Using Physiology to Predict the Responses of Ants to Climatic Warming

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24   **Abstract**

25   Physiological intolerance of high temperatures places limits on organismal responses to

26   the temperature increases associated with global climatic change. Because ants are

27   geographically widespread, ecologically diverse, and thermophilic, they are an ideal system for

28   exploring the extent to which physiological tolerance can predict responses to environmental

29   change. Here we expand on simple models that use thermal tolerance to predict the responses of

30   ants to climatic warming. We investigated the degree to which changes in the abundance of ants

31   under warming reflect reductions in the thermal niche space for their foraging. In an eastern

32   deciduous forest system in the United States with ~40 ant species, we found that for some

33   species, the loss of thermal niche space for foraging was related to decreases in abundance with

34   increasing experimental climatic warming. However, many ant species exhibited no loss of

35   thermal niche space. For one well-studied species, *Temnothorax curvispinosus*, we examined

36   both survival of workers and growth of colonies (a correlate of reproductive output) as functions

37   of temperature in the laboratory, and found that the range of thermal tolerances for colony

38   growth was much narrower than for survival of workers. We evaluated these functions in the

39   context of experimental climatic warming and found that the difference in the responses of these

40   two attributes to temperature generates differences in the means and especially the variances of

41   expected fitness under warming. The expected mean growth of colonies was optimized at

42   intermediate levels of warming (2 – 4 °C above ambient), yet the expected variance

43   monotonically increased with warming. In contrast, the expected mean and variance of the

44   survival of workers decreased when warming exceeded 4 °C above ambient. Together, these

45   results for *T. curvispinosus* emphasize the importance of measuring reproduction (colony

46   growth) in context of climatic change: indeed, our examination of the loss of thermal niche space

47 with the larger species pool could be missing much of the warming impact due to these analyses

48 being based on survival rather than reproduction. We suggest that while physiological tolerance

49 of temperature can be a useful predictive tool for modeling responses to climatic change, future

50 efforts should be devoted to understanding the causes and consequences of variability in models

51 of tolerance calibrated with different metrics of performance and fitness.

52

53 *Keywords*: ants, climate change, fitness components, niche loss, temperature, thermal tolerance

54

55 **Introduction**

56   Global changes in land-use and climate ensure that species are increasingly likely to

57 encounter novel environments (Grimm et al. 2008). This places a renewed urgency on

58 understanding biological responses to environmental novelty. However, because these changes

59 are occurring at a global scale with potential impacts on millions of species, it is challenging to

60 develop predictions for how each species might respond. To add to the issue, recent models of

61 global biodiversity suggest that conservation planning based on the patterns of global diversity of

62 well-studied vertebrate taxa including birds, mammals, and amphibians, may not cover the

63 diversity of less-studied invertebrate taxa (Jenkins et al. in press; see also Lawton et al. 1998 for

64 similar findings at the regional scale). Together, these limits on conservation planning demand a

65 predictive framework that reduces the dimensionality of this task by identifying key

66 characteristics of those taxa and regions that are most vulnerable to climatic change. A number

67 of frameworks have been proposed for accomplishing this task (e.g., Williams et al. 2008; Huey

68 et al. 2012). Here, we focus on a promising component of these frameworks: the predictive

69 ability of physiological tolerance of extreme temperatures. We use ants as a model system

70 because they are geographically widespread, ecologically diverse, and have the potential to

71 mediate numerous functions of ecosystems (Dunn et al. 2010; Wardle et al. 2011; Zelikova et al.

72 2011).

73   We build upon previous global-scale analyses showing that despite the greater increases

74 in temperature anticipated at higher latitudes, ants inhabiting lower latitudes tend to be the most

75 vulnerable to climatic change because environmental temperatures are close to their upper

76 thermal tolerances (Diamond et al. 2012a). A pattern similar to the global pattern was

77 recapitulated between two large-scale experimental-warming arrays, positioned at the northern

78 and southern boundaries of temperate hardwood forests in eastern North America (Pelini et al.

79 2011); these chambers mimic the range of warming anticipated by the end of the century, from

80 1.5 to 5.5 °C above ambient temperatures (IPCC 2007). We found that thermal tolerance

81 predicted the responses of ants at the low-latitude site where temperatures routinely exceed the

82 upper thermal tolerances of ants—i.e., ants with low thermal tolerances experienced declines in

83 worker abundance and foraging intensity—but not at the high-latitude site where temperatures

84 remain below the upper thermal tolerances of ants (Diamond et al. 2012b; Stuble et al. 2013).

