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

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

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22 **ABSTRACT**

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

37

38 Keywords: ants; climate change; community; elevational gradient; Formicidae; geographic range;  
39 warming experiment.

40

## 41 INTRODUCTION

42 The responses of ecological communities to climatic change depend both on environmental conditions at  
43 specific geographic locations and on the composition of and interactions between co-occurring species  
44 (Tylianakis et al. 2008, Gilman et al. 2010, Singer and Parmesan 2010, Pelini et al. 2012). Populations  
45 and species occupying different locations may vary in their tolerances for abiotic changes (Deutsch et al.  
46 2008, Tewksbury et al. 2008, Huey et al. 2009, Andrew et al. 2013, Kingsolver et al. 2013). Additionally,  
47 the indirect effects of climate change mediated by species interactions can strengthen or reverse the  
48 effects of abiotic change (Suttle et al. 2007, Rouifed et al. 2010, Pelini et al. 2011a). As a consequence, it  
49 is difficult to predict how climatic change will shape the composition and diversity of local communities  
50 at small spatial scales.

51  
52 However, at coarser grains of observation, such as latitudinal and elevational gradients, climatic  
53 differences may lead to predictable shifts in composition and diversity. In the simplest scenario, the  
54 poleward expansion of species geographic ranges may lead to an increase in diversity at higher latitudes,  
55 even though some species may disappear locally because they cannot tolerate warmer conditions. Net  
56 gains in species richness may arise because warming is unlikely to push many species above their thermal  
57 limits (Addo-Bediako et al. 2000, Deutsch et al. 2008, Tewksbury et al. 2008, Kingsolver et al. 2013).  
58 Conversely, at lower latitudes, sites should be more likely to lose species with increases in temperature  
59 because some species will exceed their critical thermal limits (Addo-Bediako et al. 2000, Deutsch et al.  
60 2008, Tewksbury et al. 2008, Kingsolver et al. 2013) or experience too few days and hours within their  
61 range of optimal foraging temperatures.

62  
63 Experiments that compare the effects of warming on communities near high- and low latitudinal range  
64 boundaries can test predictions about geographic patterns of warming effects on ecological communities.  
65 All other things being equal, “natural experiments” along elevational and latitudinal climate gradients can  
66 also predict which species can and will persist in particular climates (Ibanez et al. 2013). Differences in

67 the response of species to natural thermal gradients and to controlled warming experiments might reflect  
68 dispersal limitation, historical effects, confounded gradients in natural experiments (Gotelli and Ellison  
69 2012), or small-scale artifacts or design constraints in controlled field experiments (Wolkovich et al.  
70 2012).

71  
72 In this study, we examined community-level responses of forest ants to ongoing experimental warming in  
73 open-top chambers at a northern (Harvard Forest, Massachusetts) and a southern (Duke Forest, North  
74 Carolina) site in the eastern USA. These two sites represent the northern and southern boundaries of  
75 eastern US forests: Harvard Forest lies at the northern end of the Eastern Temperate Forests (Mixed  
76 Wood Plains) and the southern edge of the Northern Forests (Atlantic Highlands), whereas Duke Forest,  
77 within the Eastern Temperate Forests, is at the boundary between the Southeastern USA Plains and the  
78 Mississippi Alluvial and Southeast Coastal Plains (CEC 1997). Previous work in this system has  
79 demonstrated strong geographic differences in the responses of individual species to experimental  
80 warming: at the warmer southern site, ant species with higher thermal tolerances had higher worker  
81 densities and greater foraging activity in warmer chambers than did ants species with lower thermal  
82 tolerances (Diamond et al. 2012a, Stuble et al. 2013). At the cooler northern site, however, worker density  
83 of all species, regardless of their thermal tolerances, was highest in the warmer chambers. Similar  
84 responses have been observed in the soil microbial community, with larger shifts in both structure and  
85 function observed at the southern site (Cregger et al. 2014).

86  
87 Based on these previous findings, we predicted that community composition and diversity would respond  
88 differently to warming at the northern and southern sites. Specifically, because most northern species  
89 rarely experience temperatures near their upper thermal limits, their performance and abundance should  
90 not be depressed by warming (Diamond et al. 2012a). If other ant species from warmer microhabitats  
91 such as forest gaps are able to colonize the chambers, ant community composition would change and  
92 diversity would increase in the warmer chambers at Harvard Forest. In contrast, at Duke Forest we

93 predicted that ant diversity would decrease and community composition would change because many  
94 resident species experience temperatures that exceed their thermal tolerances. Within sites, we expected  
95 closely related species to respond to warming in similar ways due to shared evolutionary histories  
96 (Diamond et al. 2012b).

