



# Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests

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## Abstract

Termites are vital members of old-growth tropical forests, being perhaps the main decomposers of dead plant material at all stages of humification (decay). Termite abundance and diversity drop in selectively logged forest, and it has been hypothesised that this drop is due to a low tolerance to changing micro-climatic conditions. Specifically, the thermal adaptation hypothesis suggests that tropical species are operating at, or close to, their thermal optimum, and therefore, small temperature increases can have drastic effects on abundance, however, other climatic variables such as humidity might also cause termite abundance to drop. We tested termite tolerance to these two climatic variables (temperature and humidity). We found that termites had a higher  $CT_{max}$  than expected, and that three traits, feeding group, body sclerotisation, and nesting type, were significantly correlated with  $CT_{max}$ . We found that termite desiccation tolerance was low, however, and that all termite genera lost significantly more water in a desiccated environment than in a control. Body sclerotisation, the only trait that was tested, was surprisingly not significantly correlated with desiccation tolerance. Our results suggest that desiccation, rather than ambient temperature, may be the determining factor in dictating termite distributions in modified forests. Should climate change lead to reduced humidity within tropical rainforests, termite abundances and the rates of the functions they perform could be severely reduced.

**Keywords** Climate ·  $CT_{max}$  · Decomposition · Ectotherms · Humidity

## Introduction

Tropical forests are under increasing pressures from human activities (Koh and Wilcove 2008; Lewis et al. 2015). In SE Asia, an area with some of the oldest and most diverse of all forests, selective logging and the oil palm industry are rapidly changing forest ecosystems (Sodhi et al. 2004, 2010). How species react to these pressures is an important contemporary question in ecology (Heydon and Bulloh 1996; Asner et al. 2005; Broadbent et al. 2008; Drescher et al. 2016; Ewers et al. 2015).

When a forest is selectively logged the microclimate is altered (Hardwick et al. 2015). As the canopy cover is reduced, more sunlight reaches the understory, which combined with a reduction of transpiring leaves, raises the temperature and lowers the humidity (Hardwick et al. 2015). Temperature regulation and water retention are two mechanisms of homeostasis required by all terrestrial organisms. When these mechanisms are under stress, organisms expend energy and resources, and may consequently have reduced fitness (Miller and Stillman 2012). This is a serious problem for ectotherms in particular, as they have no internal mechanisms allowing individuals to mitigate against environmental changes (Paaijmans et al. 2013; Sgrò et al. 2016). The thermal adaptation hypothesis proposes that in the hot, aseasonal tropics, species are adapted to a narrow thermal range (Deutsch et al. 2008; Angilletta 2009; Sunday et al. 2014). Because of this limited thermal range, tropical species are expected to be living close to their thermal optimum (Deutsch et al. 2008; Angilletta 2009). This means small increases in maximum temperature, such as those experienced when a forest is logged, could have large deleterious

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effects on tropical species (Deutsch et al. 2008). This, along with a lack of their own homeostatic thermoregulatory mechanisms, may cause widespread extinctions of ectotherms in altered forests (Huey et al. 2012).

In addition to their susceptibility to changes in temperature, a number of phenotypic features make small ectotherms extremely susceptible to changes in humidity (Chown et al. 2011; Bujan et al. 2016): a large surface area–volume ratio, high metabolic rate, and relatively high fat levels (Gibbs et al. 1997; Hoffmann and Harshman 1999) increase the rate of water loss for individuals in drier environments. The tropics have been a relatively stable environment for thousands of years, meaning that species in these biomes would have faced less selective pressure for desiccation-resistant traits than species in temperate biomes (Bujan et al. 2016). Consequently, even the small reductions in humidity seen in selectively logged forest (Uhl and Kauffman 1990; Hardwick et al. 2015) could be a major factor in determining distributions of small ectotherms after disturbance. Furthermore, with droughts predicted to increase in both frequency and severity (Fu 2015), desiccation stress could also increase in primary forests, thus altering ectotherm distributions in all forest types.

The majority of insect-driven decomposition within pristine tropical forests is due to termites (Bignell and Eggleton 2000). Termites, depending on species, break down dead plant matter across the entire humification (decomposition) gradient, which ranges from recently fallen deadwood to soil (Donovan et al. 2001), thereby contributing to other vital ecological functions such as nutrient cycling and soil turnover (Holt and Coventry 1990; Holt and Lepage 2000). Termite diversity drops in selectively logged forests (Eggleton et al. 2002; Lee 2012; Luke et al. 2014; Ewers et al. 2015), leading to a significantly lower decomposition rate than in primary forest (Ewers et al. 2015).

A number of adaptations and life history traits are thought to be associated with temperature and desiccation resistance. Some species are hard-bodied, for example, and generally forage on, or close to, the surface. Increased sclerotisation is thought to allow them to withstand the higher temperatures and lower humidity of the soil surface, when compared with the buffered environment within the soil (Rajpurohit et al. 2008a; Schimpf et al. 2009).

