



# Using Historical and Experimental Data to Reveal Warming Effects on Ant Assemblages

## Citation

Resasco, Julian, Shannon L. Peline, Katharine L. Stuble, Nathan J. Sanders, Robert R. Dunn, Sarah E. Diamond, Aaron M. Ellison, Nicholas J. Gotelli, and Douglas J. Levey. 2014. "Using Historical and Experimental Data to Reveal Warming Effects on Ant Assemblages." Edited by Martin Heil. PLoS ONE 9 (2) (February 4): e88029. doi:10.1371/journal.pone.0088029. <http://dx.doi.org/10.1371/journal.pone.0088029>.

## Published Version

doi:10.1371/journal.pone.0088029

## Permanent link

<http://nrs.harvard.edu/urn-3:HUL.InstRepos:11857773>

## 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](#)

# Using Historical and Experimental Data to Reveal Warming Effects on Ant Assemblages

Julian Resasco<sup>1\*†</sup>, Shannon L. Pelini<sup>2</sup>, Katharine L. Stuble<sup>3‡</sup>, Nathan J. Sanders<sup>3§</sup>, Robert R. Dunn<sup>4</sup>, Sarah E. Diamond<sup>4¶</sup>, Aaron M. Ellison<sup>5</sup>, Nicholas J. Gotelli<sup>6</sup>, Douglas J. Levey<sup>7</sup>

<sup>1</sup>Department of Biology, University of Florida, Gainesville, FL 32611, USA

<sup>2</sup>Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, USA

<sup>3</sup>Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

<sup>4</sup>Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695, USA

<sup>5</sup>Harvard University, Harvard Forest, Petersham, MA 01366 USA

<sup>6</sup>Department of Biology, University of Vermont, Burlington, VT 05405 USA

<sup>7</sup>National Science Foundation, Arlington, VA 22230, USA

† **Current address:** Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

‡ **Current address:** Oklahoma Biological Survey, 111 E. Chesapeake Street  
Norman, OK, 73019 USA

§ **Current address:** Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark.

¶ **Current address:** Department of Biology, Case Western Reserve University, Cleveland OH 44106

\* **Corresponding author address:** Julian Resasco, Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

**email:** jresasco@colorado.edu

## 1 **Abstract**

2 Historical records of species are compared with current records to elucidate effects of  
3 recent climate change. However, confounding variables such as succession, land-use  
4 change, and species invasions make it difficult to demonstrate a causal link between  
5 changes in biota and changes in climate. Experiments that manipulate temperature can  
6 overcome this issue of attribution, but long-term impacts of warming are difficult to test  
7 directly. Here we combine historical and experimental data to explore effects of warming  
8 on ant assemblages in southeastern US. Observational data span a 35-year period (1976-  
9 2011), during which mean annual temperatures had an increasing trend. Mean summer  
10 temperatures in 2010-2011 were  $\sim 2.7$  °C warmer than in 1976. Experimental data come  
11 from an ongoing study in the same region, for which temperatures have been increased  
12  $\sim 1.5 - 5.5$  °C above ambient from 2010 to 2012. Ant species richness and evenness  
13 decreased with warming under natural but not experimental warming. These  
14 discrepancies could have resulted from differences in timescales of warming, abiotic or  
15 biotic factors, or initial species pools. Species turnover tended to increase with  
16 temperature in observational and experimental datasets. At the species level, the  
17 observational and experimental datasets had four species in common, two of which  
18 exhibited consistent patterns between datasets. With natural and experimental warming,  
19 collections of the numerically dominant, thermophilic species, *Crematogaster lineolata*,  
20 increased roughly two-fold. *Myrmecina americana*, a relatively heat intolerant species,  
21 decreased with temperature in natural and experimental warming. In contrast, species in  
22 the *Solenopsis molesta* group did not show consistent responses to warming, and  
23 *Temnothorax pergandei* was rare across temperatures. Our results highlight the  
24 difficulty of interpreting community responses to warming based on historical records or  
25 experiments alone. Because some species showed consistent responses to warming based

26 on thermal tolerances, understanding functional traits may prove useful in explaining  
27 responses of species to warming.

28

## 29 **Introduction**

30 Global climatic change has altered phenology, ranges of individual species, and  
31 community structure across many taxa (reviewed in [1]). Predicting how species  
32 assemblages will change as a result of climatic warming is a prerequisite for  
33 understanding the ecological future, but such predictions remain vexingly difficult.  
34 Observational studies of relationships between climatic trends or weather events and  
35 changes in biotic assemblages have a long history in ecology [2-6]. When historical data  
36 exist, repeated sampling and comparisons of historical and contemporary datasets can  
37 reveal assemblage-level changes that have occurred concurrent with decades of climatic  
38 change [2,7-11]. In essentially all cases, however, confounding factors (e.g., succession,  
39 pollution, changes in soil, invasion, landscape context) make it difficult to attribute  
40 observed differences solely to changes in climate [1].

41         Manipulative field experiments that simulate projected climatic change can  
42 provide a bridge between observational, correlative studies and potential mechanisms that  
43 underlie any observed patterns. These studies increase the ability to assign causation of  
44 biotic changes to abiotic variables. However, manipulative field experiments have their  
45 own limitations, such as limited replication and relatively small spatial and temporal  
46 scales. Experimental plots or chambers may not capture rare extremes in weather or  
47 interactions among climatic drivers [12]. Climatic changes in these experiments occur at  
48 a shorter time scale, so experiments may miss biotic changes that are slow to emerge.  
49 Likewise, high variation in intra- and interspecific responses may mask overall changes

50 in community composition or diversity that may occur in the long term. A combined  
51 approach of long-term observations and experimental manipulations can overcome many  
52 of the inherent limitations of detection and attribution of each approach in isolation  
53 [13,14]. A challenge of such combined approaches, however, is that they depend on a  
54 combination of data from long-term observations and from warming (or other global  
55 change) experiments in the same region on the same taxa.

56 Here we revisit a set of sites where ant assemblages were sampled ~ 35 years ago  
57 and compare changes in these assemblages through time to results from an ongoing  
58 warming experiment on an assemblage of ants in the same region. We focus on ants  
59 because they are diverse, abundant, ecologically important [15], well studied in the  
60 southeastern United States [16], and because they are among the very few animal taxa to  
61 be studied in field manipulations of climatic change [17]. Further, temperature influences  
62 many aspects of ant biology, including assemblage-level metrics such as species diversity  
63 [18-20], and population-level phenomena such as the timing of reproduction [21],  
64 dynamics of foraging behavior [22-24], limits of species ranges [25-27], and colony  
65 growth and development [28]. Specifically, we asked whether the patterns observed from  
66 the long-term resampling of ant assemblages over 35 years are congruent with results  
67 from an ongoing warming experiment that has been running continuously since 2010.

