



Common Garden Experiments Reveal Uncommon Responses across Temperatures, Locations, and Species of Ants

Citation

Pelini, Shannon L., Sarah E. Diamond, Heidi MacLean, Aaron M. Ellison, Nicholas J. Gotelli, Nathan J. Sanders, and Robert R. Dunn. Forthcoming. Common garden experiments reveal uncommon responses across temperatures, locations, and species of ants. *Ecology and Evolution*.

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1 Common Garden Experiments Reveal Uncommon Responses across Temperatures, Locations,
2 and Species of Ants

3 Running Title: Uncommon geographic ant warming responses

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16 *Keywords*: climate change, Formicidae, warming experiment, common garden, intraspecies
17 variation, interspecies variation

18 *Primary Research Article*

19

20 ABSTRACT

21 Population changes and shifts in geographic range boundaries induced by climate change have
22 been documented for many insect species. On the basis of such studies, ecological forecasting
23 models predict that, in the absence of dispersal and resource barriers, many species will exhibit
24 large shifts in abundance and geographic range in response to warming. However, species are
25 composed of individual populations which may be subject to different selection pressures and
26 therefore may be differentially responsive to environmental change. Consequently, asystematic
27 responses across populations and species to warming will alter ecological communities
28 differently across space. Common garden experiments can provide a more mechanistic
29 understanding of the causes of compositional and spatial variation in responses to warming
30 because such experiments are useful for determining if geographically separated populations and
31 co-occurring species respond differently to warming, and they provide the opportunity to
32 compare effects of warming on fitness (survivorship and reproduction). We exposed colonies of
33 two common ant species in the eastern US, *Aphaenogaster rudis* and *Temnothorax*
34 *curvispinosus*, collected along a latitudinal gradient from Massachusetts to North Carolina, to
35 growth chamber treatments that simulated current and projected temperatures in central
36 Massachusetts and central North Carolina within the next century. Regardless of source
37 location, colonies of *A. rudis*, a keystone seed disperser, experienced high mortality and low
38 brood production in the warmest temperature treatment. Colonies of *T. curvispinosus* from cooler
39 locations experienced increased mortality in the warmest rearing temperatures, but colonies from
40 the warmest locales did not. Our results suggest that populations of some common species may
41 exhibit uniform declines in response to warming across their geographic ranges, whereas other
42 species will respond differently to warming in different parts of their geographic ranges. Our

43 results suggest that differential responses of populations and species must be incorporated into
44 projections of range shifts in a changing climate.

45

46 INTRODUCTION

47 The majority of forecasts of the responses of species to climatic warming assume that
48 populations within a species are homogeneous and thus model shifts in the geographic
49 distributions of entire species (but see Buckley 2008; Richardson *et al.* 2011 for exceptions).
50 Likewise, most empirical studies of recent responses to warming focus on individual species
51 and/or locations (but see Pelini *et al.* 2011a) as invariant units of analysis. However, the rate,
52 magnitude, and direction of the responses to warming or other climatic changes by different
53 individuals in different populations of any given species may differ for at least two reasons. First,
54 populations may be locally adapted to current or historical environmental conditions (Gilman *et*
55 *al.* 2006; Pelini *et al.* 2009; Angert *et al.* 2011). Second, individuals from different populations
56 may differ in their ability to cope with local environmental changes (Magnani 2009). For these
57 reasons, models based on the assumption of uniform responses among populations within a
58 species may be misleading.

59 The methods necessary to assess if populations are locally adapted to climate or can cope with,
60 or even benefit from climatic change are well established (reviewed in Kawecki & Ebert 2004).

61 The first step is to determine experimentally whether and how individuals from distinct
62 populations vary in their ability to respond to common conditions (Grosholz 2001; Castañeda *et*
63 *al.* 2005; Pelini *et al.* 2009; Tack & Roslin 2010; Craig *et al.* 2011). The second step is to
64 conduct common garden experiments with treatments that represent different climatic regimes.

