



Heat tolerance predicts the importance of species interaction effects as the climate changes

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1 Heat tolerance predicts the importance of species interaction effects as
2 the climate changes

3

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19

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23

24 **Abstract**

25 Few studies have quantified the relative importance of direct effects of climate change on
26 communities versus indirect effects that are mediated thorough species interactions, and the
27 limited evidence is conflicting. Trait-based approaches have been popular in studies of climate
28 change, but can they be used to estimate direct versus indirect effects? At the species level,
29 thermal tolerance is a trait that is often used to predict winners and losers under scenarios of
30 climate change. But thermal tolerance might also inform when species interactions are likely to
31 be important because only subsets of species will be able to exploit the available warmer climatic
32 niche space, and competition may intensify in the remaining, compressed cooler climatic niche
33 space. Here we explore the relative roles of the direct effects of temperature change and indirect
34 effects of species interactions on forest ant communities that were heated as part of a large-scale
35 climate manipulation at high- and low-latitude sites in eastern North America. Overall, we found
36 mixed support for the importance of negative species interactions (competition), but found that
37 the magnitude of these interaction effects was predictable based on the heat tolerance of the focal
38 species. Forager abundance and nest site occupancy of heat-intolerant species were more often
39 influenced by negative interactions with other species than by direct effects of temperature. Our
40 findings suggest that measures of species-specific heat tolerance may roughly predict when
41 species interactions will influence responses to global climate change.

42

43 *Keywords:* critical thermal maximum, global climate change, ants, community ecology,
44 physiology, thermal tolerance, temperature

45

46 **Introduction**

47 Ecologists have widely acknowledged the importance of incorporating species
48 interactions into forecasts of responses to climate change (Tylianakis *et al.* 2008; Walther 2010),
49 but there are few published studies that actually succeed in this because empirical data are rare
50 and modeling tools are limited (Cahill *et al.* 2012; Angert, LaDeau & Ostfeld 2013). Empirical
51 support for the role of species interactions in shaping population persistence and growth under
52 climate change is mixed: some studies find a stronger role for direct effects of changes in climate
53 on individual species (Chu *et al.* 2016), but others find a stronger role for species interactions
54 (Suttle, Thomsen & Power 2007). On the surface, it may appear that species interactions simply
55 introduce noise into ecological forecasts owing to the inherent variability of interactions over
56 space and time, and that the magnitude of these effects can vary across different systems. But
57 recent work suggests that the magnitude of species interaction effects under climate change may
58 be predictable based on species traits that are proxies for physiological performance and habitat
59 use (Urban, Tewksbury & Sheldon 2012). For example, in grassland plant communities, the
60 indirect effects of climate change, *i.e.* those mediated through species interactions, are strongest
61 for species showing weak niche differentiation (Chu *et al.* 2016).

62 Such trait-based approaches have met with considerable success in forecasting the
63 relative performance of species—the winners and losers—under the direct effects of climate
64 change (see Pacifici *et al.* 2017 for a recent data-driven review; see also for trait-based
65 forecasting frameworks: Suding *et al.* 2008; Chown 2012; Foden *et al.* 2013). Of the many traits
66 that have been used, thermal tolerance has been an especially strong predictor of responses in a
67 warming world. For example, in forest ant communities, greater heat tolerance is positively
68 correlated with ant abundance and activity under experimental warming (Diamond *et al.* 2012,
69 2013; Stuble *et al.* 2013) and historical changes in abundance related to long-term patterns of

70 climate change in the field (Resasco *et al.* 2014). But again, these approaches lack an explicit
71 consideration of indirect effects of temperature change via altered species interactions. As
72 temperatures rise, species that have limited tolerance of high temperatures may experience more
73 density-dependent (competitive) interactions with other species as suitable thermal niche space
74 for their foraging and other activities decreases. In contrast, the subset of species in the
75 community with high heat tolerance may be subject to fewer density-dependent interactions
76 because they have broader ranges of suitable thermal niche space along which they can
77 differentiate relative to other members of the community under future warmed conditions; there
78 is also some evidence that heat tolerant species may gain competitive advantages in warmer
79 conditions (Urban *et al.* 2012). A key question then is whether heat tolerance can predict the
80 importance of competitive species interactions under warming.

