Effects of short-term warming on low and high latitude forest ant communities

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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 site

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 temper-

et al. 2009). A common ant at both sites, *A. ⸳ ⸳ ⸳ ⸳ ⸳ ⸳*, 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

scatterplot smoothing.

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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 (_ _ _) to estimate predation rates (Wilson 1971), dead adults of _ . _ _ or _ _ _ (mealworms) to estimate scavenging rates (Jeanne 1979), and milled oat grain (*A* _ _) to estimate granivory rates (Valone and Kaspari 2005). We also measured rates of removal of seeds of wild ginger (*A* _ _ _), 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

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. C. was the most abundant ant species in the southern site, and A. 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: $F_{1,43} = 62$, $<$ 0.001; richness: $F_{1,43} = 194$, $<$ 0.001; evenness: $F_{1,43} = 119$, $<$ 0.001).

Total abundance of ants increased by 240% for every 1°C increase in temperature at the southern site ($\chi^2 = 2800$; $<$ 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 ($\chi^2 = 6.9$; $=$ 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. , the most abundant ant species at the southern site, increased by 190% with temperature ($\chi^2 = 5700$; $<$ 0.001) while the abundance of A. , J-10.l11Tf4119,an7-4.v7366.641
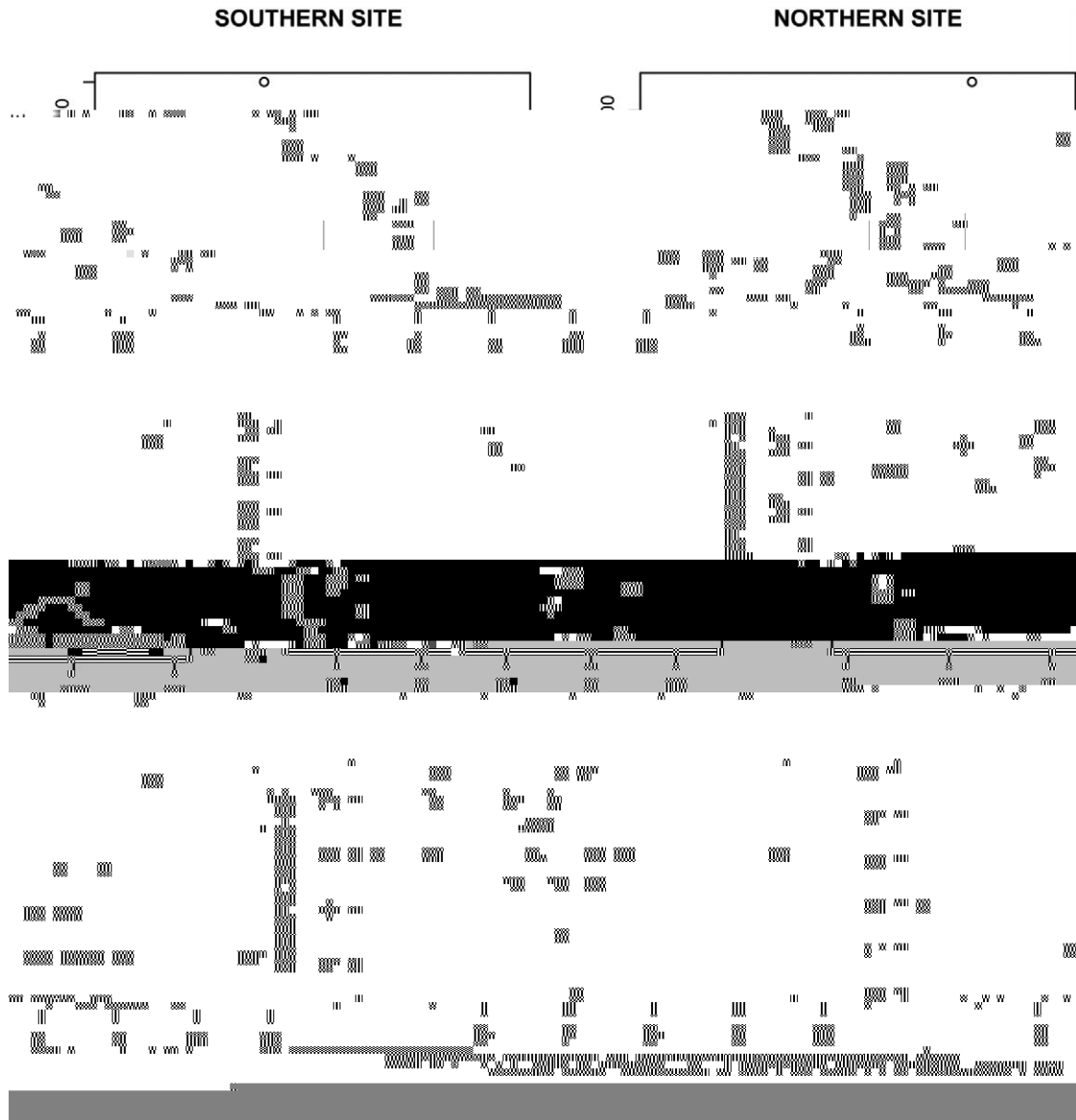
Fig. 4. Scatterplots of ant diversity measures (total ant abundance, species evenness (Hurlbert's PIE), species richness) plotted against average diurnal variation in temperature (daily maximum – daily minimum temperature) at the southern (left panels) and northern (right panels) study sites.

