Effects of Short-Term Warming On Low and High Latitude Forest Ant Communities

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1   EFFECTS OF SHORT-TERM WARMING ON LOW AND HIGH LATITUDE FOREST ANT

2   COMMUNITIES

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20

21 **ABSTRACT**

22

23 Climatic change is expected to have differential effects on ecological communities in different

24 geographic areas. However, few studies have experimentally demonstrated the effects of

25 warming on communities simultaneously at different locales. We manipulated air temperature

26 with *in situ* passive warming and cooling chambers and quantified effects of temperature on ant

27 abundance, diversity, and foraging activities (predation, scavenging, seed dispersal, nectivory,

28 granivory) in two deciduous forests at 35° and 43° N latitude in the eastern US. In the southern

29 site, the most abundant species, *Crematogaster lineolata*, increased while species evenness, most

30 ant foraging activities, and abundance of several other ant species declined with increasing

31 temperature. In the northern site, species evenness was highest at intermediate temperatures, but

32 no other metrics of diversity or foraging activity changed with temperature. Regardless of

33 temperature, ant abundance and foraging activities at the northern site were several orders of

34 magnitude lower than those in the southern site.

35

36 **KEY WORDS:** climate change; community composition; foraging; Formicidae; warming

37 experiment.

38

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42 **INTRODUCTION**

43

44 The ecological impacts of projected climatic change are likely to have a strong geographic

45 signal. For species that have geographic ranges constrained by temperature, warming may

46 facilitate population increases and range expansions at high latitudes while simultaneously

47 decreasing population sizes and contracting ranges at low latitudes (Parmesan and Yohe 2003).

48 Other studies suggest that the consequences of warming will be more severe at lower latitudes,

49 where organisms may be more sensitive to fluctuating temperatures (Deutsch et al. 2008,

50 Tewksbury et al. 2008, Dillon et al. 2010). Differential responses of populations to warming at

51 high versus low latitudes also can be accompanied by community-level changes such as

52 increases in species diversity at high latitudes and decreases in species diversity at low latitudes

53 (Menendez et al. 2006, Wilson et al. 2007).

54

55 Other factors may obscure, or even ameliorate, the geographic signal of climate change on

56 ecological communities. For example, temperature increases are expected to be more

57 pronounced at high latitudes (Solomon et al. 2007). Local adaptation to historical climates, and

58 corresponding maladaptation to new climates, also may be more pronounced at high latitudes

59 (Pelini et al. 2009). Although individual organisms at low latitudes may be more sensitive to

60 climatic change than those at high latitudes, ecological communities at low latitudes could be

61 more resilient to environmental change because they are generally more diverse (Wittebolle et al.

62 2009). Yet, because most experimental studies of the effects of warming have been conducted at

63 single sites (but see Doak and Morris 2010), it is unclear whether warming will have differential

64 effects on the structure and function of similar communities and ecosystems across latitude and

65 diversity gradients. Here, we report the results of a temperature manipulation experiment on ant

66 community composition and foraging activity in deciduous forests that was conducted

67 simultaneously at two sites, separated by 8 degrees of latitude (~1000 km), in the eastern United

68 States.

69

70 We focused on ants because they are numerically dominant in many terrestrial ecosystems, and

71 their foraging activities, including seed dispersal, nectivory, granivory, predation, and

72 scavenging, cut across many trophic levels and can affect ecosystem processes such as nutrient

73 cycling (c.f. Hölldobler and Wilson 1990, Folgarait 1998). We experimentally manipulated a key

74 component of climatic change – atmospheric warming – because temperature is correlated with

75 patterns of ant diversity and abundance (Kaspari et al. 2003, Sanders et al. 2007, Dunn et al.

76 2009), seasonal patterns of activity (Dunn et al. 2007), foraging behavior (Ruano et al. 2000),

77 and the outcomes of interactions between species (Cerdá et al. 1997, Holway et al. 2002). We

78 hypothesized that changes in air temperature would have different effects on ant abundance,

79 species richness, species evenness, and foraging activities at the two sites. We expected that ant

80 abundance, diversity and foraging activities would increase in the northern site, where cooler

81 temperatures may be limiting, while ant abundance, diversity and foraging may decrease at the

82 southern site, where many ant species are already exposed to temperatures near their thermal

83 limits.

84

85 **METHODS**

86

87 *Study Sites*

88

89   The warming experiment was conducted simultaneously at two sites, Harvard Forest ("northern

90   site") and Duke Forest ("southern site"). Harvard Forest is in central Massachusetts in the

91   northern hardwood hemlock-white pine transition zone (42° 31' 48"N, 72° 11' 24"W, 300 m

92   elevation above sea level (a.s.l.)). The mean annual temperature at Harvard Forest is 7.1° C and

93   the mean annual precipitation is 1066 mm. Our experimental site at Harvard Forest is in an ~70-

94   yr-old oak-maple stand in the Prospect Hill Tract. Duke Forest is near Hillsborough, North

95   Carolina (35° 52' 0" N, 79° 59' 45" W, 130 m a.s.l.), in the Piedmont region. The mean annual

96   temperature at Duke Forest is 15.5°C and mean annual precipitation is 1140 mm. Our

97   experimental site at Duke Forest is in an ~80-yr-old oak-hickory stand within the Eno River

98   Unit.

99

100   Harvard Forest and Duke Forest share more than 30 ant species but they differ substantially in

101   ant diversity and abundance (Pelini et al. 2011). An additional 65 species have been recorded at

102   Duke Forest but not at Harvard Forest, and an additional 12 species have been recorded at

103   Harvard Forest but not at Duke Forest. Ants are active at Harvard Forest April through

104   November while those at Duke Forest are active year-round, but peak abundance occurs May-

105   August at both sites. In our experimental chambers during the six months of this experiment, we

106   captured 16,000 individuals from 28 species at Duke Forest and fewer than 1000 individuals

107   from 9 species at Harvard Forest. Only one species, *Aphaenogaster rudis*, occurred in the

108   experimental chambers at both sites.

