

Research



Cite this article: Bujan J, Nottingham AT, Velasquez E, Meir P, Kaspari M, Yanoviak SP. 2022 Tropical ant community responses to experimental soil warming. *Biol. Lett.* **18**: 20210518.
<https://doi.org/10.1098/rsbl.2021.0518>

Received: 6 October 2021
Accepted: 7 March 2022

Subject Areas:
ecology

Keywords:
climate change, CT_{max} , ecophysiology, experimental warming, formicidae, BCI

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One paper of a special feature 'A contribution to the special feature 'Insect Decline' organised by Martin Gossner, Florian Menzel and Nadja Simons'.

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5903149>.

Community ecology

Tropical ant community responses to experimental soil warming

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

1. Introduction

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

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

We used experimental soil warming of a tropical lowland forest to test the effect of temperature increase on soil arthropods. A previous study at this site found that 4°C of warming across 2 years increased soil CO₂ emissions by 55%, mainly due to increased soil heterotrophic activity [12]. Here we test if warming, and this associated soil microbial functional change, are associated with changes at higher trophic levels. We focus on ants because they play key roles in ecosystem functioning [13]. Ants are highly thermophilic, and their activity is directly governed by temperature. However, in tropical forest, understory ants are less thermally tolerant compared to the canopy [14], and they are likely to avoid hot forest patches, as observed for army ants in tropical treefall gaps [15,16]. Tropical ants also respond to differences in resource availability by recruiting in higher numbers [17], or by relocating their colonies closer to a high-quality resource [18]. In the tropical understory, temperature promotes ant activity at baits [17]. Thus, any effects of soil warming on the abundance or quality of resource patches should be reflected in changes in ant abundance and recruitment. Warming potentially affects both nest location and ant activity; although these are not mutually exclusive aspects of ant biology, we focused on ant activity.

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

2. Material and methods

This study was conducted in the Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR) project on Barro Colorado Island (BCI) in the Panama Canal (9.15° N, 79.85° W). More details about SWELTR and BCI are available elsewhere [12,22]. Briefly, this ongoing experiment consists of 10 circular plots (five warming plots paired with five control plots), each 5 m in diameter, distributed over 1 ha of forest. Control and warming plots are 10 m apart and pairs of plots are separated by at least 20 m. The soil is heated by cables inside a stainless-steel frame encircling a 3.5 m diameter area at 1.2 m depth, so the effective heated area of the plot is 5 m in diameter. The control plots were constructed in the same way as the warming plots: steel frames (with no heating cable inside) were buried at the same depth (see [12] for more details).

We sampled the ants by placing five pitfall traps in each of the 10 plots. Each trap consisted of a 50 ml plastic centrifuge tube filled with 70% ethanol and a drop of scentless detergent. Tubes were buried so that their opening was flush with the soil surface. One trap was placed in the plot centre and the other four traps were distributed 2 m away from the centre trap, following a five-on-a-die pattern. The traps remained in the soil and were deactivated (covered) for the duration of the study apart from three 48 h sampling periods: one each in July and August 2018, and January 2019.

To determine how warming affects foraging activity, we used 10 baits per plot: five ca 20 cm outside of the warming cable and five inside. Each bait consisted of a ca 5 g mix of tuna and honey placed on white index card (7.6 × 12.7 cm). We recorded the

surface temperature of each plot at the beginning and the end of every baiting trial by aiming a portable IR thermometer at the ground (Fluke Corporation, model 62). After 1 h, we recorded the number of ants at each bait (recruitment) using a base 2 logarithmic scale. Recruitment is the short-term accumulation of ant workers at a food resource. We identified distinctive, common ants in the field (e.g. *Ectatomma ruidum* and *Odontomachus bauri*) and collected other ants for identification in the laboratory. To identify ants to species or morphospecies, we used online resources [23] and reference collections from BCI [24]. We baited monthly from June–August 2018, and January 2019, 10 days prior to pitfall trapping.

