



# Upper thermal tolerance of tropical and temperate termite species (Isoptera: Rhinotermitidae, Termitidae): a test of the climate variability hypothesis in termites

M. Janowiecki<sup>1</sup> · E. Clifton<sup>2</sup> · A. Avalos<sup>3</sup> · E. L. Vargo<sup>1</sup>

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## Abstract

Extrema in temperature tolerances are a selective factor contributing to variation between populations and species. The climate variability hypothesis (CVH) posits that organisms exposed to a wider range of temperatures are expected to have a wider thermal range. This pattern is common across many taxa. In this study, we investigate how social insects vary in thermal tolerance. We test if social role in termites influences tolerance to temperature maxima, and given ties between social roles and body size, whether it is a primary correlate. Our methods examined upper lethal limit (ULL) and dry weights of five termite species representing two families across four sites in Texas and Costa Rica. With the addition of previously recorded upper heat tolerances in the literature, we conclude that termites follow the CVH and upper heat tolerance is positively correlated with absolute latitude. Our results show a differentiation in heat tolerance by task (collected from foraging site versus from nest) for *Nasutitermes corniger* soldiers but not workers. In the remaining species, there was no ULL partitioning by caste (soldier versus worker). Body size significantly correlated with ULL with the exception of *Cornitermes walkeri*, an outlier in both body size and ULL. A better understanding of how termites cope with temperature is important for this essential wood decomposer in a changing climate.

**Keywords** Termites · Upper thermal tolerance · Climate variability hypothesis

## Introduction

The ability to adapt to habitat-specific temperature ranges is responsible for much of the global pattern of biodiversity and key metabolic strategies, e.g. ectothermy and endothermy. In social organisms, thermoregulation requires consideration of the individual as well as the nest. Social insect species' persistence in an area will depend in part on their thermal tolerance breadth, the range of survivable temperatures, and thermal tolerance diversity, the variation between individuals in a nest (Baudier 2017). Thermal tolerance diversity may be especially important in determining where a colony can thrive (Baudier et al. 2015). Though one of the oldest social insect groups (Bourguignon et al. 2015) with known, varied, complex forms of colony thermoregulation (Jones and Oldroyd 2006), information on termites thermal tolerance is lacking. This is of increasing relevance given projected global temperature increases.

Termite colonies use various means of thermoregulation (Jones and Oldroyd 2006). Passively, termites use nest architecture to facilitate ventilation, exemplified by the magnetic

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✉ M. Janowiecki  
janowiecki@tamu.edu

E. Clifton  
elizabeth.clifton@uconn.edu

A. Avalos  
arian.avalos@usda.gov

E. L. Vargo  
ed.vargo@tamu.edu

<sup>1</sup> Department of Entomology, Texas A&M University, TAMU 2475, College Station, TX 77843, USA

<sup>2</sup> Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Rd., Unit 3043, Storrs, CT 06269, USA

<sup>3</sup> USDA-ARS Honey Bee Breeding, Genetics, and Physiology Research, Baton Rouge, LA 70820, USA

*Amitermes* mounds in northern Australia and other mound building termites (Jones and Oldroyd 2006). Actively, individual termites are able to increase temperature by clustering and producing metabolic heat, as shown in two species of *Coptotermes* in Australia where the temperature of the nursery chamber of the nest is elevated by congregating workers (Greaves 1964). Contrastingly in warmer climates, *Macrotermes* decreases nest temperature through evaporative cooling by placing water on the inside of exterior walls of the nest (Darlington 1985).

The climate variability hypothesis (CVH) asserts that greater variation in environmental temperatures is matched by a larger range in organismal thermal tolerance (Janzen 1967; Stevens 1989). The pattern is robust in ectotherms, endotherms, and plants ( $n = 2740$ ) (Araújo et al. 2013), although a large portion of the variation in tolerance was found around the lower tolerance limits (Sunday et al. 2011).

Although the CVH has not been specifically tested in termites, there has been an interest in heat tolerances of a variety of termites for practical applications in pest management (Scheffrahn et al. 1997; Woodrow and Grace 1998a). Less is known about caste and environmental differences across termite species (Hu and Appel 2004; Mitchell et al. 1993; Woon et al. 2018). However, in other eusocial insects, differences in thermal tolerances were correlated to worker size (Cerdá and Retana 1997; Clémencet et al. 2010), colony size (Oyen et al. 2016; Ribeiro et al. 2012; Wendt and Verble-Pearson 2016), nest location (Baudier et al. 2015), and role (Strassmann et al. 1984) and is often explained by differences in microhabitats experienced by individuals.