65 Three broad outcomes are possible. First, all populations might exhibit increased survivorship or
66 reproduction in response to warming. Second, populations might exhibit local adaptation to
67 historical conditions, or have narrow physiological tolerances, thereby leading to population
68 declines or extinctions under warming. Third, local populations may respond idiosyncratically to

69 warming, with some populations exhibiting local adaptation/narrow physiological tolerances and
70 declining in response to temperature increases, whereas other populations cope with and/or
71 increase in response to temperature increases. All of these outcomes are possible because
72 individuals are behaviorally or phenotypically plastic and populations of individuals possess
73 genetic variation in traits that maximize fitness for different individuals in different conditions.

74 In this study, we used ants to examine variation among populations and co-occurring species
75 under expected temperature change in the eastern United States (also see Fitzpatrick *et al.* 2011;
76 Jenkins *et al.* 2011). Ants are an ideal taxon to use for multiple common-garden experiments
77 because they are responsive to temperature (Dunn *et al.* 2009) and relatively easy to maintain in
78 controlled environments. Temperature is correlated with patterns of ant diversity and abundance
79 (Sanders *et al.* 2007), seasonal patterns of activity (Dunn *et al.* 2007), overwintering mortality
80 (Sorvari *et al.* 2011), foraging behavior (Ruano *et al.* 2000), and the outcomes of interactions
81 between species (Cerdeira *et al.* 1997; Holway *et al.* 2002). Ant foraging activities modulate many
82 ecosystem processes, including decomposition, nutrient cycling, and primary production
83 (Hölldobler & Wilson 1990; Folgarait 1998; Del Toro *et al.* In press). Consequently, the extent
84 to which ants respond to climatic change, especially to local and regional changes in
85 temperature, may have cascading consequences for other taxa and for ecosystem dynamics
86 (Lensing & Wise 2006; Moya-Larano & Wise 2007). Other work has demonstrated that ant
87 community responses to warming differ across latitude (Pelini *et al.* 2011a), making ants an ideal
88 taxon for examining the underlying causes of geographic variation in the ecological responses to
89 climate change.

90 Using a common garden experiment, we tested the hypothesis that the relationship between
91 temperature and fitness will vary for ant populations sampled across a species' range. In order to

92 understand if patterns in intraspecies variation in temperature impacts on fitness are
93 generalizable, we tested the hypothesis that co-occurring, closely related species with similar
94 geographic distributions would display similar patterns in intraspecies variation in their response
95 to varying temperature; this is one of the first studies to experimentally test this hypothesis.
96 Growth chamber studies are particularly useful for examining insect responses to warming
97 because they circumvent heat- island effects associated with warming treatments applied in the
98 field (Moise & Henry 2010). We placed ant colonies in growth chambers set to summer
99 temperatures in the regions from which ants were collected as well as to mimic summer
100 temperatures in the future (Solomon *et al.* 2007). To determine if ants from different climates
101 differed in their ability to cope with shifts in temperature, and more generally to determine if
102 warming could have a net negative or positive effect on populations across the geographic ranges
103 of species, we examined associations between source location mean summer temperature and
104 experimental rearing temperature on two measures of fitness: survival and brood production.
105 Fitness differences attributed to source location temperatures would suggest that individuals
106 from different locations differed in their ability to cope with temperature change. Increases in
107 fitness with increases in rearing temperature would suggest that populations throughout species'
108 ranges will have increased fitness under warming, whereas decreases would suggest that
109 warming will have negative fitness effects across species' ranges. Fitness differences attributed
110 to interactions between source location temperatures and rearing temperature would suggest that
111 populations from different locales are affected differently by temperature shifts.