97  
98 Because both experiments and large-scale geographic patterns of diversity and species composition are  
99 used to forecast future responses to climatic change (Parry and IPCC 2007), assessing congruence  
100 between responses to experimental warming and natural warming is important. We compared the patterns  
101 in diversity and composition of ants under experimental warming with those along an elevational gradient  
102 in the Great Smoky Mountains. The elevational gradient shares many species with and spans a gradient of  
103 temperature increase similar to that generated by the warming treatments (Sanders et al. 2007).

104

## 105 **METHODS**

106 **Study system.** Ants are the numerically dominant macroinvertebrates in eastern forests (King et al.  
107 2013), contribute to important ecosystem services such as seed dispersal and nutrient cycling, and respond  
108 predictably to a variety of environmental conditions (reviewed in Del Toro et al. 2012), making them an  
109 ideal system for the study of community-level effects of warming. Other studies have demonstrated that  
110 air temperature can potentially influence ant community structure (Arnan et al. 2007, Wittman et al. 2010,  
111 Lessard et al. 2011), diversity (Kaspari et al. 2000, Sanders et al. 2007, Dunn et al. 2009, Pelini et al.  
112 2011a), colony survival (Pelini et al. 2012), worker density (Pelini et al. 2011a, Diamond et al. 2012a),  
113 foraging behavior (Ruano et al. 2000, Pelini et al. 2011a, Stuble et al. 2013), and competitive interactions  
114 (Cerda et al. 1997, 1998).

115

116 **Open-top warming chambers.** We used an open-top warming experiment at Harvard Forest,  
117 Massachusetts and Duke Forest, North Carolina, USA (design details in Pelini et al. 2011b). The warming  
118 array at each site consists of twelve 5-meter diameter ( $\sim 22 \text{ m}^3$ ) open-top chambers in a regression design

119 (Cottingham et al. 2005) that are held at ambient air temperatures (three control chambers) or are heated  
120 to one of the 0.5 °C intervals between 1.5 to 5.5°C, inclusive, above ambient air temperature (one  
121 experimental chamber for each temperature set-point). The bottoms of the chamber walls are elevated 2–3  
122 cm above the ground so that movement of ants and other arthropods into and out of the chambers is not  
123 restricted. These chambers have been operating continuously since January 2010. Four permanent pitfall  
124 traps (5 cm diameter) are located in each chamber. Each month, pitfall traps were opened and filled with  
125 60–80 mL of 95% EtOH or glycol and left uncovered for 48 hours during rain-free conditions. Ants were  
126 then extracted and identified to species using regional keys (e.g., Ellison et al. 2012); identifications were  
127 confirmed at the Harvard University Museum of Comparative Zoology (Cambridge, Massachusetts). In  
128 this study, we compared ant species occurrences in the different warming scenarios using monthly pitfall  
129 data collected from January 2010 through July 2012.

130

131 **Environmental variables.** Each chamber is fitted with environmental sensors that are linked to a data  
132 logger; environmental data are collected continuously at 1-minute intervals (Pelini et al. 2011b). We  
133 calculated the mean, minimum and maximum air temperature, and soil temperature at 2 and 6 cm, mean  
134 soil moisture, and growing degree days ( $T_{\text{base}}=15^{\circ}\text{C}$ ; “GDD”) for each chamber during January 2010-July  
135 2012. Growing degree-days were summed across all time periods, but all the other metrics were averaged  
136 over sampling periods.

137 **Measures of diversity.** Most biodiversity measurements are sensitive to sampling effort and to the  
138 abundance per sampling unit (Gotelli and Chao 2013). Measuring biodiversity in climate-change  
139 experiments is especially challenging because warming treatments will alter the activity and movement of  
140 many poikilotherms, even without changing population size or community structure (Moise and Henry  
141 2010). Thus, simultaneous decreases in abundances but increases in detection probability with warming  
142 could mask important treatment effects. Moreover, counting the number of ant workers in a trap is  
143 usually not valid statistically because the workers caught in a single trap often originated from the same

144 colony (Gotelli et al. 2011). To ameliorate these effects, we used only the incidence of each species  
145 (presence or absence) in a chamber during a monthly sampling period (Longino et al. 2002, Kaspari et al.  
146 2003, Gotelli et al. 2011). In each chamber at both sites, the sampling effort was equivalent: every  
147 chamber was sampled each month with pitfall traps open for 48 hours.