81 Using ant forager abundance and nest occupancy of forest ants in field-based climate
82 warming arrays, we tested whether the relative importance of competition, inferred from
83 negative species interaction effects, was greater for heat-intolerant species compared with heat-
84 tolerant species. In many habitats, competition among ant species for limited food and nest
85 resources is intense (Herbers 1989; Cerdá, Retana & Cros 1997), and heat-tolerant species may
86 gain competitive advantages in warmed environments (Diamond *et al.* 2016). Within the
87 experimental warming arrays, the forest floor was heated for 5 years at sites located in the
88 northern and southern regions of the eastern United States, and ant foraging activity and nest
89 occupancy were monitored approximately monthly during the growing season at each site. If the
90 available thermal niche space for heat-intolerant species shrinks in warmed habitats with
91 concomitant increases in competition for limited food and nest resources (Fig. 1), we predict a

92 negative relationship between species-specific heat tolerance and the importance of negative
93 species interaction effects on forager abundance and nest occupancy.

94

95 **Methods**

96 *Warming chambers*

97 We explored foraging and nest-use of ant communities in response to climate warming in
98 a pair of field-based experimental warming arrays. The arrays were established in comparable
99 ecotypes (deciduous forest) at two sites: a warm, southern site (Duke Forest, located in the
100 Piedmont region of North Carolina, USA) and a cool, northern site (Harvard Forest, located in
101 the New England upland region of Massachusetts, USA). This extensive gradient spanned 6.5
102 degrees of latitude, yielding a mean annual temperature difference of 5.8 °C.

103 The arrays encompassed a total of 30 open-top chambers (15 per site). At each of the two
104 sites, nine chambers experienced different levels of warming in increments of 0.5 °C from 1.5 to
105 5.5 °C above ambient temperature; each chamber remained at a constant level of warming
106 amount above ambient temperature for the five-year duration of the experiment. The chambers,
107 each 5m in diameter, warmed the forest floor year-round with thermostat-controlled forced air
108 passed over hydronic heaters. At each of the two sites, six additional chambers experienced
109 ambient temperature conditions; three of these chambers had forced air at ambient temperature,
110 and three had no forced air infrastructure (Pelini *et al.* 2011). The range of temperatures spanned
111 by the warming treatments encompasses climate projections of increased mean annual
112 temperature from 1 °C to greater than 5 °C over the next century (Intergovernmental Panel on
113 Climate Change 2014) and represents a continuous experimental gradient of increasing
114 temperature between sites where the unheated control chambers at the southern Duke Forest site
115 had similar temperatures to the warmest heated chambers at the northern Harvard Forest site.

116 The open-top chambers were also open at the bottom to allow free access to ants and other
117 invertebrates, though most ants tended to remain within the chambers. More than 98% of
118 foraging activity observed in the chambers involved workers originating from nests within the
119 chambers (Stuble *et al.* 2013).

120 Because we were interested in the influence of the effect of warming among the
121 chambers on ant communities rather than the specific temperature at the time of pitfall trapping
122 or nest box observations, we computed the mean annual temperature (MAT) for each of the
123 chambers with forced air (nine heated and three control chambers). The MAT of the chamberless
124 control plots was computed for the single set of sensors located outside the warming chambers,
125 and this average temperature was assigned as the MAT for all three of the chamberless control
126 plots. Raw temperature data were recorded at hourly intervals throughout the year via a ground-
127 based sensor network of thermistors in the chambers; MAT is the mean of all hourly
128 temperatures for the years in which the nest box censuses occurred.

129

130 *Ant censuses using pitfall trapping and artificial nest boxes*

131 At the start of the experiment in 2010, we placed four pitfall traps and four artificial nest
132 boxes into each of the 30 chambers; midway through the experiment, we added another four nest
133 boxes (Diamond *et al.* 2016). The pitfall traps (90 mL volume) contained 30 mL of propylene
134 glycol (Prestone, LowTox) at Duke Forest or ethanol at Harvard Forest and were set flush with
135 the soil surface in each chamber (Pelini *et al.* 2011; Diamond *et al.* 2012). During each sampling
136 event, traps were left out for a 48-hour sampling period. At the end of the 48-hour sampling
137 period, ants recovered in the pitfall traps were removed and preserved in 95% ethanol. All ants
138 were identified to the species level; pinned voucher specimens are retained at North Carolina

139 State University and at Harvard Forest. Each nest box was constructed from balsa wood and a
140 wood block of untreated pine (14x15x2cm). We routed a zig-zag pattern into the top of the
141 block, and cut an entryway in the side of the block. The nest box was covered on top with
142 Plexiglas and a ceramic tile. The tiles were lifted to census the ant colony visible through the
143 Plexiglas top; this observation technique provided minimal disturbance to the resident ant
144 colony. Multiple occupancy of nest boxes was never observed: at each census, nest boxes were
145 either occupied by a single colony or were empty.

