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1 **Tropical ant community responses to experimental soil warming**

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17

18 **Abstract**

19 Climate change is one of the primary agents of the global decline in insect abundance.
20 Because of their narrow thermal ranges, tropical ectotherms are predicted to be most
21 threatened by global warming, yet tests of this prediction are often confounded by other
22 anthropogenic disturbances. We used a tropical forest soil warming experiment to directly test
23 the effect of temperature increase on litter-dwelling ants. Two years of continuous warming led
24 to a change in ant community between warming and control plots. Specifically, six ant genera
25 were recorded only on warming plots, and one genus only on control plots. *Wasmannia*
26 *auropuctata*, a species often invasive elsewhere but native to this forest, was more abundant in
27 warmed plots. Ant recruitment at baits was best predicted by soil-surface temperature and ant
28 heat tolerance. These results suggest that heat tolerance is useful for predicting changes in daily
29 foraging activity, which is directly tied to colony fitness. We show that a 2-year increase in
30 temperature (of 2-4°C) can have a profound effect on the most abundant insects, potentially
31 favoring species with invasive traits and moderate heat tolerances.

32

33

34 **Keywords:**

35 Climate change, CT_{max} , ecophysiology, experimental warming, Formicidae, BCI.

36

37

38 **Introduction**

39 Global warming is predicted to negatively impact insects and other ectotherms, especially in
40 diverse habitats like tropical forests [1,2]. Isolating the role of climatic change in insect declines
41 is challenging, in part because its effects are often confounded with other factors such as habitat
42 destruction, pollution, and species invasions [3,4]. Moreover, most research on the effects of
43 climatic change on insects is correlational. For example, changes in species distributions [5],
44 biomass [6], and species richness and abundance [7] are correlated with temperature changes
45 across decades. To better understand the effect of warming on insects, we need experimental
46 warming studies directly testing the effect of temperature on insect abundance and community
47 structure *in situ*.

48 Despite the need to know the consequences of warming on tropical ecosystems, there are few
49 experimental soil warming experiments in the tropics, partially due to logistical obstacles [8,9].
50 This is problematic because tropical arthropods are largely understudied in the context of
51 climate change [10], yet global warming is considered to be the most important driver of insect
52 declines in tropical regions [11]. Given that many tropical insects tend to exhibit low variability in
53 heat tolerance [2] and possess narrow thermal safety margins [1], they are a good focal group
54 for understanding the role of climatic change in insect declines.

55 We used experimental soil warming of a tropical lowland forest to test the effect of temperature
56 increase on soil arthropods. A previous study found that 4°C of warming across 2 years
57 increased soil CO₂ emissions by 55%, mainly due to increased soil heterotrophic activity [12].
58 Here we test if warming, and this associated soil microbial functional change, are associated with
59 changes at higher trophic levels. We focus on ants because they play key roles in ecosystem

60 functioning [13]. Ants are highly thermophilic, and their activity is directly governed by
61 temperature. However, in tropical forest understory ants are less thermally tolerant compared to
62 the canopy [14] and they are likely to avoid hot forest patches, as observed for army ants in
63 tropical treefall gaps [15,16]. Tropical ants also respond to differences in resource availability by
64 recruiting in higher numbers [17], or by relocating their colonies closer to a high quality resource
65 [18]. In the tropical understory temperature promotes ant activity at baits [17]. Thus, any effects
66 of soil warming on the abundance or quality of resource patches should be reflected in changes
67 in ant abundance and recruitment. Warming potentially affects both nest location and ant
68 activity; although these are not mutually exclusive aspects of ant biology, we focused on ant
69 activity.

70 Given that tropical ectotherms experience lower temperature variability compared to the
71 temperate zone [19,20], especially in the litter [21], we hypothesized that tropical litter ants are
72 sensitive to increasing soil temperatures. Specifically, we predicted that an experimental increase
73 in soil temperature of 4°C would: 1) change litter ant community structure by favoring species
74 with higher thermal tolerance; 2) decrease species richness with warming, given that tropical
75 litter-dwelling ants generally have lower thermal limits than those in open, more insolated
76 habitats [14]; and 3) promote ant-visits to baits, as ant activity is temperature-dependent.

