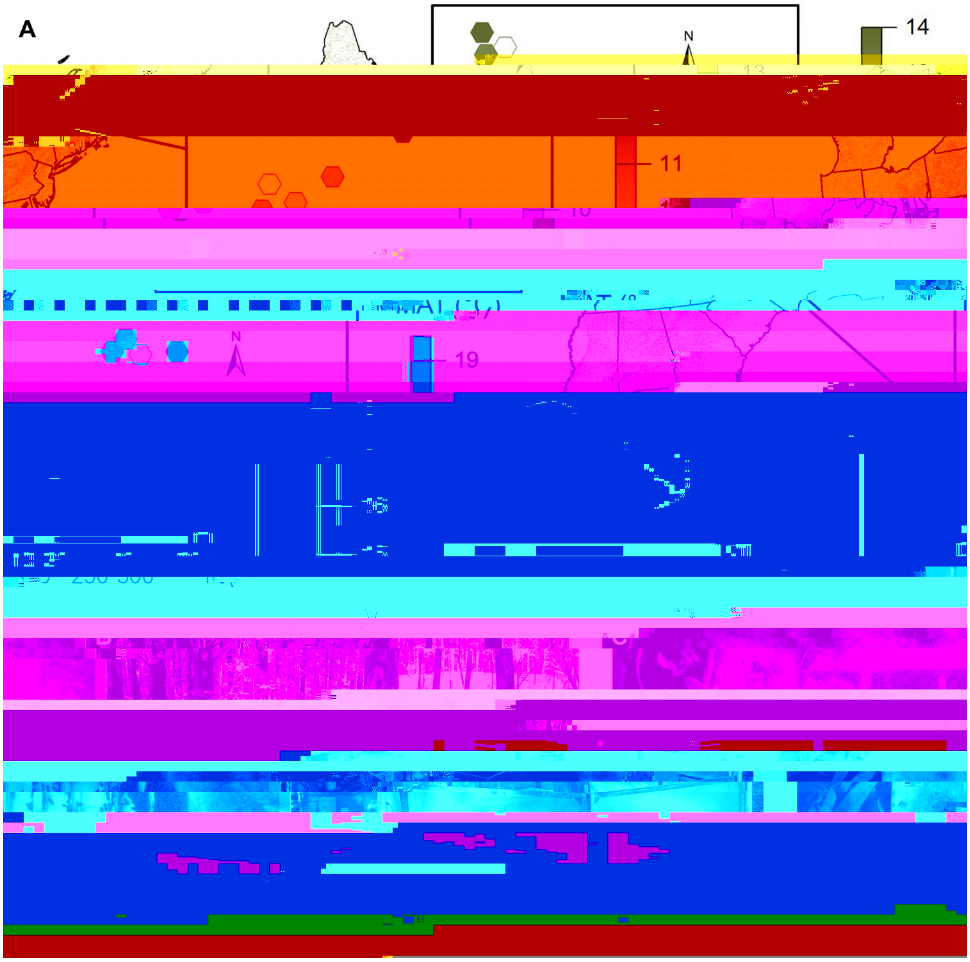
# Climatic warming destabilizes forest ant communities

**How will ecological communities change in response to climate warming? Direct effects of temperature and indirect cascading effects of species interactions are already altering the structure of local communities, but the dynamics of community change are still poorly understood. We explore the cumulative effects of warming on the dynamics and turnover of forest ant communities that were warmed as part of a 5-year climate manipulation experiment at two sites in eastern North America. At the community level, warming consistently increased occupancy of nests and decreased extinction and nest abandonment. This consistency was largely driven by strong responses of a subset of thermophilic species at each site. As colonies of thermophilic species persisted in nests for longer periods of time under warmer temperatures, turnover was diminished, and species interactions were likely altered. We found that dynamical (Lyapunov) community stability decreased with warming both within and between sites. These results refute null expectations of simple temperature-driven increases in the activity and movement of thermophilic ectotherms. The reduction in stability under warming contrasts with the findings of previous studies that suggest resilience of species interactions to experimental and natural warming. In the face of warmer, no-analog climates, communities of the future may become increasingly fragile and unstable.**

Climate-driven shifts in community structure and function are already apparent in natural systems (1



( ) Geographic position of warming arrays at Duke Forest (orange) and Harvard Forest (green) toward the center and northern boundary of temperate deciduous forest (45) and the local spatial arrangement of the chambers at each site. Color intensity indicates greater MAT, with chamberless control plots indicated by unshaded symbols. ( ) A single warming chamber at Duke Forest. Note that the diameter of each chamber is roughly 1000 ant body lengths. ( ) Nest box containing a *Crematogaster lineolata* colony, with the cover tile removed.