146 Censuses of pitfall traps and nest boxes occurred approximately monthly during the
147 growing season at each site over a span of over five years of experimental warming, from
148 January 2010 to May 2015. This sampling scheme yielded 60 pitfall samples and 41 nest box
149 observations at Duke Forest, and 37 pitfall samples and 19 nest box observations at Harvard
150 Forest. Fewer censuses occurred at Harvard Forest because the snow-free growing season is
151 much shorter there than at Duke Forest; ants generally were not collected in pitfall traps at
152 Harvard Forest between November and March. Although we were able to identify all individuals
153 from the pitfall traps to species, the taxonomic resolution of the nest box data was coarser.
154 Because we did not disturb the nest boxes by collecting individual workers, we used ant genera
155 as our taxonomic unit in several cases. At Duke Forest, the nest box taxa were identified as
156 *Aphaenogaster* spp., *Brachyponera chinensis*, *Crematogaster lineolata*, and *Temnothorax*
157 *curvispinosus*; at Harvard Forest, *Aphaenogaster* spp., *Camponotus* spp., *Myrmica* spp., and
158 *Temnothorax longispinosus*. At Duke Forest, the pitfall species included *Aphaenogaster*
159 *carolinensis*, *Aphaenogaster fulva*, *Aphaenogaster lamellidens*, *Aphaenogaster rudis*,
160 *Brachyponera chinensis*, *Camponotus castaneus*, *Camponotus pennsylvanicus*, *Crematogaster*
161 *lineolata*, *Formica pallidefulva*, *Formica subsericea*, *Myrmecina americana*, *Nylanderia*

162 *faisonensis*, *Ponera pennsylvanica*, *Solenopsis invicta*, *Solenopsis molesta*, *Stenamma impar*, and
163 *Temnothorax curvispinosus*; at Harvard Forest, *Aphaenogaster fulva*, *Aphaenogaster picea*,
164 *Aphaenogaster rudis*, *Camponotus pennsylvanicus*, *Formica subsericea*, *Lasius alienus*,
165 *Myrmica punctiventris*, *Stenamma impar*, *Temnothorax longispinosus*. For each species or
166 species group, we used five separate occurrences in two separate warming chambers as the
167 inclusion criteria for our analyses, which yielded 4 species or species groups from the nest box
168 data at each site, and 17 species at Duke Forest and 9 species at Harvard Forest from the pitfall
169 data.

170

171 *Heat tolerance*

172 Our measure of heat tolerance was the critical thermal maximum (CT_{max}), defined here as
173 the temperature at which muscle coordination of an individual forager was lost in a controlled
174 laboratory heating experiment. This metric provides an ecologically relevant measure of heat
175 tolerance because it represents the temperature at which an individual could not escape to a non-
176 lethal thermal environment (Lighton & Turner 2004). Ant workers of different species were
177 collected from forests near the warming sites; mean heat tolerance for each species was
178 computed separately for each of the two sites. Although the focal ant species are relatively
179 abundant and widespread throughout North America, and our experimental warming sites are
180 positioned within the range boundaries of these species (Lach, Parr & Abbott 2010; Gibb *et al.*
181 2017), we used site-specific heat tolerances to account for potential local adaptation throughout
182 the geographic ranges of the ant species in our analyses (*e.g.*, Warren & Chick 2013). Heat
183 tolerances were tested individually (minimum 8 individuals per species at each site) in a heat
184 block for which the temperature was increased at a slow ramping rate of $0.2\text{ }^{\circ}\text{C min}^{-1}$ starting at

185 36 °C. Because the rate of experimental temperature increase can influence the estimate of
186 thermal tolerance (Terblanche *et al.* 2011), we refit all of our statistical models using an
187 alternative measure of CT_{max} based on a fast-ramp temperature increase of 1 °C min^{-1} starting at
188 36 °C. Our models that used CT_{max} assessed with the fast ramp yielded qualitatively similar
189 results to those assessed with the slow ramp; we present the results only from the slow-ramp
190 experiment for which we were able to obtain measurements for more species.

