1 **Termites have developed wider thermal limits to cope with environmental conditions in**

2 **savannas**

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19 Key words – Adaptation; Blattodea; Ectotherms; Termitoidae; Physiology; Thermal Tolerance;

20 Tropics

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28 **Abstract**

29 The most diverse and abundant family of termites, the Termitidae, evolved in warm, wet African

30 tropical forests. Since then, they have colonised grassy biomes such as savannas. These

31 environments have more extreme temperatures than tropical forests, and greater temporal

32 fluctuations (both annually and diurnally) that are challenging for soft-bodied ectotherms. We

33 propose that that a likely mechanism that facilitated the expansion from forest to savanna was the

34 widening of physiological limits of savanna termite species in order to cope with more extreme

35 environmental conditions. We sampled termites directly from mound structures across an

36 environmental gradient in Ghana, and recorded the thermal tolerance of individual termites, both

37 critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}). We estimated colony thermal

38 tolerance by taking an average of each tested individual, and modelled these data against several

39 environmental factors (canopy cover above the mound, rainfall and temperature). We found that

40 savanna termite species had significantly higher CT_{max} values, and significantly lower CT_{min} values,

41 than forest species. In addition, areas with high canopy cover were significantly associated with low

42 CT_{max} values, and areas with higher average daily rainfall were significantly associated with higher

43 CT_{min} values. Our results suggest that the widening of thermal tolerances has occurred in savanna

44 termite species, probably in response to the more extreme temperatures found in those

45 environments.

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48 **Introduction**

49 In the terrestrial tropics, there are two dominant biomes: tropical forests and grassy biomes

50 (savannas and grasslands; Mokany, Raison and Prokushkin, 2006; Parr *et al.*, 2014). The spatial

51 distribution of these tropical environments has changed over time, as climatic conditions have

52 varied. Notably, in the late Miocene and into the Pliocene, there was a major expansion of savanna

53 grasslands (Cerling et al., 1993; Cerling et al., 1997; Davies et al., 2020; Pagani et al., 1999), which

54 coincided with the adaptive radiation of C_4 grasses (Christin et al., 2013; Bouchenak-Khelladi et al.,

55 2014), and a recession of tropical forests. The expansion of savannas offered novel habitats for

56 forest species to colonise, and while this provided opportunity for radiation of species, it also posed

57 specific challenges. Understanding how species radiating from forest to savannas have overcome

58 these challenges is vital for accurately predicting biogeographical history, making inferences of their

59 current ecology, and predicting how these species may be affected by climate change

60   Tropical forests and grassy biomes have markedly different environmental conditions. Forests have

61   greater levels of canopy connectivity, rainfall, humidity (both relative humidity and vapour pressure

62   deficit) and, typically, lower mean temperatures with a smaller thermal range (Nicholls and Wong,

63   1990; Sternberg, 2001; Tang et al., 2019). In contrast, tropical grassy biomes tend to have more

64   extreme conditions than tropical forests, both spatially with more variable light and therefore

65   temperature regimes, and also temporally over seasonal and diurnal timescales. Specifically,

66   savanna conditions vary annually with pronounced dry seasons and large variation in temperature,

67   humidity and rainfall across the year (D'Onofrio et al., 2019), but also diurnally, with the more open

68   environment allowing for more extreme differences in environmental conditions throughout a 24-

69   hour period (due to higher levels of heat, and insolation, at ground level during the day, and a

70   greater amount of heat loss during the night, when compared with forest; Hardwick et al., 2015).

71   Despite these environmental differences, a number of taxa have radiated from forests to savannas,

72   adapting to the novel environmental challenges that savannas pose. For example, adaptations of

73   grasses to open tropical environments (Bouchenak-Khelladi et al., 2014; Christin et al., 2013; Pagani

74   et al., 1999) include the notable dominance of C4 grasses in savannas, compared with the

75   prevalence of C3 grasses in tropical forests (Adjorlolo et al., 2012; Still et al., 2014;

76   Solofondranohatra et al., 2018). The generally more open canopy of savannas increases light

77   availability for grass species which, coupled with the increased temperatures and decreased water