The aim of this paper was to directly test the CVH using a panel of tropical and temperate termite species. Specifically, we: (1) contrast heat tolerance across temperate and tropical species; (2) examine if there is caste- or task-specific partitioning of heat tolerance; and (3) address how body size contributes to heat tolerance. We hypothesize that if termites adhere to predictions proposed by the CVH, temperate species will have a higher upper thermal tolerance than tropical species, approximating a wider thermal breadth; that colonies partition heat tolerance with tasks or castes exposed to more temperature variability able to withstand a wider range of temperatures; and that body size contributes to the variation in heat tolerance within and between species.

## Materials and methods

### Sample collection and identification

Termites were collected for this study from two locations in Texas, United States, and two locations in Costa Rica (Table 1, Fig. 1). In Texas, the sites were the Hill Country State Natural Area (SNA) in the Edwards Plateau in

west Texas and a city park in Texas City, Texas which is a part of the Gulf Coast prairie ecotype (Table 1, Fig. 1b). In Costa Rica, termites were collected from two research stations operated by the Organization for Tropical Studies: La Selva Biological Station in a lowland rainforest (35 m elevation) and Las Cruces Biological Station in a premontane wet forest (1200 m elevation) (Table 1, Fig. 1c). Nineteen climatic variables were extracted from WorldClim Global Climate Data (Fick and Hijmans 2017) for each sample site. Samples were collected alive with aspirators and soft forceps and thermal tolerance trials were run on 24 individuals per caste (soldier and worker) for each colony. Following the thermal trials, individuals were stored in 100% ethanol for morphological and genetic analyses. These specimens are maintained in the Rollins Structural and Urban Entomology Facility, Texas A&M University, United States and voucher specimens are deposited in the Texas A&M University Insect Collection (#734).

When possible, collected termites were morphologically identified with dichotomous keys (Banks et al. 1918; Emerson 1952; Nickle and Collins 1992). These identifications were confirmed by sequencing the 16S section of mitochondrial DNA. Genomic DNA was extracted from entire bodies of individual specimens using a salting-out procedure with in-house reagents (Sambrook and Russell 2001). The 16S region was amplified with the primers: LR-J-13007 (5'-TTACGCTGTTATCCCTAA-3') (Kambhampati and Smith 1995) and LR-N-13398 (5'-CGCCTGTTTATCAAAAACAT-3') (Simon et al. 1994). Consensus sequences were created from alignment of both directions for each sample in Geneious 9.1.8 (Kearse et al. 2012). Sequences were subjected to BLAST searches of sequences in GenBank to determine similarity and species identification.

### Thermal tolerance analysis

The upper lethal limit (ULL) was calculated for 24 individuals per experimental group according to Esch et al. (2017). Termites were placed individually in 1.5 mL plastic Eppendorf tubes capped with cotton in a digital heat block (Thermo Scientific Compact Digital Dry Bath/Block Heater, double block capacity, model 88871002, temperature control accuracy and uniformity at  $37\text{ °C} \leq \pm 0.5\text{ °C}$ ). The block temperature began at  $33\text{ °C}$  and increased by  $1\text{ °C}$  every 5 min (Esch et al. 2017). After each 5 min exposure, the tube was examined under a dissecting microscope to determine whether there was visible movement. When the termite no longer moved during a 5 s period, it was declared deceased and the previous temperature (the highest temperature it survived) was recorded as its ULL.

**Table 1** Collection localities and climate data (Fick and Hijmans 2017) for samples collected from Texas, U.S.A. and Costa Rica

Location	Country: State/ Province	Geographical coordinates	Species col- lected	Average daily temperature fluctuation (°C)	Seasonal tem- perature fluctua- tion (standard deviation *100)	Annual tem- perature range (maximum temperature of warmest month–mini- mum tempera- ture of coldest month) (°C)	Permit number
Hill Country State Natural Area	United States: Texas	29.629118, – 99.184520	Termitidae: <i>Tenuirostritermes cinereus</i>	12.56	691.28	31.12	Texas Parks and Wildlife 2018_ R2_RGV_04
Texas City	United States: Texas	29.393290, – 94.945346	Rhinotermiti- dae: <i>Coptotermes formosanus</i>	7.78	622.91	24.52	Not required
La Selva Bio- logical Station	Costa Rica: Heredia	10.429584, – 84.005308	Rhinotermiti- dae: <i>Coptotermes testaceus</i> Termitidae: <i>Nasutitermes corniger</i>	8.17	77.53	10.59	R-007-2018-OT- CONAGEBIO
Las Cruces Biological Station	Costa Rica: Puntarenas	8.787079, – 82.95954	Rhinotermiti- dae: <i>Coptotermes testaceus</i> Termitidae: <i>Cornitermes walkeri</i>	9.83	82.51	11.91	R-007-2018-OT- CONAGEBIO