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

We used generalized linear mixed effect models (*glmmTMB* function) with Poisson distribution to analyse the effect of warming on litter ant abundance and species richness. We checked for model overdispersion using diagnostic plots in the DHARMA package [25]. Experimental treatment was used as a fixed effect and plot and month of sampling as random effects. We separately tested responses of numerically dominant genera (abundance greater than 5%): *Ectatomma*, *Labidus*, *Pheidole*, *Solenopsis* and *Wasmannia*. To determine how warming affected the number of ants recruited at baits, we used ground temperature (average of baiting start and end temperatures) as the fixed effect instead of treatment. In this way we accounted for forest heterogeneity and temporal changes in temperature. Average ground temperature was significantly higher on warming plots ($\chi^2 = 9.04$, d.f. = 1, $p = 0.0027$). We used the same abundance threshold (greater than 5%) when analysing recruitment at baits and ran separate models for the four numerically dominant genera. We used abundance data to analyse the differences in ant community composition (pitfalls) and recruitment (baits) using non-metric multi-dimensional scaling (NMDS) with Bray–Curtis distances [26]. We ran separate tests for species-level and genus-level abundances across all months of sampling. We used analysis of similarity (ANOSIM) to test for the significance of observed differences [27]. All analyses were done with the R statistical program [28]. The data supporting the findings of this study are available in figshare [29].

3. Results

Collectively, the 150 pitfall trap samples captured 1395 individual ants, representing 44 species in 19 genera and 5 subfamilies (electronic supplementary material, table S1, figure S1A). The 400 baits placed in SWELTR plots attracted 6585 individual ants, representing 29 species in 14 genera and 6 subfamilies (electronic supplementary material, table S2 and figure S1B).

Ant community composition, recorded with pitfalls, differed between experimental treatments (figure 1a; NMDS: $R^2 = 0.988$, stress = 0.109; ANOSIM: $p = 0.0044$), with six genera recorded only on warming plots and one genus only on control plots. We also observed community-level differences at the species level (electronic supplementary material, figure S2), with two species positively and two negatively affected by warming (electronic supplementary material, figure S3). In pitfall traps, total ant abundance and species richness were similar between treatments ($\chi^2_{\text{abundance}} = 0.87$, d.f. = 1, $p = 0.35$; $\chi^2_{\text{richness}} = 0.003$, d.f. = 1, $p = 0.96$). However, soil warming