Termites also have a range of nesting strategies and this may enhance their eco-physiological tolerances. Species nest in a number of strata of the forest, allowing them to exploit a range of different habitats and food sources (Li et al. 2015). Termites that nest in different strata will potentially have different adaptations to protect themselves from varying environmental stresses, as there is a range of microclimates within tropical forests. Typically, the higher strata are hotter and drier (Ozanne et al. 2003; Scheffers et al. 2013), and arboreal species could, therefore, heat up and dry out more

rapidly. Life histories, then, could shape thermal adaptation, providing various benefits that allow certain genera to persist in an otherwise unfavourable environment. It is assumed that some traits confer protection against heat or desiccation, however, these have not been studied in detail in termites. For example, there are a variety of building types that might buffer against the environment, allowing greater control over the conditions experienced within the structures (Korb 2003; Jones and Oldroyd 2006). These differences in life histories could provide an insight into differing thermal tolerances, and therefore, the genera that are more at risk from higher levels of environmental stress.

Despite the functional importance of termites within tropical forests, their tolerances to changing microclimatic conditions have not previously been examined. Here, we provide an insight into the morphological and life history characteristics of termites that shape their tolerances. We ascertain the upper thermal boundary ( $CT_{max}$ ) for a number of termite genera, and the applicability of the thermal adaptation hypothesis is discussed.

We test a number of hypotheses about the relative thermal and desiccation sensitivity of termites, with all hypotheses based on the same underlying rationale that species inhabiting and/or foraging in more extreme environments will be less sensitive to microclimatic extremes. For example, we predict higher  $CT_{max}$  for: (1) termites with hard rather than soft bodies; (2) termites with arboreal rather than ground nests; (3) termites that construct thin carton nests; and (4) termites that feed higher up the humification gradient than those lower down. (5) We also expect to detect caste differences in  $CT_{max}$ , as different castes are exposed to different ambient conditions. Finally, we predict (6) that increased body sclerotization will confer a higher desiccation tolerance as has previously been demonstrated for other insects (Appel and Tanley 1999; Singh et al. 2009).

## Materials and methods

### Sampling area

All sampling occurred within Sabah, in East Malaysia, on the island of Borneo, between February and June 2016. A major El Niño event occurred during this sampling period and this may have affected the diversity of termites we collected for this study. The samples were collected from the lower areas of Maliau Basin Conservation Area (4.85°N, 116.84°E), an area of old growth mixed dipterocarp forest.

### Termite collection

We located termite colonies within mounds or deadwood within the forest, systematically searching new,

undisturbed areas of the forest day by day to increase likelihood of new colony discovery. Once a colony was located, we removed a portion of the colony structure or feeding substrate (such as infested deadwood or soil) containing termites and placed it in a cool-box for transportation to the laboratory. Time between sampling and the beginning of laboratory experiments was minimised (mean = 30 min, SD = 18 min) to reduce stress to the termites. Because we were unable to conduct the experiment at the point of sampling, we were unable to quantify the impact of the transportation time on the results. Termites were not acclimatised to laboratory conditions because preliminary tests suggested this reduced fitness.

All collected termites were identified to genus, and morphological and life history data was taken from the literature and our own observations. Feeding groups were categorised using the criteria outlined in Donovan et al. (2001), which splits termites into one of five groups (I, II, IIF, III, and IV) based on their family and feeding preference along the humification gradient. Nesting strategies were recorded in the field, when sampled at colony centres, and corroborated using Inward et al. (2007). If termites were not sampled at colony centres, nesting strategy was assigned after identification. Four categories of nesting strategy were identified; (1) soil nesting, (2) wood nesting, (3) wood nesting with carton structures, and (4) mound structures. Body sclerotisation was treated categorically as either hard- or soft-bodied, with a termite categorised as soft-bodied if the gut was visible through the abdomen at a magnification rate of  $100\times$  (i.e. the abdomen was so unsclerotised that its wall was translucent or transparent). Only soldier and worker castes were studied and dimorphic differences within castes were not considered in this experimentation. Nesting layer had three categorical variables; Arboreal, Terrestrial, Subterranean, based upon the typical location of their colony centre. If the colony centre could not be located, nesting layer was assigned after identification.

### Thermal tolerance

To obtain values of upper thermal tolerance ( $CT_{max}$ ) for all genera collected in the field, we used a ramping procedure based on methods outlined in Terblanche et al. (2011). Twenty individual termites were placed into unique glass vials and submerged in a water bath (Grant Instruments TXF200). The temperature of the water was then increased at a rate of  $0.2\text{ }^{\circ}\text{C}$  per minute, which was the fastest rate at which the temperature within the tubes and the temperature of the water remained constant. We defined  $CT_{max}$  as the temperature at which individuals lost all motor control and so were completely still.