191

192 *Statistical analyses for the species interactions and temperature models*

193 To explore the influence of species interactions (specifically, negative interactions; see
194 below) and temperature on nest site occupancy, we used the nest box data and constructed
195 generalized linear models with a binomial error structure, in which the proportion of nest boxes
196 occupied was the response variable, and chamber temperature and the proportion of nest boxes
197 occupied by a single non-focal species were separately considered as predictor variables. We
198 used AIC to determine whether models with temperature or non-focal species nest box
199 occupancy were better predictors of focal species nest box occupancy. To quantify the
200 importance of temperature relative to negative species interactions, we developed a binomial
201 response variable in which we assigned a score of 0 when models with temperature as a predictor
202 were more important, *i.e.* they had the lowest AIC value by 2 or more units, and we assigned a
203 score of 1 when models with the non-focal species as a predictor were more important, again
204 having the lowest AIC value by 2 or more units. In cases where the difference in AIC between
205 temperature and negative species interaction models was less than two, we assigned a score of
206 0.5. For each focal species, we computed the mean proportion of times the species interaction

207 models were selected as the best-fitting models, *i.e.* as an indicator of the overall importance of
208 species interactions versus temperature.

209 Of course ants engage in many types of species interactions from competition to
210 predation to mutualism and involve both other ant species and non-ant species (Lach *et al.* 2010).
211 As competition among ant species for limited food and nest resources is a major driver of ant
212 performance and distribution (Cerda, Arnan & Retana 2013), we focus on competitive species
213 interactions among ants in our experimental warming arrays. We infer competitive interactions
214 from negative effects of non-focal species on focal species, and as a consequence, we do not
215 distinguish between specific mechanisms of competition (*e.g.*, more contact-based interactions
216 such as aggression or nest defense versus more diffuse interactions such as exploitative
217 competition over shared food resources; see Diamond *et al.* 2016 for a full discussion of this
218 issue). Hereafter we refer to negative species interaction effects, as these were the effects we
219 were able to quantify with our experiments, and intend these effects as a proxy for general
220 competitive interactions among ant species within our warming arrays. Because we were
221 specifically testing the hypothesis that competition intensifies for heat-intolerant species in
222 warmed environments, for models that indicated species interactions were more important, we
223 restricted further consideration of these models to those where the effect of the non-focal species
224 on the focal species was negative. For models that indicated temperature effects were more
225 important, we did not restrict our models based on the sign of the effect. We also performed
226 comparable analyses in which the sign of the species interaction coefficient was not restricted to
227 be negative and found qualitatively similar results to our focal analyses, so we present only those
228 analyses with the negative species interaction coefficient for consistency with our hypothesis.
229 We then explored whether heat tolerance explained the importance of negative species

230 interactions using a generalized linear model with a quasi-binomial error structure. We used F -
231 tests to assess the statistical significance of chamber temperature, because these tests are most
232 appropriate for models in which dispersion is estimated by the method of moments (Crawley
233 2007).

234 To explore the influence of negative species interactions and temperature on forager
235 abundance, we used the pitfall data and constructed a second series of generalized linear models
236 with a Poisson error structure, in which the number of foragers (workers) was considered the
237 response variable, and chamber temperature and a single non-focal species abundance were
238 separately considered as predictor variables. We again used the AIC-based model selection
239 approach to compute the overall importance of negative species interactions and examined its
240 relationship with heat tolerance.

241

242 **Results**

243 At both the northern and southern sites, and for both the pitfalls and nest boxes, forager
244 abundance and nest box occupancy were negatively related to the heat tolerance of individual
245 species (Figs. 2,3). Heat tolerance was a significant predictor of the importance of negative
246 species interactions on forager abundance (pitfall data) ($F = 8.72$, $P = 0.00735$, $df = 1$), and there
247 were no effects of site ($F = 0.0263$, $P = 0.873$, $df = 1$) or an interaction between site and CT_{\max}
248 ($F = 0.105$, $P = 0.749$, $df = 1$), indicating that this relationship was consistent between sites.