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).

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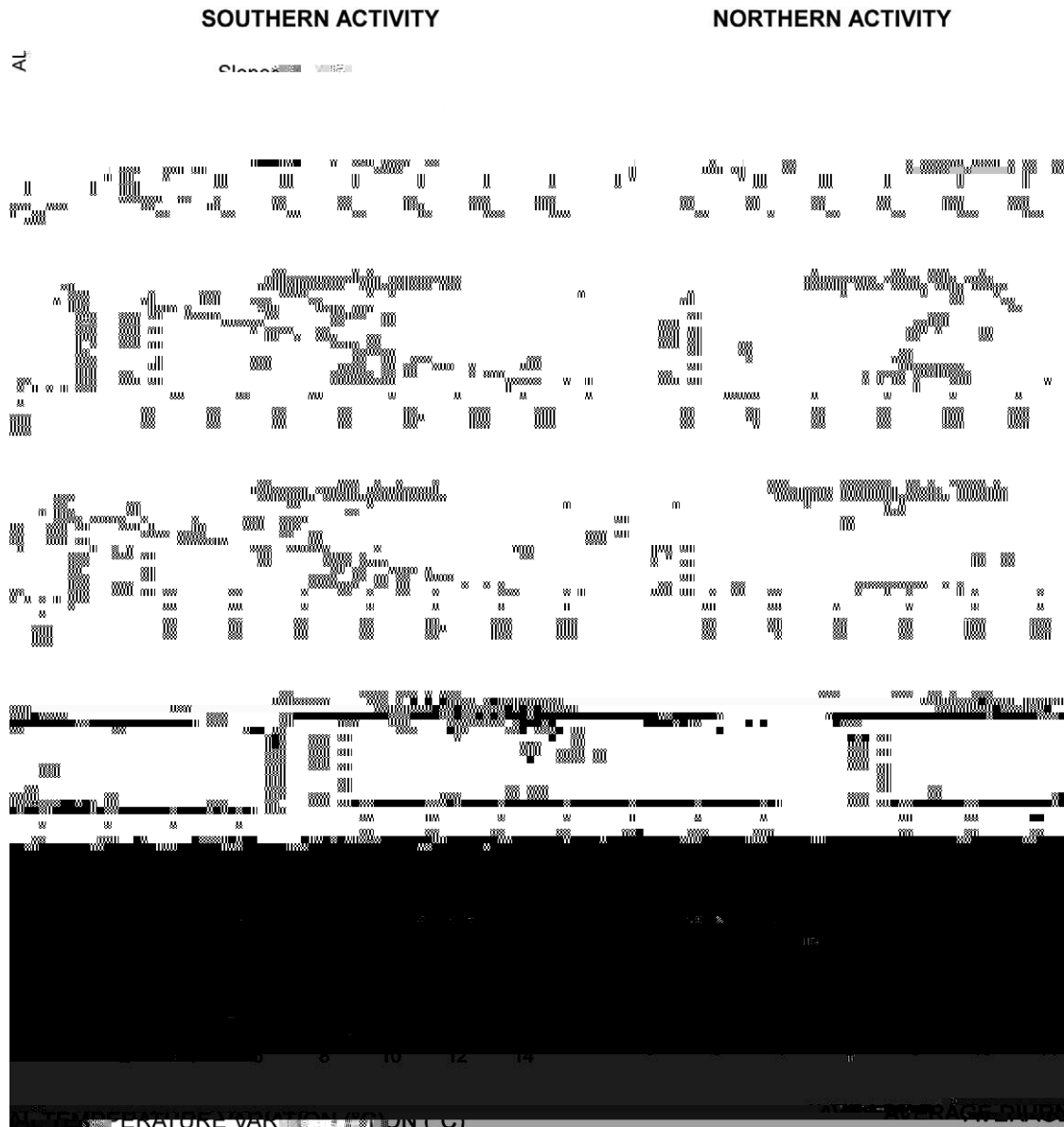
time that the abundance of *C.* increased, species evenness and overall ant foraging activities decreased with increasing temperature. We suggest that this result may be due to competitive displacement by *C.* of other species in the chambers. Altered dominance patterns driven by climatic change have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

Acknowledgments

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