### Desiccation tolerance

We quantified the desiccation tolerance of termites by measuring the rate of water loss in an environment where the air was dried experimentally. We focussed on four genera (*Macrotermes*, *Hospitalitermes*, *Microcerotermes*, and *Dicuspiditermes*), which were chosen because of their high abundance, distinctive nest structures, range of thermal tolerances and varying responses to selective logging (Luke et al. 2014).

Workers were sampled from a single colony at a time and divided into groups. Group size varied between five and 15 termites depending on the quantity of termites collected, and the weight of the individual termites—larger-bodied species had smaller groups. Where possible, 20 groups of termites were collected per colony and were standardised with an equal number of termites, however, some sampling trips yielded lower numbers of termites than expected. As such, we collected 191 groups from 12 unique colonies. Termite groups were weighed and then placed in glass vials and randomly assigned to either treatment or control. The treatment vials contained 5 g of silica gel which reduced the humidity to 30% (SD = 4.5%); the humidity within control vials was 76% (SD = 8%). All 20 vials were placed in a water bath which was set to a constant  $30\text{ }^{\circ}\text{C}$ . This temperature was chosen as it was the average ambient maximum air temperature in the laboratory. At each of five time-points (10, 30, 60, 120, and 180 min) we removed four vials for analysis: three treatment vials and a single control. The weight of each termite group was recorded, and weight change was assumed to be due to water loss.

Because a large-bodied termite might lose a larger absolute amount of water than a small-bodied termite, we standardised weight change by the total body water content of each genus. To determine total body water content, we weighed samples containing approximately 50 termites, all of the worker caste, placed them in a drying oven for 24 h at  $60\text{ }^{\circ}\text{C}$ , and then weighed them again. We used insects taken from different colonies to those used in the desiccation experiment; if we were to repeat the experiment we would use the same insects used in the desiccation experiment. We subtracted the dry weight from the fresh weight to estimate body water content. We divided the weight loss observed in the desiccation experiments by the average body water content of that genus to calculate the proportion of total body water that had been lost at each time point in the desiccated environment.

### Statistical analysis

We analysed all data using the R statistical package version 3.2.2 (R Core Team 2015). Linear mixed effects models (package lme4, Bates et al. 2015) were fitted to the data,

from both the thermal and desiccation experiments, and simplified until minimal adequate models were attained. Tukey's post-hoc tests were used to determine differences between levels of categorical factors (package multcomp, Hothorn et al. 2008).