109

110   *Minichamber design and deployment*

111

112   We altered air temperatures in the forest understory near the forest floor by using passively

113   heated and cooled minichambers (Lessard et al. 2010, Wittman et al. 2010). Each minichamber

114   was a table-shaped frame of 1.3-cm-diameter PVC pipe that supported a 1×1 m open-top frame

115   57 cm above the ground. Previous work on ant communities has documented ant responses to

116   both abiotic and biotic changes caused by these treatments in similar sized plots (e.g., Kaspari et

117   al. 2003, Sanders et al. 2007, McGlynn et al. 2009). A common ant at both sites, *Aphaenogaster*

118   *rudis*, has foraging and nest emigration distances shorter than 1m (Smallwood 1982). To reduce

119   temperatures, we covered the top frame of 10 of the minichambers at each site with a 1×1 m

120   piece of shade cloth mesh that reduced solar gain by 80% but allowed for rain penetration to the

121   soil surface. To raise temperatures in 10 of the minichambers at each site, we attached clear

122   polyethylene sheeting to the top and along each side down to a height of 9 cm above the soil.

123   We punched 25 6-mm-diameter holes in a uniform pattern in the top polyethylene to allow for

124   rain penetration. We also established 10 control minichambers, which were PVC frames only.

125   We secured the legs of the minichambers to the ground with iron rods.

126

127   Under the forest canopy at both sites, we arranged the 30 minichambers in a completely

128   randomized design, with neighboring minichambers being separated by at least five meters. We

129   deployed the minichambers in April 2009, when many ant species actively move their nests

130   (Smallwood 1982). We left the minichambers in place until the experiment was ended in

131   September 2009.

132

133   *Temperature*

134

135   We recorded air and soil temperatures in all of the northern minichambers with thermistors

136   connected to a Campbell Scientific data logger (CR100, Logan, Utah). At the southern site, we

137   measured air temperature in seven randomly-chosen minichambers of each treatment (i.e., 21 out

138   of the 30 minichambers) using iButton® electronic temperature sensors (Dallas Semiconductors,

139   Dallas, TX). We shielded all air temperature sensors from direct sun and rain and placed them 5

140   cm above the litter layer beneath the minichambers.

141

142   Though the minichamber treatments were implemented as one-factor ANOVA design with three

143   treatment levels (cooling, warming, control), there was substantial variation in temperature

144   within treatment groups due to microhabitat and other variables not manipulated in this study.

145   Thus, we treated the temperature manipulation as a continuous variable and used regression to

146   determine the effects of variation in temperature on ant assemblage composition and foraging

147   activities (Inouye 2001, Cottingham et al. 2005). We note that both regression and ANOVA are

148   linear models of identical mathematical form, and unlike ANOVA, regression analysis can

149   identify potential nonlinearities in associations between temperature and ant response variables

150   (Cottingham et al. 2005, Meyers et al. 2009).

151

152   Though variation in soil temperature is also an important determinant of ant community structure

153   and foraging activities, we used air temperature data in analyses of temperature effects on ant

154   composition and activity because soil temperature was not measured at the southern site. Soil

155   temperatures did track air temperatures similarly in the three minichamber treatments (i.e., the

156   differences between average soil and air temperatures were the same in the three treatments) at

157   Harvard Forest (ANOVA: $F_{2,37}$= 1.6, P= 0.21; Figure 1). We are confident that the associations

158   we report between air temperature and ant community structure and foraging activities reflect

159   real responses to temperature change. Finally, we also calculated the average daily range of

160   temperatures by subtracting the daily minimum from the maximum for each minichamber and

161   used this variable to test whether or not diurnal variation in temperature affected the ant

162   communities that we studied.

163

164   *Ant Community Composition*

165

166   In September 2009, we terminated the experiment and collected all of the leaf litter within each

167   minichamber to sample ants. We extracted, identified and counted ants from all organic matter

168   and loose surface soil in the 1 m^2 area using Winkler extractors (Fischer 1998). We used general

169   linear models with Poisson error distributions to examine relationships between total ant

170   abundance and species richness with average temperature and diurnal variation in temperature at

171   both sites. We estimated species evenness using Hurlbert's PIE (probability of an interspecific

172   encounter; Hurlbert 1971) for each minichamber. This diversity index is equivalent to the slope

173   of an individual-based rarefaction curve measured at its base (Olsweski 2004). We used general

174   linear models to examine the relationship between PIE and temperature in the southern site, but

175   because of strong departures from normality in data from the northern site, we examined these

176   latter data using locally weighted scatterplot smoothing.

