



Plant shade enhances thermoregulation of internal environments in *Trinervitermes trinervoides* mounds

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ABSTRACT

Microhabitats may be crucial in buffering organisms from temperature extremes, particularly given increases in maximum temperature associated with global climate change. For example, thermoregulation in termite mounds is influenced by prevailing ambient conditions, and plant canopies may reduce external temperatures, in turn lowering internal temperatures. This buffering may be crucial during heat waves. Whether this happens, and to what extent, remains equivocal, however. We tracked internal temperatures in eight inhabited and six uninhabited *Trinervitermes trinervoides* mounds, half of each group of which were shaded by vegetation. *T. trinervoides* seek to maintain internal mound temperatures at c. 20 °C in winter and c. 30 °C in summer. Temperatures were logged for 72 h in winter, and again in summer. Internal temperatures of uninhabited mounds mirrored those of external temperatures, with temperatures varying by c. 15 °C, although shading was associated with some buffering of internal temperatures. Internal temperatures within inhabited mounds were far less variable, varying by c. 6 °C over the course of our study. In summer, exposed inhabited mounds maintained temperatures c. 29.5 °C, whilst shaded inhabited mounds were c. 27.5 °C. In winter, mean internal temperatures of exposed and shaded inhabited mounds were very similar, at 21.8 and 22.0 °C, respectively. Internal mound temperature varied significantly with external (ambient) temperature, mound activity, temperature, shading, and to a small extent, mound volume. The buffering effect of shade was evident in summer (c. 2 °C) but not in winter, suggesting that the benefit of such temperature modulation may be most important when ambient temperatures reach heat extremes, e.g. during heat waves.

1. Introduction

Species' range shifts in response to climate change are happening far faster than anticipated, with distributions moving poleward almost 17 km per decade (Chen et al., 2011), highlighting the importance of climate limits to species' persistence. Microclimates associated with vegetation may offer refuge from extreme temperatures, however (Scheffers et al., 2014). Termites (Blattodea) use behavioural and physiological means to maintain internal nest temperatures within narrow ranges, which ultimately enable them to expand their species' niche (Korb and Linsenmair 2000). Mound building termites maintain a homeostatic environment within nests through nest site selection and orientation, and by controlling internal temperatures and humidity by manipulating mound structure and using other behavioural and

physiological mechanisms (Field and Duncan, 2013; Jones and Oldroyd, 2006; Korb and Linsenmair, 1998, 2000). The orientation of the mound influences the amount of solar radiation received and the time of day when the highest radiation is received (Jacklyn, 1992; Jones and Oldroyd, 2006). Structural features are important for retaining heat, while others are effective in dissipating it (Theraulaz, 1998). Internal temperatures of mounds are therefore influenced by ambient temperatures, intensity of solar radiation, metabolism of the termites and fungi, mound shape, nest depth and opening and closing of mound chimneys (Korb and Linsenmair, 2000).

Maintenance of a steady internal climate within the mound is vital for termite colony survival. For example, *Macrotermes* spp. (Macrotermitinae) are unable to digest the lignin in the wood that they collect, so they farm *Termitomyces* fungus to break down the lignin, which grow

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optimally within the narrow temperature range of 29–32 °C (Wood and Thomas, 1989). Although the regulation of temperature and humidity within mounds of *Macrotermes* spp. has received some attention (e.g., Korb and Linsenmair, 1998; Korb and Linsenmair, 2000; Joseph et al., 2016; Joseph et al., 2018, Bardunias et al., 2020), far less is known about the mound thermoregulation capabilities of non-*Macrotermes* spp. termites such as the snouted harvester termite, *Trinervitermes trinervoides* (Field and Duncan, 2013). *Trinervitermes* spp. are not known to cultivate fungi inside their mounds (Uys, 2002; Adam et al., 2008), but temperature can still crucially influence larval development (Mukerji, 1970), making it necessary that internal temperatures are maintained within suitable ranges. In winter, *T. trinervoides* maintain internal mound temperatures c. 20 °C, and in summer, c. 30 °C (Field and Duncan, 2013), suggesting inhabited mound thermoregulation. A study conducted in the Sahel and Sudan found that although the two regions had very different ambient temperatures, the internal temperatures of *Trinervitermes* mounds did not differ significantly between the two regions (Aiki et al., 2019).