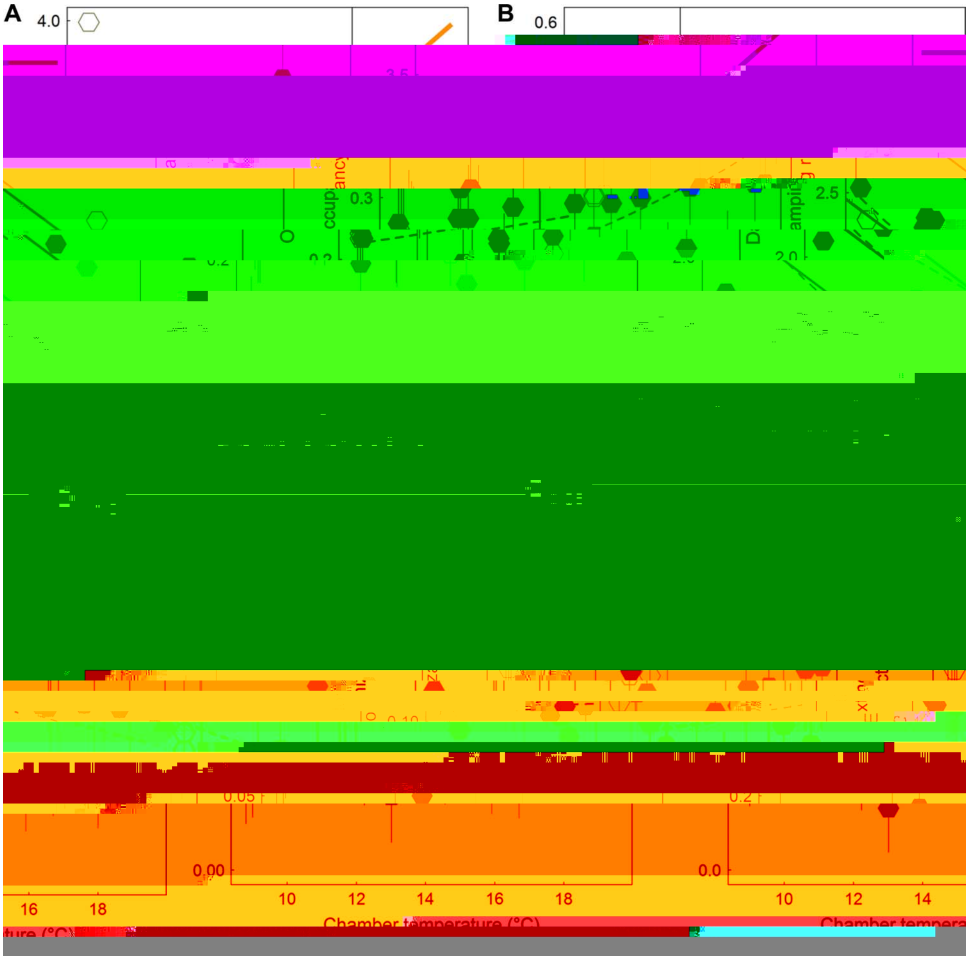
records within each chamber and estimated the species-specific monthly binomial probability of colonization, extinction, and occupancy. Colonization and extinction were defined operationally as appearances and disappearances between consecutive censuses of a species in a nest box. Nest box occupancy per chamber ranged from 0.10 to 0.33 at Duke Forest and from 0.07 to 0.22 at Harvard Forest, with considerable dynamic turnover between consecutive monthly censuses and frequent replacement of one species by another with no intervening vacancy (table S1). Multiple occupancy of nest boxes was never observed: At each census, nest boxes were either occupied by a single colony or empty. These data suggest that nest boxes provided adequate nesting sites but were still sufficiently limited to reflect the dynamics of interactions and associations among species. Note that periodic nest box censuses provide indirect evidence of interactions among species through shifts in nest box usage as opposed to direct observations of interactions. Here and elsewhere, we refer to altered species interactions under climate change in a general sense, but because we acknowledge the possibility (albeit one that we consider unlikely) that some or all of the shifts in nest box usage in our experiment may be simple associations among species absent any interactions, we refer to the results from our experiment as shifts in species associations (see Results and Discussion for a full discussion of the nature of species interactions and associations in our system).