177

178   *Foraging activities*

179

180   We recorded the rate at which ants removed different kinds of baits to assess effects of

181   temperature on foraging activities. We used Demerara sugar grains (Signature Brands, Ocala,

182   FL) to estimate nectivory rates, live adult termites (*Reticulatermes flavipes*) to estimate predation

183   rates (Wilson 1971), dead adults of *R. flavipes* or *Tenebrio molitor* (mealworms) to estimate

184   scavenging rates (Jeanne 1979), and milled oat grain (*Avena sativa*) to estimate granivory rates

185   (Valone and Kaspari 2005). We also measured rates of removal of seeds of wild ginger (*Asarum*

186   *canadense*), a native forest understory species that occurs at both sites and that has seeds with

187   eliasomes that are commonly dispersed by ants in the eastern US (Hölldobler and Wilson 1990).

188

189   We conducted the bait removal experiments at both sites in August through early September

190   2009. On each census day, we used only one bait type. In each minichamber, we placed one 55-

191   cm-diameter plastic petri dish with ten units of bait and recorded the number of bait units

192   remaining at 30-minute intervals for two hours. We quantified removal of bait as the area under

193   the curve of the number of baits removed versus time. This measure of activity integrates time to

194   discovery, number of foragers, and rate of removal. To adjust for outliers, we used robust

195   regression to examine the relationship between foraging activities and temperature at both sites.

196

197   All statistical analyses were performed in R (version 2.9.0, R Development Core Team 2007) or

198   EcoSim (Version 7.0, Gotelli & Entsminger 2009).

199

200   **RESULTS**

201

202   *Temperature*

203

204   Average temperatures during the experiment at the southern and northern sites were 22.8 ± 0.3°C

205   and 17.5 ± 0.4°C across treatments, respectively. Warming and cooling minichamber treatments

206   increased and decreased average temperatures ~0.3°C relative to controls at both sites (Figure 2).

207   In addition, diurnal variation in air temperature (i.e. difference between daily minimums and

208   maximums) did not differ across minichamber treatments (southern site ANOVA: $F_{2,17}=1.7$,

209   P=0.22; northern site ANOVA: $F_{2,27}=2.9$, P=0.07).

210

211   *Ant Community Composition*

212

213   We collected a total of 16,421 individuals and 28 ant species at the southern site and 780

214   individuals and 9 ant species at the northern site. *Crematogaster lineolata* was the most abundant

215   ant species in the southern site, and *Aphaenogaster rudis* was the most abundant ant species in

216   the northern site. Overall, ant abundance (i.e., number of individuals across all ant species),

217   species richness, and evenness (PIE) were significantly higher at the southern site than at the

218   northern site (abundance: $F_{1,43}=62$, *P* <0.001; richness: $F_{1,43}=194$, *P* <0.001; evenness: $F_{1,43}=119$,

219   *P* <0.001).

220

221   Total abundance of ants increased by 240% for every 1°C increase in temperature at the southern

222   site ($X^2 = 2800$; *P* < 0.001), but was not associated with average temperature at the northern site

223   (Figure 3, upper panels). Species evenness decreased by 60% with 1°C increase in average

224   temperature in the southern site ($X^2 = 6.9$; *P* = 0.009) and was highest at intermediate

225   temperatures in the northern site (Figure 3, middle panels). Species richness was not associated

226   with average temperature at either site (Figure 3, lower panels). Species evenness also was

227   highest at intermediate levels of diurnal variation in temperature in the northern site, but no other

228   metrics of ant community composition were associated with diurnal variation in temperature

229   (Figure 4). The abundance of *C. lineolata*, the most abundant ant species at the southern site,

230   increased by 190% with temperature ($X^2 = 5700$; $P < 0.001$) while the abundance of

231   *Aphaenogaster rudis*, the most common ant at the northern site did not vary with temperature (X^2

232    $= 1.7$; $P = 0.19$).

233

234   *Foraging Activities*

235   Across temperatures, foraging activities were higher at the southern site (seed dispersal: 700%;

236   nectivory: 130%; granivory: 1000%; predation: 200%; scavenging: 650%). However, when

237   foraging activity was standardized to account for differences in abundance at the two sites, per

238   capita foraging activities were substantially higher at the northern site (seed dispersal: 200%;

239   nectivory: 700%; granivory:16%; predation: 700%; scavenging: 300% higher at the northern

240   site).

241

242   At the southern site, per degree of warming, seed dispersal, nectivory, and granivory decreased

243   approx. 50% from the site averages for these activities (Figure 5, left panels). At the northern

244   site, none of the foraging activities were altered substantially by temperature (Figure 5, right

245   panels). Diurnal variation in temperature was negatively associated with nectivory and granivory

246   at the southern site and weakly positively associated with scavenging at the northern site (Figure

247   6).

248

249

250 **DISCUSSION**

251 Climatic change is expected to have differential effects on ecological communities in different

252 geographic areas, but forecasts of climatic change based on global or even large-scale regional

253 climatic patterns are unlikely to provide accurate assessments of short-term, small-scale changes

254 in temperature, which ultimately regulates local ant abundance, richness, and foraging activities

255 (Wehner et al. 1992, Cerdá et al. 1997, Azcarate et al. 2007, Chong and Lee 2009). Furthermore,

256 few studies have experimentally demonstrated the effects of warming on communities

257 simultaneously at different locales (but see Doak and Morris 2010). Our experimental results

258 suggest that even modestly warmer average daytime temperatures can have large impacts, some

259 mediated disproportionately by abundant species, on ant communities at lower latitudes.

260 However, at higher latitudes, observed responses were much weaker and in general they may be

261 slower than observed in other studies (cf. Parmesan and Yohe 2003).