## Experimental design

We determined the variation in ULL between colonies of *Tenuirostritermes cinereus* (Buckley) by testing three different colonies from a single site in Texas. We examined the difference in heat tolerance determined by location. One species, *Coptotermes testaceus*, was collected at both sites in Costa Rica. The ULL was compared between sites within Costa Rica to determine the variation of ULL for a species on a relatively small scale (within a country). To test the climate variability hypothesis, we compiled the five species examined in this study along with all other records of other studies of the upper thermal tolerance in termites (Mitchell et al. 1993; Sponsler and Appel 1991; Woodrow and Grace 1998b) (Table 2). The correlations of absolute latitude and nineteen bioclimatic variables to upper thermal tolerance were plotted and the significance was tested with Spearman's correlation test in R v-3.4.1 (R Core Team 2013).

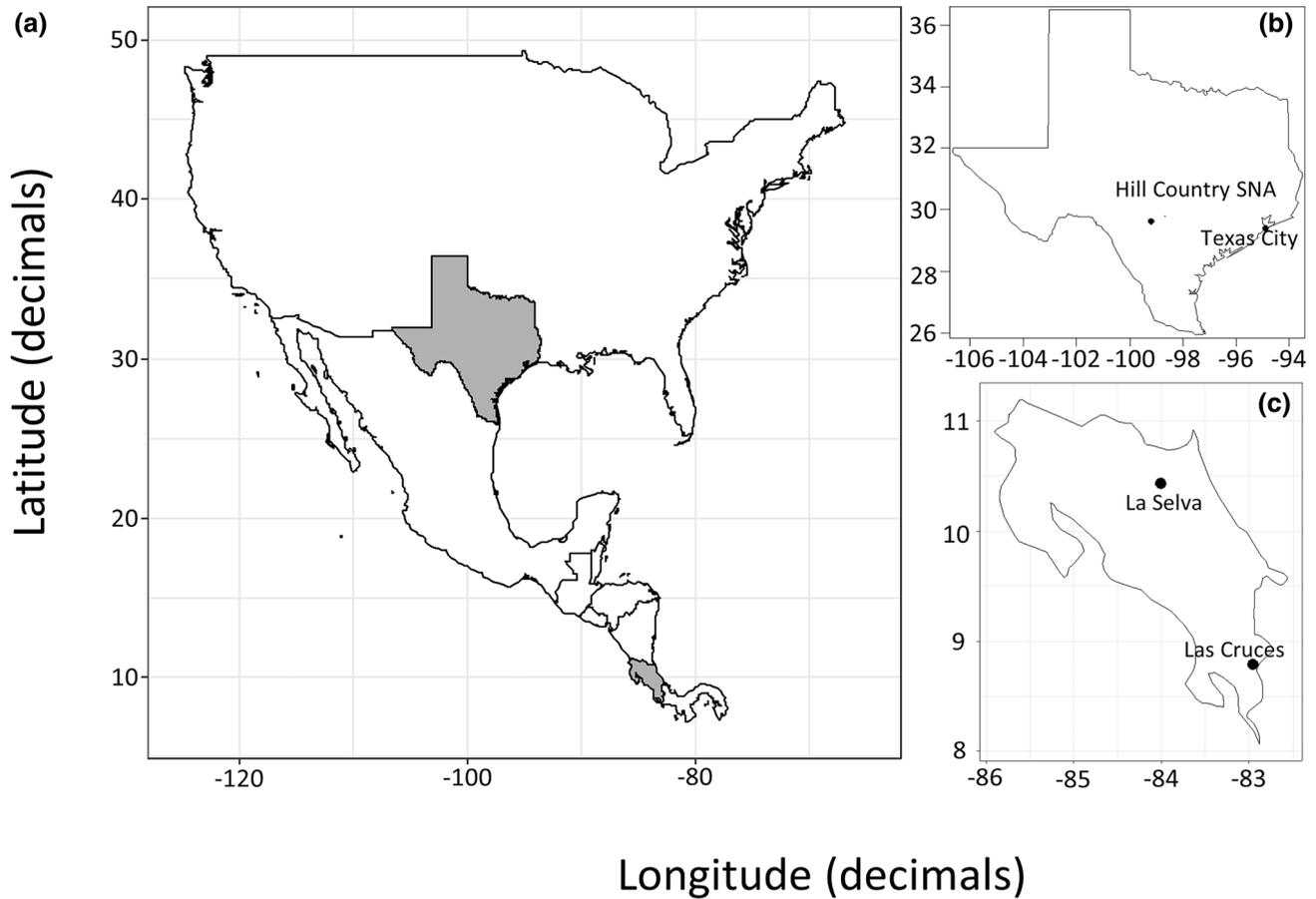
To test for a partitioning of heat tolerance by task, we examined *Nasutitermes corniger* (Motschulsky) because its conspicuous arboreal nests were convenient to sample. We collected soldiers and workers in La Selva from three arboreal nests and from three food sources (fallen logs) on