Mounds of *Macrotermes* often harbour evergreen plant species with thick foliage (Van der Plas et al., 2013; Joseph et al., 2014) which provide microclimates significantly cooler than the surrounding matrix (Korb and Linsenmair, 1998; Joseph et al., 2016). Most mound-building species in hot, dry environments are said to locate their mounds under shade (Sands, 1965; Lee and Wood, 1971) although others are completely exposed. Mound vegetation has been found to modulate *Macrotermes*' internal mound temperatures, an effect that increased with increasing ambient temperatures (Joseph et al., 2016). Yet elsewhere, the contribution of plant shade to *Macrotermes*' mound internal temperature stability was concluded to be negligible, suggesting that internal mound temperatures may be more influenced by mound size (Ndlovu and Pérez-Rodríguez, 2018).

Mounds of *Trinervitermes trinervoides* termites enrich the soil with macro- and micro-nutrients that promote num-num plant (*Carissa bispinosa*) growth (Nampa and Ndlovu, 2019) next to the mounds. Here, we investigate whether plant growth over and around *T. trinervoides* mounds provides a microclimate that influences maintenance of stable temperatures within mounds. We document 24-h internal mound temperature profiles in summer and in winter, within inhabited as well as uninhabited termite mounds, and investigate whether shade provided by num-num shrubs modulates fluctuations in internal mound temperature. Given that *T. trinervoides* seem to keep internal mound temperatures at different temperatures in different seasons, we expected to find the internal mound environment maintained within narrow limits, but for these limits to differ between seasons. We also anticipated that mound size and the presence of shrub canopy could buffer internal mound temperatures from ambient conditions.

2. Methods

2.1. Study site

This study was conducted at Nylsvley Nature Reserve (24° 39' 17.28" S, 28° 41' 27.6" E) in Limpopo province, South Africa. The approximately 40 km² reserve lies at the intersection of three different geological formations with five distinct soil groups (Jones et al., 2013) on the seasonally inundated floodplain of the Nyl river (Rowberry, 2011). This Afrotropic region receives about 600 mm of rainfall per year and is characterised by a warm wet summer from October to April, with mean maximum temperatures of 35 °C, and a cool dry winter between May and September with mean minimum temperatures of –2 °C (Rowberry, 2011). Most termite mounds in the reserve are compact dome-shaped mounds of Snouted harvester termites (*Trinervitermes* spp.), with a few large *Macrotermes* spp. mounds. North of the Nyls river region is dominated by relatively taller *Trinervitermes* spp. compact mounds (mean height = 61.03 ± 32.04 cm; Nampa and Ndlovu, 2019), compared to the shorter *T. rhodesiensis* mounds (less than 38 cm in

height) found in regions south of the river (Ferrar, 1982). Different castes from the study mounds located north of the river were collected and positively identified as *Trinervitermes trinervoides* (Sjöstedt) (Termitidae: Nasutitermitinae) by an entomologist at the University of the Free State, South Africa.

2.2. Sampling methods

The study was carried out in 2017 at the end of summer (March) and in mid-winter (July), to capture seasonal variations in internal mound temperatures as affected by prevailing ambient conditions. *T. trinervoides* mounds of similar sizes (approximately 1 m in height and diameter) were carefully selected for this study. A total of 14 mounds were used, of which eight were inhabited and six uninhabited; within each group, half of the mounds were exposed while the other half were shaded. Mounds were deemed as shaded if the entire mound was covered by Num-num canopy. Exposed mounds were totally exposed to sunlight throughout the day with no observed shading from any surrounding vegetation.

Mounds of *T. trinervoides* termites are dome-shaped above ground, usually with an extensive subterranean network of tunnels, which include passageways to holes that open onto the surface from which they leave to harvest grass (Adam et al., 2008). In rocky habitats, the subterranean passageways appear to be much reduced (Field and Duncan, 2013), although our site was not particularly rocky, so underground structures are likely well developed.