112 METHODS

113 *Common garden*

114 The focal taxa for these experiments were populations of *Aphaenogaster rudis* Mayr and
115 *Temnothorax curvispinosus* Mayr from Massachusetts to North Carolina (33.6 - 42.5°; Table 1).
116 These two ant species co-occur across forests in the eastern US (Pelini *et al.* 2011a). While *T.*
117 *curvispinosus* is recognized as a species (Mackay 2000), *A. rudis* is a species complex (Umphrey
118 1996) currently undergoing taxonomic revision (Bernice DeMarco, *unpublished data*). In order
119 to determine if patterns observed in our focal species were similar to those for other species, we
120 also included a subset of colonies of other species that co-occur with the focal species: *A. fulva*
121 Roger, *Camponotus chromaiodes* Bolton, *Crematogaster lineolata* Say, *Tapinoma sessile* Say,
122 and *Temnothorax longispinosus* Roger (Table 1). We placed single queen colonies in artificial
123 nest boxes and allowed them to acclimate to laboratory conditions for two weeks before placing
124 them into growth chambers at North Carolina State University lab facilities. Artificial nests were
125 plastic containers (390cm³) with sand, water tubes plugged with cotton (to maintain humidity),
126 and a food source (Bhatkar & Whitcomb 1970). When brood or males were collected with the
127 colonies, we removed them so as to assess more accurately survival and reproductive output of
128 the colony throughout the duration of the experiment.

129 We placed colonies in their artificial nest boxes into one of three growth chamber temperature
130 treatments, with temperatures determined from long-term temperature records from Harvard
131 Forest, Massachusetts (21°C summer mean); Duke Forest, North Carolina (26°C summer mean)
132 and Miami, Florida (31°C summer mean); the 26°C treatment represents projected warming for
133 Massachusetts before 2100, and the warmest treatment, 31°C, represents the forecast temperature
134 for Massachusetts beyond 2100 and for North Carolina before 2100 (Solomon *et al.* 2007).
135 Chamber temperatures fluctuated diurnally, i.e., temperatures were ramped up/down by 1.2°C
136 per hour) between the average minimum (at 3am) and maximum (at 3pm) temperatures for each

137 location (Massachusetts: 16-26°C; North Carolina: 21-31°C; Florida: 26-36°C), and day-length
138 was 14 hours long in all chambers.

139 We checked nests daily to ensure constant water and food supply. We censused ant colonies in
140 July before transferring them to the growth chambers, again 10 days after the start of the
141 experiment, and finally at the end of the experiment in September (59 days total). At each
142 census, we recorded the presence or absence of brood and the number of workers in each colony.

143 *Data analysis*

144 First, we used generalized linear mixed models (R version 2.9.0; R Development Core Team
145 2007) to test whether survival and brood production (binomial response variables) were
146 significantly affected by source-location temperature (fixed effect) and/or rearing temperature
147 (fixed effect), across all species (random effect) and both census periods (random effect). To
148 determine if patterns found across our entire species pool were consistent with those for the focal
149 species, *Aphaenogaster rudis* and *Temnothorax curvispinosus*, for which we had broader
150 geographic coverage, we ran similar models examining the effects of source-location
151 temperature, rearing temperature, and species as fixed effects, and census period as a random
152 effect. We also included a species \times source-location temperature term to determine if the ability
153 of colonies from different source locations to cope with temperature change was similar in both
154 focal species. In addition, we also included a species \times rearing temperature term in this model to
155 determine if the two focal species differed in their responses to rearing temperature, regardless of
156 source location. Lastly, because both species \times source-location temperature and species \times rearing
157 temperature had significant effects on survival of the two focal species, we examined in more
158 detail the separate responses of *A. rudis* and *T. curvispinosus*. For each of these two species, we

159 modeled survival as a function of source-location temperature, rearing temperature and their
160 interaction. Significant interactions between source-location temperature and rearing temperature
161 revealed if colonies from different locales were affected differently by similar temperatures,
162 which may be due to adaptive differences such as local adaptation. We extracted the mean
163 summer (warmest quarter) temperatures at the source locations from WorldClim (Hijmans *et al.*
164 2005).