the forest floor. Partitioning by caste was determined for all species collected and compared between soldiers and workers from the same colony.

Finally, to determine the influence of body size on the upper thermal limit, the dry weight of 10 individuals per experimental group was determined following the methods of Haverty and Nutting (1975). Termites were placed individually in weigh boats and maintained in an oven at 60 °C. The weight was recorded daily with an analytical balance (RADWAG AS 220.R2, readability 0.1 mg) until it was constant to the nearest 0.1 mg. The correlation between body mass and upper lethal limit was plotted and the significance was tested with Spearman's correlation test in R v-3.4.1 (R Core Team 2013).

## Results

From the four sites in Costa Rica and Texas, a total of five species of termites representing two families were identified using 16S sequencing: *Coptotermes formosanus* Shiraki, *C. testaceus* (L.) (Rhinotermitidae), *Tenuirostritermes cinereus*, *Nasutitermes corniger*, and *Cornitermes*



**Fig. 1** a Map of collection localities. b Texas, c Costa Rica

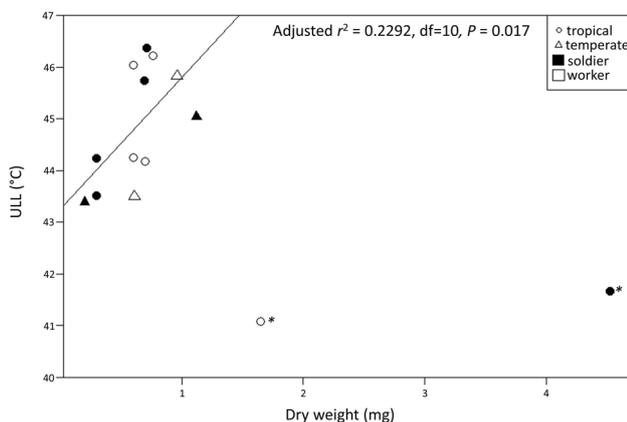
**Table 2** Species examined for climate variability hypothesis

Family	Species	Absolute latitude	Caste(s)	Upper thermal tolerance (°C)	Citation
Hodotermitidae	<i>Hodotermes mossambicus</i> (Hagen)	29°	Worker	47.93	Mitchell et al. (1993)
Hodotermitidae	<i>Hodotermes mossambicus</i>	27°	Worker	16.69	Mitchell et al. (1993)
Kalotermitidae	<i>Neotermes connexus</i> Snyder	21.29925°	Worker	51	Woodrow and Grace (1998b)
Kalotermitidae	<i>Incisitermes immigrans</i> (Light)	21.29925°	Worker	51.3	Woodrow and Grace (1998b)
Kalotermitidae	<i>Cryptotermes brevis</i> (Walker)	21.29925°	Worker	51.3	Woodrow and Grace (1998b)
Rhinotermitidae	<i>Reticulitermes flavipes</i> Kollar	32.6082°	Worker/Soldier	46.4/46.7	Sponsler and Appel (1991)
Rhinotermitidae	<i>Coptotermes formosanus</i> Shiraki	32.6082°	Worker/Soldier	48/46.7	Sponsler and Appel (1991)
Rhinotermitidae	<i>Coptotermes formosanus</i>	29.39329°	Worker/Soldier	45.83/45.04	This study
Rhinotermitidae	<i>Coptotermes formosanus</i>	21.29925°	Worker	47.9	Woodrow and Grace (1998b)
Rhinotermitidae	<i>Coptotermes testaceus</i> (L.)	10.42958°	Worker/Soldier	46.04/45.74	This study
Rhinotermitidae	<i>Coptotermes testaceus</i>	8.787079°	Worker/Soldier	46.37/46.22	This study
Termitidae	<i>Tenuirostritermes cinereus</i> (Buckley)	29.629118°	Worker/Soldier	43.5/43.38	This study
Termitidae	<i>Nasutitermes corniger</i> (log) (Motschulsky)	10.429584°	Worker/Soldier	44.75/43.92	This study
Termitidae	<i>Nasutitermes corniger</i> (tree)	10.429584°	Worker/Soldier	44.43/44.21	This study
Termitidae	<i>Cornitermes walkeri</i> Snyder	8.787079°	Worker/Soldier	41.08/41.67	This study