To determine mound volume, we measured mound height, breadth and width using a rigid measuring tape. We then calculated mound volume using the formula for volume of an ellipsoid, divided by two. Therefore, we used:

We tried to ensure comparable mound sizes in all treatments, but to account for effects associated with mound size, we also included mound volume as a possible explanatory variable in our models (see section 2.3. below).

Holes were drilled into the side of mounds, at 2 cm above ground level, to a depth of approximately half the diameter of the mound, to reach the mound core. Evidence of termite activity was noted by extensively looking for termites, or evidence of termites, inside and around the mound before the loggers were inserted. Internal mound and ambient temperature were measured to the nearest 0.1 °C using data loggers (EL-USB-5, Lascar electronics). Loggers were calibrated in a natural convection laboratory oven (MRC, DNO 20, 1100 W, 20 l) at 30 °C prior to data collection. Each logger was attached to a 60 cm flexible steel wire (to allow easy retrieval of the logger afterwards) and placed inside a 50 cm × 5 cm PVC pipe. The outer end of the pipe was tightly sealed with a thick polyurethane insulation foam. Loggers inside pipes were then inserted inside the mounds in the evening (around 16h00 – 18h00) and the drilled holes were quickly sealed with a mud mixture made from the drilled soil substrate and water. About 10 cm of the logger attachment steel wire remained protruding from the mound for later retrieval. Another logger, used to record ambient conditions, was placed on top of a 1 m pole and left totally exposed to sunlight throughout the day with no observed shading from any surrounding vegetation. All data loggers were left in place for at least 72 h and were programmed to record temperature at 30-min intervals. Loggers were retrieved at the end of each sampling session and the mound was subsequently sealed again.

2.3. Data analysis

To capture how mound internal temperature varies as a function of external temperature, we calculated ΔT , i.e., the external temperature minus internal temperature. This measure therefore reflects the difference between external and internal temperatures, which should be linear with external temperature, although the intercept, and perhaps slope, of the relationship might vary for different seasons, inhabited vs.

uninhabited status, and with and without shading. We therefore constructed a series of generalised linear mixed models (GLMMs), using R package “nlme” (Pinheiro et al., 2021), with ΔT (continuous) as the dependent variable, external temperature (continuous), mound activity (categorical: inhabited vs. uninhabited), shade cover (categorical: open vs shaded), and mound volume (continuous: mound size in cm^3) as fixed effects, and mound identity (categorical) as random effect. We included interactions between mound activity and external temperature and mound activity and season, between shade cover and season, and shade cover and external temperature, and season and external temperature, to account for the differences in mean temperature and the different temperatures at which *T. trinervoides* aim to maintain their nests, in winter and summer. We used the “dredge” function in the package “MuMIn” (Barton, 2020) to identify models within two units of that with the lowest AICc, that thus have substantial support for being the best models (Burnham and Anderson, 2002). No other models were within 2 AICc units of the best model, so we did not need to conduct model averaging. We calculated variance explained by fixed (marginal R^2) and fixed and random effects (conditional R^2) for the best model (Nakagawa and Schielzeth, 2013). Residuals were plotted against fixed values and quantile-quantile plots to assess constant error variance and normality of errors for the best model.

3. Results

Temperature profiles of all 14 mounds were successfully recorded at 30 min intervals during both sampling seasons. There was a strong effect of ambient temperature on internal mound temperature profiles (Fig. 1 and Fig. 2). The effect changed seasonally but was more pronounced on uninhabited mounds. Temperature profiles of exposed uninhabited mounds mirrored those of ambient temperatures in both seasons. Both inhabited and uninhabited mounds under shade had fairly constant

internal temperature profiles during both seasons. Overall, internal temperature changes stayed within narrow limits ($\pm 6^\circ\text{C}$) in inhabited mounds during the 24-h period in both seasons, while temperature changes in uninhabited mounds varied more ($\sim 15^\circ\text{C}$).