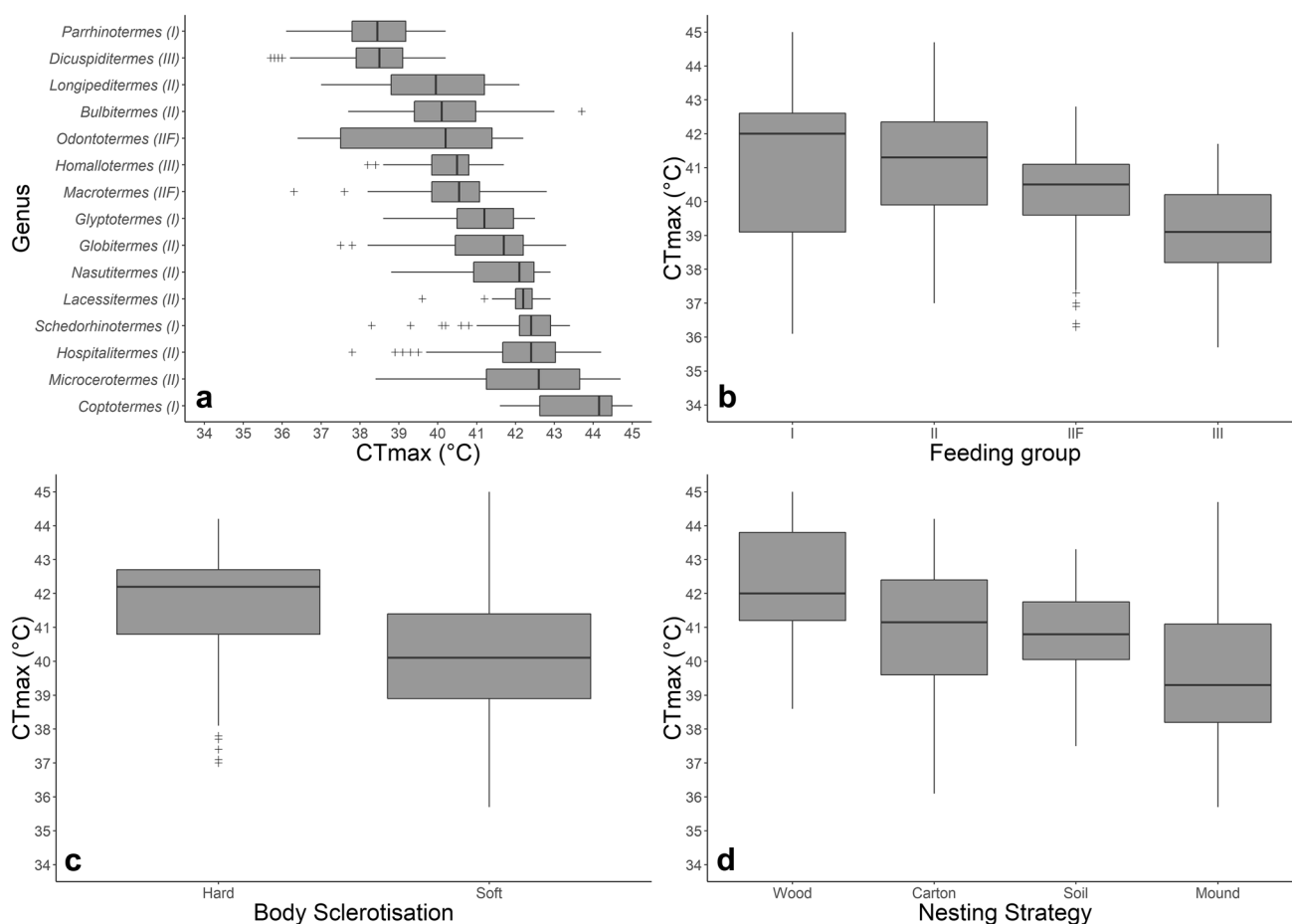
We tested the impact of five fixed effects on  $CT_{max}$ : body sclerotisation, feeding group, nesting strategy, nesting layer and caste. We fitted all five fixed effects in a single model that included colony identity as a random effect, allowing for the possibility that individuals collected from the same colony and at the same time are likely to exhibit similar responses. The maximal model was simplified using a backwards stepwise process using likelihood ratio tests to compare models. The remaining significant factors were retained in the final model, and likelihood ratio tests were used on this model to calculate the overall significance of each explanatory variable.

To analyse the desiccation tolerance data, we modelled the percentage of body water lost against three fixed effects and all interactions: time, treatment and body sclerotisation; with colony identity included as a random effect. Profile confidence intervals were calculated to determine the significance of the explanatory variables and their interactions.

## Results

### Thermal tolerance

A total of 1171 individuals were tested, collected from 45 unique colonies and representing 15 genera.  $CT_{max}$  varied by 5.25 °C across the 15 genera (Fig. 1a), with body sclerotisation, feeding group and nesting strategy all explaining a statistically significant part of the observed variation.



**Fig. 1** Boxplots displaying  $CT_{max}$  data of the termites. For **b–d**, all genera were grouped into displayed groups. **a** A boxplot of each genera's  $CT_{max}$ , in numerical order from lowest (top) to highest. Low outliers were attributed to injured individuals. The numerals within the parentheses correspond to the feeding group of each genus. **b** A comparison of the  $CT_{max}$  of the four feeding groups that were found. The average  $CT_{max}$  sequentially decreases through the humification gradi-

ent. No group IV true soil feeders were found. **c** A comparison of the  $CT_{max}$  of hard and soft-bodied termites. **d** A comparison of the  $CT_{max}$  of the four nesting strategies found. Nesting strategy was classified using recent literature (Inward et al. 2007), and field observations. The thick central line indicates the median, the box the interquartile range, higher whisker the upper adjacent value and the lower whiskers the lower adjacent value

Feeding group was significantly correlated with  $CT_{max}$  (Fig. 1c, likelihood ratio test,  $\chi^2 = 12.04$ ,  $P = 0.007$ ,  $df = 3$ ). Hard bodied termites had a significantly higher  $CT_{max}$  than soft-bodied termites (Fig. 1b, likelihood ratio test,  $\chi^2 = 8.64$ ,  $P = 0.003$ ,  $df = 1$ ), with an average of  $1.29^\circ\text{C}$  ( $SD = 0.45$ ) higher than soft-bodied termites (Tukey test,  $z = -2.846$ ,  $P = 0.004$ ).  $CT_{max}$  was highest in feeding group I and sequentially decreased along the humification gradient, with a  $2.70^\circ\text{C}$  ( $SD = 0.90$ ) difference between the highest and lowest groups (Tukey test,  $z = -2.991$ ,  $P = 0.013$ ). Nest type was weakly correlated with  $CT_{max}$  (Fig. 1d, likelihood ratio test,  $\chi^2 = 8.05$ ,  $P = 0.045$ ,  $df = 3$ ). Termites that built mounds had the lowest  $CT_{max}$  and wood nesting termites the highest. However, the post-hoc pairwise comparisons were not statistically significant (Tukey test,  $z < 1.900$ ,  $P > 0.208$ ). Nest layer was not significantly correlated with  $CT_{max}$  (likelihood ratio test,  $\chi^2 = 3.65$ ,  $P = 0.056$ ,  $df = 1$ ). Finally, caste was also not significantly correlated with  $CT_{max}$  (likelihood ratio test,  $\chi^2 = 0.11$ ,  $P = 0.74$ ,  $df = 1$ ), however, the only two castes that were tested were the soldier (511 individuals) and worker (660 individuals) castes.