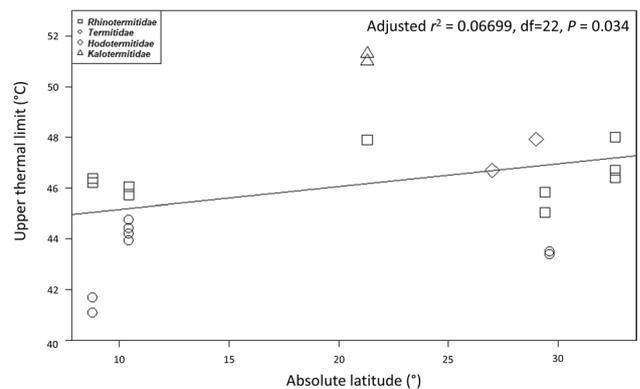
*walkeri* Snyder (Termitidae) (Table 1). A preliminary test of ULL for three colonies of *T. cinereus* in Texas showed no significant difference between colonies. Therefore, we used 24 soldiers and 24 workers from a single colony to represent each species for the following analyses, with the exception of the *N. corniger* samples where we used three nests and three logs to test partitioning by task.

### Difference of ULL by location

Within Costa Rica, there was no significant difference in the ULL of *C. testaceus* collected from two sites at different altitudes although a trend was observed in soldiers ( $P=0.0928$ ). Comparing temperate and tropical climates, most temperate samples (triangles) had a lower than average ULL for their body weight compared to tropical samples (circles) since they were mostly below the best fit line of the correlation between body weight and ULL (Fig. 2). With the addition of previous studies of upper thermal limits (Table 2), there is a positive correlation between absolute latitude and ULL (adjusted  $r^2=0.06699$ ,  $df=22$ ,  $P=0.034$ ) (Fig. 3). Additionally, four bioclimatic variables significantly predicted ULL. Specifically, ULL is positively correlated with temperature seasonality (adjusted  $r^2=0.0438$ ,  $df=22$ ,  $P=0.034$ ), and negatively correlated with mean temperature of the wettest quarter (adjusted  $r^2=-0.000352$ ,  $df=22$ ,  $P=0.016$ ), warmest quarter (adjusted  $r^2=-0.000352$ ,  $df=22$ ,  $P=0.033$ ), and precipitation of the warmest quarter (adjusted  $r^2=-0.0003518$ ,  $df=22$ ,  $P=0.027$ ). These results show that tropical termites have lower thermal limits than temperate termites and this pattern is shaped by a combination of temperature and precipitation factors which shape microhabitat variation.



**Fig. 2** Correlation of dry weight (mg) to upper lethal limit ( $^{\circ}\text{C}$ ) for temperate (triangle symbols) and tropical species (circle symbols) excluding the outlier, *Cornitermes walker*, marked by asterisks



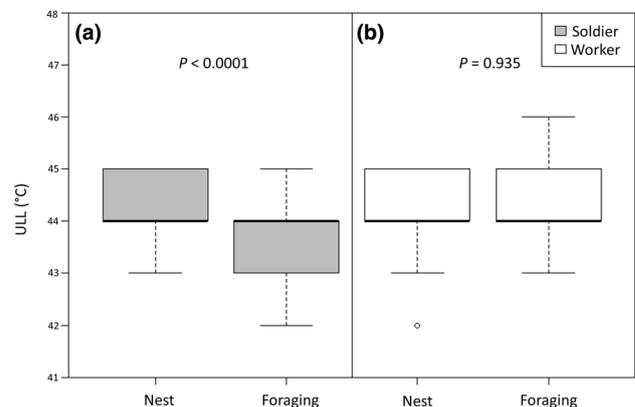
**Fig. 3** Correlation of absolute latitude (deg) to upper lethal limit ( $^{\circ}\text{C}$ ) for various families of termites [additional data from: (Mitchell et al. 1993; Sponsler and Appel 1991; Woodrow and Grace 1998b)]