68

## 69 **Materials and Methods**

### 70 *Study systems*

71 We conducted this study at two sites approximately 450 km apart: Savannah River Site  
72 (SRS), a National Environmental Research Park, South Carolina, (33.21 N, 81.41 W; 80-  
73 130 m above sea level [29]) and Duke Forest, North Carolina (35.52 N, 79.59 W, 130 m

74 above sea level). Permission to conduct this research was granted by the Office of the  
75 Duke Forest and the Savannah River Ecology Laboratory. This research did not involve  
76 endangered or protected species. At SRS, our sampling areas were in two stands of turkey  
77 oak (*Quercus laevis*) forest (a map and description of the study site are in [30]). At Duke  
78 Forest, our experimental site is located in an oak-hickory (*Quercus-Carya*) forest.

79 *Historic data: Savannah River Site*

80 Data on ants at SRS were collected by Van Pelt and Gentry [30] in the summer (date  
81 unspecified) of 1976 and by one of us (JR) in the summers of 2010 and 2011, using the  
82 same sampling areas and similar methodology. Van Pelt and Gentry [30] used 148 mL  
83 (diameter not specified) plastic-vial pitfall traps baited with either sugar (30 traps) or  
84 peanut butter (10 traps) solutions. They also used baited containers and collected by hand,  
85 but because sampling effort for, and ant abundances obtained from these techniques were  
86 not reported, we used only their pitfall-trap data (“Scrub Oak” in Table 2 in [30]). In July  
87 2010 and 2011, we sampled with 55 mL, 28.6mm inner-diameter plastic-vial pitfall traps  
88 baited either with sugar (34 and 28 traps in 2010 and 2011, respectively) or peanut butter  
89 solutions (7 and 10) inserted into the forest floor flush with the ground surface. We  
90 placed traps 15 m apart along transects, interspersed in the sites described in Van Pelt and  
91 Gentry [30]. We randomized the placement of trap types. In both collection periods (one  
92 each year), pitfall traps were left open for 24 hours. We sorted and identified ants to  
93 species, except for two taxonomically difficult groups (*Solenopsis molesta* group and  
94 *Aphaenogaster rudis* complex) in which individuals were combined. To compare the two  
95 datasets we used current synonyms for species, based on the taxonomic history provided  
96 in Bolton’s [31] updated catalog at [http://www.antwiki.org/wiki/New\\_General\\_Catalogue](http://www.antwiki.org/wiki/New_General_Catalogue).

97 To assess the extent of climatic warming between the historic and present-day  
98 sampling periods, we obtained data on monthly temperatures between 1976 and 2011  
99 from the nearest weather station, Aiken 5SE, approximately 15 km away, in Aiken, SC  
100 (33.49N, 81.70W; SC State Climatology Office <http://www.dnr.sc.gov/climate/sco/>).  
101 Missing data (~12% of months) were filled in using data from the second-nearest weather  
102 station, Bush Field (KAGS), approximately 25 km away, in Augusta, GA (33.38N  
103 81.97W; National Oceanic and Atmospheric Administration; <http://www.noaa.gov/>).  
104 Mean summer temperatures (June, July, and August) were approximately 2.7°C warmer  
105 in 2010-2011 than in 1976 (Fig. 1). We recognize that extreme warm temperature  
106 anomalies, like those in southeastern United States in 2010 and 2011 are an important  
107 aspect of climate change [32]. Over the intervening years, mean annual temperatures also  
108 showed an increasing trend (Fig. 1).

#### 109 *Duke Forest warming experiment*

110 The Duke Forest warming experiment consists of 12 octagonal, open-top chambers, each  
111 built around a > 20 cm dbh oak (*Quercus*) tree. Chambers are constructed of wooden  
112 frame walls covered in greenhouse sheeting. Each chamber is 5 m in diameter, 1.5 m high  
113 (~ 22 m<sup>2</sup>), and has a 3-cm gap along the bottom to allow ants to enter and exit. Nine  
114 chambers have been heated with warm air since January 2010 in a regression design at  
115 0.5 °C intervals ranging from 1.5 to 5.5°C above ambient temperature; three additional  
116 chambers serve as ambient controls. Air temperature is monitored within each chamber.  
117 Details of the experimental design are provided in Pelini et al. [17]. Within each chamber,  
118 we have collected data on ants since 2009 using four pitfall traps (90 mL, 50 mm  
119 diameter) filled to approximately one-third of their volume with propylene glycol. Traps  
120 were left open for a 48-h sampling period. We identified collected ants to species and

121 deposited voucher specimens at North Carolina State University. To correspond with  
122 SRS data, Duke Forest pitfall data from only summer months (June, July, and August) of  
123 2010-2012 were used. Most of the ants detected in pitfall traps in the chambers come  
124 from colonies that are located in the chambers [33].

#### 125 *Statistical Analyses*

126 Data from pitfall traps provide a combined estimate of ant activity and density because a  
127 change in either activity or density will affect the rate at which ants fall into the traps [34].  
128 Despite this drawback, pitfall traps are commonly used in studies such as ours because  
129 they are easy to standardize and have little impact on soil, litter, or ant populations  
130 [35,36]. Because high numbers of individuals recruited to baited pitfall traps at SRS, we  
131 measured activity-density as number of traps with a given species present. In contrast,  
132 non-baited pitfall traps at Duke Forest did not recruit high numbers of workers and there  
133 were relatively few per chamber, so we measured activity-density as number of  
134 individuals per chamber of a given species. Relative activity-density (analogous to  
135 relative abundance) was calculated as the activity-density of a given species divided by  
136 the sum of the activity-densities of all species.

137 Differences in species richness between sampling periods at SRS were estimated  
138 from sample-based rarefaction (to adjust for sampling effort) on incidence data from both  
139 2010 and 2011 pitfall trap data using EstimateS [37]. To estimate species evenness, we  
140 calculated Hurlbert's PIE (probability of interspecific encounter, [38]). PIE varies  
141 between 0 and 1, with greater values indicating greater evenness. We used PIE as a  
142 metric of evenness because it is robust to differences in sample size and is intuitive to  
143 interpret as the probability that two individuals randomly drawn are from a different  
144 species. To estimate species turnover, we calculated Bray-Curtis distance (a measure of



145 community dissimilarity) on relative activity-density of ant species [39] among sampling  
146 periods at SRS and among temperature treatments at Duke Forest. Bray-Curtis distance  
147 varies between 0 and 1, with greater values indicating greater dissimilarity between  
148 assemblages.

149 We examined the relationship between temperature and species richness,  
150 evenness, and the relative activity-density of each species that occurred at both sites. We  
151 also used Mantel tests with 10,000 permutations to examine the association between  
152 pairwise temperature differences and species turnover at both sites. For Duke Forest data,  
153 we used temperature differences among chambers. For SRS data, we used mean summer  
154 temperature differences among sampled years.