In summer, ambient temperatures fluctuated greatly with maximum temperatures of 37°C recorded around midday (11h00–13h00), while minimum temperatures of 15°C were recorded in the early morning hours between 02h00–04h00. Internal temperatures of exposed uninhabited mounds were relatively constant at mean = $29.5 \pm 2.72^\circ\text{C}$ (\pm standard deviation), while shaded inhabited mounds had slightly lower mean temperatures of $27.5 \pm 2.24^\circ\text{C}$. Exposed uninhabited mounds had internal mean temperatures = $23.7 \pm 5.67^\circ\text{C}$, while shaded mounds were slightly lower at mean = $23.3 \pm 5.72^\circ\text{C}$ (Fig. 1). For uninhabited mounds, maximum internal temperatures were 35°C for unshaded, 33°C for shaded mounds. For inhabited mounds, maximum internal temperatures were 34°C for unshaded, 33°C for shaded mounds.

During winter, the ambient temperature maximum was 21°C , recorded around 13h00–14h00, with a minimum of c. 3.5°C between 02h00–04h00. Internal temperatures of exposed inhabited mound temperatures remained relatively constant (mean = $21.8 \pm 2.62^\circ\text{C}$), as were those of shaded mounds (mean = $22.0 \pm 2.23^\circ\text{C}$). For uninhabited mounds, exposed mounds had mean temperatures of $11.38 \pm 4.56^\circ\text{C}$, shaded of $11.2 \pm 4.42^\circ\text{C}$, and internal temperature fluctuated with ambient temperatures never exceeding 20°C (Fig. 2).

The best model found ΔT varied significantly with season, mound activity, external temperature, and shade, with significant interactions between activity and season and external temperature, and shade and season, and season and external temperature. These fixed effects explained 87.7% of the variation in the data, mound identity, the random effect, explained a further 0.4%. The relationship of ΔT with external temperature (Fig. 3) shows a significant linear relationship for