249 Heat tolerance also predicted effects of negative species interactions on nest site
250 occupancy (nest box data) ($F = 9.19$, $P = 0.0291$, $df = 1$), and there was a significant effect of
251 site ($F = 8.29$, $P = 0.0346$, $df = 1$), but not of the interaction between site and CT_{\max} ($F = 0.0224$,
252 $P = 0.888$, $df = 1$). Specifically, negative species interactions were overall more important at the
253 high-latitude site than at the low-latitude site.

254 In each of the four response-type-by-site datasets, the total number of observations of
255 each species during the course of the warming experiment was uncorrelated with CT_{\max} , which
256 suggests that sampling bias was not responsible for the relationships between CT_{\max} and negative
257 species interaction effects that were observed (Duke Forest pitfall: $r = 0.113$, $P = 0.665$, $df = 15$;
258 Duke Forest nest box: $r = 0.382$, $P = 0.618$, $df = 2$; Harvard Forest pitfall: $r = -0.469$, $P = 0.202$,
259 $df = 7$; Harvard Forest nest box: $r = -0.906$, $P = 0.0939$, $df = 2$).

260

261 Discussion

262 Although the direct effects of climate change on communities have been studied in some
263 detail, the indirect effects of climate change, while being discussed as potentially important, are
264 largely understudied (Buckley 2013; Urban *et al.* 2016). There are few tests of the importance of
265 indirect effects of climate change via altered species interactions, and even fewer that examine
266 whether these outcomes are predictable based on species traits (Moritz & Agudo 2013;
267 Ockendon *et al.* 2014). In this study, experimental warming of forest ant communities at high
268 and low latitude sites within the eastern United States revealed that the importance of negative
269 species interactions in determining forager abundance and nest site occupancy was predictable
270 from measures of heat tolerance: heat-intolerant species were more strongly driven by negative
271 species interactions compared with more heat-tolerant species. Together, these results suggest a
272 variable, but predictable, role for altered species interactions in shaping community responses to
273 climate change.

274 Recent work in grassland plant communities has linked climatic niche differentiation
275 between interacting species to the magnitude of species interaction effects, such that species with
276 more climatically similar niches exhibited greater species interaction effects (Chu *et al.* 2016).

277 However, the main finding of Chu and colleagues—that the direct effects of climate are much
278 stronger than indirect effects of species interactions—contrasts with a number of plant and
279 animal studies showing a stronger role for species interactions (Suttle *et al.* 2007; Ockendon *et*
280 *al.* 2014). In terms of whether the direct effects of temperature versus species interactions are
281 more important in shaping ant community forager abundance and nest site occupancy, our results
282 reveal mixed support, because we found cases where temperature was more important and cases
283 where negative species interactions were more important (Figs. 2,3). Uniquely however, our
284 study shows how this variation can be explained by heat tolerance of the focal species alone,
285 with heat-intolerant species exhibiting higher values of the importance of negative species
286 interaction effects.

287 Biogeographers have long been interested in this question of species interactions and
288 whether they are predictable across latitude. Although historically the assumption has been that
289 biotic interactions are more important (often quantified as the intensity of interactions or the
290 degree of specialization between interaction species) at lower latitudes, recent work has revealed
291 mixed support for this hypothesis (Schemske *et al.* 2009; Moles *et al.* 2011; Ollerton 2012). Our
292 results partially challenge the species interaction-latitude hypothesis, because the nest box data
293 revealed overall greater importance of negative species interactions at the higher latitude site
294 compared with the lower latitude site (Fig. 2). However, we did not detect a site effect in models
295 of negative species interactions using pitfall trap data. It is possible that negative species
296 interactions are more difficult to detect with pitfall data than with nest box data, where
297 competition for nest sites and resources near nest sites is based on interference and direct species
298 interactions rather than use of shared resources by foragers; alternatively, the sample sizes were
299 smaller for the nest box data, so perhaps the site effect is an artefact of limited sampling. Future

300 tests of the species interaction-latitude hypothesis may be facilitated by the rapid accumulation
301 of thermal tolerance data sets (Sunday *et al.* 2014; Gunderson & Stillman 2015) and species
302 interaction data (Vázquez *et al.* 2007).