155

## 156 **Results**

157 A total of 56 ant species was recorded across both periods and sites (Table 1). Seventy-  
158 six percent of the species that occurred at Duke Forest were present at SRS, either in the  
159 samples collected for this study or other studies ([40], Resasco and Booher unpublished  
160 data). However, only four of these species occurred in historical samples, present-day  
161 samples at SRS, and present-day samples in the warming experiment: *Crematogaster*  
162 *lineolata*, *Myrmecina americana*, *Solenopsis molesta* (species group), and *Temnothorax*  
163 *pergandei*.

164 Estimated species richness decreased by approximately 35% at SRS between  
165 1976 and 2010-2011 (33% by 2010; 37% by 2011). This difference is outside the present-  
166 day 95% confidence interval constructed after rarefying to equivalent sample sizes (1976  
167 observed species richness: 21; 2010 and 2011 rarefied species richness 95% CI: 12-14;

168 Fig. 2A). In contrast, three years of experimental warming at Duke Forest have, as of yet,  
169 shown no effect on species richness ( $\beta = -0.01$ ;  $SE = 0.35$ ;  $r^2 < 0.001$ ;  $P = 0.99$ ; Fig. 2B).

170 Evenness decreased by approximately 10% at SRS between 1976 and 2010-2011  
171 (12% by 2010; 8% by 2011). This difference is outside of the present-day 95%  
172 confidence interval constructed after rarefying to equivalent sample sizes (1976 observed  
173 PIE: 0.91; 2010 and 2011 rarefied species richness 95% CI: 0.79-0.84; Fig. 2C). As with  
174 species richness, differences in evenness were not apparent in the experimental warming  
175 treatments at Duke Forest ( $\beta = 0.005$ ;  $SE = 0.01$ ;  $r^2 = 0.03$ ;  $P = 0.62$ ; Fig. 2D).

176 Bray-Curtis distance (species turnover) was positively related to mean summer  
177 temperature differences at SRS, although the relationship was not statistically significant  
178 (Mantel  $r = 0.90$ ;  $P = 0.33$ ). At Duke Forest we found that as temperature differences  
179 among warming chambers increased, Bray-Curtis distance tended to increase (Mantel  $r =$   
180  $0.22$ ;  $P = 0.06$ ).

181 The relative activity-density of *Crematogaster lineolata* more than doubled  
182 between the 1976 sampling period and the present-day sampling period at SRS (Fig. 3A).  
183 Similarly, there was a trend towards a positive relationship between the extent of  
184 warming and *Crematogaster lineolata* relative activity-density in the experimental  
185 chambers at Duke Forest ( $\beta = 0.04$ ;  $SE = 0.02$ ;  $r^2 = 0.27$ ;  $P = 0.08$ ; Fig. 3B).

186 The relative activity-density of *Myrmecina americana* and the *Solenopsis molesta*  
187 species group decreased between sampling periods at SRS (Fig. 3C,E). At Duke Forest,  
188 the relative activity-density of *Myrmecina americana* also decreased ( $\beta = -0.01$ ;  $SE =$   
189  $0.003$ ;  $r^2 = 0.39$ ;  $P = 0.03$ ; Fig. 3 D) but the relative activity-density of the *Solenopsis*  
190 *molesta* group did not show any relationship with temperature ( $\beta = 0.01$ ;  $SE = 0.015$ ;  $r^2 =$

191 0.12;  $P = 0.40$ ; Fig. 3F). *Temnothorax pergandei* was rare at both sites and did not appear  
192 to respond to warming at either site (Fig. 3G,H).

193

## 194 **Discussion**

195 Our results, taken together, suggest that at least some of the long-term responses of  
196 species are congruent with the short-term responses of species to warming. Species  
197 turnover (Bray-Curtis distance) exhibited similar, positive trends at SRS and Duke Forest,  
198 although the increases were not statistically significant. When we looked at species-  
199 specific responses for four species collected in all sampling periods at both sites, we  
200 found similarities between SRS and Duke for the numerically dominant species,  
201 *Crematogaster lineolata* and for *Myrmecina americana* (Fig. 3A-D). Although we  
202 detected declines in ant species richness and evenness over a period of several decades at  
203 SRS, we did not find congruent results over a period of several years at the experimental  
204 warming site (Duke Forest; Fig. 2). Further, species in the *Solenopsis molesta* group  
205 responded variably across the sites, decreasing with time at SRS while not responding to  
206 temperature at Duke Forest. We note, however, that the poor taxonomy of the *Solenopsis*  
207 *molesta* species group complicates such comparisons.

208 Many factors may have contributed to the observed differences in the responses to  
209 warming of the ant assemblages at SRS and Duke Forest. The nature and timescale of  
210 warming is an obvious difference: at Duke Forest the warming was applied rapidly and  
211 maintained over a period of several years, whereas at SRS the warming was incremental  
212 and variable over 35 years. Differences in microclimate, local community structure, and  
213 land-use also may have played a role in driving variation in the responses to warming of

214 the two assemblages. For example, there is evidence of successional maturation of forest  
215 stands at SRS that has not occurred during the three years of warming at Duke Forest.  
216 Van Pelt and Gentry [30] describe the habitat as a “subclimax forest” but do not provide  
217 vegetation data to allow a direct comparison with current conditions. Further, the  
218 presence of ant species such as *Dorymyrmex* sp., *Forelius pruinosus*, *Nylanderia*  
219 *arenivaga*, *Pheidole davisii*, *Pheidole metallescens*, *Pheidole crassicornis*,  
220 *Pogonomyrmex badius*, and *Trachymyrmex septentrionalis* in the 1976 SRS data but not  
221 the present-day data suggests that the sampling sites likely were more open and xeric  
222 during the original sampling period. This potential difference is important because  
223 succession can result in large changes in animal assemblages [41,42] including  
224 assemblages of ants [43].

225         Other potential drivers include altered precipitation regimes, changes in leaf litter,  
226 and shifts in species interactions. The important point is that observed shifts in the ant  
227 assemblage at SRS have multiple explanations, whereas those at Duke Forest most  
228 parsimoniously are attributable directly to warming. We also have reported high intra-  
229 and interspecies variation in ant responses to warming in the Duke Forest warming  
230 experiment [24,25,33,44-46]. Such high variation in short-term responses of ants to  
231 warming may mask patterns of diversity and composition that eventually result in the  
232 longer term.