### Partitioning of ULL by task or caste

In *N. corniger*, there was a difference in ULL for termites collected in the foraging site (log) vs the nest for the soldiers ( $P < 0.0001$ ) but not the workers ( $P=0.935$ ) (Fig. 4). For the remaining species tested, there was no difference in ULL between the castes (soldier and worker) ( $P > 0.95$ ).

### Correlation of ULL to body weight

When examining all samples, body weight and ULL are not significantly correlated ( $P=0.66$ ) (Fig. 2). However, this is primarily due to the *C. walkeri* outlier with much larger body weight (more than 4  $\times$ ) and much lower ULL than all other samples. If *C. walkeri* is excluded from the correlation, there is a significant correlation between body weight and ULL (adjusted  $r^2=0.2292$ ,  $df=10$ ,  $P=0.017$ ) (Fig. 2).



**Fig. 4** Upper lethal limit for *Nasutitermes corniger* individuals that were foraging compared to those collected in the nest, **a** soldiers, **b** workers

## Discussion

This first test of the climate variability hypothesis in termites shows that they do indeed follow the pattern of tropical species having a narrower range of thermal breadth, as approximated through the upper thermal limit, compared to temperate species. This is likely caused by the greater daily and seasonal temperature fluctuation in the temperate sampling areas (Texas, United States) compared to the tropical sampling locations (Costa Rica) (Table 1). The ULL increases as seasonality increases, indicating that exposure to a wider range of temperatures increases the ability to withstand these temperatures. These patterns would likely be even more pronounced if the lower thermal limit were measured since Sunday et al. (2011) found a majority of the increase in thermal breadth came from the lower limit.

In *N. corniger*, there was a partitioning of task for soldiers but not for workers. Soldiers in the nest were able to withstand higher temperatures than soldiers in the foraging site (log). In the remaining species, we found no difference in ULL by caste. For 15 genera of termites in Borneo, Woon et al. (2018) also found no difference in upper thermal tolerance for soldiers and workers. These observations do not align with Mitchell et al. (1993), however, which found a separation of upper and lower thermal limits by caste (specifically, workers and larvae) in *Hodotermes mossambicus*. This difference may be explained because Mitchell et al. (1993) were comparing age within a caste whereas we compared between castes.

With the exception of *C. walkeri*, body weight is a good predictor of ULL. However, *C. walkeri* is a much larger than the other species examined in this study and this may explain why this species does not align to the pattern. This finding contrasts results from *Reticulitermes flavipes* and *C. formosanus* where no correlation between worker body mass and thermal tolerance was detected (Hu and Appel 2004), suggesting a complex relationship between body mass and thermal tolerance when considering different species. Hu and Appel (2004) instead attributed the variation in thermal tolerance to seasonality. Our study also had a lower ULL for *C. formosanus* (worker: 45.83 °C, soldier: 45.04 °C) compared to other studies by Woodrow and Grace (1998b) (worker: 47.9 °C) as well as Sponsler and Appel (1991) (worker: 48 °C, soldier: 46.7 °C). This difference is particularly surprising because Sponsler and Appel (1991) measured the critical thermal maximum, the temperature where the termite could still move one body length when probed, which should be a lower temperature than the lethal limit measured in this study. This underlines the degree of possible variation within a species at a broader scale than examined in this study.

A better understanding of termite thermal tolerances has important implications for wood decomposition in a warming climate. Termites are critical in recycling resources from wood back to the soil (Eggleton and Tayasu 2001) and represent a biomass equal to humans (Bar-On et al. 2018). Currently, climate projections highlight increasing mean global temperature and the frequency of extreme events (Pachauri et al. 2014). This change will likely impact tropical species more than temperate species, since we found that temperate termites were able to withstand a relatively higher temperature, indicating a wider range of tolerance. Future work is needed to characterize the lower thermal limits of termites, as well as thermal tolerance across a broader termite phylogeny. The latter can provide insight into how other evolutionary factors contribute to established thermal breadth and intraspecific thermal diversity. Results from this study and future studies are important to understanding how termites will navigate a changing climate.

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