148 For each chamber, the resulting data were organized as an incidence matrix in which each row is a  
149 species, each column is a sampling period, and the entries indicated incidence (0 or 1) of each species at  
150 each sampling period. In addition to calculating the number of species per sampling unit (“species  
151 density” sensu Gotelli and Colwell 2001), we also calculated indices that are unbiased by sample size:  
152 PIE—the probability of an interspecific encounter, or the chance that two randomly drawn incidences  
153 represent two different species (Hurlbert 1971)— the first two Hill numbers (Hill 1973), and the  
154 asymptotic species diversity that would be found with maximum sampling effort (the Chao2 index; Chao  
155 1987). Hill numbers are modified measures of species richness that take into account relative abundance.  
156 The first Hill number is equivalent to the exponent of the Shannon index, and it weights all species  
157 equally. The second Hill number is the inverse of the Simpson index, and is related to PIE. This index  
158 places more weight on common species.

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

164

165 To examine the effects of environmental variables on diversity, we used linear regressions to determine if  
166 species density, Chao2, PIE, Hill.1, or Hill.2 were significantly associated with Site, GDD, soil moisture.  
167 We also included Site  $\times$  GDD and Site  $\times$  soil moisture interaction terms in these models to determine if  
168 the diversity-climate relationships differed between sites. To yield more precise parameter estimates, we



169 used a weighted linear regression model for Chao2, with the weights being proportional to the inverse of  
170 the estimated variance for Chao2. Because some extrapolations of species richness can have a very large  
171 estimated variance, this procedure down-weights those highly uncertain estimates in the regression  
172 models.

173

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

183

184 As described in Gotelli et al. (2010), we analyzed the model with and without detection errors. In the first  
185 model, we assumed there were no errors in detection and that all species present in each chamber were  
186 detected in pitfall catches. This analysis is based on the observed incidence matrix. In the second  
187 variation, we assumed there were detection errors and that some rare species were present that were not  
188 detected in any of the pitfall traps. For this analysis, we estimated the number of missing species with the  
189 Chao2 estimator. We added additional rows to represent these additional rare species in the analysis, and  
190 assigned relative abundances to be less than one half of the relative abundance of the rarest species in  
191 each community (see Gotelli et al. 2010 for details).

192

193 To determine if closely related species responded similarly to the temperature manipulation, we used the  
194 *phylosig* function from the R library *phytools* (Revell 2012) to estimate Blomberg's K (Blomberg et al.  
195 2003) for the coefficients from regression models of species-incidence counts versus GDD. Phylogenetic  
196 sampling error was incorporated using the methods described in Ives et al. (2007). The phylogeny of  
197 Moreau and Bell (2013) was used in analyses for both study sites; but because this phylogeny is resolved  
198 only to genus, we treated unknown species relationships as terminal polytomies.

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

203

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

205

## 206 **RESULTS**

207 With the exception of PIE, diversity increased with GDD and soil moisture and was higher at the southern  
208 study site (Table 2). PIE increased significantly with GDD and also was higher at the southern site. The  
209 relationship between diversity and climate between sites (i.e., site × GDD) was statistically significant for  
210 Chao2, which increased significantly with GDD at the southern site but was not significantly associated  
211 with GDD at the northern site (Table 2). At the southern site, asymptotic species richness (Chao2)  
212 decreased significantly with warming at a loss rate of one species per 2,400 GDD (~ 1°C) (Figure 1).  
213 Species density (the number of species per unit area), PIE, and other diversity indices did not respond  
214 significantly to warming or to changes in soil moisture at either study site (Table 2). Species composition  
215 at the southern site differed more with temperature than expected by chance (Figure 2a), although the  
216 significance of this effect depended on the data transformation and the inclusion of undetected species in

217 the model (untransformed:  $p = 0.020$  and  $0.020$ ; square root-transformed:  $p = 0.143$  and  $0.193$  for  
218 undetected species included or excluded, respectively).

219

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

224

225 With increasing GDD at the southern site, *Aphaenogaster rudis* decreased in incidence, whereas  
226 *Crematogaster lineolata* and *Crematogaster vermiculata* increased in incidence (see Figure 3a for linear  
227 regression coefficients and significance levels). With increasing GDD at the northern site, *Camponotus*  
228 *herculeanus* decreased significantly in incidence, whereas *Myrmica pinetorum* marginally increased in  
229 incidence with increasing temperature (Figure 3b).