262

263 At the more species-rich southern site, the abundance of *Crematogaster lineolata*, the most

264 abundant species at that site, increased with temperature. Warming may have resulted in

265 acceleration of successful brood production and development, or *C. lineolata* may have moved

266 from cooler patches to the small islands of heat formed by the treatment (Moise and Henry

267 2010). Both effects are likely to occur as increases in mean temperatures create new thermal

268 landscapes in which some, but not all, patches are warmer than current conditions. At the same

269 time that the abundance of *C. lineolata* increased, species evenness and overall ant foraging

270 activities decreased with increasing temperature. We suggest that this result may be due to

271 competitive displacement by *C. lineolata* of other species in the chambers. Altered dominance

272   patterns driven by climatic change have been shown in other systems and may be a common

273   feature of the earliest responses of communities to warming (e.g., Kardol et al. 2010).

274

275   In contrast to the strong responses we observed at the southern site, we observed relatively weak

276   responses at the northern site, even though foraging of colonies at the northern site is likely to be

277   limited by cold temperatures (cf. Hölldobler and Wilson 1990). Among community measures,

278   only species evenness was associated with temperature, reaching highest values at intermediate

279   temperatures. These responses were opposite of our initial predictions. It is possible that the

280   overall low ant abundance at the northern site limits the ability to detect responses. Greater

281   increases in temperature may be needed before the abundances of northern populations increase.

282   Alternatively, it may be the case that the structure and dynamics of more temperate ant

283   communities are not limited exclusively by temperature. Several studies now exist in which

284   northern populations of insects do not experience changes in population sizes with warming

285   (e.g., Adler et al. 2007, Pelini et al. 2009).

286

287   The different responses of ant communities to temperature at our two study sites also could be

288   associated with other factors that co-vary with latitude. Although the two study sites do share

289   many ant species and occur in similar deciduous forests, they differ dramatically in ant

290   abundance, diversity and foraging activity. Furthermore, historical differences in climate,

291   particularly temperature, and differences in seasonality may have been strong selective agents

292   that constrain responses to temperature. For example, cold temperate species may have higher

293   thermal maxima relative to ambient temperatures (Deutch et al.) such that species at higher

294   latitudes have to be warmed more to experience fitness consequences.

295

296 By manipulating temperature only during spring and summer, we focused on the effects of

297 warming on rates of foraging, development and potentially mortality during the active period of

298 ants in the two regions and avoided potential confounding effects of warming on winter survival.

299 When ants are most active, they respond to warming by shifts in foraging (and food intake)

300 and/or shifts in development in their present locations. At the hottest temperatures we observed

301 at the southern site, they may also respond through reduced activity or even mortality. Ants also

302 may track environmental conditions by moving their colonies. Such a response to climatic

303 change is also seen in other animals (Moise and Henry 2010). Outside of the minichambers at

304 both sites, we have observed multiple, within-season relocations of colony sites by

305 *Aphaenogaster rudis*, and other studies provide similar evidence for the redistribution of ant

306 colonies during a single season (Hölldobler and Wilson 1990, Foitzik et al. 2004, McGlynn et al.

307 2009, Lessard et al. 2010). Just as for birds and mammals, actual responses to climatic change

308 inevitably reflect a mix of behavioral responses to warming, such as local shifts in habitat use,

309 and demographic responses. A third possibility is that individual foragers may move into

310 treatments areas to forage. Future studies should consider the effects of warming during cooler

311 periods on ant community composition and activity.

312

313 As the climate changes, trophic cascades and ecosystem processes dependent on ants are likely

314 to change in tandem. (Folgarait 1998, Petchey et al. 1999, Lensing and Wise 2006, Suttle et al.

315 2007, Barton et al. 2009, Harmon et al. 2009, O'Connor et al. 2009, Gilman et al. 2010, Traill et

316 al. 2010). We found this to be the case at our southern site, where we observed decreases in rates

317 of granivory, seed dispersal, and nectivory. Such changes suggest that ant responses to climatic

318 change may have cascading consequences for species dependent upon particular ants, such as

319 ant-dispersed plants (Gove et al. 2007) or insects tended for honeydew in exchange for

320 protection by ants (Stadler and Dixon 2008). More detailed, long-term studies of the responses of

321 ants to climatic change, both observational and experimental, are needed to improve the forecasts

322 of these changes.

323

324

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326

331

332   **LITERATURE CITED**

333

334   Adler, L. S., P. De Valpine, J. Harte, and J. Call. 2007. Effects of long-term experimental

335   warming on aphid density in the field. Journal of the Kansas Entomological Society 80:156-

336   168.

337

338   Azcarate, F. M., E. Kovacs, and B. Peco. 2007. Microclimatic conditions regulate surface

339   activity in harvester ants Messor barbarus. Journal of Insect Behavior 20:315-329.

340

341   Barton, B. T., A. P. Beckerman, and O. J. Schmitz. 2009. Climate warming strengthens indirect

342   interactions in an old-field food web. Ecology 90:2346-2351.

343

344   Cerda, X., J. Retana, and S. Cros. 1997. Thermal disruption of transitive hierarchies in

345   Mediterranean ant communities. Journal of Animal Ecology 66:363-374.

346

347   Chong, K. F. and C. Y. Lee. 2009. Influences of Temperature, Relative Humidity and Light

348   Intensity on the Foraging Activity of Field Populations of the Longlegged Ant, Anoplolepis

349   gracilipes (Hymenoptera: Formicidae). Sociobiology 54:531-539.