165

166 RESULTS

167 Interspecies Models—Survival decreased with increasing rearing temperature (all species:
168 $\chi^2=5800$; $P<0.001$; focal species: $\chi^2=3800$; $P<0.001$) but increased with source-location
169 temperature (all species: $\chi^2=4.3$; $P=0.037$; focal species: $\chi^2=500$; $P<0.001$) (Figure 1). Brood
170 production also decreased with increasing rearing temperature (all species: $\chi^2=19$; $P<0.001$; focal
171 species: $\chi^2=18$; $P<0.001$). In our focal species model of survival, the species \times source-location
172 temperature and species \times rearing temperature terms also were significant ($\chi^2=1900$; $P<0.001$;
173 $\chi^2=6000$; $P<0.001$, respectively).

174 Intraspecies Models—Survival of both *Aphaenogaster rudis* and *Temnothorax curvispinosus*
175 decreased with increasing rearing temperature ($\chi^2=120$; $P<0.001$ and $\chi^2=36$; $P<0.001$,
176 respectively) but increased with source-location temperature ($\chi^2=200$; $P<0.001$ and $\chi^2=17$;
177 $P<0.001$, respectively) (Figure 1, lower panels). Interactions between source-location and rearing
178 temperature also were significant, but different, for both species (*A. rudis*: $\chi^2=270$; $P<0.001$ and
179 *T. curvispinosus*: $\chi^2=30$; $P<0.001$). More specifically, *A. rudis* colonies from warmer locations
180 had higher survival than those from cooler locations in the low and intermediate rearing

181 temperatures, but all colonies had high mortality in the warmest rearing temperature (Figure 2,
182 upper panel). In contrast, *T. curvispinosus* colonies from different source locations did not differ
183 significantly in survival except in the warmest rearing temperature, where colonies from two of
184 the three warmest source locations had relatively high survival compared to their cooler source-
185 location counterparts (Figure 2, lower panel).

186

187 DISCUSSION

188 Species are composed of individual populations, which may be subject to different selection
189 pressures. Some will go extinct locally or globally, some will migrate, and some will increase in
190 size (Pelini *et al.* 2009). Increasing temperatures may have negative fitness effects for
191 populations that are locally adapted to and/or have narrow physiological tolerances of
192 temperature and positive fitness effects for other populations with broader physiological
193 tolerances of temperature. If different populations respond differently to climatic warming, then
194 extrapolating to a single, overall response of the given species may be unwise or unwarranted.
195 Furthermore, a species' potential to adapt to future climatic change may be reduced if some
196 populations perform well while others decline under warming and causes a reduction in genetic
197 diversity (Collevatti 2011). In aggregate (at the species level), all eight ant species that we
198 studied in this common garden experiment exhibited decreased survival and brood production
199 with increased warming. However, we observed strong differences among species and
200 populations within particular species. Colonies of both focal species, *Temnothorax curvispinosus*
201 and *Aphaenogaster rudis*, from warmer locales had higher survival and brood production under
202 warmer temperatures than those from cooler sites. Survival decreased with increasing

203 temperatures for *A. rudis* from all locales. The results for *T. curvispinosus* were very similar,
204 with one exception: colonies of *T. curvispinosus* from the warmest locale experienced increased
205 fitness in the warmer temperatures. Together, these findings suggest that for many of the species
206 in our study system, warming may be detrimental. However, where responses differ among
207 populations within species, warming affects southern populations (from warmer climates) less
208 than it does northern populations (from cooler climates). This latter result suggests that
209 forecasted distributions of ant species in a warmed world, whether based on physiology or
210 distributional data, do not account for intraspecific variability and may be inaccurate.