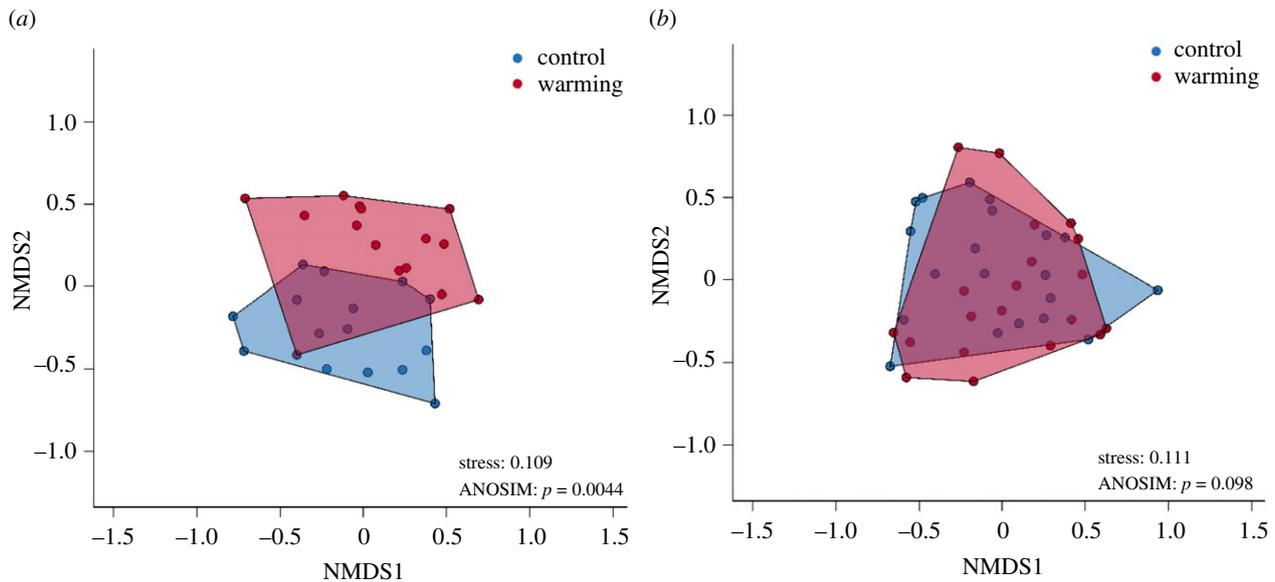


Figure 1. NMDS ordination plots comparing ant community composition in samples from *warming* and *control* plots. NMDS is based on genus abundance data from pitfall samples across three months of trapping (a) and four months of baiting (b).

tripled the abundance of *Wasmannia* in pitfall traps relative to controls (electronic supplementary material, figure S3; $p = 0.012$). Other abundant genera did not show a significant response to warming (electronic supplementary material, table S3).

Soil surface temperature of plots during baiting trials promoted ant recruitment to baits (electronic supplementary material, figure S4; $\chi^2 = 56.8$, d.f. = 1, $p < 0.001$). We found the same pattern of soil surface temperature best-predicting recruitment to baits (electronic supplementary material, figure S4) at the genus level: *Wasmannia* (electronic supplementary material, table S4; $p = 0.0002$), *Ectatomma* ($p = 0.0279$), *Azteca* ($p < 0.001$) and *Pheidole* ($p = 0.003$). However, species richness at baits could not be predicted by temperature ($\chi^2 = 1.03$, d.f. = 1, $p = 0.31$). In contrast with the differences in community composition observed for pitfall traps, the composition of ants at baits was similar between controls and warming treatments at genus (figure 1b) and species levels (electronic supplementary material, figure S2).

Recruitment peaked in genera with medium heat tolerances, so a quadratic function fit the data better (AIC = 53.8) than a linear function (AIC = 58.9), although both models were significant. Critical thermal maximum predicted 53% of ant recruitment at baits, regardless of the warming treatment (figure 2; $F_{2,17} = 9.4$, $p = 0.002$). None of the examined thermoregulatory traits (CT_{max} , CT_{min} or mass) was a significant predictor of the genus-level abundance of ants in pitfalls between warmed and control plots (electronic supplementary material, table S5).

4. Discussion

Climatic change is among the most important threats to insect biodiversity. Here we show that experimental warming of soil in a tropical forest changed the composition and activity of ant communities. The changes were dominated by increased activity of a single genus—*Wasmannia*—on warmed plots. *Wasmannia auropunctata* is native to Panama but is invasive in many other tropical regions [30]. The increased occurrence of *W. auropunctata* observed in this study differs from patterns

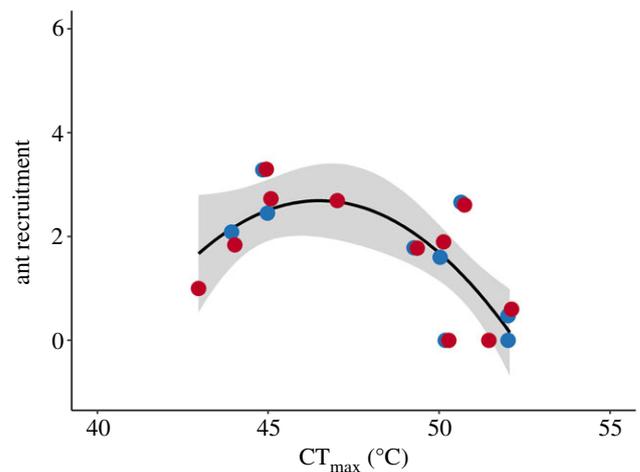


Figure 2. The number of ants at baits (ant recruitment) versus critical thermal maximum (CT_{max}). Each point is the log-transformed total genus abundance across 200 baits placed within warming plots (red) or 200 baits in control (blue) plots. Grey area represents 95% confidence interval of the model: $y = -0.08x^2 + 7.6x - 174.2$, $R^2 = 0.53$.

shown for invasive ants in their invasive range, where populations are declining either because of climatic changes [31] or for unknown reasons [32]. In accordance with our prediction warming promoted ant recruitment at baits, but it was the highest in ants with moderate CT_{max} . Thus, resource acquisition on warming plots was governed by temperature and heat tolerance.