230

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

237

238 We recorded a total of 72 species in the Great Smoky Mountains dataset and in the chambers at the two  
239 study sites. The Smoky Mountain dataset shared 18% and 10% of this species list with the southern and  
240 northern sites, respectively. Approximately 7% of the species were shared by all three sites; 30% were  
241 found only at the southern site, 19% only in the Great Smoky Mountains, and 11% only at the northern

242 study site. Species density significantly increased with temperature in the Great Smoky Mountains ( $F_{1,27} =$   
243 40;  $p = <0.001$ ; Figure 4).

244

## 245 **DISCUSSION**

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

257

258 Previous work in this study system suggests that the variable responses of these ant species may be  
259 predictable based on the thermal tolerance ( $CT_{max}$ ) of these species (Diamond et al. 2012a, Stuble et al.  
260 2013). Specifically, the relationships between experimental warming and ant worker densities and  
261 foraging were significantly associated with  $CT_{max}$ , but only for ants at the southern study site. Applying  
262 the same approach to this dataset of species incidence, we found that  $CT_{max}$  was not significantly  
263 associated with the incidence~GDD slope (see Figures 2 and 3) ( $F_{1,18} = .2.8$ ,  $p = 0.11$ ). Although ants with  
264 higher  $CT_{max}$  may be more active in higher temperatures (Diamond et al. 2012a, Stuble et al. 2013), other  
265 processes such as thermoregulation (Sunday et al. in press) or changes in nest architecture (Jones and  
266 Oldroyd 2007) may allow ant species to persist in the short run in environments that exceed their  $CT_{max}$ .

267 In the long run, these acclimations may lead to a reduction in colony size and eventual extirpation  
268 (Sinervo 2010).

269

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

279

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

291

292 Our study suggests that ant community responses to warming in lower latitudes are more likely to  
293 experience decreases in diversity and changes in composition than those at higher latitudes (Colwell et al.  
294 2008). Future research efforts should assess the consequences of abundance increases of thermophilic  
295 species, which could exert strong indirect effects of warming through species interactions.

296

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307

308 **LITERATURE CITED**

309

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455

456 **TABLES**

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

<b>Environmental variable</b>	<b>Southern Site</b>	<b>Northern Site</b>
Latitude (decimal degrees)	35.9	42.5
Elevation (meters 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 2cm 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)	$17 \times 10^3$ - $30 \times 10^3$	$5.4 \times 10^3$ - $14 \times 10^3$

459 Notes: Temperature and soil moisture values are based on conditions during 48 hour pitfall  
 460 sampling periods across the 30 month study period. In contrast, Growing Degree Days are accumulated  
 461 across the 30 month study period ( $T_{base}=15^{\circ}\text{C}$ ). “Southern Site” is Duke Forest (North Carolina, USA);  
 462 “Northern Site” is Harvard Forest (Massachusetts, USA).

463

464 **Table 2. ANOVA table for diversity metrics modeled as a function of site, Growing Degree Days**  
 465 **(GDD), soil moisture, and site-GDD and site-soil moisture interactions.**  
 466

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

467 Notes: We used a weighted linear regression model for Chao2, with the weights being  
468 proportional to the inverse of the estimated variance for Chao2. Because some extrapolations of species  
469 richness can have a very large estimated variance, this procedure down weights those highly uncertain  
470 estimates in the regression models. Sites are as in Table 1.

471 \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001

472

473

474 **FIGURES**

475

476 **Figure 1. Regression plots for Mean ( $\pm$  SE) Chao2 and PIE as a function of the number of Growing**  
477 **Degree Days (GDD) and Soil Moisture at the Southern (open circles) and Northern (filled circles)**  
478 **study sites.** “Southern Site” is Duke Forest (North Carolina, USA); “Northern Site” is Harvard Forest  
479 (Massachusetts, USA). We found only one statistically significant relationship ( $P < 0.05$ ): Chao2  
480 estimates of diversity decreased significantly with GDD at the southern site. We used a weighted linear  
481 regression model for Chao2, with the weights being proportional to the inverse of the estimated variance  
482 for Chao2. Because some extrapolations of species richness can have a very large estimated variance, this  
483 procedure down-weights those highly uncertain estimates in the regression models. The line of best fit for  
484 Chao2 is based on this weighted linear regression model. Growing degree-days were summed across all  
485 time periods.