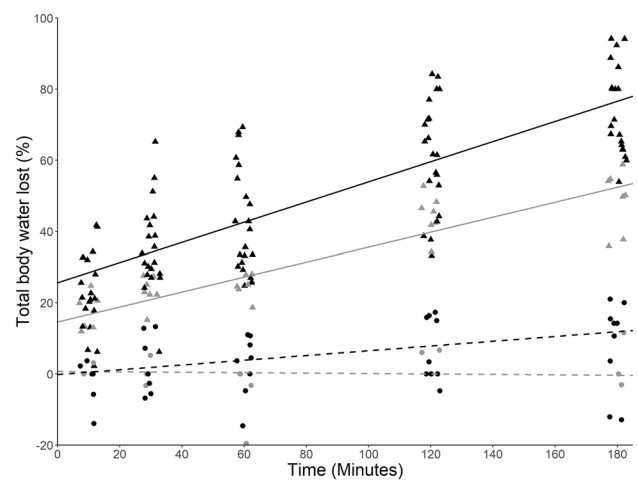
## Desiccation tolerance

Termites lost significantly more water in the desiccated than the control treatment [Fig. 2, 95% CI (8.294, 27.517)]. There was no significant difference in percentage water loss between hard and soft-bodied termites [Fig. 2, 95% CI (-10.043, 15.670)]. The rate of water loss over time was higher in the desiccated environment [Fig. 2, 95% CI (0.073, 0.257)], however, there was no significant difference in the rate of water loss between the two body types [Fig. 2, 95% CI (-0.069, 0.111)].

## Discussion

Termites varied strongly in their tolerances to both temperature and desiccation stress, and these tolerances varied systematically with various morphological and life history traits. Our results largely conform to our hypotheses, supporting the general pattern that species inhabiting and/or foraging in more extreme environments are more resilient to microclimatic stresses. This pattern could, however, have important implications for the maintenance of termite-mediated ecosystem processes, such as decomposition, in forests that have undergone selective logging and are further threatened by future climate change.

Position along the humification gradient was associated with  $CT_{max}$  in line with our hypothesis. The higher up the gradient the higher the  $CT_{max}$ . However, both the most thermal-tolerant genus, *Coptotermes*, and the least tolerant, *Parrhinotermes*, are found in feeding group I. Both *Coptotermes*



**Fig. 2** Water loss in termites through time. Each point corresponds to a unique group of termites, and their weight loss at point of weighing. Termites were split into one of two classes: hard bodied termites, represented by the black points and lines; and soft-bodied, represented by the grey points and lines. Termites were exposed to one of two environments: a desiccated environment, represented by triangular points and solid lines; or a control environment, represented by the circular points and dashed lines. Negative values are attributed to water absorption from the tube environment during the experiment and measurement error. The data points are jittered

and *Parrhinotermes* are found within the same family, Rhinotermitidae, suggesting that  $CT_{max}$  is not evolutionarily conserved within a clade. This is further supported by the variation displayed in feeding group II, all of which are in the monophyletic Termitidae. Feeding groups IIF and III (which contain genera of the termitids), however, all had a  $CT_{max}$  that was significantly lower than feeding group I. We sampled no genera from feeding group IV, the true soil-feeders, as they are extremely rare in the Sabah community.

As expected, hard-bodied termites had a higher  $CT_{max}$  than soft-bodied termites. Other studies on different insect groups have shown the opposite pattern (Kellermann et al. 2012; Parkash et al. 2012), with higher levels of sclerotisation correlating with a lower  $CT_{max}$ . However, these studies were conducted across altitudinal or latitudinal gradients rather than within a single study site, therefore, they may not be directly comparable. Hard-bodied termites may have acquired a higher  $CT_{max}$  as a bi-product of a mechanism designed to offer better protection from predation while foraging on the hotter, drier surface as compared to their soft-bodied subterranean counterparts.