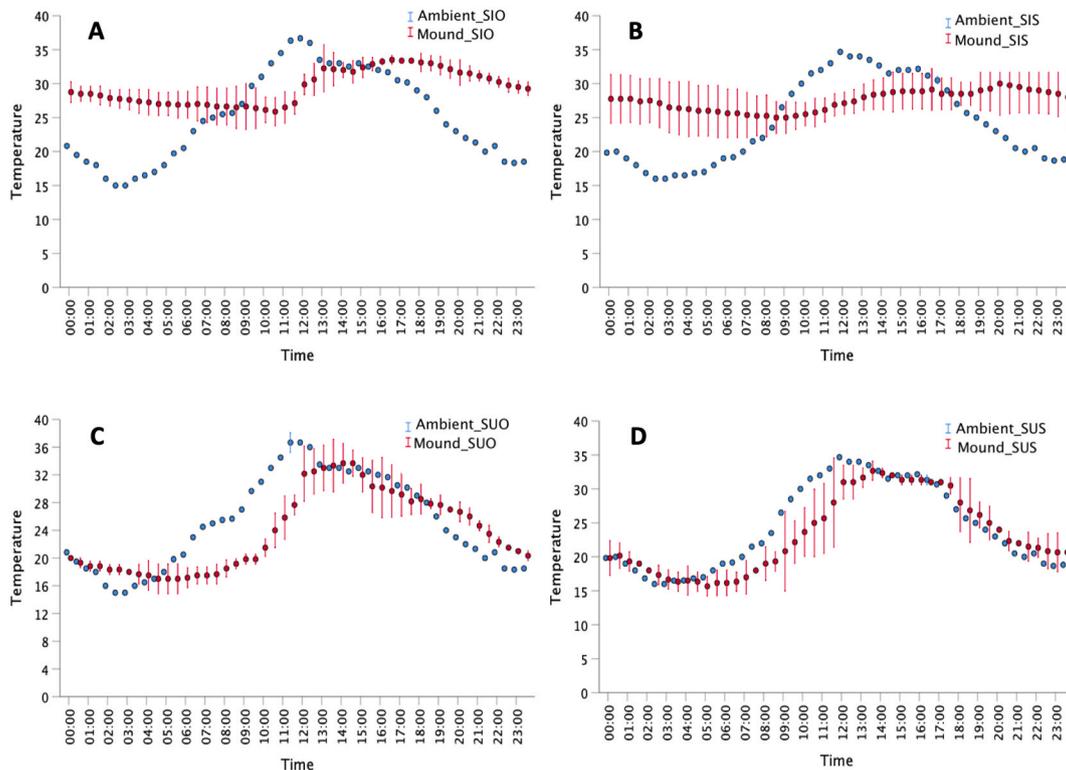


Fig. 1. Mean internal mound (*Trinervitermes trinervoides*) and ambient temperature ($^\circ\text{C}$) profiles at Nylsvley nature reserve during the summer season. Temperature was recorded at 30 min intervals over a 24-h period. A: exposed uninhabited mounds, B: inhabited mounds under num-num (*Carissa bispinosa*) shade; C: exposed uninhabited mounds, and D: uninhabited mounds under num-num shade. [SIO = Summer Inhabited Open; SIS = Summer Inhabited Shade; SUO = Summer Uninhabited Open; SUS = Summer Uninhabited Shade].