233         For the subset of species shared among the SRS and Duke Forest samples,  
234 physiological tolerance appears to explain some of their responses to warming. The  
235 activity-density of the numerically dominant species, *Crematogaster lineolata*, increased  
236 with warming at both SRS and Duke Forest (Fig. 3A,B). In addition, samples at Duke  
237 Forest have documented greater nest box colonization by this species in the warmest

238 chambers (unpublished data). Previous work from the Duke Forest site and surrounding  
239 areas has linked increasing abundance and foraging intensity of *C. lineolata* with greater  
240 tolerance of high temperatures than that of co-occurring species [24,25,47]. Indeed, *C.*  
241 *lineolata* has one of the highest critical thermal maxima (temperature of loss of ant  
242 muscular coordination), 46.1 °C, among the 20 most common species at Duke Forest  
243 (data at: <http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf113>). In  
244 contrast, *Myrmecina americana* showed congruent declines with temperature at SRS and  
245 at Duke Forest (Fig. 3 C,D). This species has the lowest critical thermal maximum,  
246 38.8 °C, among the species collected at Duke Forest.

247         The increased activity-density of *Crematogaster lineolata* in both the  
248 observational and the experimental studies might lead to subsequent effects on the rest of  
249 the ant assemblage. For instance, if *Crematogaster lineolata* benefits from warming by  
250 increasing foraging, evenness of the assemblage could be reduced by competitive  
251 displacement [44]; such results have also been observed for plant assemblages [48].  
252 Effects of warming on species interactions have been demonstrated in a variety of aquatic  
253 and terrestrial systems [49,50] including plant-herbivore [51], host-parasitoid [52], and  
254 trophic interactions [14,53-56], ultimately influencing the composition of communities.  
255 Exploring how ongoing warming mediates interactions among species and in turn  
256 influences the structure and dynamics of species assemblages is a central challenge in  
257 global-change research [49,50].

258         In summary, our results from observational data of shifts in activity-density in  
259 two individual ant species were similar to those of the experimental data, but overall  
260 responses of ant assemblages largely differed between observational and experimental  
261 studies. Species-specific responses may be linked to functional traits [57] such as thermal

262 tolerance [24,25,57], whereas uncontrolled variables in observational studies and site-  
263 specific differences may mask assemblage-level changes [12]. Our study highlights  
264 challenges and the importance of assessing alternative explanations when drawing on  
265 experimental data to make stronger inferences from historical datasets about impacts of  
266 climate change.

267

## 268 **Acknowledgments**

269 We thank Hannah Penn for assistance in the lab; John Blake and the USDA Forest  
270 Service-Savannah River for logistic support; and Rob Fletcher, Sanford Porter, Scott K.  
271 Robinson, and Todd Palmer for useful feedback on this manuscript.

272

## 273 **Financial Disclosure**

274 Funding was provided by a National Science Foundation Graduate Research Fellowship  
275 (DGE-0802270) to JR, a National Science Foundation Dissertation Improvement Grant  
276 (NSF- 1208974) to KS, a US Department of Energy PER award (DEFG02-08ER64510) to  
277 RRD, NJS, AME, and NJG, and a National Science Foundation Dimensions of  
278 Biodiversity grant (NSF-1136703) to NJS, RRD, AME, and NJG. The funders had no  
279 role in study design, data collection and analysis, decision to publish, or preparation of  
280 the manuscript.

281

## 282 **Figure Legends**

283 Fig. 1. Annual, summer, and winter mean monthly temperatures near the Savannah River  
284 Site (South Carolina, United States) from 1976 to 2011.

285

286 Fig. 2. Relationships between temperature and ant species richness (A-B), evenness (C-  
287 D) at Savannah River Site (A, C) and Duke Forest (B, D). Dots for Savannah River Site  
288 represent sampling periods and dots for Duke Forest represent warming chambers.  
289 Warmer colors indicate warmer temperatures.

290

291 Fig. 3. Relationships between temperature and species relative activity-densities for ant  
292 species that occurred at both Savannah River Site and Duke Forest. Species are: A-B)  
293 *Crematogaster lineolata*, C-D) *Myrmecina americana*, E-F) *Solenopsis molesta* group,  
294 G-H) *Temnothorax pergandei*. Dots for Savannah River Site represent sampling periods  
295 and dots for Duke Forest represent warming chambers where the species occurred.  
296 Warmer colors indicate warmer temperatures.