303 Although it is useful to identify traits that predict the magnitude of direct versus indirect
304 effects of temperature change on communities, ultimately we are interested in the consequences
305 of these changes, *i.e.* whether these changes result in population increase, decrease, or even local
306 extirpations. Simulation models have shown that heat-tolerant species are able to outcompete and
307 even eradicate less heat-tolerant species under changing climates (Urban *et al.* 2012). Our results
308 support this finding: forager abundance and nest occupancy were driven more by direct effects of
309 temperature than by negative interactions with other species (Figs. 2,3) and our previous work in
310 this system has shown substantial advantages to warming for the most heat-tolerant species with
311 respect to colony size and growth, forager abundance, and ability to hold nest sites (Diamond *et*
312 *al.* 2012, 2013, 2016; Stuble *et al.* 2013). Indeed, recent laboratory work on the temperature-
313 dependence of colony growth components in forest ants, showed that heat tolerant species appear
314 to be limited primarily by access to heat for brood production and development requirements
315 (Penick *et al.* 2017).

316 Our findings appear to be robust, because we detected a negative relationship between
317 heat tolerance and the importance of negative species interactions using both ant forager
318 abundance and nest occupancy data each at two distinct locations. Despite this, there are some
319 limitations and caveats with our analysis. With forager abundance data from pitfall trapping and
320 occupancy data from nest box observations, we still lack direct evidence of each competitive
321 interaction (inferred by negative effects of non-focal species on focal species abundance and nest
322 occupancy) in the experiment. This criticism is perhaps most strongly levied against the ant

323 forager abundance data obtained with pitfall trapping, where interactions are potentially more
324 diffuse compared with the nest box occupancy data. In contrast, interactions are more direct for
325 the nest box data as single colonies of different species compete directly for occupancy of nest
326 sites. Of course our approach somewhat buffers against this possibility because we are directly
327 competing models of forager abundance or nest box occupancy based on temperature change
328 against those with the abundance or presence of a non-focal species as a predictor. The results
329 from another experimental manipulation of temperature (in this case, using shading treatments)
330 and its impacts on ant communities are also illuminating here. Species were spatially segregated
331 at bait stations at low temperatures but not at high temperatures, and species with weak thermal
332 niche differentiation segregated more frequently at baits than species with greater differentiation,
333 collectively suggesting that species-specific thermal performance can drive the competitive
334 landscape (Wittman *et al.* 2010).

335 Further, the restriction of our analyses to ant species that were active during the growing
336 season enabled us to identify an exception that proves the rule. The winter ant, *Prenolepis*
337 *imparis*, is a unique species in forest ant communities, because it is active during the cooler
338 months when few other ant species are foraging, but relatively inactive during the warm months
339 when most other species are active (Dunn, Parker & Sanders 2007; Ellison *et al.* 2012). In our
340 analyses, the winter ant had a low heat tolerance (39.6 °C) but was not strongly affected by
341 negative species interactions (its mean importance value for negative species interactions, or the
342 fraction of models where non-focal species responses were a better predictor than temperature,
343 was < 0.1). Such a result is what we would expect for a species with a winter-active phenotype
344 and one which is unlikely to interact with many other ant species.

345 Our results suggest when species interactions may be important to consider in models of
346 responses to climate change: negative species interactions tend to be more important for heat-
347 intolerant species, consistent with a model in which warming reduces available thermal niche
348 space and increases competitive interactions for species with lower heat tolerances (Fig. 1).
349 However, it is necessary to explore the extent to which these patterns generalize over different
350 types of interactions (for example, competition versus predation, parasitism, or mutualism), taxa,
351 and geographic location. In terms of ecological forecasting and management implications, the
352 key question is whether we can safely ignore species interactions, and develop forecasts based on
353 single-species models calibrated with climatic variables (Chu *et al.* 2016). The evidence so far is
354 decidedly mixed. Here we suggest a potential trait-based approach to this question, using heat
355 tolerance as a general guide for when negative species interactions are more likely to influence
356 responses to global climate change.

357

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484

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489

490 **Data Availability**

491 All data are available on the Harvard Forest Data Archive
492 (<http://harvardforest.fas.harvard.edu/harvard-forest-data-archive>), dataset hf-113.