77 **Materials and Methods**

78 This study was conducted in the Soil Warming Experiment in Lowland Tropical Rainforest
79 (SWELTR) project on Barro Colorado Island (BCI) in the Panama Canal (9.15°N, 79.85°W). More
80 details about SWELTR and BCI are available elsewhere [12,22]. Briefly, this ongoing experiment

81 consists of ten circular plots (5 warming plots paired with 5 control plots), each 5 m in diameter
82 distributed over 1 ha of forest. Control and warming plots are 10 m apart, and pairs of plots are
83 separated by at least 20 m. The soil is heated by cables inside a stainless-steel frame encircling a
84 3.5 m diameter area at 1.2 m depth, so the effective heated area of the plot is 5 m in diameter.
85 The control plots were constructed in the same way as the warming plots: steel frames (with no
86 heating cable inside) were buried at the same depth (see [12] for more details).

87 We sampled the ants by placing five pitfall traps in each of the ten plots. Each trap consisted of
88 a 50 mL plastic centrifuge tube filled with 70% ethanol and a drop of scentless detergent. Tubes
89 were buried so their opening was flush with the soil surface. One trap was placed in the plot
90 center and the other four traps were distributed 2 m away from the center trap, following a five-
91 on-a-die pattern. The traps remained in the soil and were deactivated (covered) for the duration
92 of the study apart from three 48 h sampling periods: one each in July and August 2018, and
93 January 2019.

94 To determine how warming affects foraging activity, we used 10 baits per plot: five ca. 20 cm
95 outside of the warming cable, and five inside. Each bait consisted of a ca. 5 g mix of tuna and
96 honey placed on white index card (7.6 × 12.7 cm). We recorded the surface temperature of each
97 plot at the beginning and the end of every baiting trial by aiming a portable IR thermometer at
98 the ground (Fluke Corporation, model 62). After 1 h we recorded the number of ants at each
99 bait (recruitment) using a base 2 logarithmic scale. Recruitment is the short-term accumulation
100 of ant workers at a food resource. We identified distinctive, common ants in the field (e.g.,
101 *Ectatomma ruidum*, *Odontomachus bauri*) and collected other ants for identification in the lab.
102 To identify ants to species or morphospecies we used online resources [23] and reference

103 collections from BCI [24]. We baited monthly from June-August 2018, and January 2019, 10 days
104 prior to pitfall trapping.

105 Last, we tested how thermoregulatory functional traits affect abundance and recruitment on
106 warming plots by calculating genus-level averages for critical thermal limits (CT_{max} , CT_{min}), and
107 body size (dry mass) using data from prior studies of BCI ants [14,21]. Because these traits were
108 highly correlated (Pearson coefficient range: 0.72-0.84), we used them separately in generalized
109 linear models. We used AIC model selection to test which of the functional traits, in addition to
110 treatment, best explained ant abundance and recruitment.

111 We used generalized linear mixed effect models (*glmmTMB* function) with Poisson distribution
112 to analyze the effect of warming on litter ant abundance and species richness. We checked for
113 model overdispersion using diagnostic plots in DHARMA package [25]. Experimental treatment
114 was used as a fixed effect and plot and month of sampling as random effects. We also tested
115 responses of numerically dominant genera (abundance >5%): *Ectatomma*, *Labidus*, *Pheidole*,
116 *Solenopsis*, and *Wasmannia*. To determine how warming affected the number of ants recruited
117 at baits we used ground temperature (average of baiting start and end temperatures) as the
118 fixed effect instead of treatment. This way we accounted for forest heterogeneity, and temporal
119 changes in temperature. Average ground temperature was significantly higher on warming plots
120 ($\chi^2=9.04$, $df=1$, $p=0.0027$). We used the same abundance (>5%) threshold when analyzing
121 recruitment at baits and ran separate models for the four numerically dominant genera. We
122 used abundance data to analyze the differences in ant community composition (pitfalls) and
123 recruitment (baits) using non-metric multidimensional scaling (NMDS) with Bray Curtis
124 distances[26]. We ran separate tests for species level and genus level abundances across all

125 months of sampling. We used analysis of similarity (ANOSIM) to test for significance of observed
126 differences [27]. All analyses were done with the R statistical program [28]. The data supporting
127 the findings of this study will be available in figshare [29].