We also found that nest type significantly affected  $CT_{max}$ , with genera that nested in mounds having the lowest thermal  $CT_{max}$  of the genera studied, as expected. This is likely to be due to the thick walls providing a barrier against the external conditions that keep the internal nest at a constant, cool temperature. Some species of mound-building termite, including African savanna species of *Macrotermes*, have complex

gas-flow systems that work to refresh the air inside the nest (Korb 2003). This aspect of nest building is unstudied in the SE Asian genera, but could help explain this result. Contrary to what was predicted, genera that form carton nests (the nest type which provides the least amount of environmental buffering) did not have the highest  $CT_{max}$ ; wood-nesting species did. Only two soil nesting genera were found, which is much lower than expected in old growth forests (Eggleton et al. 1999; Luke et al. 2014).

Despite average ambient temperature varying by approximately 4 °C between the canopy and the understory at our study site (Hardwick et al. 2015), nesting layer did not significantly affect  $CT_{max}$ . This suggests that foraging location is more important than nest location in defining  $CT_{max}$ . We also found no significant effect of caste on  $CT_{max}$ . This suggests that within a colony,  $CT_{max}$  is equal, although no juveniles or reproductives were tested, which are two castes vital for the survival of the colony (Roisin 2000). Changing temperatures could alter colony survival not by impacting the fitness of the worker or soldier castes, but by altering fertility rates or other vital processes that support the colony.

A large proportion of the variation in  $CT_{max}$  was explained by the random effect of colony identity. Due to the relatively coarse taxonomic scale at which we are working, these differences may be explained by species-level differences, as  $CT_{max}$  may not be conserved at a genus-level in termites. Nest location could also influence the variation in  $CT_{max}$ . Nests located in areas with relatively extreme microclimates, such as treefall gaps, could be home to colonies with a higher  $CT_{max}$  than those located in the shade, for example.

All genera have a  $CT_{max}$  that is significantly higher than any ambient temperature within an old growth tropical forest. The average highest daily temperature in the old growth forest study zone in Sabah was roughly 26 °C (Hardwick et al. 2015), but the lowest  $CT_{max}$  we quantified was 35.7 °C (Fig. 1, *Dicuspiditermes*), with the lowest average  $CT_{max}$  for an individual genus being 38.4 °C (Fig. 1, *Parrhinotermes*). So why do these small ectotherms have such a high upper thermal limit? The thermal adaptation hypothesis posits that it should be much closer to the temperatures experienced in the forest (Angilletta 2009), but our data appears to contradict that. We did, however, not record ground surface temperature, which would provide more insight into the temperatures that termites experience (particularly the ground foraging species), which could be much closer to their  $CT_{max}$ .

Although ambient temperature has been an effective variable for predicting changes in species distributions in previous studies (Parmesan and Yohe 2003; Root et al. 2003), our study, and a number of other recent studies (Clusella-Trullas et al. 2011; Kellermann et al. 2012), suggest it may not be the best measure to use for ectotherms. Clusella-Trullas et al.

(2011) suggested that temperature variation and precipitation might play a larger role than average ambient temperature in determining the  $CT_{max}$  of larger ectotherms. Furthermore, the interaction between precipitation and temperature has been shown to have an effect on insect  $CT_{max}$  (Kellermann et al. 2012). This suggests that future studies into the effects of microclimate change on small invertebrates should study a suite of microclimatic conditions alongside temperature, with an obvious candidate being desiccation stress.

Our results show that humidity could play a larger role in dictating termite distributions than has previously been acknowledged. They also suggest that body sclerotisation does not affect desiccation tolerance, which contradicts previous studies of other ectotherms (Parkash et al. 2008; Rajpurohit et al. 2008b). However, we only tested one hard-bodied genus (*Hospitalitermes*) and used a simplified binary classification. The large amount of variation in water loss of the soft-bodied genera, may have contributed to the lack of significant difference between the body types. In addition, factors such as body size and diet could play a role in rate and amount of water loss and should be investigated.

Our findings are concerning. They suggest that all termites are heavily affected by a drop in humidity, thus humidity decreases, and not temperature increases, could be the leading factor in dictating the observed termite diversity decline in logged forest systems (Luke et al. 2014). Despite these worrying results, some termites do thrive in desiccated environments and should be studied further. If  $CT_{max}$  is a driver of species distributions (McGill et al. 2006; Diamond et al. 2013), our results suggest that termites consuming more decomposed plant matter appear to be less resistant than those feeding higher up the humification gradient, which could be cause for alarm in selectively logged forest, as whole functional groups could be lost. We have shown that the worker and soldier caste have a higher thermal tolerance than previously thought, however, more study should be done into their experienced temperature and other castes, such as reproductives, to fully understand the impact of temperature changes on termite colony survival.