350

351   Cottingham, K. L., J. T. Lennon, and B. L. Brown. 2005. Regression versus ANOVA -

352   Response. Frontiers in Ecology and the Environment 3:358-358.

353

354 Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and

355   P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude.

356   Proceedings of the National Academy of Sciences of the United States of America 105:6668-

357   6672.

358

359 Dillon, M. E., G. Wang, and R. B. Huey. 2010. Global metabolic impacts of recent climate

360   warming. Nature 467:704-706.

361

362 Doak, D. F., and W. F. Morris. 2010. Demographic compensation and tipping points in climate-

363   induced range shifts. Nature 467:959-962.

364

365 Dunn, R. R., C. R. Parker, M. Geraghty, and N. J. Sanders. 2007. Reproductive phenologies in a

366   diverse temperate ant fauna. Ecological Entomology 32:135-142.

367

368 Dunn, R. R., et al. 2009. Climatic drivers of hemispheric asymmetry in global patterns of ant

369   species richness. Ecology Letters 12:324-333.

370

371 Fisher, B. L. 1998. Ant diversity patterns along an elevational gradient in the Reserve Naturelle

372   Integrale dAndringitra and on the western Masoala Peninsula, Madagascar. Fieldiana

373   (Zoology) 90:39-67.

374

375 Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review.

376   Biodiversity and Conservation 7:1221-1244.

377

378   Foitzik, S., V. L. Backus, A. Trindl, and J. M. Herbers. 2004. Ecology of Leptothorax ants:

379   impact of food, nest sites, and social parasites. Behavioral Ecology and Sociobiology 55:484-

380   493.

381

382   Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework

383   for community interactions under climate change. Trends in Ecology & Evolution 25:325-

384   331.

385

386   Gotelli, N.J., and G.L. Entsminger Acquired Intelligence Inc. & Kesey-Bear. 2001. EcoSim: Null

387   models software for ecology. Version 7.0.

388   <http://homepages.together.net/~gentsmin/ecosim.htm>

389

390   Gove, A. D., J. D. Majer, and R. R. Dunn. 2007. A keystone ant species promotes seed dispersal

391   in a "diffuse" mutualism. Oecologia 153:687-697.

392

393   Harmon, J. P., N. A. Moran, and A. R. Ives. 2009. Species Response to Environmental Change:

394   Impacts of Food Web Interactions and Evolution. Science 323:1347-1350.

395

396   Hölldobler, B., and E.O. Wilson. 1990. The Ants. Belknap Press, Cambridge, Massachusetts,

397   U.S.A.

398

399   Holway, D. A., A. V. Suarez, and T. J. Case. 2002. Role of abiotic factors in governing

400   susceptibility to invasion: A test with argentine ants. Ecology 83:1610-1619.

401

402   Hurlbert, S. H. 1971. Nonconcept of Species Diversity - Critique and Alternative Parameters.

403   Ecology 52:577.

404

405   Inouye, B. D. 2001. Response surface experimental designs for investigating interspecific

406   competition. Ecology 82:2696-2706.

407

408   Jeanne, R. L. 1979. A Latitudinal Gradient in Rates of Ant Predation. Ecology 60:1211-1224.

409

410   Kardol, P., C. E. Campany, L. Souza, R. J. Norby, J. F. Weltzin, and A. T. Classen. 2010.

411   Climate change effects on plant biomass alter dominance patterns and community evenness

412   in an experimental old-field ecosystem. Global Change Biology 16:2676-2687.

413

414   Kaspari, M., M. Yuan, and L. Alonso. 2003. Spatial grain and the causes of regional diversity

415   gradients in ants. American Naturalist 161:459-477.

416

417   Lensing, J. R. and D. H. Wise. 2006. Predicted climate change alters the indirect effect of

418   predators on an ecosystem process. Proceedings of the National Academy of Sciences of the

419   United States of America 103:15502-15505.

420

421

422   Lessard, J. P., T. E. Sackett, W. N. Reynolds, D. A. Fowler, and N. J. Sanders. 2010.

423   Determinants of the detrital arthropod community structure: the effects of temperature and

424   resources along an environmental gradient. Oikos 120:333-343.

425

426   McGlynn, T. P., R. M. Fawcett, and D. A. Clark. 2009. Litter Biomass and Nutrient

427   Determinants of Ant Density, Nest Size, and Growth in a Costa Rican Tropical Wet Forest.

428   Biotropica 41:234-240.

429

430   Menendez, R., A. G. Megias, J. K. Hill, B. Braschler, S. G. Willis, Y. Collingham, R. Fox, D. B.

431   Roy, and C. D. Thomas. 2006. Species richness changes lag behind climate change.

432   Proceedings of the Royal Society B-Biological Sciences 273:1465-1470.

433

434   Meyers, R. H., D. C. Montgomery, and C. M. Anderson-Cook. 2009. Response Surface

435   Methodology: Process and Product Optimization using Designed Experiments. Third edition.

436   John Wiley & Sons, New York, USA.

437

438   Moise, E. R. D. and H. A. L. Henry. 2010. Like moths to a street lamp: exaggerated animal

439   densities in plot-level global change field experiments. Oikos 119:791-795.

440

441   O'Connor, M. I., M. F. Piehler, D. M. Leech, A. Anton, and J. F. Bruno. 2009. Warming and

442   resource availability shift food web structure and metabolism. Plos Biology 7: e1000178.

443

444   Olsweski, T. D. 2004. A unified mathematical framework for the measurement of richness and

445   evenness within and among multiple communities. Oikos 104:377-387.

446

447   Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts

448   across natural systems. Nature 421:37-42.