211 Because *A. rudis* populations responded negatively to temperature increases regardless of their
212 location of origin, we forecast that severe warming will negatively affect populations of this
213 species across its entire range. As the primary disperser of many forest understory herbs (Ness *et*
214 *al.* 2009), reductions in *Aphaenogaster* populations are likely to have ramifying consequences in
215 many forests (e.g., Rodriguez-Cabal *et al.* 2012). Unlike *A. rudis*, *T. curvispinosus* colonies from
216 warmer, southern locales performed well under warming whereas their counterparts from cooler,
217 northern locales did not. Southern *T. curvispinosus* populations may have more genetic diversity
218 in traits related to physiological tolerances than northern colonies. We also observed noticeably
219 increased foraging activity in *Aphaenogaster rudis* (S. Diamond, personal observation) and
220 running speeds in *Temnothorax curvispinosus* (H. MacLean, unpublished data) in the warmer
221 temperature treatments, suggesting that some of the mortality associated with warming may be
222 due to changes in behavioral and physiological traits (e.g., Dillon *et al.* 2010).

223 The findings from this laboratory common garden experiment complement those from recent
224 field warming manipulations in the same system with many of the same ant species. In field
225 warming experiments, we found increases in abundance under warming up to 5°C for low

226 latitude (North Carolina) populations of species with higher thermal tolerances, including
227 *Crematogaster lineolata* (and see Pelini *et al.* 2011a) and *T. curvispinosus*, but not for
228 *Aphaenogaster rudis* and other species with lower thermal limits. Abundances of species at a
229 higher latitude site (Massachusetts) increased under warming regardless of their thermal
230 tolerances (Diamond *et al.* in review). The data from the laboratory common garden experiment
231 reported here, together with data from our previous field experiments, suggest that the responses
232 of ants to warming will vary across populations within and across species (also see Fitzpatrick *et*
233 *al.* 2011; Jenkins *et al.* 2011 for modeling of ant communities under climate change).

234 Future studies should address how such changes could have cascading consequences for
235 species interactions and ecosystem processes (Traill *et al.* 2010) that are localized and are not
236 well projected by current models that assume uniform responses of species across their entire
237 range. Multiple observational and experimental approaches should be integrated because
238 complex abiotic (e.g., humidity, rainfall) and biotic (e.g., interactions with predators/prey or
239 plants) changes associated with climatic change can be captured by field manipulations but
240 separated by common garden laboratory experiments.

241

242 ACKNOWLEDGEMENTS

243 Funding was provided by a US DOE PER award (DE-FG02-08ER64510) to R.R. Dunn, A. M.
244 Ellison, N. J. Gotelli and N. J. Sanders. We would like to thank Adam Clark, Israel Del Toro,
245 David General, Benoit Guenard, Chris Hirsch, Neil McCoy, Mike Pelini, James Trager, and
246 Kaitlin Uppstrom for ant collection; Adriana Cardinal-De Casas, Beth Carton, Jarrett Clifton,
247 Colin Funaro, Britne Hackett, Nina Rountree and Scott Waring for assistance with ant rearing

248 and censusing; and Carole Saravitz and Janet Shurtleff for technical support and permission to
249 use NCSU phytotron facilities. We also thank three anonymous reviewers for comments that
250 improved the manuscript.

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355

356

357 TABLES

358

359 **Table 1. Source locations (decimal degrees), mean summer temperatures (WorldClim,**
 360 **Hijmans *et al.* 2005) at source locations, and number of colonies placed into three growth**
 361 **chamber temperature treatments from each species.** For species x sampling locations with
 362 fewer than 3 colonies, priority was given to the intermediate (26°C) and warmest (31°C)
 363 temperature treatments. Black text indicates focal species; non-focal species are gray.