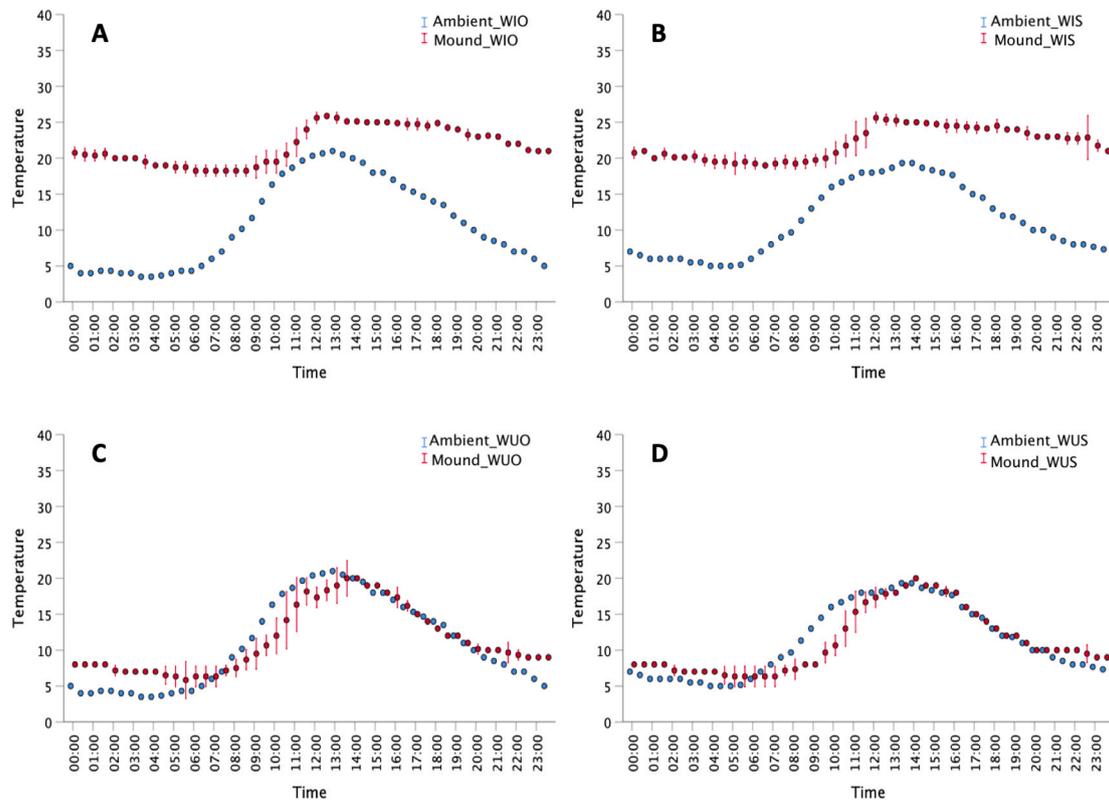


Fig. 2. Mean internal mound (*Trinervitermes trinervoides*) and ambient temperature ($^{\circ}\text{C}$) profiles at Nylsvley nature reserve during the winter season. Temperature was recorded at 30 min intervals over a 24-h period. A: exposed inhabited mounds, B: inhabited mounds under num-num (*Carissa bispinosa*) shade; C: exposed uninhabited mounds, and D: uninhabited mounds under num-num shade. [WIO = Winter Inhabited Open; WIS = Winter Inhabited Shade; WUO = Winter Uninhabited Open; WUS = Winter Uninhabited Shade].

inhabited mounds, that differs between winter and summer, but no such relationship for uninhabited mounds. There was weak support for an influence of mound volume on ΔT (Table 1). ΔT was significantly lower for inhabited mounds, reflecting termites' diligent activity in keeping mound internal temperatures within certain ranges.

4. Discussion

The structure of *T. trinervoides* mounds alone provided little buffer against ambient temperature fluctuations, with mean temperatures inside uninhabited mounds tracking external temperatures in both seasons (Figs. 1 and 2). Termites actively maintain the internal temperature of a mound, keeping it within narrow temperature ranges. Shade provided by *C. bispinosa* reduced external temperatures, although it appears as if this effect for mound internal temperatures is small, or only important at high temperatures. Thus a difference is seen between shaded and unshaded inhabited mounds in summer, but not in winter, and similarly, mean temperatures in shaded and unshaded uninhabited mounds only differed by c. 0.5°C , but maximum internal temperatures reached by unshaded uninhabited mounds were $\sim 2^{\circ}\text{C}$ greater than that reached by shaded uninhabited mounds. The highest external ambient temperature we recorded was 36.6°C , roughly 6°C above that which *T. trinervoides* would require inside the mound during summer. Elsewhere, where external air temperatures reached 40.3°C , inhabited mounds were significantly associated with percentage shade (Joseph et al., 2018). Shade may, therefore, only be important for internal mound temperature and thermoregulation during hotter spells.

Uninhabited mounds, although lacking termites to regulate internal temperatures and produce metabolic heat, did not exponentially increase as might be expected with influence of ambient temperatures (Joseph et al., 2016), but instead remained slightly below external temperatures, perhaps because of the soil insulation properties that the

mound structure naturally provides, which should buffer against ambient temperatures (Wood and Thomas, 1989). Similarly, in winter, the interior of uninhabited mounds did not drop as low as external ambient temperatures, suggesting that some buffering from cold temperatures is achieved by the structure itself. Mounds of *Macrotermes bellicosus* tend to be more dome shaped, with thicker walls in cooler environments (Korb and Linsenmair, 1998; Jones and Oldroyd, 2006). The mounds of *Trinervitermes* in this study are dome shaped, which may explain some architectural contribution to regulation of mound temperatures. Termites can use metabolic heat and clustering together to achieve stable temperatures, and termites have been found to achieve 20°C differences through metabolic heat (Greaves, 1964 in Jones and Oldroyd, 2006).

We found seasonal changes in temperature, and whether or not mounds were inhabited strongly determined internal mound temperature profiles. It appears that, in general, *T. trinervoides* termites struggle to maintain higher optimal mound temperatures during winter, which may explain why the species tends to be uninhabited during cold winter months (Adam et al., 2018). The energetic costs of opening the mound, going out to forage, and later returning to the mound, sealing it, and using metabolic activity to heat up the mound interior could be very costly (Sands, 1965).