85   Temperature can have both indirect and direct impacts on fitness. In ants, increases in

86 temperature can limit the amount of time available for foraging if temperatures approach or

87 exceed the thermal tolerances of workers, with subsequent limits on colony growth. In contrast,

88 temperature can directly impact colony growth through physiological constraints on the

89 production of brood and the lifespan of workers (Porter 1988; Calabi and Porter 1989; Asano and

90 Cassill 2011). Theory suggests colony growth should be a strong correlate of fitness in ants

91 (Oster and Wilson 1979), and this has been borne out empirically, as larger colonies maintain

92 larger territories (Adams 1990; Tschinkel et al. 1995), deploy more foragers (Tschinkel 2011),

93   and have a higher probability of producing reproductives (Tschinkel 1993; Cole and Wiernasz

94   2000).

95   Here we further explore the mechanisms underlying the responses of ants to climatic

96   warming. Specifically, we examine how (1) reductions in foraging time (the amount of thermal

97   niche space for foraging that exceeds the upper thermal tolerance of an ant species) correspond

98   with changes in the abundance of ants under experimental warming, and (2) how estimates of

99   vulnerability of particular species under climatic change are altered by the choice of performance

100   or component of fitness employed, i.e. the survival of workers versus a more comprehensive

101   metric of fitness, colony growth.

102

103   **Materials and Methods**

104   *Warming chambers*

105   The details of our warming chambers are presented elsewhere (Pelini et al. 2011), but

106   briefly, the high-latitude (42° N) site at Harvard Forest and the relatively low-latitude (36° N)

107   site at Duke Forest each contain 12 open-top experimental plots (5 m in diameter). At each site,

108   nine chambers are heated by the addition of warmed air in a regression design of 0.5 °C

109   increasing intervals from 1.5 to 5.5 °C above ambient air temperature, and three chambers are

110   unheated controls. The chambers add a fixed amount of heat (according to the target amount of

111   warming), such that increases in mean temperature are achieved (target and actual differences

112   between chamber temperatures and ambient chambers are on average within 0.3 °C) without

113   alterations to the variance in temperature. Because previous work in this system showed that ants

114   are more vulnerable to climatic change (and exhibit much stronger responses to warming) at the

115   low-latitude site (Duke Forest) than at the high-latitude one (Harvard Forest), we focus

116   exclusively on Duke Forest in the analyses presented here. The chambers at Duke Forest have

117   been heated continuously since January 2010; we present data through January 2013,

118   representing three full years of warming and its impact on the performance of ants.

119

120   *Loss of thermal niche space under warming*

121   We first estimated the thermal niche using kernel density distributions of air temperatures

122   in the chambers during peak activity periods for foraging (hours 10 through 18 during the

123   reproductive season when colonies are growing: May through September). Given that we are

124   focusing on peak periods for foraging, it is likely these temperature distributions estimate the

125   available thermal niches for ants foraging in the chambers. It is possible ants are not actively

126   foraging during this entire period; therefore, we focus our analyses and interpretations on

127   alterations to the time available for foraging, rather than the time of active foraging. We then

128   calculated how much of the thermal niche was lost, specifically how much of the thermal niche

129   (computed using kernel density estimation, which disperses the mass of the empirical cumulative

130   density function over a regular grid, on the air temperatures of the warming chambers)

131   (Silverman 1986) exceeded the upper thermal tolerance of a given ant species (critical thermal

132   maximum, CT_{max}, defined as the temperature at which muscular coordination is lost; see

133   Diamond et al. [2012b] for original data and methods for estimating CT_{max}) (Figure 1 A).

134   Because the air temperature data among the different warming chambers were recorded at the

135   same times and on the same scale (hourly over the course of three years), the total areas under

136   the kernel density curves are the same, ensuring that the loss of thermal niche space can be

137   directly compared among chambers. In general, our thermal-niche-loss models assume that

138   temperature is the major driver of the activity of ants, and do not include the impacts of other

139   abiotic and biotic variables.

140   Finally, we compared the slope of the relationship between the fraction of thermal niche

141   space lost and the degree of warming in the chambers ("thermal-niche-loss slope") with the slope

142   of the relationship between the abundance of ants (natural log transformed) and the degree of

143   warming in the chambers ("thermal-accumulation slope"). Although the thermal-accumulation

144   slope and thermal-niche-loss slope share the degree of warming as denominators, we present

145   these results as slopes to ensure equal representation among species. Qualitatively similar results

146   were obtained when examining the abundance of ants (natural log transformed) as a function of

147   the loss of thermal niche space as when examining the thermal-accumulation slope as a function

148   of the thermal-niche-loss slope; further, the similarity in results indicates that deviations from

149   linearity of the abundance of ants as a function of the degree of warming do not strongly

150   influence our results. Most species exhibit strong linear components in their responses to

151   warming in the chambers (Appendix F of Diamond et al. 2012b, but see *Temnothorax*

152   *curvispinosus*, described below), so we focus on linear rather than quadratic terms in models of

153   abundance as a function of warming to be able to compare responses among ant species.