486

487 **Figure 2. Thermal trends in community composition at (A) Southern Site and (B) Northern Site.**

488 Sites are as in Figure 1. For each site, we used bootstrapping and hierarchical modeling (modified from  
489 Gotelli et al. 2010) to estimate the slope of incidence as a function of GDD (pooled across the entire study  
490 period) for each species. Here we show the linear trends for all species plotted against GDD for both the  
491 observed and one randomized community.

492

493 **Figure 3. Ant species responses to warming at (A) Southern Site and (B) Northern Site.** Sites are as  
494 in Figure 1. The slope of incidence as a function of growing degree days (GDD) is presented in context of  
495 ant phylogenetic history (Moreau and Bell 2013). The magnitudes and directions of the slopes of  
496 incidence as a function of GDD slopes indicated by distance from the zero line and positive/negative  
497 values, respectively); significance is indicated by asterisks: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . The  
498 slopes have been scaled, but not centered, such that shaded circles always correspond with positive



499 slopes. Data for *Protomagnathus americanus* are not included in the figure because this species is not  
500 represented in Moreau's phylogeny; the results for this species are: slope= 2.3E-05, se=6.2E-05; p=0.72.

501

502 **Figure 4. Ant species richness as a function of mean air temperature at sites in the Smoky**

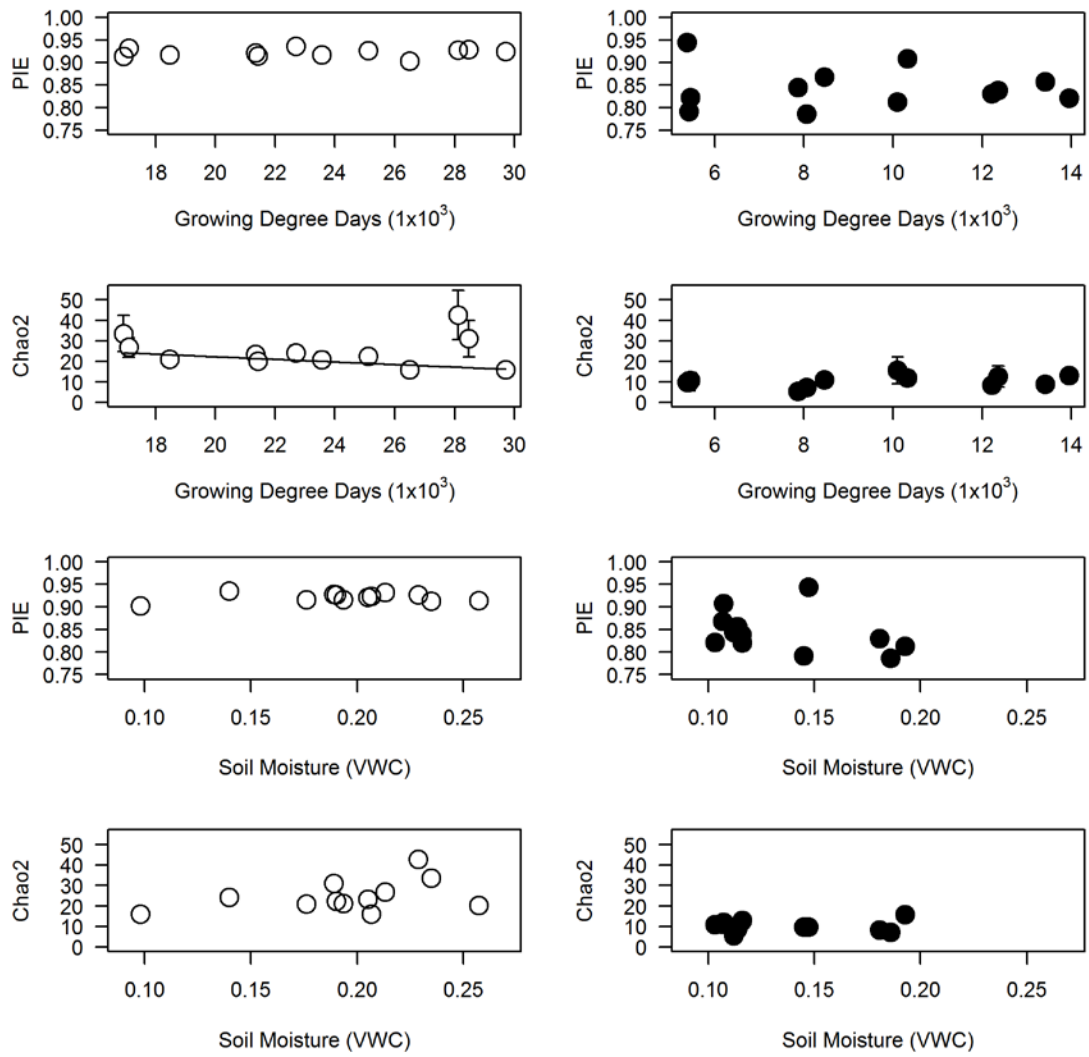
503 **Mountains (triangles; upper panel) and Southern (filled circles) and Northern (open circles)**

504 **experimental chambers (lower panel).** Sites are as in Figure 1. Solid lines represent statistically

505 significant relationships ( $P < 0.05$ ); dashed are non-significant.