Although temperatures in inhabited mounds remained relatively stable throughout winter and summer, we found significant differences in internal mound temperatures between the two seasons as might be expected: *T. trinervoides* have been found to maintain internal mound temperatures within narrow limits of 20°C in winter and around 30°C in summer (Field and Duncan, 2013). The temperature stability profile remained similar in the two seasons (Fig. 3). Species in studies elsewhere have been found to vary in the critical thermal maxima and minima (CT_{max} and CT_{min} , respectively) that can be tolerated. *Coptotermes formosanus* and *Reticulitermes flavipes* have been found to have higher CT_{max}

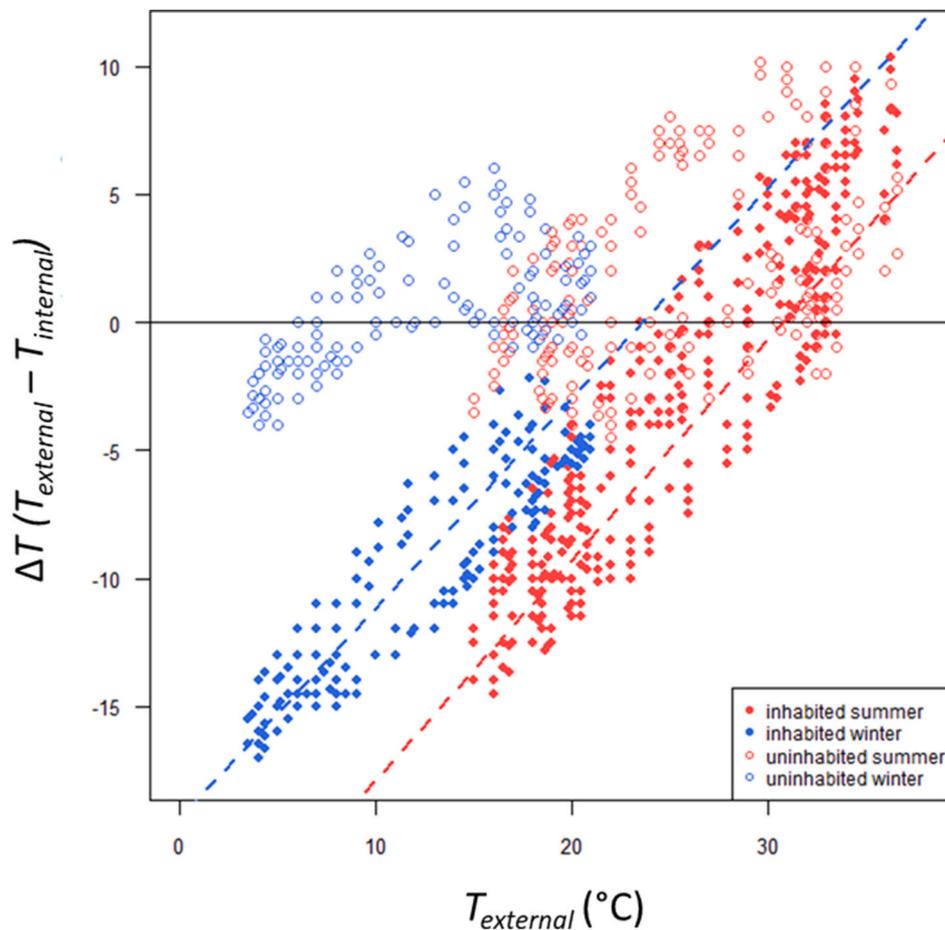


Fig. 3. The relationship between $\Delta T_{external-internal}$ and $T_{external}$, for inhabited and uninhabited mounds, Red points indicate summer, blue, winter; closed circles denote inhabited mounds, open circles uninhabited mounds. Plotted dashed red and blue lines indicate the fit of the model for inhabited mounds in summer and winter, respectively.

Table 1
Coefficients from the best model explaining ΔT (i.e., External [ambient] temperature – internal temperature) of *Trinervitermes trinervoides* mounds.