154   Abundance data for 20 species were obtained from monthly pitfall trapping from January 2010 to

155   January 2013 in the chambers (most observations occurred during the growing season), and

156   represent the accumulation of individuals in each chamber since the beginning of heating the

157   chambers in January 2010. We expected that species with greater loss of thermal niche space

158   would have flat or negative relationships between abundance and the degree of warming in the

159   chambers.

160

161 *Survival of workers and growth of colonies under warming*

162   For one focal species, *Temnothorax curvispinosus*, we estimated the survival of workers

163 and growth of colonies as functions of temperature in the laboratory. We used Weibull functions,

164 the best-fitting functions among Gaussian and quadratic functions that were also considered

165 (AIC was the basis for comparing fits to the data; see Angilletta [2006]); when the Weibull and

166 Gaussian functions had comparable fits to the data, the Weibull was preferred owing to

167 theoretical predictions of skew in curves describing performance as a function of temperature

168 (Schoolfield 1981). The *T. curvispinosus* colonies originated from North Carolina, USA, at sites

169 near the Duke Forest experimental warming chambers. Colonies were maintained in growth

170 chambers under diurnally fluctuating thermal regimes with mean temperatures of 21, 26, and 31

171 °C for two months (each diurnal range was 10 °C; 14:10 L:D; n = 12, 11, and 12 colonies per

172 temperature treatment, respectively), after which time, we assessed both production of brood and

173 survival of workers within each colony, which served as an estimate of colony growth (see Pelini

174 et al. 2012 for original data and details on rearing ants; all colonies had queens). Both metrics

175 were expressed relative to the initial size of the colony, and the ordinate of each function was

176 determined by the maximum proportion of surviving workers or number of brood produced.

177   Although life-table analyses of ant colonies that would allow the computation of

178 comprehensive measures of fitness, i.e. net reproductive rate (R_0), are relatively nascent for this

179 taxon (Ingram et al. in press), the growth of an ant colony may serve as a useful proxy of the

180 colony's fitness. The probability that a colony will produce reproductives tends to be higher for

181 larger colonies than for smaller ones (Tschinkel 1993; Gordon and Wagner 1997; Cole and

182 Wiernasz 2000). Additionally, larger colonies may provide a buffer against environmental

183 uncertainty (Cassill 2002), and this could lead to higher lifetime fitness benefits. Regardless of

184   the precise mechanism, growth of the colony is almost certainly a more comprehensive estimate

185   of fitness than is the more often studied survival of workers.

186   We evaluated the worker-survival and colony-growth functions with the air temperature

187   data from the experimental warming chambers during the growing season (May through

188   September), available at a temporal resolution of one hour over the course of three years since

189   heating began in the chambers. The resulting distributions of expected survival of workers and

190   growth of colonies were transformed (log-inverse and square root, respectively) to meet

191   normality assumptions for estimating means and standard deviations; we present summary

192   statistics that were back-transformed to the original scale of the data. The natural history of

193   *Temnothorax* sp. ensures that air temperatures are likely to be particularly relevant for this

194   group's physiological performance because *Temnothorax* sp. lives in fallen acorns, walnuts, and

195   twigs, and is intimately tied to its nest, such that the ability of these ants to behaviorally

196   thermoregulate and avoid stressful air temperatures is limited (Mitrus 2013).

197

198   **Results and Discussion**

199   *Global and regional responses to warming*

200   Ants and several other ectothermic taxa are likely to be more vulnerable to climatic

201   change in the tropics compared with more temperate regions (Deutsch et al. 2008; Huey et al.

202   2009; Diamond et al. 2012a; but see Walters et al. 2012). These findings are contrary to previous

203   expectations that ectotherms inhabiting higher latitudes would be more vulnerable owing to the

204   greater amounts of warming anticipated in these regions. The basis of increased tropical

205   vulnerability appears to be related to biogeographic patterns in thermal adaptation; tropical

206   ectotherms have evolved in thermally invariant environments and tend to exhibit narrower ranges

207   of thermal tolerance compared with temperate and higher-latitude ectotherms (Janzen 1967;

208   Brattstrom 1968, 1970). Because tropical ectotherms experience environmental conditions

209   already close to their thermal optima and upper thermal tolerances, even small increases in

210   environmental temperature can lead to population decline or extirpation (Deutsch et al. 2008).