128 **Results**

129 Collectively, the 150 pitfall trap samples captured 1,395 individual ants, representing 44 species
130 in 19 genera and 5 subfamilies (Table S1, Fig. S1A). The 400 baits placed in SWELTR plots
131 attracted 6,585 individual ants, representing 29 species in 14 genera and 6 subfamilies (Table S2,
132 Fig. S1B).

133 Ant community composition, recorded with pitfalls, differed between experimental treatments
134 (Fig. 1; NMDS: $R^2=0.988$, Stress=0.1099; ANOSIM: $p=0.006$), with six genera recorded only on
135 warming plots, and one genus only on control plots. We also observed community level
136 differences at the species level (Fig. S2), with two species positively and two negatively affected
137 by warming (Fig. S3). In pitfall traps, total ant abundance and species richness were similar
138 between treatments ($\chi^2_{abundance}=0.87$, $df=1$, $p=0.35$; $\chi^2_{richness}=0.003$, $df=1$, $p=0.96$). But soil
139 warming tripled the abundance of *Wasmannia* in pitfall traps relative to controls (Fig. S3,
140 $p=0.012$). Other abundant genera did not show a significant response to warming (Table S3).

141 Soil-surface temperature of plots during baiting trials promoted ant recruitment to baits (Fig. S4,
142 $\chi^2=56.8$, $df=1$, $p<0.001$). We found the same pattern of soil-surface temperature best predicting
143 recruitment to baits (Fig. S4) at the genus level: *Wasmannia* (Table S4; $p=0.0002$), *Ectatomma*
144 ($p=0.0279$), *Azteca* ($p<0.001$) and *Pheidole* ($p=0.003$). However, species richness at baits could
145 not be predicted by the temperature ($\chi^2=1.03$, $df=1$, $p=0.31$). In contrast to the differences in

146 community composition observed for pitfall traps, the composition of ants at baits was similar
147 between control and warming treatments at genus (Fig. 1) and species level (Fig. S2).
148 Recruitment peaked in genera with medium heat tolerances, so a quadratic function fit the data
149 better (AIC=53.4) than a linear function (AIC=58.9), although both models were significant.
150 Critical thermal maximum predicted 53% of ant recruitment at baits, regardless of the warming
151 treatment (Fig. 2; $F_{2,17}=9.4$, $p=0.002$). None of the examined thermoregulatory traits (CT_{max} , CT_{min} ,
152 or mass) was a significant predictor of the genus level abundance of ants in pitfalls between
153 warmed and control plots (Table S5).

154 **Discussion**

155 Climatic change is among the most important threats to insect biodiversity. Here we show that
156 experimental warming of soil in a tropical forest changed the composition and activity of ant
157 communities. The changes were dominated by increased activity of a single genus—
158 *Wasmannia*—on warmed plots. *Wasmannia auropunctata* is native to Panama but is invasive in
159 many other tropical regions [30]. The increased occurrence of *W. auropunctata* observed in this
160 study differs from patterns shown for invasive ants in their invasive range, where populations are
161 declining either because of climatic changes [31] or for unknown reasons [32]. In accordance
162 with our prediction, warming promoted ant recruitment at baits, but it was the highest in ants
163 with moderate CT_{max} . Thus, resource acquisition on warming plots was governed by temperature
164 and heat tolerance.