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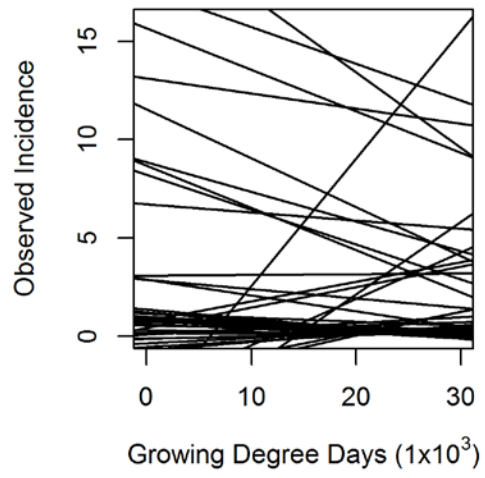
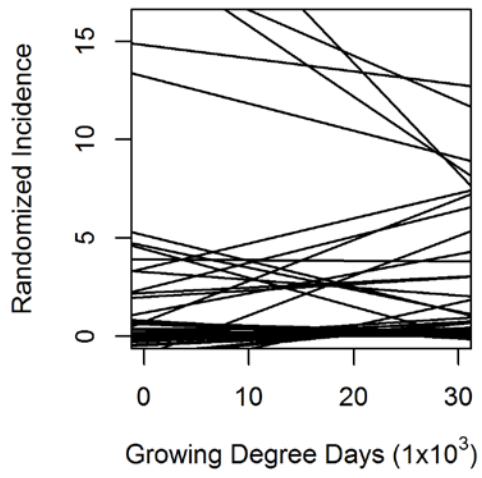


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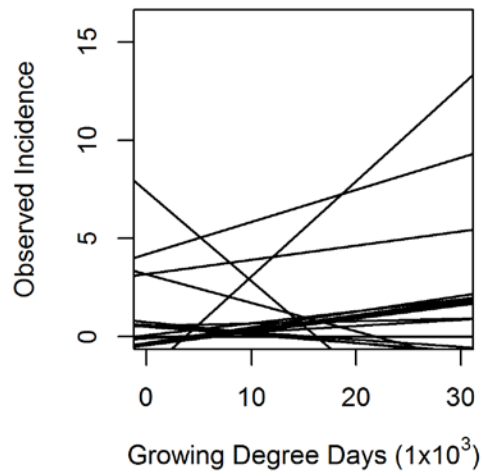
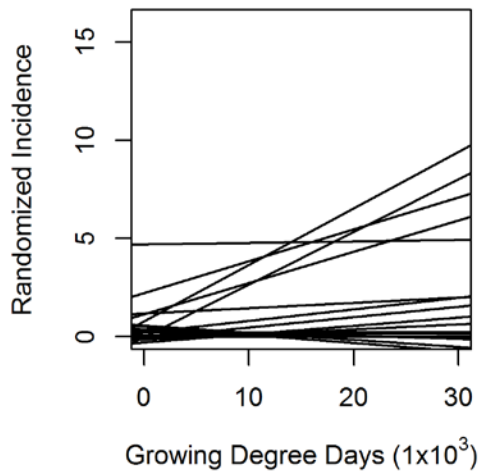
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Figure 1