211   Interestingly, this global pattern of increased vulnerability of species living closer to the

212   equator appears to hold even among sites at higher and lower latitudes within the temperate zone.

213   The responses of ants to experimental climatic warming suggest that those from lower temperate

214   latitudes are more vulnerable to warming compared with those from higher temperate latitudes.

215   At our low-latitude site, the critical thermal maximum (CT_{max}, an ecologically relevant metric of

216   thermal tolerance based on the survival of workers in our study) predicted both general activity

217   (Diamond et al. 2012b) and foraging activity (Stuble et al. 2013), such that species with lower

218   CT_{max} values were less abundant and exhibited reduced foraging activity in the warmest

219   experimental chambers. Air temperatures in the warmest experimental chambers can exceed the

220   CT_{max} values of some ant species, but the question arises as to how much of the thermal niche

221   space is lost for the species inhabiting the chambers, and whether this relates to changes in their

222   abundance when subjected to warming?

223

224   *Loss of thermal niche space under warming*

225   Here, we quantified the relationship between the degree of the thermal niche space lost

226   (i.e. how much of the temperature distributions of the chambers exceeded the CT_{max} of a

227   particular ant species) and the changes in abundance of ant species under the experimental

228   manipulations of temperature (Figure 1 B, C). Our models of thermal niche loss are a measure of

229   the reduction of the time available for foraging. Reductions in available foraging time could

230   contribute to reductions in colony performance by reducing the quantity or quality of food

231   retrieved. Reductions in thermal niche space might also lead to an increase in competition since

232   there is less thermal space in which organisms can distribute their activity (Urban et al. in press).

233   Interestingly, even with 5.5 °C of warming, we found that the majority of the 20 species we

234   examined experienced no loss of thermal niche space. However, of the 35% of species that

235   exhibited significant losses of thermal niche space, 71% exhibited significant or trending

236   declines in abundance with experimental warming (Figure 1 C). Thus, for some species with low

237   thermal tolerances, the loss of thermal niche space can be sufficient to drive reductions in

238   foraging and potentially in colony size. It is important to note that these models were constructed

239   with survival-based CT_{max}, and temperature can have differential impacts via different

240   components of performance and fitness. How warming impacts not only survival, but other

241   components of fitness, particularly reproduction, is an important, but open, question in many

242   systems.

243

244   *Impacts of warming via different fitness components*

245   Estimates of tolerance frequently are based on proxies or components of fitness such as survival,

246   body size, or development time. Few estimates of tolerance are based on more comprehensive

247   metrics such as net reproductive rate (R_0) and intrinsic rate of increase (*r*), largely owing to the

248   practical limits of obtaining these data (Ingram et al. in press). For example, ideally our models

249   of thermal niche loss would be calibrated with more comprehensive metrics of fitness rather than

250   the survival of workers, but only data on survival are presently available to cover the diversity of

251   ant species present in the experimental warming chambers. Yet importantly, in some cases these

252   more comprehensive metrics of tolerance can have narrower ranges compared with other metrics

253   such as survival (reviewed by Angilletta 2009; Kingsolver et al. 2011). Because many estimates

254   of vulnerability to climatic change are based on survival, we may be misestimating potential

255   impacts: survival functions can determine conditions that are immediately lethal, but populations

256   may stop growing before lethality is reached (i.e. when $R_0 < 1$ or $r < 0$), which over time can

257   contribute to local extirpation.

258   We used the acorn ant, *Temnothorax curvispinosus*, to illustrate how estimates of

259   vulnerability to climatic change might be altered by the choice of tolerance metric used in the

260   context of a colonial ectotherm. *Temnothorax curvispinosus* is a relatively heat-tolerant ant, with

261   a mean CT_{max} of 43.4 °C (using a dynamic-temperature ramping method of assessing thermal

262   tolerance) (Diamond et al. 2012b). As a consequence, this species experienced no reductions in

263   thermal niche space under experimental climatic warming (Figure 1 B). From ant colonies reared

264   in the laboratory under different thermal treatments (Pelini et al. 2012), we were able to estimate

265   the survival of workers and the growth of colonies, a more comprehensive metric of fitness

266   related to R_0 (see above), as functions of temperature. We found that the worker-survival

267   function lies outside the function that describes the growth of colonies; indeed, on the warm end

268   of the function, the upper tolerances of these two attributes differed by 8.3 °C (colony growth

269    $CT_{max} = 34.1$ °C; survival $CT_{max} = 42.4$ °C, an estimate that is relatively close to that using the

270   dynamic-temperature method presented above; Figure 2 A). *Temnothorax curvispinosus* thus

271   appears to survive much higher temperatures than those that colony growth of colonies.

