



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

Citation

Pelini, Shannon L., Mark Boudreau, Neil McCoy, Aaron M. Ellison, Nicholas J. Gotelli, Nathan J. Sanders, and Robert R. Dunn. Forthcoming. Effects of short-term warming on low and high latitude forest ant communities. *Ecosphere*.

Published Version

<http://www.esajournals.org/loi/ecsp>

Permanent link

<http://nrs.harvard.edu/urn-3:HUL.InstRepos:4892936>

Terms of Use

This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Other Posted Material, as set forth at <http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA>

Share Your Story

The Harvard community has made this article openly available.
Please share how this access benefits you. [Submit a story](#).

[Accessibility](#)

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

3
4
5 Shannon L. Pelini^{1,†}, Mark Boudreau^{2,5}, Neil McCoy², Aaron M. Ellison¹, Nicholas J. Gotelli³,
6 Nathan J. Sanders⁴, and Robert R. Dunn²

7
8 ¹Harvard Forest, Harvard University, Petersham, MA 01366

9 ²Department of Biology, North Carolina State University, Raleigh, NC 27695

10 ³Department of Biology, University of Vermont, Burlington, VT 05405

11 ⁴Department of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN

12 37996 *and* Center for Macroecology, Evolution and Climate, Department of Biology,
13 University of Copenhagen, Denmark

14 ⁵Current address: Department of Biological and Agricultural Engineering, University of Georgia,
15 Griffin, GA 30223

16 [†]Email: spelini@fas.harvard.edu

17

18

19

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

39 **CORRESPONDING AUTHOR:** spelini@fas.harvard.edu

40

41

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 m² 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 $22.8 \pm 0.3^{\circ}\text{C}$
205 and $17.5 \pm 0.4^{\circ}\text{C}$ across treatments, respectively. Warming and cooling minichamber treatments
206 increased and decreased average temperatures $\sim 0.3^{\circ}\text{C}$ 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

325 **ACKNOWLEDGEMENTS**

326

327 Funding was provided by a US DOE PER award (DE-FG02-08ER64510) to R.R. Dunn, A. M.
328 Ellison, N. J. Gotelli and N. J. Sanders. We thank A. Koltz, M. VanScoy, I. Del Toro, S. Menke,
329 C. Hirsch, J. Boudreau, R. Tizon, C. Hart, D. Rodriguez, J. Chandler and J. Trombley for field
330 assistance and technical support.

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 Olszewski, 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 \pm 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**

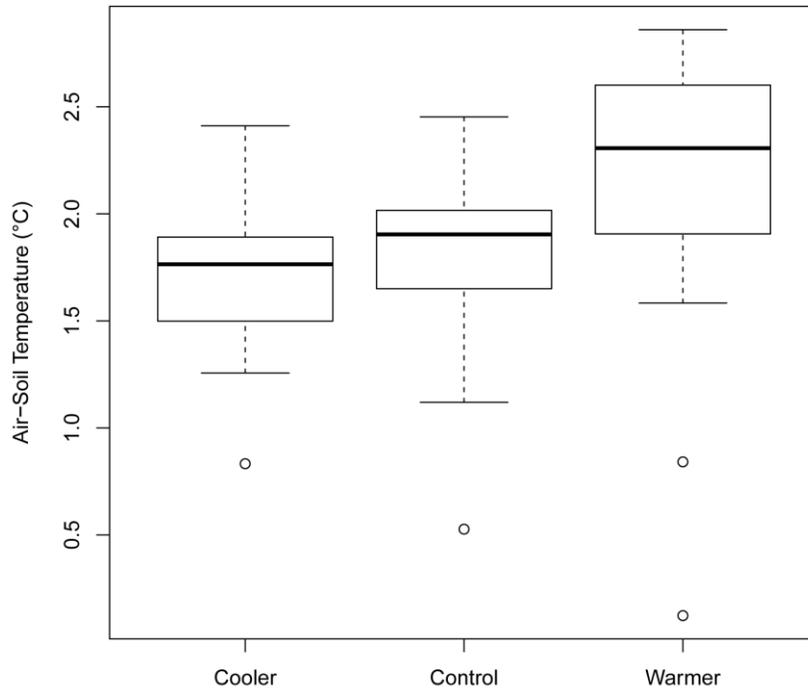
546 **the southern (left panels) and northern (right panels) study sites.** This measure of activity