297

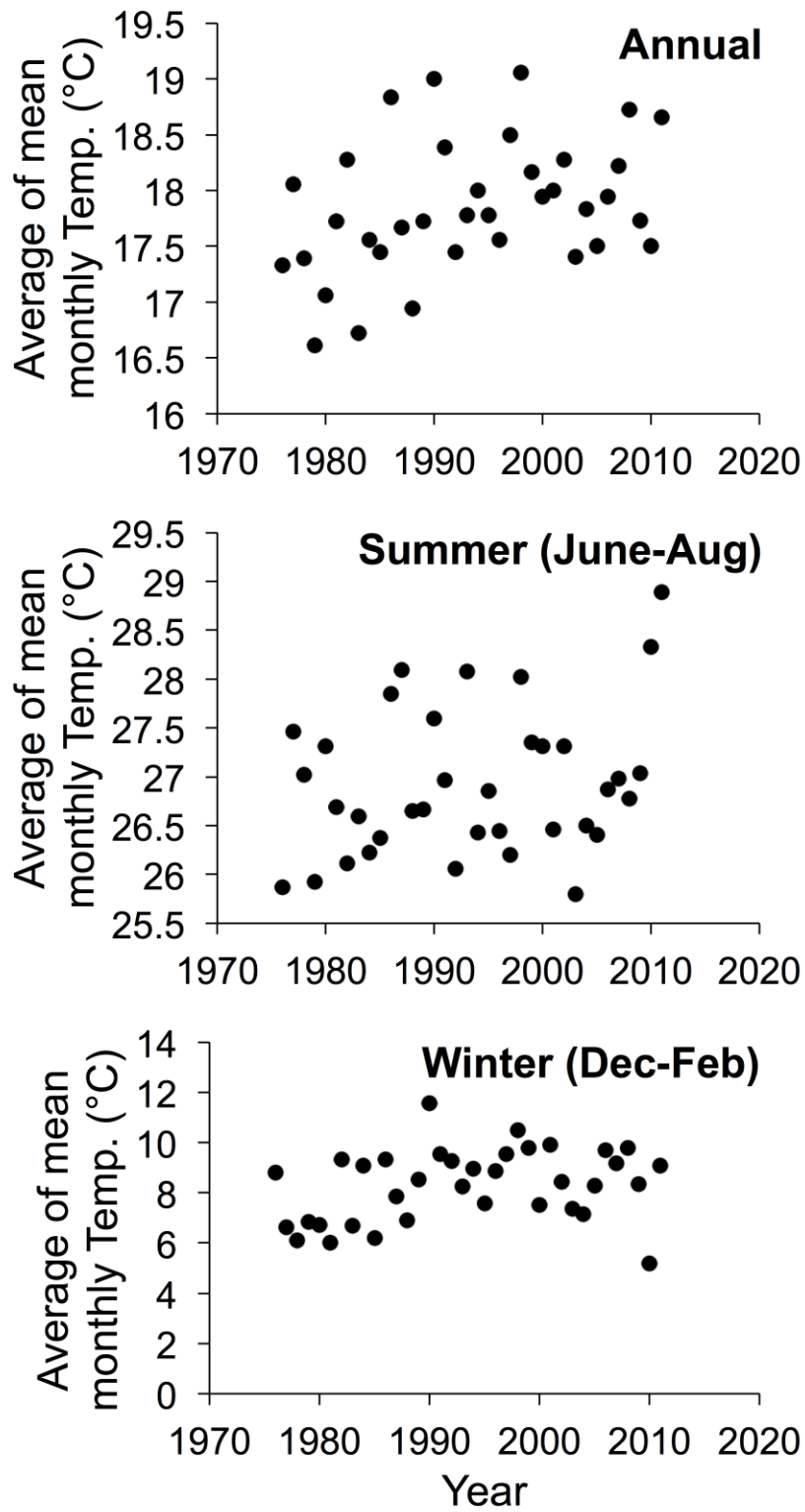


Figure 1



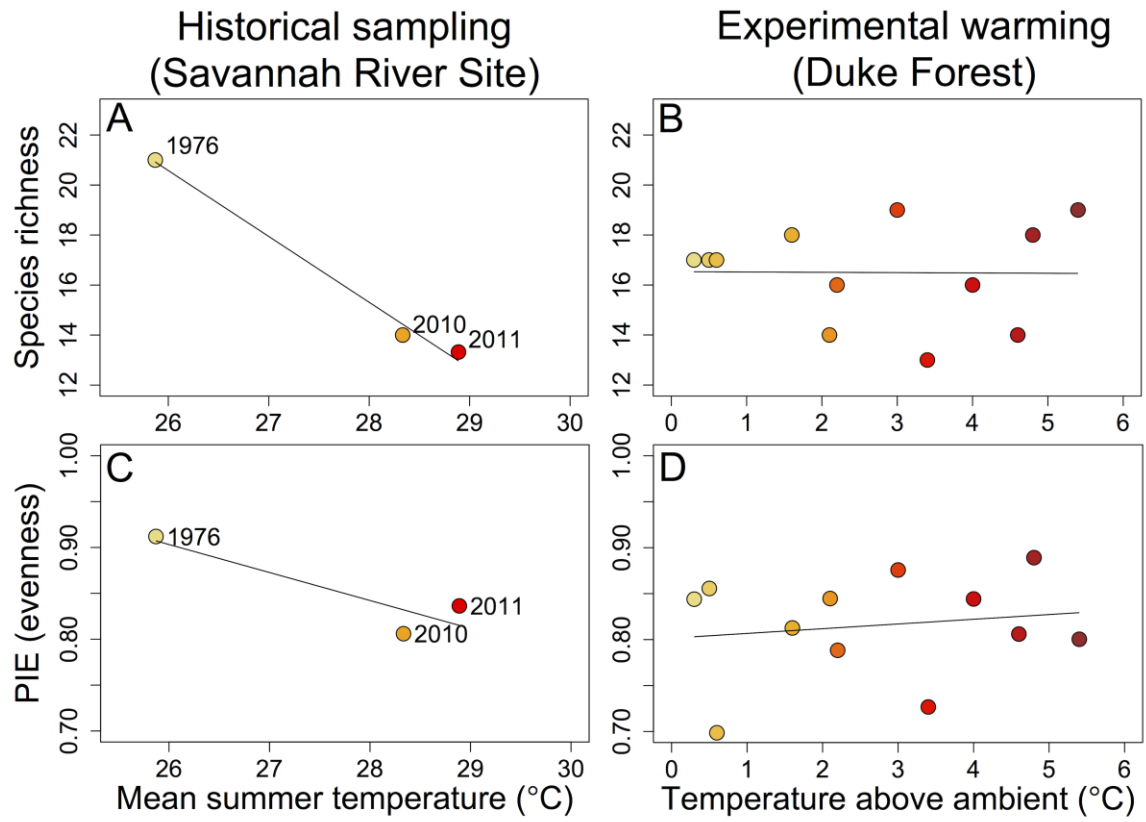
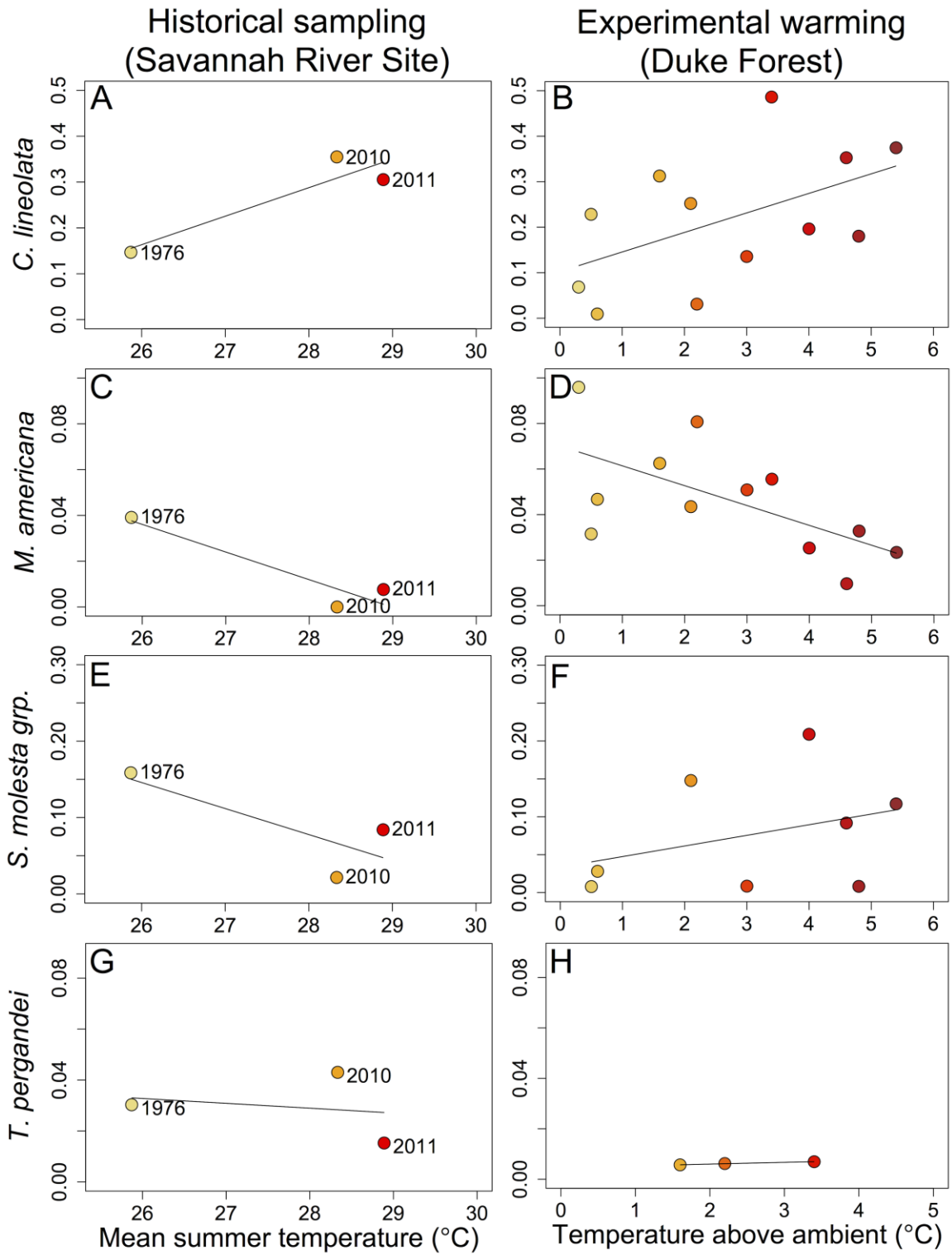