272   When we used these functions to examine the distribution of survival of workers and of

273   growth of colonies in the context of the environmental temperatures in our experimental

274   warming chambers, we found that while expected mean survival began to decline sharply in only

275   those warming chambers that were > 4 °C above ambient conditions (Figure 3 A), expected

276   mean growth of colonies exhibited a somewhat different pattern, with chambers having moderate

277   amounts of warming ($2 - 4$ °C) yielding the highest growth, and very cool and very warm

278   chambers yielding the lowest growths (Figure 3 B). Because the absolute range of temperatures

279   during the growing season across all chambers (5.9 – 41.5 °C) falls within the limits of the

280   survival function (3.8 – 42.4 °C), the decrease in expected mean survival would appear to result

281   from the skewness of the function, i.e. that survival declines more rapidly on the warm end of the

282   curve above the optimal temperature for survival than on the cool end (Figure 2 A). For expected

283   mean growth, both skewness (again, decreasing more steeply at temperatures higher than the

284   optimum) and breadth—optimal temperatures not being frequently reached in the cool chambers

285   (minimum temperature for colony growth was estimated at 11.6 °C) or being frequently

286   exceeded in the warm chambers (maximum temperature for colony growth was estimated at 34.1

287   °C)—appear to result in moderate amounts of warming leading to the greatest growth.

288   Interestingly, the pattern for expected mean growth of colonies as a function of the

289   degree of warming in the chambers was more functionally similar (optimized at intermediate

290   amounts of warming) to the pattern of observed abundances in the chambers (Figure 3 A,C)

291   compared with expected mean survival, which decreased only at very high levels of warming

292   (Figure 3 B). Principal components (PC) analysis using different amounts of warming as 'traits'

293   and different types of performance curves as 'replicates' revealed that the loadings on PC1 were

294   all of the same sign when comparing the spline fits of colony growth and abundance as functions

295   of warming, but the loadings on PC1 changed signs (both from low to intermediate temperatures

296   and intermediate to high temperatures) when comparing the spline fits of survival and abundance

297   as functions of warming, indicating more substantial differences in curve shape in the latter case

298   (see Izem and Kingsolver 2005 for details of the modeling approach). The similarity in colony

299   growth and abundance patterns as functions of warming suggests that the pitfall trapping method

300   of estimating performance may in fact capture more inclusive metrics of performance such as

301   colony growth. This result is somewhat surprising given the inherent differences between our

302 field and laboratory experiments of ant responses to warming, particularly the differences in

303 timescale (three years of warming in the field versus two months in the laboratory). The field

304 results represent the impacts of warming throughout the colony-growth season and

305 overwintering, whereas the laboratory results represent only the impacts throughout a portion of

306 the colony-growth season. It is perhaps encouraging that the field and laboratory results are in

307 agreement for the responses of *T. curvispinosus* to warming; however, in general, more research

308 is needed on the mechanisms underlying organismal responses to warming throughout ontogeny

309 (e.g. Williams et al. 2012).

310   In contrast to the variance in expected survival which decreased along with decreases in

311 expected mean survival in the warming chambers, the variance in expected colony growth

312 increased with greater warming (Figure 3 A, B). Indeed, while there are more frequent

313 opportunities for achieving the highest levels of colony growth in the warmest (+ 5.5 °C)

314 chamber, *T. curvispinosus* is expected to even more frequently experience temperatures at which

315 the colony cannot grow, leading to an overall reduction in expected mean colony growth in the

316 warmest chambers (Figure 2 C, D). Further, because the experimental chambers alter the mean,

317 but not the variance, of environmental temperature, the anticipated increases in temperature-

318 variance with global climatic change (IPCC 2007) may exacerbate the current pattern of

319 increased variance in expected fitness for *T. curvispinosus*, and possibly for other species.

