foraging, development and potentially mortality during the active period of ants in the two regions and avoided potential confounding effects of warming on winter survival. When ants are most active, they respond to warming by shifts in foraging (and food intake) and/or shifts in development in their present locations. At the hottest temperatures we observed at the southern site, they may also respond through reduced activity or even mortality. Ants also may track environmental conditions by moving their colonies. Such a response to climatic change is also seen in other animals (Moise and Henry 2010). Outside of the mini-

chambers at both sites, we have observed multiple, within-season relocations of colony sites by *Aphaenogaster rudis*, and other studies provide similar evidence for the redistribution of ant colonies during a single season (Hölldobler and Wilson 1990, Foitzik et al. 2004, McGlynn et al. 2009, Lessard et al. 2010). Just as for birds and mammals, actual responses to climatic change inevitably reflect a mix of behavioral responses to warming, such as local shifts in habitat use, and demographic responses. A third possibility is that individual foragers may move into treatments areas to forage. Future studies should consider the effects of warming during cooler periods on ant community composition and activity.

As the climate changes, trophic cascades and ecosystem processes dependent on ants are likely to change in tandem. (Folgarait 1998, Petchey et al. 1999, Lensing and Wise 2006, Suttle et al. 2007, Barton et al. 2009, Harmon et al. 2009, O'Connor et al. 2009, Gilman et al. 2010, Traill et al. 2010). We found this to be the case at our southern site, where we observed decreases in rates of granivory, seed dispersal, and nectivory. Such changes suggest that ant responses to climatic change may have cascading consequences for species dependent upon particular ants, such as ant-dispersed plants (Gove et al. 2007) or insects tended for honeydew in exchange for protection by ants (Stadler and Dixon 2008). More detailed, long-term studies of the responses of ants to climatic change, both observational and experimental, are needed to improve the forecasts of these changes.

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