449

450   Pelini, S. L., J. D. K. Dzurisin, K. M. Prior, C. M. Williams, T. D. Marsico, B. J. Sinclair, and J.

451   J. Hellmann. 2009. Translocation experiments with butterflies reveal limits to enhancement

452   of poleward populations under climate change. Proceedings of the National Academy of

453   Sciences of the United States of America 106:11160-11165.

454

455   Pelini, S. L., F. P. Bowles, A. M. Ellison, N. J. Gotelli, N. J. Sanders, R. Dunn. 2011. Heating up

456   the forest: Open-top chamber warming manipulation of arthropod communities at Harvard

457   and Duke forests. Methods in Ecology and Evolution. doi: 10.1111/j.2041-

458   210X.2011.00100.x.

459

460   Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming

461   alters food-web structure and ecosystem function. Nature 402:69-72.

462

463   R Development Core Team. 2007. R: a language and environment for statistical computing. R

464   Foundation for Statistical Computing, Vienna, Austria.

465

466   Ruano, F., A. Tinaut, and J. J. Soler. 2000. High surface temperatures select for individual

467   foraging in ants. Behavioral Ecology 11:396-404.

468

469   Sanders, N. J., J. P. Lessard, M. C. Fitzpatrick, and R. R. Dunn. 2007. Temperature, but not

470   productivity or geometry, predicts elevational diversity gradients in ants across spatial grains.

471   Global Ecology and Biogeography 16:640-649.

472

473   Smallwood, J. 1982. Nest relocation in ants. Insectes Sociaux 29:138-147.

474

475   Solomon, S. et al., editors. 2007. Contribution of Working Group I to the Fourth Assessment

476   Report of the Intergovernmental Panel on Climate Change. Cambridge University Press,

477   New York, USA.

478

479   Stadler, B., and A.F.G. Dixon. 2008. Mutualism: Ants and their insect partners**.** Cambridge

480   University Press, Cambridge, UK.

481

482   Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland

483   responses to changing climate. Science 315:640-642.

484

485   Tewksbury, J. J., R. B. Huey, and C. A. Deutsch. 2008. Ecology - Putting the heat on tropical

486   animals. Science 320:1296-1297.

487

488   Traill, L. W., M. L. M. Lim, N. S. Sodhi, and C. J. A. Bradshaw. 2010. Mechanisms driving

489   change: altered species interactions and ecosystem function through global warming. Journal

490   of Animal Ecology 79:937-947.

491

492   Wehner, R., A. C. Marsh, and S. Wehner. 1992. Desert Ants on a Thermal Tightrope. Nature

493   357:586-587.

494

495   Wilson, E.O. 1971. The insect societies. Harvard University Press, Cambridge, Massachusetts,

496   USA.

497

498   Wilson, R. J., D. Gutierrez, J. Gutierrez, and V. J. Monserrat. 2007. An elevational shift in

499   butterfly species richness and composition accompanying recent climate change. Global

500   Change Biology 13:1873-1887.

501

502   Wittebolle, L., M. Marzorati, L. Clement, A. Balloi, D. Daffonchio, K. Heylen, P. De Vos, W.

503   Verstraete, and N. Boon. 2009. Initial community evenness favours functionality under

504   selective stress. Nature 458:623-626.

505

506   Wittman, S. E., N. J. Sanders, A. M. Ellison, E. S. Jules, J. S. Ratchford, and N. J. Gotelli. 2010.

507   Species interactions and thermal constraints on ant community structure. Oikos 119:1056-

508   1056.

509

510   Valone, T. J. and M. Kaspari. 2005. Interactions between granivorous and omnivorous ants in a

511   desert grassland: results from a long-term experiment. Ecological Entomology 30:116-121.

512   FIGURES

513   **Figure 1. Average difference between air and soil temperature June- August in the**

514   **northern minichambers.** "Cooler" minichambers represent PVC frames covered with shade

515   cloth, "Control" minichambers are PVC frames only, and "Warmer" minichambers have PVC

516   frames covered with plastic.

517

518   **Figure 2. Average temperatures June-August in the southern (left) and northern (right)**

519   **minichambers.** "Cooler" minichambers represent PVC frames covered with shade cloth,

520   "Control" minichambers are PVC frames only, and "Warmer" minichambers have PVC frames

521   covered with plastic. Temperatures were recorded in only 21 out of the 30 minichambers at the

522   southern site.

523

524   **Figure 3. Scatterplots of ant diversity measures (total ant abundance, species evenness**

525   **(Hurlbert's PIE), species richness) against average temperature at the southern (left**

526   **panels) and northern (right panels) study sites.** Symbol sizes for each replicate are

527   proportional to the square root of abundance of the most common species at each site

528   (*Crematogaster lineolata* at the southern study site and *Aphaenogaster rudis* at the northern

529   study site).

530

531   **Figure 4. Scatterplots of ant diversity measures (total ant abundance, species evenness**

532   **(Hurlbert's PIE), species richness) plotted against average diurnal variation in**

533   **temperature (daily maximum- daily minimum temperature) at the southern (left panels)**

534   **and northern (right panels) study sites.**

535

536

537 **Figure 5. Scatterplots of ant foraging activities ((bait units removed)*minutes) against**

538 **average temperature at the southern (left panels) and northern (right panels) study sites.**

539 This measure of activity integrates time to discovery, number of foragers, and rate of removal.

540 Slopes and standard errors of the regression lines are shown. Best-fit lines are presented for

541 activities where the slope ± SE of temperature versus bait units removed*minutes did not cross

542 zero.