Species	Source locations (decimal degrees)	Mean summer temperature (°C)	Rearing temperature (# colonies)		
			21°C	26°C	31°C
Aphaenogaster rudis	33.63°, -91.79°	26.1	1	2	2
	35.78°, -78.80°	24.8	0	1	0
	36.04°, -79.07°	24.1	5	4	5
	39.89°, -74.58°	22.3	0	1	0
	40.02°, -83.01°	22.1	0	0	1
	42.53°, -72.19°	18.5	4	4	4
Temnothorax curvispinosus	35.76°, -78.68°	24.8	12	11	12
	38.57°, -77.37°	23.7	0	1	1
	39.64°, -74.66°	22.6	0	0	1
	40.44°, -74.27°	22.4	1	1	1
	41.84°, -70.67°	20.4	2	2	3
	42.35°, -72.19°	18.5	2	2	2
Aphaenogaster carolinensis	35.78°, -78.68°	24.7	0	0	1
	38.51°, -90.83°	23.8	0	0	1
Aphaenogaster fulva	38.51°, -90.83°	23.8	1	1	1
Camponotus chromaiodes	38.51°, -90.83°	23.8	0	1	1
Crematogaster lineolata	36.04°, -79.07°	24.1	0	1	1
	40.58°, -76.75°	21.2	0	1	1
	42.53°, -72.19°	18.5	0	1	0
Tapinoma sessile	38.51°, -90.83°	23.8	0	0	1
	40.02°, -83.01°	22.1	1	1	2
Temnothorax longispinosus	42.53°, -72.19°	18.5	2	1	2

364

365 FIGURES

366

367 **Figure 1. Scatterplots of survival (at final census) as a function of mean rearing**

368 **temperature - source-location summer temperatures.** Upper left panel shows data for all

369 species considered in the experiment; upper right shows all species except for *Aphaenogaster*

370 *rudis* and *Temnothorax curvispinosus*; lower left shows *A. rudis*; and lower right shows *T.*

371 *curvispinosus* survival. Positive *x*-axis values indicate cases when experimental temperatures

372 were higher than those at colony source locations, and negative values indicate cases when

373 rearing temperatures were lower. Lines represent locally-weighted scatterplot smoothing

374 (function *loess* in R). In plots with multiple species (upper panels), species are shown in different

375 colors: green = *Aphaenogaster carolinensis*; blue = *A. fulva*; gray = *A. rudis*; black =

376 *Camponotus chromaiodes*, purple = *Crematogaster lineolata*, orange = *Tapinoma sessile*, light

377 blue = *Temnothorax curvispinosus*; brown = *Temnothorax longispinosus*. For *Aphaenogaster*

378 *rudis* and *Temnothorax curvispinosus* (bottom panels), colors represent mean summer

379 temperatures at source locations: *A. rudis* - darkred = 26.1°C, red = 24.8°C, orangered = 24.1°C,

380 orange = 22.3°C, yellow = 22.1°C, tan = 18.5°C; *T. curvispinosus* - darkred = 24.8°C, red =

381 23.7°C, orangered = 22.6°C, orange = 22.4°C, yellow = 20.4°C, tan = 18.5°C.

382 **Figure 2. Mean survival (at final census) of *Aphaenogaster rudis* (upper panel) and**

383 ***Temnothorax curvispinosus* (lower panel) as a function of rearing temperature.** Error bars

384 represent 95% binomial proportion confidence intervals. Lines are colored by source locations

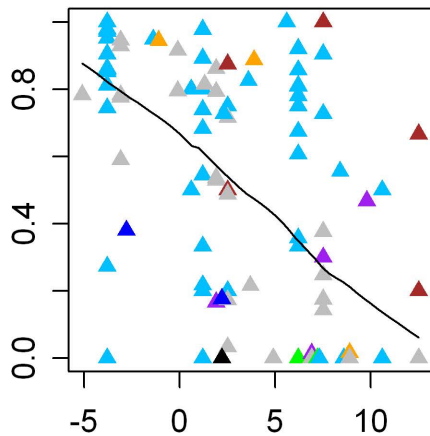
385 such that the coolest location is tan and the warmest is darkred. Colors represent mean summer

386 temperatures at source locations: *A. rudis* - darkred = 26.1°C, orangered = 24.1°C, tan = 18.5°C;