165 We did not find changes in species richness after 2 years of warming. Similar warming
166 experiments conducted at two temperate sites also found species richness unchanged after

167 warming [33,34]. Moreover, a warming experiment at a low latitude oak-hickory forest showed
168 that <10% of temperate zone ants in the sampled community responded to warming, and most
169 of those species increased in abundance [35]. Similarly, we found that only 9% (4/44) species
170 responded to warming (Fig. S3). In accordance with findings from experimental and natural
171 warming [36], we found that temperature increase has a selective impact on ants, with some
172 species are not affected while others are either positively or negatively impacted by warming
173 (Fig. S3). The abundance of *W. auropunctata* in the BCI forest increased in response to
174 experimental substrate addition, specifically carbohydrates [37]. This suggests that changes in
175 resource availability observed across warming plots [12] might be a mechanism for an increase
176 in *W. auropunctata*, similar to increased activity of tropical ants observed following long-term
177 fertilization with phosphorus [17]. Although *W. auropunctata* forms low-density populations in
178 its native range, an increase in disturbance can increase recruitment and nest density [38]. The
179 increase we observed in response to warming is unlikely to be caused by the disturbance that
180 accompanied the warming treatment, because control plots underwent the same level of
181 disturbance.

182 At the community level we found differences in abundance at pitfalls, but not baits (Fig.
183 1). Pitfall traps sample ant activity throughout the whole day, so trapping ants during the night
184 might be one reason why we found distinct community on warming plots. Air temperature and
185 warmed soil should show the greatest temperature difference at night, so nighttime baiting
186 trials would test the hypothesis that night foragers are more affected by soil warming.

187 In our experiment, the soil temperature was 4°C higher than ambient when averaged
188 across the soil profile, and the soil surface temperature was about 3°C warmer than ambient

189 [12]. Both of these values are still far from the CT_{max} of any of the leaf litter ants in this forest
190 [14]. Within the range of CT_{max} measured for temperate zone ants, maximum CT_{max} being 46°C
191 [34,39], our results are in accordance with the finding that heat tolerant ants are more abundant
192 at baits. However, our ant community included canopy ants with thermal tolerances exceeding
193 50°C, which rarely forage on the forest floor. Because of this we found a unimodal response of
194 ant recruitment and heat tolerance. Such unimodal response to warming was also recorded for
195 ants across temperate forests, where genera with moderate CT_{max} increased in their incidence
196 after 20 years [40]. An increase in incidence of ants with moderate thermal tolerances might be
197 the overall ant response to raising temperatures.

198 In summary, we show that warming in a tropical forest can have a profound effect on ant
199 communities, potentially favoring species with moderate heat tolerance and invasive traits.
200 Favoring species with invasive properties might have detrimental effects for the community
201 structure, as warming can destabilize ant communities [41]. Additionally, warming changed rates
202 of soil organic matter cycling [12], which together with warming could have cascading effects on
203 the rest of the soil food web. Thus, we need a better understanding of the effects of warming on
204 insects in the tropics where insects tolerate narrow thermal ranges.