543

544 **Figure 6. Scatterplots of ant foraging activities ((bait units removed)*minutes) against**

545 **average diurnal variation in temperature (daily maximum- daily minimum temperature) at**
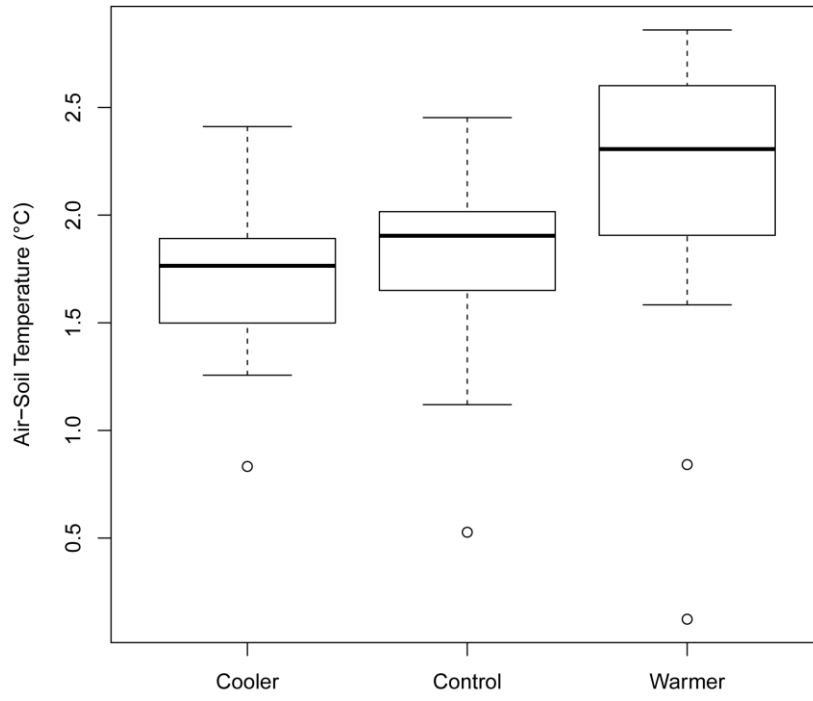
546 **the southern (left panels) and northern (right panels) study sites.** This measure of activity

547 integrates time to discovery, number of foragers, and rate of removal. Slopes and standard errors

548 of the regression lines are shown. Best-fit lines are presented for activities where the slope ± SE

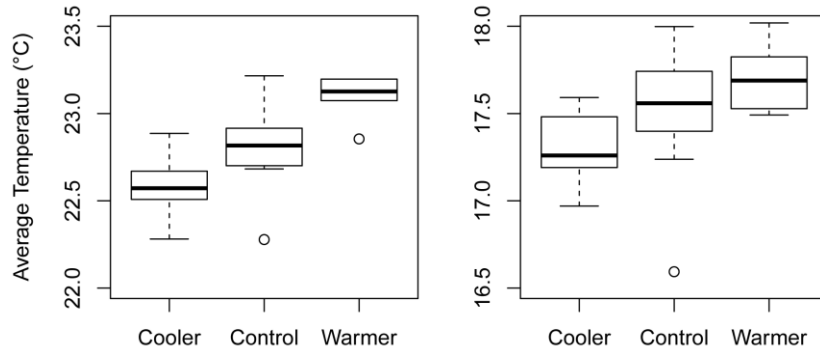549 of temperature versus bait units removed*minutes did not cross zero.