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 \pm SE

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

550



551

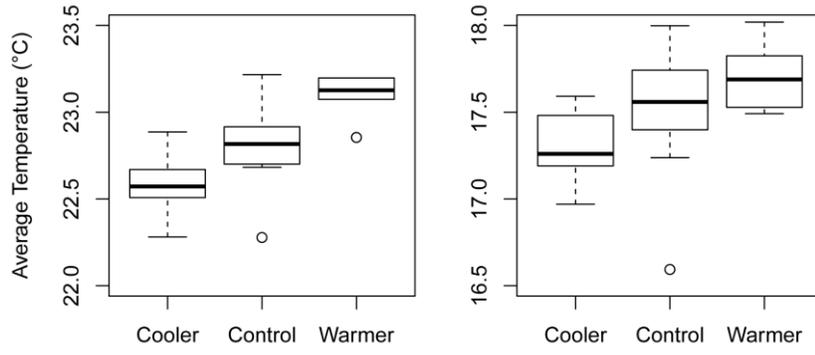
552

553

554

555

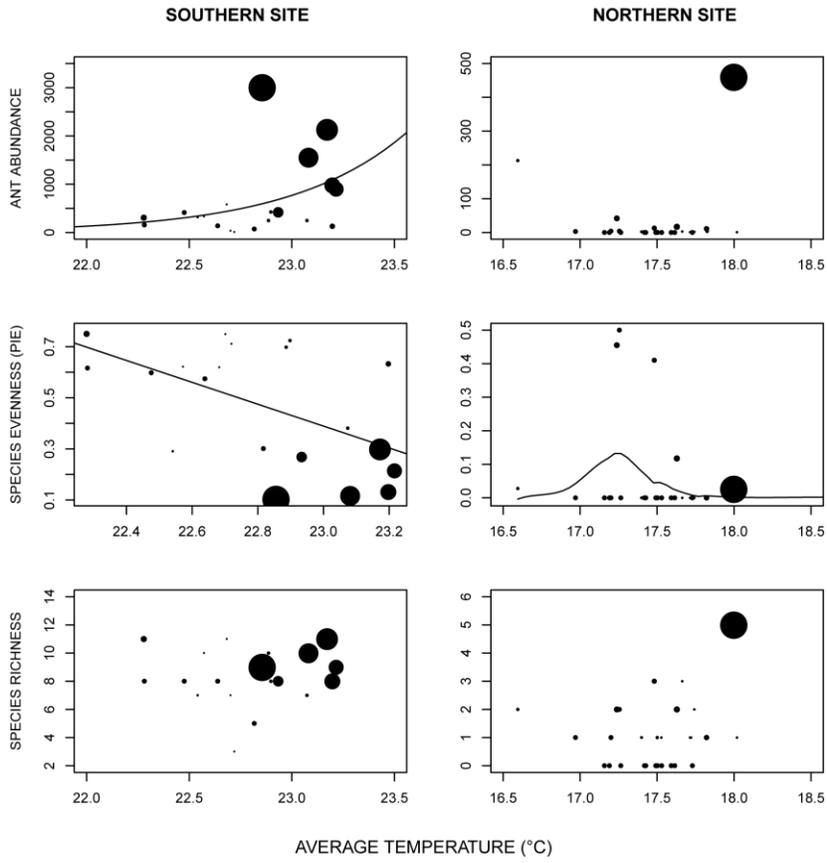
556



557

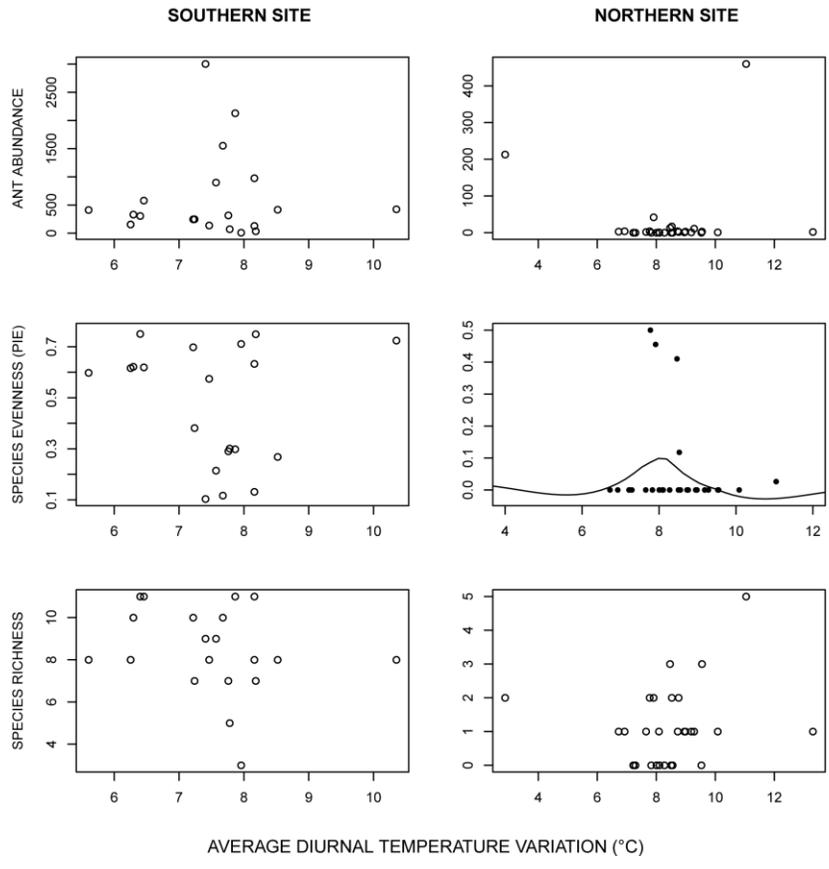
558

559



560

AVERAGE TEMPERATURE (°C)



561

AVERAGE DIURNAL TEMPERATURE VARIATION (°C)