We used multiple regression models with a quasi-binomial error structure [generalized linear models (GLMs)] to tease apart the effects of MAT in each chamber and the presence of other species on responses to warming. There were few cases in which colonization, occupancy, or extinction was affected by only MAT, as is often assumed for many species distribution models. Instead, the responses of species depended on both temperature and other species. Most species were connected to one or two other species in simple networks of positive and negative associations mediated by temperature (Fig. 2 and table S2). The responses of individual species to warming and to the presence of other species were complex and idiosyncratic, and these responses were different for colonization, extinction, and occupancy (Fig. 2).

At Duke Forest, *C. lineolata* and, to a lesser degree, *Aphaenogaster* spp. were the most strongly influenced by the direct effects of warming. With increasing warming, the probability of nest box occupancy by C. lineolata significantly increased and the probability of extinction decreased (figs. S2 to S4 and table S3). Aphaenogaster spp. exhibited decreased occupancy and colonization with increasing temperature (figs. S2 and S3 and table S3). For the remaining two focal species, Brachyponera chinensis and Temnothorax curvispinosus, occupancy, colonization, and extinction did not respond significantly to increasing chamber temperature. We found some cases in which occupancy of a focal species responded to temperature or other species, but we did not detect effects on colonization or extinction, possibly because of limited sample sizes (figs. S3 and S4 and table S3).

Although there is good evidence for the direct effects of temperature on C. lineolata and Aphaenogaster spp., there were also indirect effects of temperature on nest box occupancy, colonization, and extinction that were mediated by its effects on co-occurring species (Fig. 2 and table S2). For example, the presence of C. lineolata was negatively associated with Aphaenogaster spp. occupancy and colonization; the presence of B. chinensis (a newly arrived exotic species at Duke Forest) was negatively associated with C. lineolata occupancy, and there was a significant interaction of MAT and T. curvispinosus occupancy on C. lineolata colonization.

At Harvard Forest, Camponotus spp., Myrmica spp., and Temnothorax longispinosus were the most strongly influenced by the direct effects of warming. Nest box occupancy and colonization of Myrmica spp. decreased with warming (figs. S5 and S6 and table S4), whereas occupancy by Camponotus spp. and T. longispinosus (fig. S5 and table S4)



( ) Damping ratio, ( ) occupancy, ( ) colonization, and ( ) extinction as functions of MAT (°C) for ant communities inhabiting nest boxes at Duke Forest (orange) and Harvard Forest (green); chambered plots are represented by filled symbols, and chamberless control plots are represented by open symbols. For the damping ratio, dashed lines represent simple linear regressions; the solid lines are from an analysis of covariance (ANCOVA) with separate intercepts for site and a common slope for MAT (Table 1). For occupancy, colonization, and extinction, mean proportions and binomial 95% confidence intervals are presented; dashed lines are predicted values from quasi-binomial GLMs (Table 1). Inset panels depict the null expectations for stability, occupancy, colonization, and extinction under a simple model of increasing activity of thermophilic ectotherms at higher temperatures.

These Markov models predicted a consistent shift in equilibrium species composition through time, with a set of thermophilic "winner" species becoming more common and an approximately equal number of "loser" species becoming less common. At Duke Forest, the equilibrium frequency of the thermophilic C. lineolata increased with warming, whereas the equilibrium frequencies of Aphaenogaster spp., T. curvispinosus, and empty patches either decreased or exhibited little change (fig. S8 and table S6). These shifts reflect the change in transition probabilities in the individual matrices: The transition (empty→C. lineolata) increased at higher temperatures, whereas the transitions (C. lineolata→Aphaenogaster spp.) and (C. lineolata→T. curvispinosus) decreased at higher temperatures. At Harvard Forest, there was a nonsignificant trend at higher temperatures toward a greater equilibrium frequency of the relatively thermophilic T. longispinosus (fig. S9 and table S6). Individual transition probabilities as functions of chamber temperature supported this result: The transition (T. longispinosus→empty) trended negatively with increased warming (table S7). Analyses of individual transition probabilities reinforced the results of the species association GLMs (Fig. 2), which revealed evidence of indirect effects of warming at Harvard Forest. Although the transition (Myrmica spp.→Myrmica spp.) significantly increased with warming, there was also an increase in the transition (Myrmica spp.→T. longispinosus) with warming. The change in species associations with increasing temperature was further reflected in a decrease in the transitions (Aphaenogaster spp.→Myrmica spp.) and (Myrmica spp.→Aphaenogaster spp.) with warming.