493

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497

498 **Figure Legends**

499 **Figure 1.** Conceptual diagram of how temperature rise may predictably influence the availability
500 of thermal niche space and the importance of competitive interactions based on heat tolerance. In
501 the top panel, bars represent the thermal niche ranges of different species, with more heat-
502 tolerant species represented in warmer colors. The gray shading indicates the current range of
503 mean environmental temperatures and the red shading indicates the future range of mean
504 environmental temperatures. The non-overlapping gray shading indicates the thermal niche space
505 being lost with climate change, and the non-overlapping red shading indicates the thermal niche

506 space being gained with climate change. In general, heat-intolerant species tend to lose thermal
507 niche space with climate change. The bottom panel shows how the negative effects of
508 competition may intensify for heat-intolerant species as they lose thermal niche space under
509 climate change.

510

511 **Figure 2.** The importance of negative species interactions in determining nest site occupancy as
512 a function of heat tolerance. Importance is calculated as the mean proportion of models where
513 species interactions were more important than temperature (by 2 AIC units) in determining nest
514 site occupancy. Above the dashed line at 0.5, species interactions are more important; below the
515 line, temperature is more important for nest site occupancy. Predicted values and their standard
516 errors from a model with heat tolerance and site as explanatory variables are shown in solid
517 lines.

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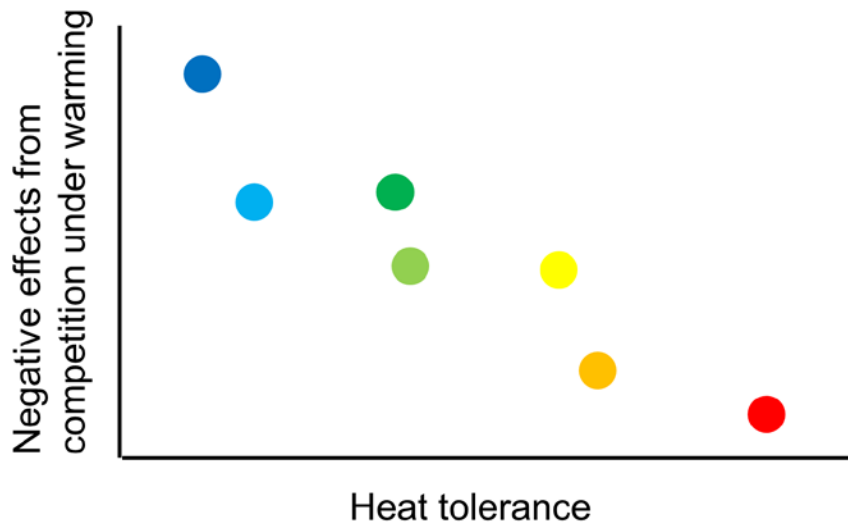
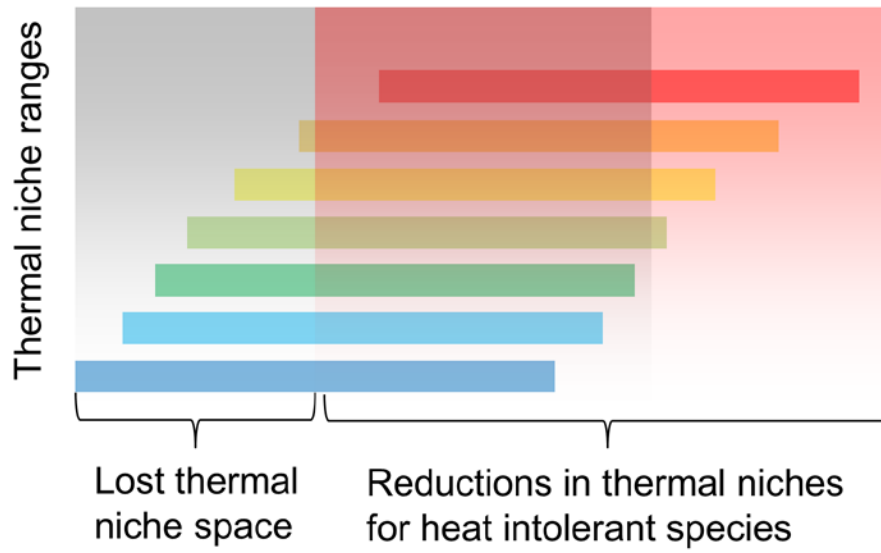
519 **Figure 3.** The importance of negative species interactions in determining forager abundance as a
520 function of heat tolerance. Importance is calculated as the mean proportion of models where
521 species interactions were more important than temperature (by 2 AIC units) in determining
522 forager abundance. Above the dashed line at 0.5, species interactions are more important; below
523 the line, temperature is more important for nest site occupancy. Predicted values and their
524 standard errors from a model with heat tolerance as an explanatory variable are shown in solid
525 lines.