320   *Temnothorax curvispinosus* and the many other species in the genus *Temnothorax*

321 represent somewhat unique cases because their entire colonies are exposed to changes in surface

322 temperature since they nest inside acorns, walnuts, or twigs on the forest floor. This constraint

323 should also be present in ants that nest arboreally, but ground-nesting species generally have

324 more depth to thermoregulate by transporting brood deeper underground to escape excessive

325 temperatures at the surface (e.g. Penick and Tschinkel 2008). While these species should be

326 buffered from negative effects of warming outside their nests, thermophilic species may be able

327 to take advantage of surface-warming by tracking higher temperatures inside their nests to

328 produce brood earlier in the season or to expand the amount of time that optimal brood-rearing

329 temperatures are present at some depth inside their nests. Future work is needed to determine

330 how species with different nesting habits and different temperature preferences for rearing of

331 brood may respond to warming.

332   One component currently missing from these analyses is how generation time varies as a

333 function of temperature. For social ectotherms, generation time may be related to both the age

334 when reproductives are first produced (the ergonomic phase of colony growth, after Oster and

335 Wilson 1979) and to the lifespan of the queen (Ingram et al. in press). While individual workers

336 might be relatively short lived, queens—the functional reproductive unit for social ectotherms—

337 exhibit considerable variability in lifespan, extending from several months of age to nearly 30

338 years (Keller 1998). In addition, the rate of the colony's growth should affect the duration of the

339 ergonomic phase; faster colony growth should correlate with decreases in the amount of time

340 required before the first reproductives are produced. For ants, and perhaps for other social

341 ecotherms, one way to cope with the large variance in generation time is to estimate the

342 longevity of colonies based on other physiological and demographic parameters (Shik et al.

343 2012); however, these models still need to be expressed within a temperature-dependent

344 framework.

345   Because temperature affects the fitness metrics r (intrinsic rate of increase) and R_0 (net

346 reproductive rate) differently owing to generation time (Huey and Berrigan 2001), and because

347 the incorporation of generation time into models of the vulnerability of ectotherms to climatic

348 change has been suggested to produce qualitatively different results from models lacking this

349 component (Walters et al. 2012), estimating generation time is especially important. Our

350 analyses from ants, and others from ectotherms more generally, indicate greater vulnerability in

351 the tropics (Deutsch et al. 2008; Huey et al. 2009; Diamond et al. 2012a). However, Walters et

352 al. (2012) recently suggested that the increased turnover (i.e., shorter generation time) in warmer

353 regions could recoup this increased vulnerability, particularly because shorter generation times

354 could speed adaptive evolution, allowing tropical ectotherms to respond sufficiently rapidly to

355 warming despite their thermal specialization and reduced genetic variation. From the perspective

356 of conservation planning, the qualitative differences in predictions for large-scale regional

357 vulnerability of ectotherms to climatic change is far from ideal, and points to the need to

358 integrate ecological and evolutionary models.

359

360 *Conclusions*

361   In this study, we expanded upon previous work in this system which established a strong

362 positive relationship between changes in the abundance of ants under warming and their upper

363 thermal tolerances. Specifically, we examined the relationship between temperature and

364 performance both in context of alterations to the thermal niches for foraging under experimental

365 climatic warming, and how the choice of tolerance metric—the survival of workers versus a

366 more comprehensive fitness metric, colony growth—influenced expected fitness under warming.

367 Here, we provide results that suggest the loss of thermal niche space for foraging among 20 ant

368 species at one site is somewhat related to decreases in abundance with experimental climatic

369 warming, but that we may be underestimating the loss of niche space when calibrating models

370 with the survival of workers rather than colony growth. In support of this idea, we found that for

371   one well-studied species, the range of thermal tolerance for the survival of workers was much

372   broader than for the growth of colonies. Further, this difference in the range and shape of the

373   relationship between fitness components and temperature induced differences in expected means

374   and variances of fitness under warming.

375   We suggest that understanding how physiological performance is influenced by current

376   and anticipated changes in temperature can serve as a useful baseline model (the focus of our

377   study), with additional effort directed at understanding how this relationship is moderated by

378   physiological acclimation, adaptation, behavior, and alterations to the biotic background (see

379   Table 1 for a summary of the components of thermal-tolerance models for the responses of

380   ectothermic species to climatic warming). Indeed, the models that we explored in this study

381   assume thermal tolerances to be fixed, yet tolerances can be altered via acclimation, adaptive

382   evolutionary responses, or may fail to fully capture organismal vulnerability in the face of

383   behavioral compensatory responses. Further, our models are based on air temperatures rather

384   than on body temperatures, yet in some cases air temperatures may be poor indicators of

385   environmental pressures, as body temperatures can differ substantially from air temperatures

386   (Table 1). Improving estimates of relevant environmental parameters and of components of

387   fitness along environmental gradients will often necessarily trade off with research effort and

388   investment; however, to be able to assess the most useful predictors of the responses of species

389   to climatic change, detailed estimates both of the environment and of organismal responses are

390   critical. We concur with recent calls for increased physiological and demographic data for

391   ectothermic species inhabiting the topics and lower temperate zone where the impacts of

392   warming may be the greatest, and for which we have the fewest data.