	Value	Std. Error	DF	t-value	p-value
(Intercept)	-7.37	0.56	1324	-13.1	<0.0001
Inhabited	-18.64	0.59	10	-31.6	<0.0001
Season: Winter	4.70	0.47	1324	10.1	<0.0001
External temperature	0.31	0.02	1324	17.4	<0.0001
Shaded	0.93	0.30	10	3.1	0.0104
Mound size (volume, cm ³)	6×10^{-6}	2.6×10^{-6}	10	2.2	0.0553
Inhabited x Winter	1.84	0.37	1324	4.9	<0.0001
Inhabited x External temperatures	0.55	0.02	1324	26.8	<0.0001
Winter x Shaded	-0.83	0.24	1324	-3.4	0.0007
Winter x External temperature	-0.14	0.02	1324	-6.7	<0.0001

and lower CT_{min} in summer and winter, respectively (Hu and Appel, 2004). This raises the intriguing possibility that *T. trinervoides* may also vary in the temperatures they can tolerate in different seasons, although this needs to be investigated. If this species can tolerate different temperature ranges in different seasons, temperature extremes in either direction may pose less of a threat to this species than anticipated. It is also possible that *T. trinervoides* has greater flexibility between seasons in internal nest temperatures, because this species does not cultivate

fungi (Adam et al., 2018), which are sensitive to extreme temperature fluctuations (Abe et al., 2000). Nevertheless, termites do require some stability in temperature for optimal functioning of the colony, and here, *T. trinervoides* maintained mound conditions within the ranges of 24–34 °C in summer and 18–26 °C in winter.

In winter, temperatures of mounds correlated with the lower ambient temperatures, however, both exposed and shaded inhabited mounds maintained temperatures much higher (mean 21.9 °C) than ambient temperatures (mean 11.1 °C). This suggests that the termites modified the temperature to ensure the best internal environment for development of instars and alates, since during these times *T. trinervoides* termites never leave the mound (Field and Duncan, 2013; Adam et al., 2018). Ambient temperature was slightly higher under shade than in the open in winter. This could be because in the colder season, the plant canopy creates a warmer microhabitat protected from the cold wind in the open.

A recent study on savanna *Macrotermes* spp. found the contribution of plant shade towards the internal temperature stability was negligible and hence it was suggested that the size of termite mound plays a significant role in buffering the mound interior against external conditions (Ndlovu and Pérez-Rodríguez, 2018). We selected *T. trinervoides* mounds in this study to be within a narrow size range to reduce the effects of mound size on internal temperature. Nevertheless, mound size still emerged as a significant factor explaining internal mound temperatures. Smaller sized, and therefore, temperature vulnerable mounds of *T. trinervoides* may be particularly reliant on microclimates provided by plant canopies in hot climates (Sands, 1965; Lee and Wood, 1971).

Global change has seen a combination of heavy grazing, increased

atmospheric CO₂ concentrations and changes to fire regimes that have led to changes in the composition of savannas, with an increase in the woody over the grassy component (O'Connor et al., 2014). It is possible that the loss of *T. trinervoides* primary food source (i.e., grass) could also threaten colony survival, as much as, or perhaps even more than, temperature changes. Nevertheless, thermoregulation remains a challenge for species as climate changes.

The question arises as to how might *Trinervitermes* species survive in the face of extreme temperature fluctuations. The two possible adaptations are that the mounds of *T. trinervoides* may increase in volume to counteract the effects of ambient temperature as predicted for *Macrotermes* spp. (Ndllovu and Pérez-Rodríguez, 2018), or the seemingly small role of microclimates provided by plant shade may be more noticeable at higher and lower ambient temperatures. This prediction can be tested by future studies during heat waves, or using heating treatments, which reflect anticipated future conditions. The buffering effect of shade was evident in summer (c. 2 °C) but not in winter, suggesting that the benefit of such temperature buffering may be most important when ambient temperatures reach heat extremes, e.g., during heat waves. Microhabitats, and the microclimates associated with them, are emerging as important refuges from climatic extremes, both with latitudinal (e.g., Joseph et al., 2016; Scheffers et al., 2014) and altitudinal (e.g., Muluvhahotho et al., 2021) changes in climate.

Author statement

MN: Conceptualization; methods, fieldwork; writing.
GN: Fieldwork, methods, writing.
GSJ: Analysis, writing.
CLS: Analysis, writing.

Ethical statement

The authors assert that all procedures contributing to this work comply with applicable ethical standards of the Animal Ethics Committee of the University of the Free State (Ref: UFS-HSD2017/0337).

Declaration of competing interest

The authors declare none.

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