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## References

- Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. OUP, Oxford
- Appel A, Tanley M (1999) Water composition and loss by body color and form mutants of the German cockroach (Dictyoptera: Blattellidae). *Comp Biochem Physiol A Mol Integr Physiol* 122:415–420
- Asner GP, Knapp DE, Broadbent EN, Oliveira PJC, Keller M, Silva JN (2005) Selective logging in the Brazilian Amazon. *Science* 310:480–482
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw.* <https://doi.org/10.18637/jss.v067.i01>
- Berry NJ, Phillips OL, Lewis SL, Hill JK, Edwards DP, Tawatao NB, Ahmad N, Magintan D, Khen CV, Maryati M et al (2010) The high value of logged tropical forests: lessons from northern Borneo. *Biodivers Conserv* 19:985–997
- Bignell DE, Eggleton P (2000) Termites in ecosystems. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbioses, ecology*. Springer, Dordrecht, pp 363–387
- Broadbent E, Asner G, Keller M, Knapp D, Oliveira P, Silva J (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol Conserv* 141:1745–1757
- Bujan J, Yanoviak SP, Kaspari M (2016) Desiccation resistance in tropical insects: causes and mechanisms underlying variability in a Panama ant community. *Ecol Evol* 6:6282–6291
- Chown SL, Sørensen JG, Terblanche JS (2011) Water loss in insects: an environmental change perspective. *J Insect Physiol* 57:1070–1084
- Clusella-Trullas S, Blackburn TM, Chown SL (2011) Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *Am Nat* 177:738–751
- Coley P, Barone J (1996) Herbivory and plant defenses in tropical forests. *Annu Rev Ecol Syst* 27:305–335
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105:6668–6672
- Diamond SE, Penick CA, Pelini SL, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR (2013) Using physiology to predict the responses of ants to climatic warming. *Integr Comp Biol* 53:965–974
- Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. *Trends Ecol Evol* 11:255–260
- Donovan SE, Eggleton P, Bignell DE (2001) Gut content analysis and a new feeding group classification of termites. *Ecol Entomol* 26:356–366
- Drescher J, Rembold K, Allen K, Beckschäfer P, Buchori D, Clough Y, Faust H, Fauzi AM, Gunawan D, Hertel D et al (2016) Ecological and socio-economic functions across tropical land use systems after rainforest conversion. *Philos Trans R Soc Lond B Biol Sci* 371:20150275
- Edwards DP, Larsen TH, Docherty TDS, Ansell FA, Hsu WW, Derhé MA, Hamer KC, Wilcove DS (2011) Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proc Biol Sci* 278:82–90
- Eggleton P, Homathevi R, Jones DT, MacDonald JA, Jeeva D, Bignell DE, Davies RG, Maryati M (1999) Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. *Philos Trans R Soc Lond B Biol Sci* 354:1791–1802
- Eggleton P, Bignell D, Hauser S, Dibog L, Norgrove L, Madong B (2002) Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. *Agric Ecosyst Environ* 90:189–202
- Ewers RM, Boyle MJW, Gleave RA, Plowman NS, Benedick S, Bernard H, Bishop TR, Bakhtiar EY, Chey VK, Chung AYC et al (2015) Logging cuts the functional importance of invertebrates in tropical rainforest. *Nat Commun* 6:6836
- Fu R (2015) Global warming-accelerated drying in the tropics. *Proc Natl Acad Sci USA* 112:3593–3594
- Gibbs AG, Chippindale AK, Rose MR (1997) Physiological mechanisms of evolved desiccation resistance in *Drosophila melanogaster*. *J Exp Biol* 200:1821–1832
- Griffiths HM, Ashton LA, Walker AE, Hasan F, Evans TA, Eggleton P, Parr CL (2017) Ants are the major agents of resource removal from tropical rainforests. *J Anim Ecol* 87.1:293–300
- Hardwick SR, Toumi R, Pfeifer M, Turner EC, Nilus R, Ewers RM (2015) The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives changes in microclimate. *Agric For Meteorol* 201:187–195
- Heydon MJ, Bulloh P (1996) The impact of selective logging on sympatric civet species in Borneo. *Oryx* 30:31
- Hoffmann AA, Harshman LG (1999) Desiccation and starvation resistance in *Drosophila*: patterns of variation at the species, population and intrapopulation levels. *Heredity* 83:637–643
- Holt J, Coventry R (1990) Nutrient Cycling in Australian Savannas. *J Biogeography* 17:427–432
- Holt JA, Lepage M (2000) *Termites: evolution, sociality, symbioses, ecology*. Springer Science & Business Media, Berlin, pp 389–407
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363
- Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos Trans R Soc Lond B Biol Sci* 367:1665–1679
- Inward DJG, Vogler AP, Eggleton P (2007) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Mol Phylogenet Evol* 44:953–967
- Janzen DH (1971) Seed predation by animals. *Annu Rev Ecol Syst* 2:465–492
- Jones JC, Oldroyd BP (2006) Nest thermoregulation in social insects. *Adv Insect Physiol* 33:153–191
- Kellermann V, Overgaard J, Hoffmann AA, Fløjgaard C, Svenning JC, Loeschcke V (2012) Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proc Natl Acad Sci USA* 109:16228–16233
- Koh LP, Wilcove DS (2008) Is oil palm agriculture really destroying tropical biodiversity? *Conserv Lett* 1:60–64
- Korb J (2003) Thermoregulation and ventilation of termite mounds. *Naturwissenschaften* 90:212–219
- Lee SH (2012) Effects of environmental perturbation on the territory size of subterranean termites: a simulation study. *J Asia Pac Entomol* 15:457–463
- Lewis SL, Edwards DP, Galbraith D (2015) Increasing human dominance of tropical forests. *Science* 349:827–832
- Li HF, Lan YC, Fujisaki I, Kanzaki N, Lee HJ, Su NY (2015) Termite assemblage pattern and niche partitioning in a tropical forest ecosystem. *Environ Entomol* 44:546–556
- Luke SH, Fayle TM, Eggleton P, Turner EC, Davies RG (2014) Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodivers Conserv* 23:2817–2832
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185
- Miller N, Stillman J (2012) Physiological optima and critical limits. *Nat Educ Knowl* 3.10:1
- Osazuwa-Peters OL, Jiménez I, Oberle B, Chapman CA, Zanne AE (2015) Selective logging: do rates of forest turnover in stems,