A



B

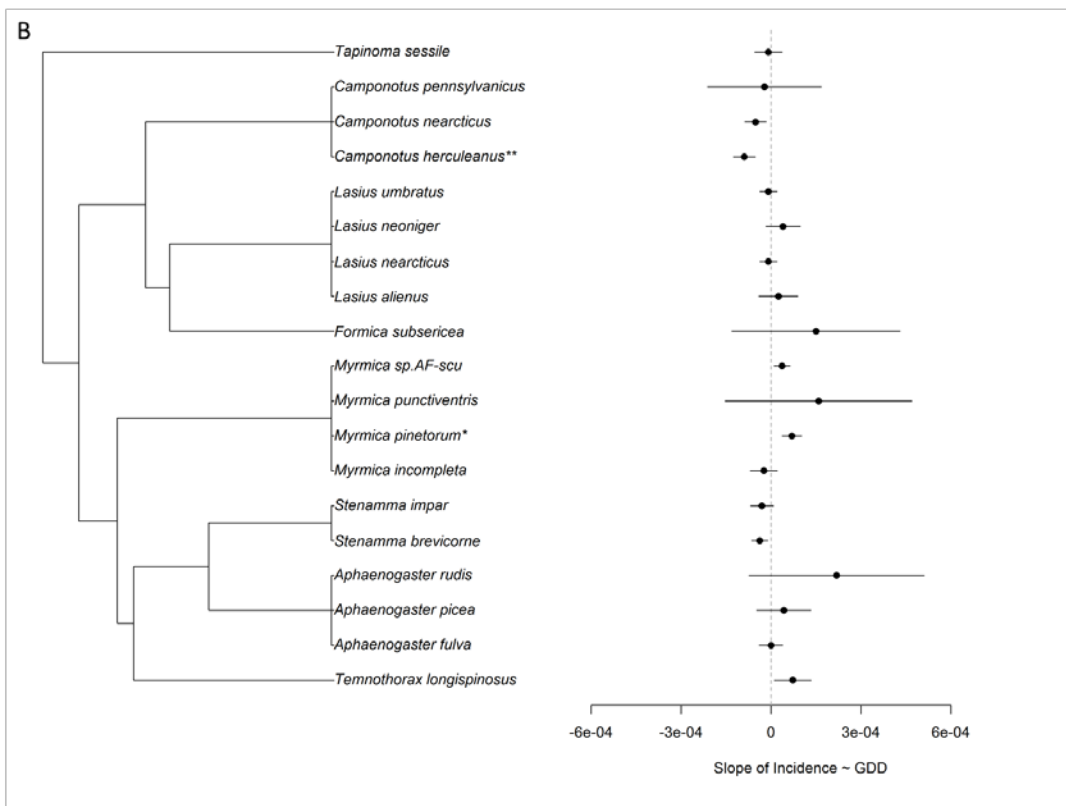
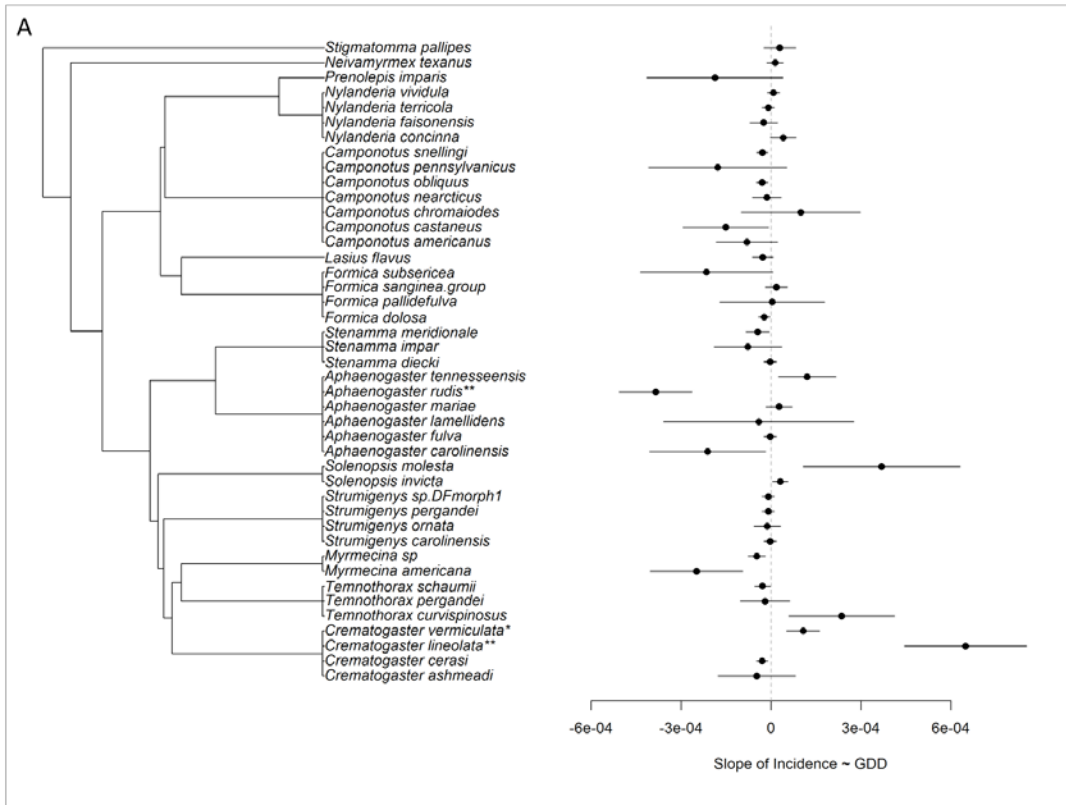