Figure 2



307

308

309

Figure 3

311 Table 1 Species list for Savannah River Site and Duke Forest for this study. Values  
 312 indicate species relative activity-density at the indicated site or time.  
 313

Species	SRS 1976	SRS 2010	SRS 2010	Duke Forest 2010-12
<i>Aphaenogaster ashmeadi</i> (Emery)	0.029	0.054	0.122	
<i>Aphaenogaster fulva</i> (Roger)				0.001
<i>Aphaenogaster lamellidens</i> (Mayr)				0.046
<i>Aphaenogaster mariae</i> (Forel)				0.001
<i>Aphaenogaster rudis</i> complex		0.172	0.130	0.301
<i>Aphaenogaster tennesseensis</i> (Mayr)				0.004
<i>Aphaenogaster treatae</i> (Forel)	0.089	0.022	0.008	
<i>Camponotus americanus</i> (Mayr)				0.006
<i>Camponotus castaneus</i> (Latreille)				0.034
<i>Camponotus chromaiodes</i> (Bolton)				0.024
<i>Camponotus nearcticus</i> (Emery)				0.002
<i>Camponotus pennsylvanicus</i> (DeGeer)			0.008	0.101
<i>Camponotus socius</i> (Roger)	0.077			
<i>Crematogaster ashmeadi</i> (Mayr)				0.008
<i>Crematogaster lineolata</i> (Say)	0.147	0.355	0.305	0.235
<i>Crematogaster minutissima</i> (Mayr)		0.000	0.008	
<i>Crematogaster vermiculata</i> (Emery)				0.002
<i>Dorymyrmex</i> sp.	0.019			
<i>Forelius pruinosus</i> (Roger)	0.040			
<i>Formica dolosa</i> (Buren)	0.010	0.054	0.023	
<i>Formica pallidefulva</i> (Latreille)		0.011	0.000	0.017
<i>Formica sanguinea</i> group				0.020
<i>Formica subsericea</i> (Say)				0.019
<i>Hypoponera opacior</i> (Forel)		0.011		
<i>Lasius interjectus</i> (Mayr)				0.001
<i>Myrmecina americana</i> (Weber)	0.039		0.008	0.050
<i>Myrmecina</i> sp.				0.002
<i>Neivamyrmex texanus</i> (Watkins)				0.027
<i>Nylanderia faisonensis</i> (Forel)		0.183	0.183	0.001
<i>Nylanderia arenivaga</i> (Wheeler)	0.019			
<i>Nylanderia parvula</i> (Mayr)	0.132	0.011		
<i>Nylanderia concinna</i> (Trager)				0.001
<i>Nylanderia terricola</i> (Buckley)				0.001
<i>Pheidole davisii</i> (Wheeler)	0.010			
<i>Pheidole dentata</i> (Mayr)	0.069	0.022	0.069	
<i>Pheidole dentigula</i> (Smith)		0.000	0.031	
<i>Pheidole metallescens</i> (Emery)	0.010			
<i>Pheidole morrissi</i> (Forel)	0.029	0.022		

<i>Pheidole crassicornis</i> (Emery)	0.050			
<i>Pogonomyrmex badius</i> (Latreille)	0.010			
<i>Ponera pennsylvanica</i> (Buckley)				0.018
<i>Prenolepis imparis</i> (Say)				0.005
<i>Pseudomyrmex ejectus</i> (Smith)	0.010			
<i>Stigmatomma pallipes</i> (Haldeman)				0.003
<i>Strumigenys bunki</i> (Brown)				
<i>Strumigenys carolinensis</i> (Brown)				0.001
<i>Strumigenys ornata</i> (Mayr)		0.022	0.008	0.001
<i>Strumigenys pergandei</i> (Emery)				0.001
<i>Strumigenys</i> sp (DFmorphX)				0.001
<i>Solenopsis molesta</i> group.	0.156	0.022	0.084	0.059
<i>Stenamma</i> cf. <i>impar</i>				0.001
<i>Stenamma impar</i> (Forel)				0.001
<i>Temnothorax pergandei</i> (Emery)	0.030	0.043	0.015	0.002
<i>Temnothorax schaumii</i> (Roger)				0.001
<i>Temnothorax curvispinosus</i> (Mayr)				0.013
<i>Trachymyrmex septentrionalis</i> (McCook)	0.010			

---

314

315



317 **References**

318

319 1. Parmesan C (2006) Ecological and evolutionary responses to recent climate change.

320 *Annu Rev Ecol Evol Syst* 37: 637-669. doi:

321 10.1146/Annurev.Ecolsys.37.091305.110100.

322 2. Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature*

323 369: 448. doi: 10.1038/369448a0.

324 3. Barry JP, Baxter CH, Sagarin RD, Gilman SE (1995) Climate-related, long-term faunal

325 changes in a California rocky intertidal community. *Science* 267: 672-675. doi:

326 10.1126/Science.267.5198.672.

327 4. Brown JH, Valone TJ, Curtin CG (1997) Reorganization of an arid ecosystem in

328 response to recent climate change. *Proc Natl Acad Sci USA* 94: 9729-9733. doi:

329 10.1073/Pnas.94.18.9729.

330 5. Holbrook SJ, Schmitt RJ, Stephens JS (1997) Changes in an assemblage of temperate

331 reef fishes associated with a climate shift. *Ecol Appl* 7: 1299-1310. doi:

332 10.2307/2641215.