- species composition and functional traits decrease with time since disturbance? A 45 year perspective. For *Ecol Manag* 357:10–21
- Ozanne CMP, Anhuf D, Boulter SL, Keller M, Kitching RL, Körner C, Meinzer FC, Mitchell AW, Nakashizuka T, Dias PLS et al (2003) Biodiversity meets the atmosphere: a global view of forest canopies. *Science* 301:183–186
- Paaijmans KP, Heinig RL, Seliga RA, Blanford JJ, Blanford S, Murdock CC, Thomas MB (2013) Temperature variation makes ectotherms more sensitive to climate change. *Glob Change Biol* 19:2373–2380
- Parkash R, Rajpurohit S, Ramniwas S (2008) Changes in body melanization and desiccation resistance in highland vs. lowland populations of *D. melanogaster*. *J Insect Physiol* 54:1050–1056
- Parkash R, Chahal J, Sharma V, Dev K (2012) Adaptive associations between total body color dimorphism and climatic stress-related traits in a stenothermal circumtropical *Drosophila* species. *Insect Science* 19:247–262
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Rajpurohit S, Parkash R, Ramniwas S, Singh S (2008a) Variations in body melanisation, ovariule number and fecundity in highland and lowland populations of *Drosophila melanogaster* from the Indian subcontinent. *Insect Sci* 15:553–561
- Rajpurohit S, Parkash R, Ramniwas S (2008b) Body melanization and its adaptive role in thermoregulation and tolerance against desiccating conditions in drosophilids. *Entomol Res* 38:49–60
- Roisin Y (2000) Diversity and evolution of caste patterns. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbioses, ecology*. Springer, Dordrecht, pp 95–119
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60
- Scheffers B, Phillips B, Laurance W, Sodhi N, Diesmos A, Williams S (2013) Increasing arboreality with altitude: a novel biogeographic dimension. *Proc R Soc Lond B Biol Sci* 280:20131581
- Schimpf NG, Matthews PGD, Wilson RS, White CR (2009) Cockroaches breathe discontinuously to reduce respiratory water loss. *J Exp Biol* 212:2773–2780
- Sgrò CM, Terblanche JS, Hoffmann AA (2016) What can plasticity contribute to insect responses to climate change? *Annu Rev Entomol* 61:433–451
- Singh S, Ramniwas S, Parkash R (2009) Fitness consequences of body melanization in *Drosophila immigrans* from montane habitats. *Entomol Res* 39:182–191
- Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. *Trends Ecol Evol* 19:654–660
- Sodhi NS, Koh LP, Clements R, Wanger TC, Hill JK, Hamer KC, Clough Y, Tscharntke T, Posa MRC, Lee TM (2010) Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol Conserv* 143:2375–2384
- Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc Natl Acad Sci USA* 111:5610–5615
- Team R (2015) R: a language and environment for statistical computing (Internet). R Foundation for Statistical Computing, Vienna
- Terblanche JS, Hoffmann AA, Mitchell KA, Rako L, le Roux PC, Chown SL (2011) Ecologically relevant measures of tolerance to potentially lethal temperatures. *J Exp Biol* 214:3713–3725
- Uhl C, Kauffman J (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71:437–449
- Wearn OR, Carbone C, Rowcliffe JM, Bernard H, Ewers RM (2016) Grain-dependent responses of mammalian diversity to land use and the implications for conservation set-aside. *Ecol Appl* 26:1409–1420