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Figure 2

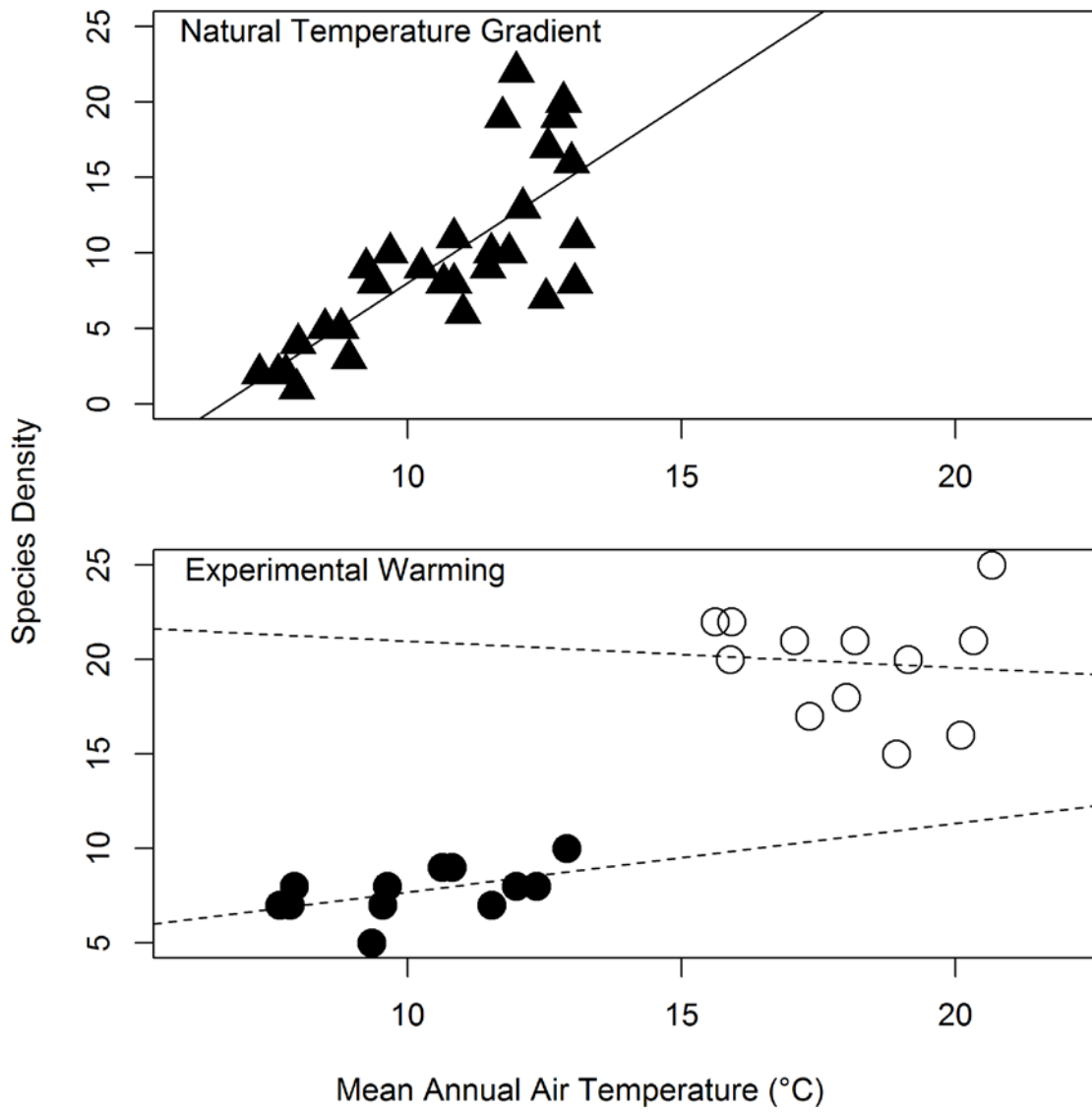


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Figure 3



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Figure 4