333 6. Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their

334 Grinnellian niche through a century of climate change. *Proc Natl Acad Sci USA*

335 106: 19637-19643. doi: 10.1073/Pnas.0901562106.

336 7. Sagarin RD, Barry JP, Gilman SE, Baxter CH (1999) Climate-related change in an

337 intertidal community over short and long time scales. *Ecol Monogr* 69: 465-490.

338 doi: 10.1890/0012-9615(1999)069[0465:Crciai]2.0.Co;2.

339 8. Smith JR, Fong P, Ambrose RF (2006) Dramatic declines in mussel bed community

340 diversity: Response to climate change? *Ecology* 87: 1153-1161. doi:

341 10.1890/0012-9658(2006)87[1153:Ddimbc]2.0.Co;2.

- 342 9. Chen I-C, Shiu H-J, Benedick S, Holloway JD, Cheye VK, et al. (2009) Elevation  
343 increases in moth assemblages over 42 years on a tropical mountain. *Proc Natl*  
344 *Acad Sci USA* 106: 1479-1483. doi: 10.1073/Pnas.0809320106.
- 345 10. Damschen EI, Harrison S, Grace JB (2010) Climate change effects on an endemic-  
346 rich edaphic flora: Resurveying Robert H. Whittaker's Siskiyou sites (Oregon,  
347 USA). *Ecology* 91: 3609-3619. doi: 10.1890/09-1057.1.
- 348 11. Tingley MW, Beissinger SR (2013) Cryptic loss of montane avian richness and high  
349 community turnover over 100 years. *Ecology* 94: 598-609. doi: 10.1890/12-  
350 0928.1.
- 351 12. Wolkovich EM, Cook BI, Allen JM, Crimmins TM, Betancourt JL, et al. (2012)  
352 Warming experiments underpredict plant phenological responses to climate  
353 change. *Nature* 485: 494-497. doi: 10.1038/Nature11014.
- 354 13. Dunne JA, Saleska SR, Fischer ML, Harte J (2004) Integrating experimental and  
355 gradient methods in ecological climate change research. *Ecology* 85: 904-916.  
356 doi: 10.1890/03-8003.
- 357 14. Harley CDG (2011) Climate change, keystone predation, and biodiversity loss.  
358 *Science* 334: 1124-1127. doi: 10.1126/Science.1210199.
- 359 15. Hölldobler B, Wilson EO (1990) *The Ants*. Belknap Press of Harvard University  
360 Press.
- 361 16. MacGown JA (2013) *Ants (Formicidae) of the southeastern United States*.  
362 ([http://mississippientomologicalmuseum.org.msstate.edu//Researchtaxapages/  
363 Formicidaehome.html](http://mississippientomologicalmuseum.org.msstate.edu//Researchtaxapages/Formicidaehome.html)).
- 364 17. Pelini SL, Bowles FP, Ellison AM, Gotelli NJ, Sanders NJ, et al. (2011) Heating up  
365 the forest: Open-top chamber warming manipulation of arthropod communities at

- 366 Harvard and Duke Forests. *Methods Ecol and Evol* 2: 534-540. doi:  
367 10.1111/J.2041-210x.2011.00100.X.
- 368 18. Kaspari M, Yuan M, Alonso L (2003) Spatial grain and the causes of regional  
369 diversity gradients in ants. *Am Nat* 161: 459-477. doi: 10.1086/367906.
- 370 19. Sanders NJ, Lessard J-P, Fitzpatrick MC, Dunn RR (2007) Temperature, but not  
371 productivity or geometry, predicts elevational diversity gradients in ants across  
372 spatial grains. *Global Ecology and Biogeography* 16: 640-649. doi:  
373 10.1111/J.1466-8238.2007.00316.X.
- 374 20. Dunn RR, Agosti D, Andersen AN, Arnan X, Bruhl CA, et al. (2009) Climatic drivers  
375 of hemispheric asymmetry in global patterns of ant species richness. *Ecology*  
376 *Letters* 12: 324-333. doi: 10.1111/J.1461-0248.2009.01291.X.
- 377 21. Dunn RR, Parker CR, Geraghty M, Sanders NJ (2007) Reproductive phenologies in a  
378 diverse temperate ant fauna. *Ecol Entomol* 32: 135-142. doi: 10.1111/j.1365-  
379 2311.2006.00839.x.
- 380 22. Porter SD, Tschinkel WR (1987) Foraging in *Solenopsis invicta* (Hymenoptera:  
381 Formicidae) effects of weather and season. *Environ Entomol* 16: 802-808.
- 382 23. Ruano F, Tinaut A, Soler JJ (2000) High surface temperatures select for individual  
383 foraging in ants. *Behav Ecol* 11: 396-404. doi: 10.1093/Beheco/11.4.396.
- 384 24. Stuble KL, Pelini SL, Diamond SE, Fowler DA, Dunn RR, et al. (2013) Foraging by  
385 forest ants under experimental climatic warming: A test at two sites. *Ecol Evol* 3:  
386 482-491. doi: 10.1002/Ece3.473.
- 387 25. Diamond SE, Nichols LM, McCoy N, Hirsch C, Pelini SL, et al. (2012) A  
388 physiological trait-based approach to predicting the responses of species to  
389 experimental climate warming. *Ecology* 93: 2305-2312. doi: 10.1890/11-2296.1.



- 390 26. Korzukhin MD, Porter SD, Thompson LC, Wiley S (2001) Modeling temperature-  
391 dependent range limits for the fire ant *Solenopsis invicta* (Hymenoptera:  
392 Formicidae) in the United States. *Environ Entomol* 30: 645-655.
- 393 27. Morrison LW, Porter SD, Daniels E, Korzukhin MD (2004) Potential global range  
394 expansion of the invasive fire ant, *Solenopsis invicta*. *Biol Invasions* 6: 183-191.  
395 doi: 10.1023/B:Bin.0000022135.96042.90.
- 396 28. Porter SD (1988) Impact of temperature on colony growth and developmental rates of  
397 the ant, *Solenopsis invicta*. *J Insect Physiol* 34: 1127-1133. doi: 10.1016/0022-  
398 1910(88)90215-6.
- 399 29. Workman SW, McLeod KW (1990) Vegetation of the Savannah River Site: Major  
400 community types. United States Department of Energy, Savannah River Site,  
401 SRO-NERP-19:1-137.
- 402 30. Van Pelt AF, Gentry JB (1985) The ants (Hymenoptera: Formicidae) of the Savannah  
403 River Plant, South Carolina. United States Department of Energy, Savannah River  
404 Site, SRO-NERP-14:1-56.
- 405 31. Bolton B (1995) A new general catalogue of the ants of the world. Harvard  
406 University Press.
- 407 32. Hansen J, Sato M, Ruedy R (2012) Perception of climate change. *Proc Natl Acad Sci*  
408 USA 109: E2415-E2423. doi: 10.1073/Pnas.1205276109.
- 409 33. Stuble KL (2013) Ant community dynamics and the effects of global warming  
410 [dissertation]. Knoxville, TN: University of Tennessee.
- 411 34. Woodcock BA (2005) Pitfall trapping in ecological studies. In: Leather SR, editor.  
412 Insect sampling in forest ecosystems. Oxford: Blackwell.
- 413 35. Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WLJ, et al. (2000)  
414 Field techniques for the study of ground-dwelling ants: An overview, description,