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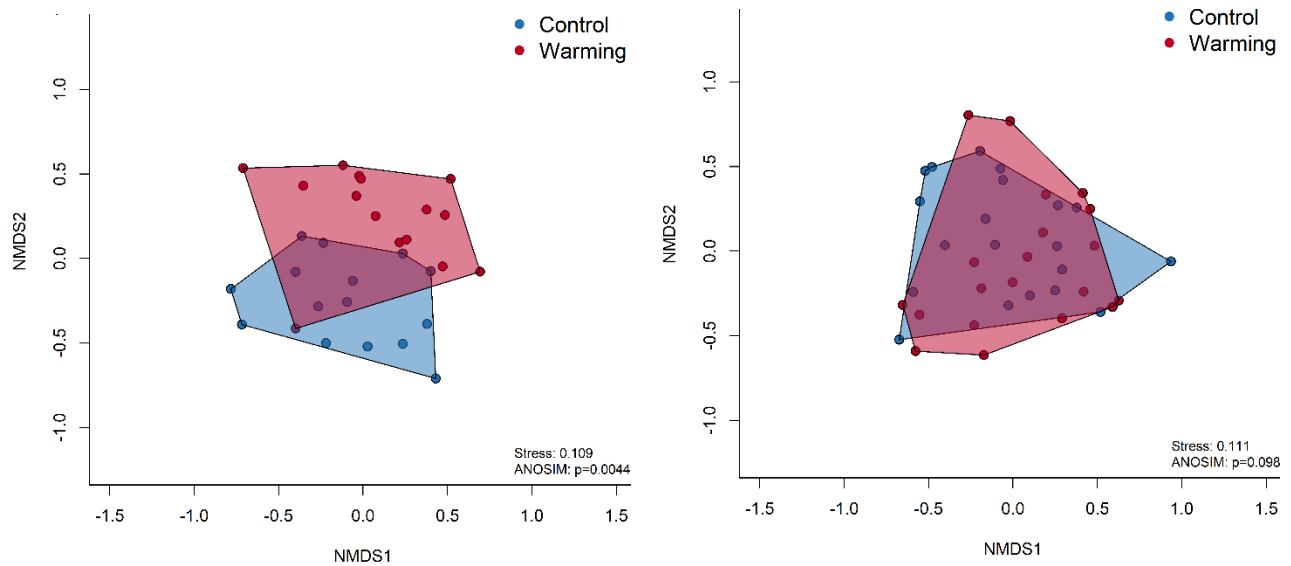
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213

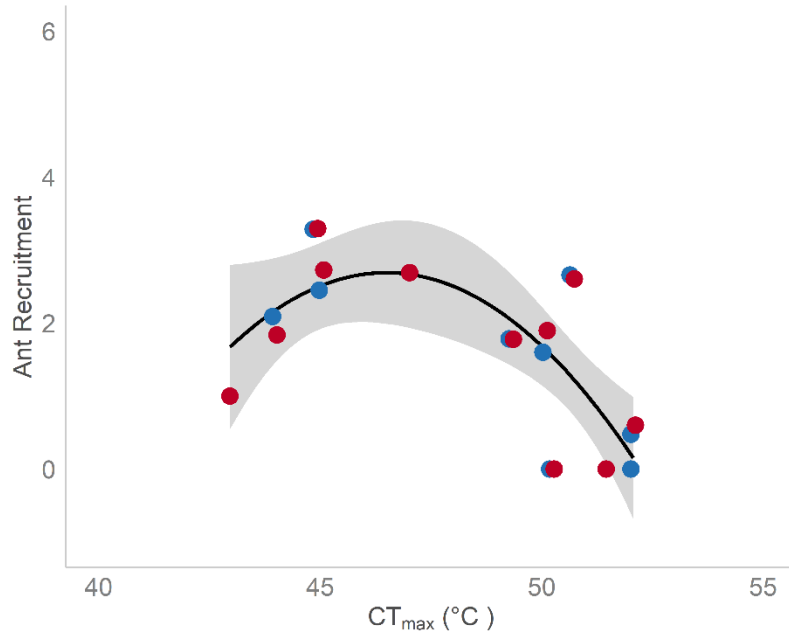
214 **Figures**

215

216



217 Figure 1. Non-metric multidimensional scaling ordination plots comparing ant community
218 composition in samples from *warming* and *control* plots. NMDS is based on genus abundance
219 data from pitfall samples across three months of trapping (left) and four months of baiting
220 (right).



221

222

223 Figure 2. The number of ants at baits (*Ant Recruitment*) vs. critical thermal maximum (CT_{max}).

224 Each point is the log-transformed total genus abundance across 200 baits placed within

225 *warming* plots (red) or 200 baits in *control* (blue) plots. Gray area represents 95% confidence

226 interval of the model: $y = -0.08x^2 + 7.6x - 174.2$, $R^2 = 0.53$.

227

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