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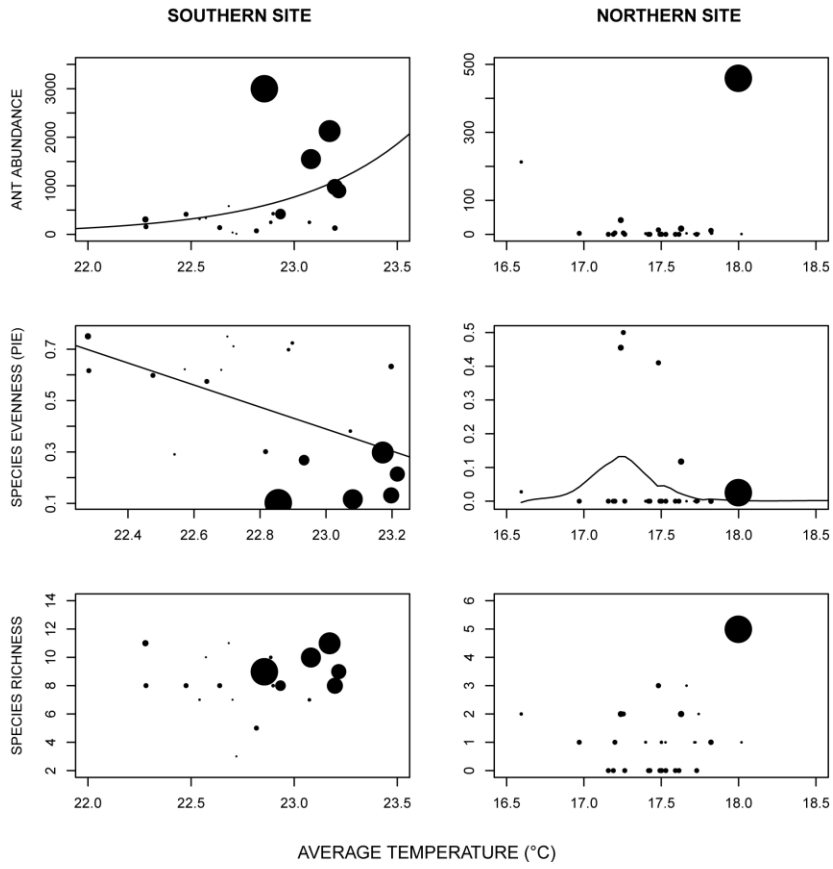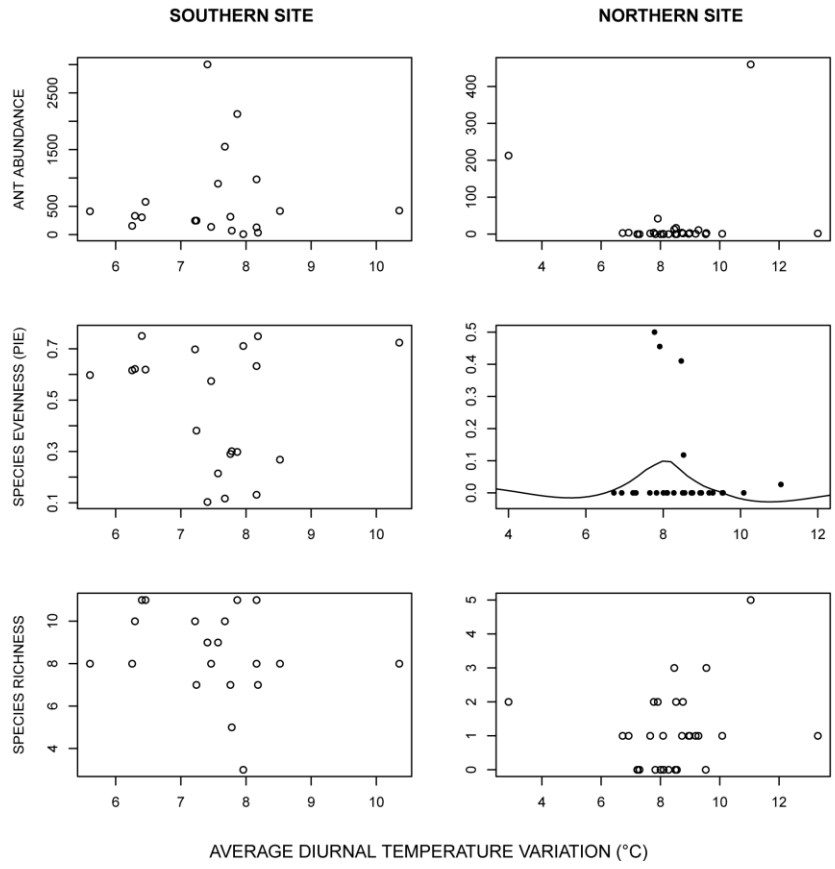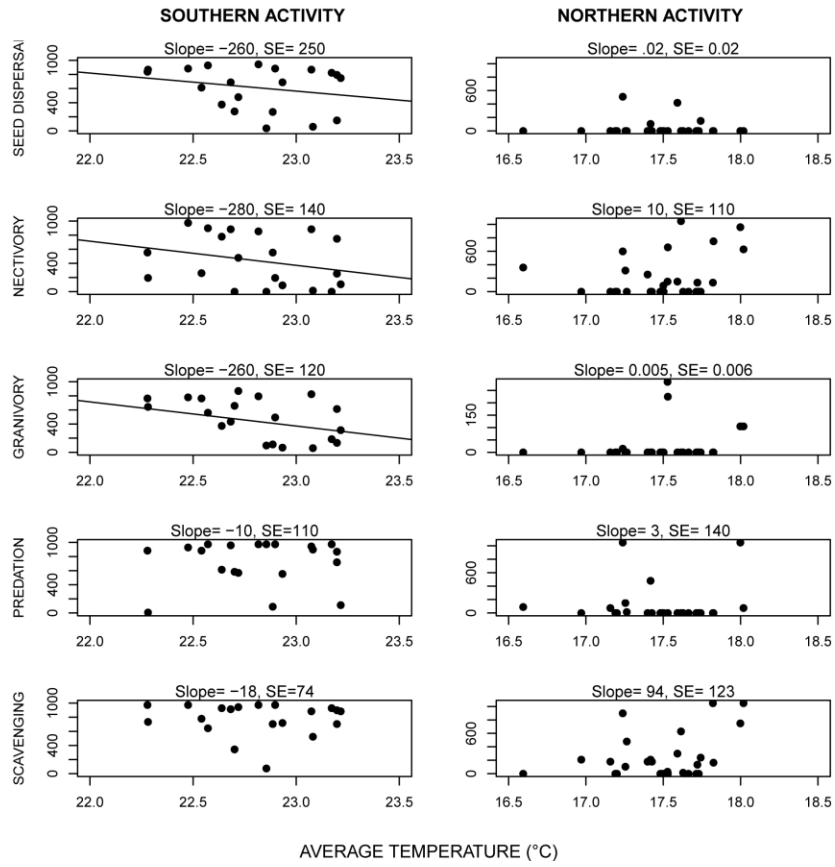555

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SOUTHERN SITE   NORTHERN SITE

561   AVERAGE DIURNAL TEMPERATURE VARIATION (°C)

562   AVERAGE TEMPERATURE (°C)

563   AVERAGE DIRUNAL TEMPERATURE VARIATION (°C)