The net effect of these altered species associations was the consistent reduction in the damping ratio of the transition matrix under warmer temperatures (Fig. 3A). This ratio measures the relative speed at which a perturbed system returns to its equilibrium (Lyapunov stability). Collectively, MAT and additive effects of site accounted for 35% of the variation among chambers in the damping ratio (Table 1). Thus, as temperatures increased, community stability decreased and did so at both sites. The stability and occupancy patterns predicted by the Markov models were not affected by using different criteria for including species in the model or by incorporating the possibility of measurement error in the estimation of transition probabilities (see "Alternative demographic and transition matrix model specifications" in the Supplementary Materials).

To understand the mechanisms that disrupt community stability with warming, we analyzed the relationship between the Lyapunov stability of a matrix and its individual transition elements. Although the Lyapunov exponent reflects nonadditive contributions of all the transition elements in the matrix (16), the best correlate of the Lyapunov stability is the sum of the diagonal transition elements, which measures the probability that the system remains unchanged from one time step to the next (resistance). The higher the probability of species persistence from one time period to the next, the lower the Lyapunov stability (table S8). At the southern site and in warm chambers, persistence of colonies was high, community resilience was low, and the return to equilibrium was slow. In contrast, at the northern site and in cool chambers, persistence of colonies was low, assemblage resilience was high, and the return to equilibrium was fast. When not perturh60s3.896d3121223

and extinction probabilities as the equilibrium frequency in the island-mainland variation of Levins' (40) metapopulation model

$$(\text{Occupancy}) = \frac{\mathsf{p}(\text{Colonization})}{\mathsf{p}(\text{Colonization}) + \mathsf{p}(\text{Extinction})}$$

We further used colonization and extinction probabilities to estimate turnover

$$(\text{Turnover}) = \frac{\mathsf{p}(\text{Colonization}) * \mathsf{p}(\text{Extinction})}{\mathsf{p}(\text{Colonization}) + \mathsf{p}(\text{Extinction})}$$

All statistical models were performed using R version 3.2.2, Fire Safety (41). For each of the focal species at each site, we fit models of the proportion of nest boxes that were occupied, those that were colonized, and those that went extinct as functions of chamber MAT. Owing to issues with dispersion not equal to 1, we used GLMs with a quasi-binomial error structure. We conducted similar quasi-binomial GLMs for community-wide occupancy, colonization, and extinction at Duke Forest and Harvard Forest separately. We also fit models of the proportion of nest boxes that were inhabited by the focal species in one census point and persisted to the next census point. Like the occupancy, colonization, and extinction models, we used quasi-binomial GLMs to examine the impact of MAT of the chambers on persistence. We used $F$ tests to assess the statistical significance of chamber temperature, because these tests are most appropriate for models where dispersion is estimated by moments (42).

We explored the effects of nonfocal species presence or absence over the course of the census period on each of the focal species responses (occupancy, colonization, and extinction) at each site. For each focal species and response variable, we constructed four models: (i) a main effect of chamber MAT, (ii) a main effect of nonfocal species presence or absence, (iii) both main effects of MAT and nonfocal species presence or absence, and (iv) both main effects plus the interaction of MAT and nonfocal species. We chose the best-fitting model among these four on the basis of the lowest Akaike information criteria (AIC) score (43). To obtain AIC values, we initially fit all models with a binomial error structure; we then refit the best-fitting models using a quasi-binomial error structure to obtain the correct SEs for the estimates.

We constructed a transition matrix for each chamber at each site, pooling observations across nest boxes within a chamber and transforming the raw counts to probabilities, such that columns sumns(t)-2747eci r234.8.014[(turt.600.2(e)-S1.6(iti)-2.7(f7e)-266.robabia(obser(m9(7h6(e.2(5.9(c)e25.68ct

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