We did not find changes in species richness after 2 years of warming. Similar warming experiments conducted at two temperate sites also found species richness unchanged after warming [33,34]. Moreover, a warming experiment at a low latitude oak-hickory forest showed that less than 10% of temperate zone ants in the sampled community responded to warming, and most of those species increased in abundance [35]. Similarly, we found that only 9% (4/44) of species responded to warming (electronic supplementary material, figure S3). In accordance with findings from experimental and natural warming [36], we found that temperature increase had a selective

impact on ants, with some species not affected while others were either positively or negatively impacted by warming (electronic supplementary material, figure S3). A resource supplementation experiment found that the abundance of *W. auropunctata* in the BCI forest increased five-fold in response to carbohydrate addition [37]. This suggests that changes in resource availability observed across warming plots [12] might be a mechanism for an increase in *W. auropunctata*, similar to increased activity of tropical ants observed following long-term fertilization with phosphorus [17]. Although *W. auropunctata* forms low-density populations in its native range, an increase in disturbance can increase recruitment and nest density [38]. The increase we observed in response to warming is unlikely to be caused by the disturbance that accompanied the warming treatment, because control plots underwent the same level of disturbance.

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

In our experiment, the soil temperature was 4°C higher than ambient when averaged across the soil profile, and the soil surface temperature was about 3°C warmer than ambient [12]. Both of these values are still far from the CT_{max} of any of the leaf litter ants in this forest [14]. Within the range of CT_{max} measured for temperate zone ants, maximum CT_{max} being 46°C [34,39], our results are in accordance with the finding that heat-tolerant ants are more abundant at baits. However, our ant community included canopy ants with thermal tolerances exceeding 50°C, which rarely forage on the forest floor. Because of this we found a unimodal response of ant recruitment and heat tolerance. Such a unimodal response to warming was also recorded for ants across temperate forests, where genera with moderate CT_{max} increased in their incidence in the past 20 years [40]. An increase in the incidence of ants with moderate thermal

tolerances might be the overall ant response to raising temperatures.

We show that warming in a tropical forest can have a profound effect on ant communities, potentially favouring species with moderate heat tolerance and invasive traits. Our finding that warming increased the abundance of species with invasive potential points to a wider destabilizing effect of warming on the ant community structure, thus extending an observation made in temperate forest [41] to the tropics. Observed changes in the ant community, together with higher rates of soil organic matter cycling [12], may have cascading effects on the rest of the soil food web. In summary, our findings illustrate the sensitivity of tropical ant communities to warming, and highlight the need for further study of the effects of warming on insects in the tropics where their thermal ranges are narrow.

Ethics. The experiments in this study comply with the current laws of the Republic of Panama.

Data accessibility. The data supporting the findings of this study are available in figshare [29].

Authors' contributions. J.B.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft and writing—review and editing; A.T.N.: conceptualization, funding acquisition, investigation, methodology, project administration, resources and writing—review and editing; E.V.: investigation, project administration and writing—review and editing; P.M.: conceptualization, methodology, resources, writing—review and editing; M.K.: conceptualization, investigation and writing—review and editing; S.P.Y.: conceptualization, funding acquisition, investigation, methodology, resources and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. This research was funded by the NSF grant no. DEB-1252614 to S.P.Y., and J.B. received funding from the Programme de la Famille Sandoz-Monique de Meuron pour la relève universitaire. A.T.N. was supported by a UK NERC grant no. NE/T012226. P.M. was supported by UK NERC grant no. NE/K01627X/1.

Acknowledgements. We thank Melissa Caño and the staff of the Smithsonian Tropical Research Institute for logistical support in Panama. Thanks to Kane Lawhorn and Julio Rodriguez for help in the field. We thank Dr Benjamin Turner for comments on an earlier version of the manuscript. This study complies with the current laws of the Republic of Panama.

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