393

394   **Acknowledgements**

407

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528 **Figure legends**

529 *Figure 1*. The relationship between the degree of loss of the thermal niche space and the density

530 of ant workers, each expressed as a function of the degree of warming of the chambers. (A)

531 Conceptual diagram for the loss of thermal niche space when temperatures exceed CT_{max}; the

532 temperature profile in the warmest chamber (+5.5 °C) and the CT_{max} of *Nylanderia faisonensis*, a

533 species with one of the lowest CT_{max} values (37 °C) that occurs in our warming chambers, are

534 shown; the remaining CT_{max} values (19 species) are indicated by hash marks along the x-axis;

535 note that some species exhibit no loss of thermal niche space. (B) A sample calculation of the

536 loss of thermal niche space as a function of the degree of warming in the chambers using *N.*

537 *faisonensis*. (C) The thermal-accumulation slope (± 1 SE) as a function of the thermal-niche-loss

538 slope (± 1 SE).

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540 *Figure 2*. Laboratory-estimated colony-growth and survival functions for *Temnothorax*

541 *curvispinosus* in the context of air temperatures from the warming chambers. (A) Colony growth

542 (solid line) and survival (dashed line) as functions of temperature (°C), with the estimated critical

543 thermal maximum for each indicated as G CT_{max} and S CT_{max}, respectively. (B) Distributions

544 (using kernel density estimation) of air temperatures of the +0 and +5.5 °C warming chambers.

545 (C) Distributions (using kernel density estimation) of the colony-growth function evaluated using

546 air temperatures of the chambers, with results from the +0°C (light grey bars) and +5.5°C (dark

547 grey bars) chambers shown. (D) Distributions (using kernel density estimation) for the worker-

548 survival function evaluated using air temperatures of the chambers, with results from the +0°C

549 (light grey bars) and +5.5°C (dark grey bars) chambers shown.

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551   *Figure 3*. Expected colony growth and survival of *Temnothorax curvispinosus* under the

552   temperatures measured in the experimental climatic-warming chambers and observed changes in

553   abundance in the warming chambers. (A) Expected mean and standard deviation of colony

554   growth, obtained by applying air temperatures of the chambers to the laboratory-estimated

555   colony-growth function, expressed as a function of the degree of warming in the chambers. (B)

556   Expected mean and standard deviation of survival, obtained by applying air temperatures of the

557   chambers to the laboratory-estimated survival function, expressed as a function of the degree of

558   chamber warming in the chambers. (C) The natural log of abundance of *T. curvispinosus* as a

559   function of the degree of warming of the chambers. In each panel, smoothing splines are used to

560   visualize the patterns of responses.

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574 **Table 1** Components of predictive models of the responses of ectothermic species to climatic

575   warming based on thermal tolerance.

Components of the model			References
Thermal environment	Spatio-temporal resolution of environmental temperature	Finer spatial and temporal resolution allows computation of the variability of fitness	Bonebrake and Deutsch (2012)
	Air temperature versus body temperature	Body temperatures are often more reflective of organismal performance than are air temperatures	Gilman et al. (2006)
Physiology	Short-term versus long-term population dynamics	Survival can allow estimation of immediate relative vulnerability across space, time, or species, but reproductive output and generation time are needed to understand long-term vulnerability	Kingsolver et al. (2011)
Moderators	Phenotypic plasticity	Warmer conditions can increase upper thermal tolerances (within generations)	Somero (2010)
	Behavioral plasticity	Behaviorally mediated thermoregulation can avoid body temperatures exceeding upper thermal tolerances	Kearney et al. (2009)
	Adaptive evolutionary responses	Warmer conditions can select for increased upper thermal tolerances (across generations)	Walters et al. (2012)
	Biotic background	Alterations to resources, competitors, predators, and pathogens can improve or exacerbate responses to warming	Tylianakis et al. (2008)