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Current mean environmental temperature range Future mean environmental temperature range



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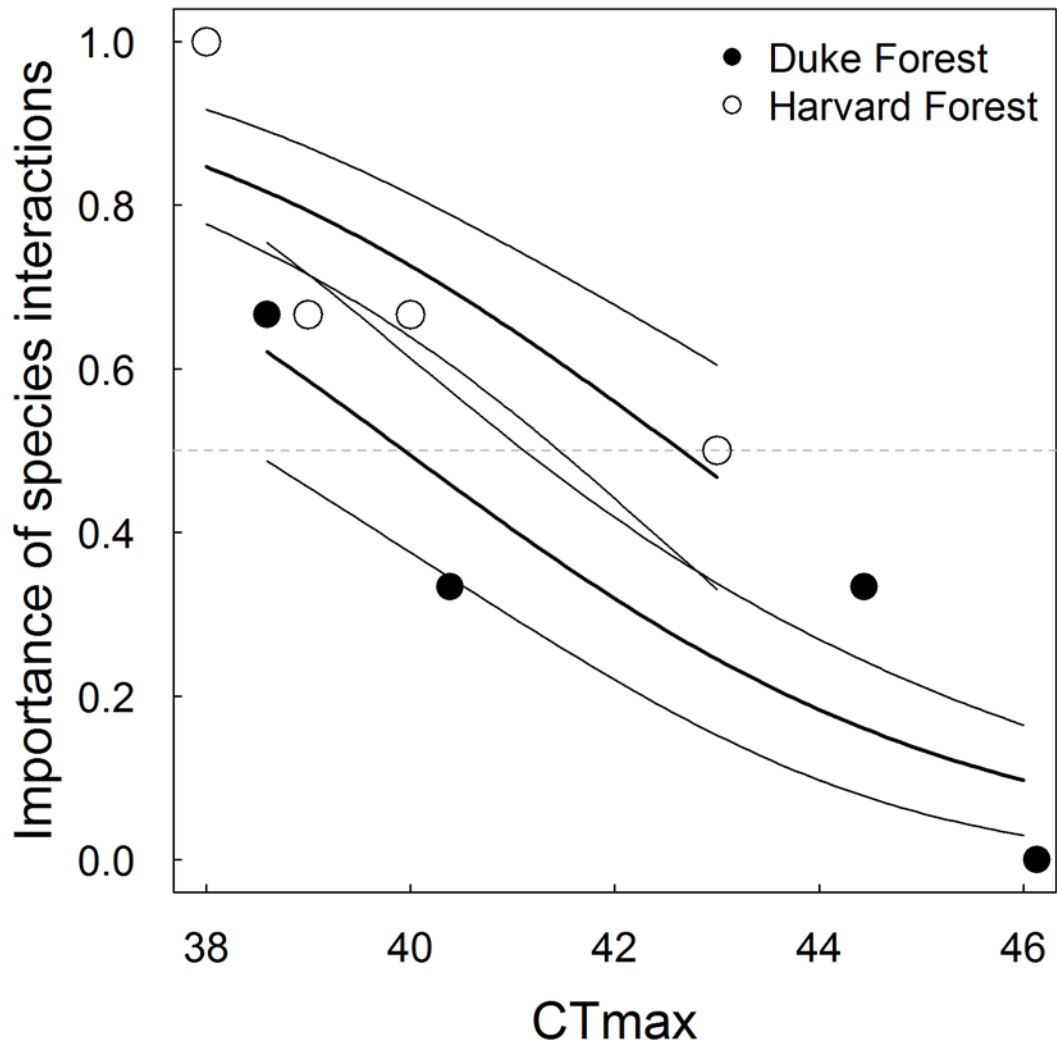
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