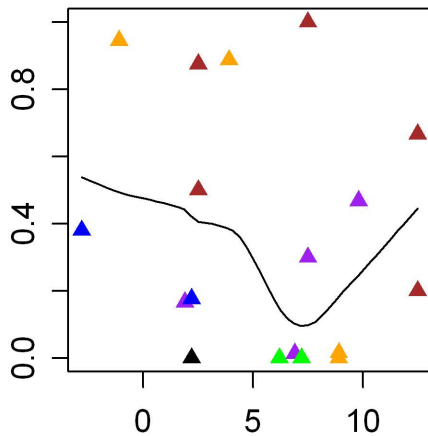
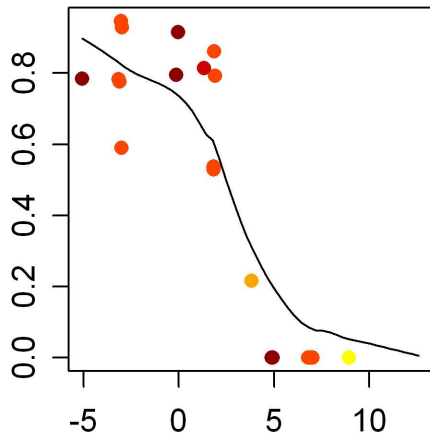
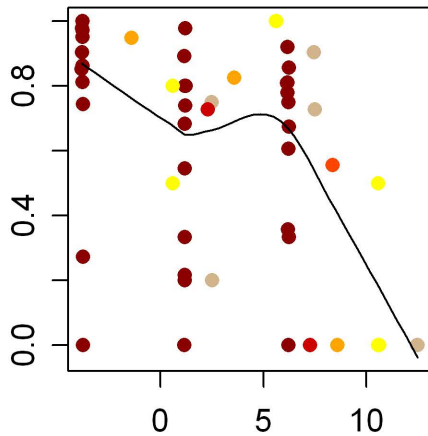
387 *T. curvispinosus* - darkred = 24.8°C, red = 23.7°C, orange = 22.4°C, yellow = 20.4°C, tan =

388 18.5°C. Points are jittered along the x-axis so that points of overlap between different source
389 locations can be visible. Rearing temperatures were 21°C, 26°C, and 31°C.

All species

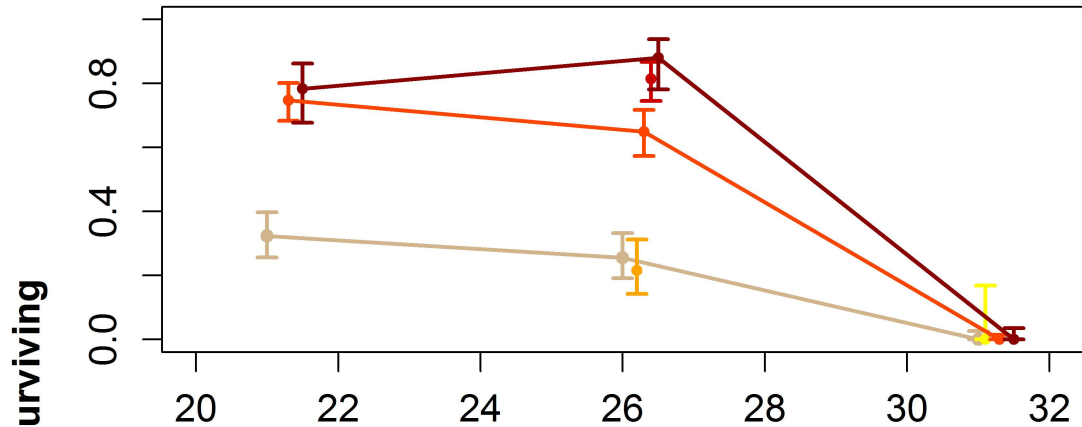


Non focal species

*Aphaenogaster rudis**Temnothorax curvispinosus*

Relative Temperature (°C)

Aphaenogaster rudis



Temnothorax curvispinosus