415 and evaluation. In: Agosti D, Majer JD, Alonso LE, Schultz TR, editors. *Ants:*  
416 *Standard methods for measuring and monitoring biodiversity.* Washington DC:  
417 *Smithsonian Institution Press.*

418 36. Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera:  
419 Formicidae): biodiversity sampling and statistical analysis for myrmecologists.  
420 *Myrmecol News* 15: 13-19.

421 37. Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared  
422 species from samples. 9.1.0 ed.

423 38. Hurlbert SH (1971) Nonconcept of species diversity: Critique and alternative  
424 parameters. *Ecology* 52: 577-586. doi: 10.2307/1934145.

425 39. Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, et al. (2011) Navigating  
426 the multiple meanings of beta diversity: A roadmap for the practicing ecologist  
427 *Ecol Lett* 14: 19-28. doi: 10.1111/J.1461-0248.2010.01585.X

428 40. Resasco J (2013) Environmental changes affecting dominant ant species [dissertation].  
429 Gainesville, FL: University of Florida.

430 41. Robinson WD (1999) Long-term changes in the avifauna of Barro Colorado Island,  
431 Panama, a tropical forest isolate. *Conserv Biol* 13: 85-97. doi: 10.1046/J.1523-  
432 1739.1999.97492.X.

433 42. Smith VG (1928) Animal communities of a deciduous forest succession. *Ecology* 9:  
434 479-500. doi: 10.2307/1929416.

435 43. Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration.  
436 *Conserv Biol* 18: 302-309. doi: 10.1111/J.1523-1739.2004.00151.X.

437 44. Pelini SL, Boudreau M, McCoy N, Ellison AM, Gotelli NJ, et al. (2011) Effects of  
438 short-term warming on low and high latitude forest ant communities. *Ecosphere*  
439 2: art62. doi: 10.1890/ES11-00097.1.

- 440 45. Pelini SL, Diamond SE, MacLean H, Ellison AM, Gotelli NJ, et al. (2012) Common  
441 garden experiments reveal uncommon responses across temperatures, locations,  
442 and species of ants. *Ecol Evol* 2: 3009-3015. [10.1002/ece3.407](https://doi.org/10.1002/ece3.407).
- 443 46. Diamond SE, Penick CA, Pelini SL, Ellison AM, Gotelli NJ, et al. (2013) Using  
444 physiology to predict the responses of ants to climatic warming. *Integr Comp Biol*  
445 53: 965-974. [doi:10.1093/icb/ict085](https://doi.org/10.1093/icb/ict085).
- 446 47. Diamond SE, Sorger DM, Hulcr J, Pelini SL, Del Toro I, et al. (2012) Who likes it  
447 hot? A global analysis of the climatic, ecological, and evolutionary determinants  
448 of warming tolerance in ants. *Glob Change Biol* 18: 448-456. [doi:](https://doi.org/10.1111/J.1365-2486.2011.02542.X)  
449 [10.1111/J.1365-2486.2011.02542.X](https://doi.org/10.1111/J.1365-2486.2011.02542.X).
- 450 48. Kardol P, Company CE, Souza L, Norby RJ, Weltzin JF, et al. (2010) Climate change  
451 effects on plant biomass alter dominance patterns and community evenness in an  
452 experimental old-field ecosystem. *Glob Change Biol* 16: 2676-2687. [doi:](https://doi.org/10.1111/J.1365-2486.2010.02162.X)  
453 [10.1111/J.1365-2486.2010.02162.X](https://doi.org/10.1111/J.1365-2486.2010.02162.X).
- 454 49. Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013) Climate change and the  
455 past, present, and future of biotic interactions. *Science* 341: 499-504. [doi:](https://doi.org/10.1126/Science.1237184)  
456 [10.1126/Science.1237184](https://doi.org/10.1126/Science.1237184).
- 457 50. Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and  
458 species interactions in terrestrial ecosystems. *Ecol Lett* 11: 1351-1363. [doi:](https://doi.org/10.1111/J.1461-0248.2008.01250.X)  
459 [10.1111/J.1461-0248.2008.01250.X](https://doi.org/10.1111/J.1461-0248.2008.01250.X).
- 460 51. de Sassi C, Lewis OT, Tylianakis JM (2012) Plant-mediated and nonadditive effects  
461 of two global change drivers on an insect herbivore community. *Ecology* 93:  
462 1892-1901. [doi: 10.1890/11-1839.1](https://doi.org/10.1890/11-1839.1).

- 463 52. Romo CM, Tylianakis JM (2013) Elevated temperature and drought interact to reduce  
464 Parasitoid effectiveness in suppressing hosts. *PLoS One* 8: e58136. doi:  
465 10.1371/journal.pone.0058136.
- 466 53. Barton BT, Beckerman AP, Schmitz OJ (2009) Climate warming strengthens indirect  
467 interactions in an old-field food web. *Ecology* 90: 2346-2351. doi: 10.1890/08-  
468 2254.1.
- 469 54. Jochum M, Schneider FD, Crowe TP, Brose U, O'Gorman EJ (2012) Climate-induced  
470 changes in bottom-up and top-down processes independently alter a marine  
471 ecosystem. *Philos Trans R Soc Lond B Biol Sci* 367: 2962-2970. doi:  
472 10.1098/Rstb.2012.0237.
- 473 55. Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, et al.  
474 (2009) Ecological dynamics across the Arctic associated with recent climate  
475 change. *Science* 325: 1355-1358. doi: 10.1126/Science.1173113.
- 476 56. Shurin JB, Clasen JL, Greig HS, Kratina P, Thompson PL (2012) Warming shifts top-  
477 down and bottom-up control of pond food web structure and function. *Philos*  
478 *Trans R Soc Lond B Biol Sci* 367: 3008-3017. doi: 10.1098/Rstb.2012.0243.
- 479 57. Foden WB, Butchart SHM, Stuart SN, Vié J-C, Akçakaya HR, et al. (2013)  
480 Identifying the world's most climate change vulnerable species: A systematic  
481 trait-based assessment of all birds, amphibians and corals. *PLoS One* 8: e65427.  
482 doi: 10.1371/journal.pone.0065427.

483

484

485