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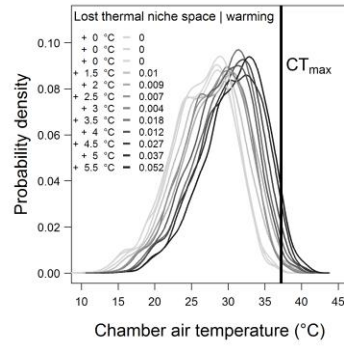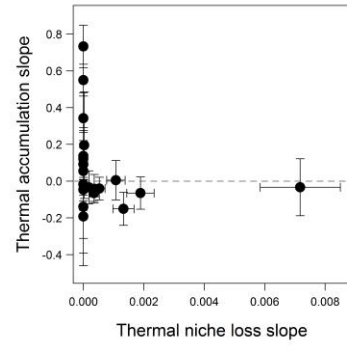
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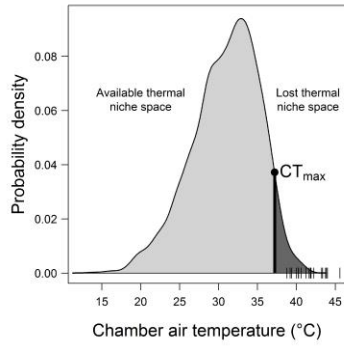
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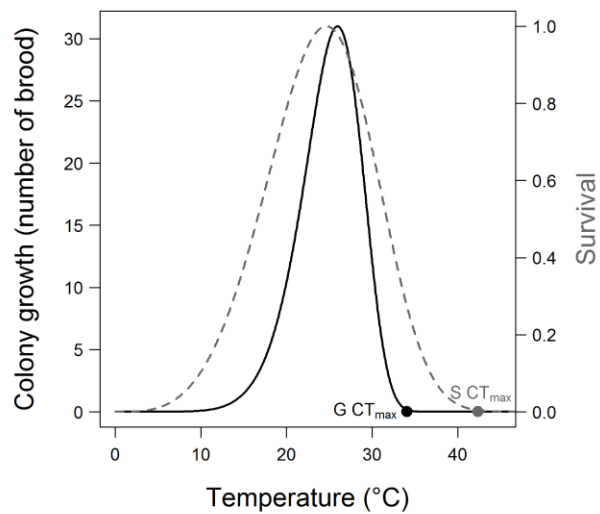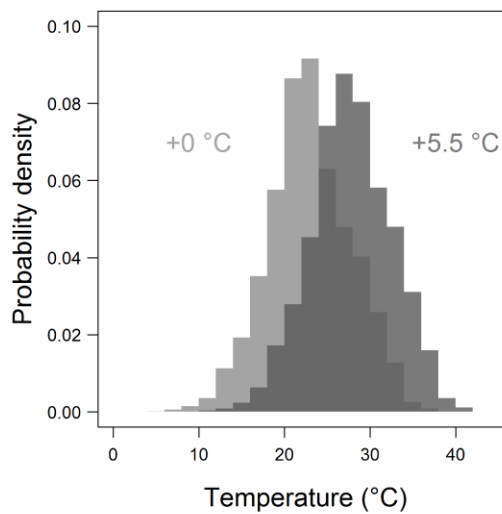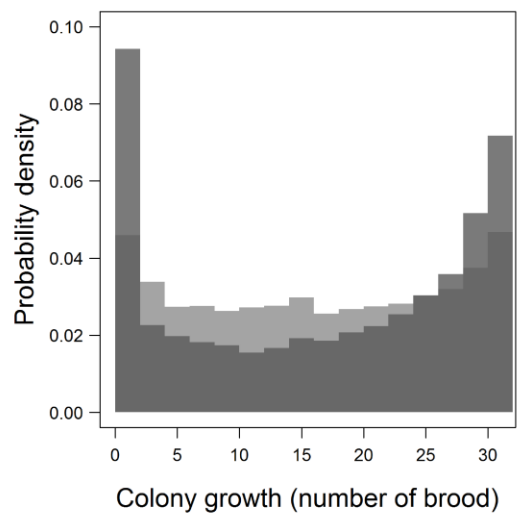
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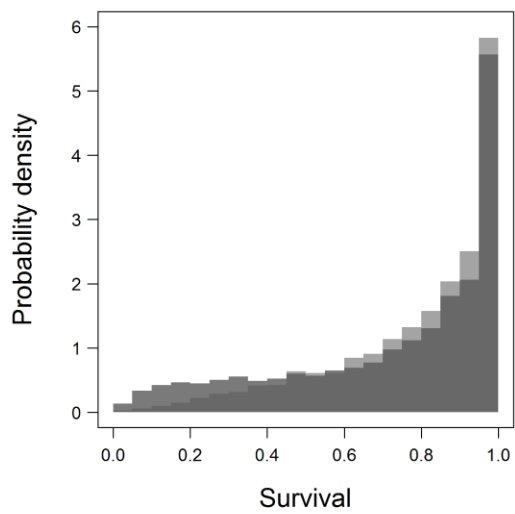590

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