78   availability, makes C_4 photosynthesis more efficient than C_3 (Still et al., 2014; Solofondranohatra et

79   al., 2018). In contrast, in forests the low understory light levels and higher water availability favour

80   C_3 photosynthesis over C_4 (Pearcy and Ehleringer, 1984; Solofondranohatra et al., 2018). Savanna

81   grasses are also commonly taller and more tussocky, which allows them to compete for light more

82   efficiently (Solofondranohatra et al., 2018). In addition, savanna species tend to be harder to

83   decompose, with a higher a C:N ratio, which also facilitates burning (Simon and Pennington, 2012;

84   Solofondranohatra et al., 2018). Forest grass species, on the other hand, tend to be creeping, low-

85   stature species, with large leaves to maximise light intake in the understory, and have structures to

86   minimise self-shading (Solofondranohatra et al., 2018). Closely related plant species can therefore

87   have very different evolutionary strategies to maximise their fitness in different tropical biomes.

88   Closely related animal species can also have radically different adaptations in different tropical

89   environments. *Bicyclus* butterflies, important pollinators in both tropical African forest and savanna

90   ecosystems (Dierks and Fischer, 2008), evolved a suite of traits when they colonised savannas from

91   tropical forests, including diapause during the dry season, probably triggered by the lack of available

92   suitable surfaces (grasses) for oviposition, which is in contrast to the forest species of *Bicyclus*, which

93   do not have a period of diapause and are able to reproduce all year round (Halali et al., 2020).

94   However, little is known about how other invertebrate groups may have adapted to the novel

95   environment that savannas present. The Termitidae, the most abundant and diverse group of

96   termites (henceforth all mention of termites refers to the Termitidae family), also evolved inside

97   tropical forests in central Africa (Eggleton, 2000; Aanen and Eggleton, 2005; Bourguignon et al.,

98   2015). Since then they have radiated from forests into more open tropical environments (Aanen and

99   Eggleton, 2005). Forests typically have higher generic and species richness than savannas, although

100   some genera occur in both habitats. However, despite these shared genera, there are almost no

101   shared species between the two environments (Evouna Ondo et al., unpublished data), suggesting

102   that while genera have radiated into savannas, they have since speciated and adapted to savanna

103   environments. Similar to *Bicyclus* butterflies, savanna environments would have posed new

104   challenges to colonising termite species. Termites are soft-bodied ectotherms, and extremely

105   susceptible to desiccation (Heath et al., 1971; Willmer, 1982), and would be challenged by the higher

106   temperatures and lower humidity in savannas. Yet, despite the more extreme conditions, termites

107   have colonised, diversified, and become ecologically dominant in savannas, with a comparable level

108   of biomass to large ungulates or elephants (Dangerfield et al., 1998; Støen et al., 2013). Termites are

109   the dominant soil invertebrate across tropical ecosystems, contributing to multiple ecosystem

110   processes including decomposition, nutrient cycling and bioturbation (Bottinelli et al., 2015; Fox-

111   Dobbs et al., 2010; Joseph et al., 2014; Jouquet et al., 2016; Turner, 2019). As ecosystem engineers,

112   they influence these processes at landscape scales (Davies et al., 2014; Davies et al., 2016a), altering

113   the spatial distribution of nutrients and, as a result, plant species distributions (Davies et al., 2016b;

114   Davies et al., 2016a; Joseph et al., 2014; Støen et al., 2013).

115   How termites have been able to colonise and to adapt to savanna conditions is currently uncertain.

116   Termites have very different life history traits compared with other invertebrates (Poissonnier et al.,

117   2018; Porter and Hawkins, 2001; Roisin, 2000); most termite species produce complex nest

118   structures, and/ or live underground (Jones and Oldroyd, 2006; Noirot and Darlington, 2000). These

119   subterranean environments could protect and buffer termites from extreme environmental

120   conditions, maintaining stable and ideal nest conditions (Gouttefarde et al., 2017; Jones and

121   Oldroyd, 2006; Korb, 2003). The adaptation of nest structures to provide more efficient

122   thermoregulatory properties, such as altering the external shape to interact with the external

123   temperature to maintain more stable internal conditions (Ocko et al., 2017; Singh et al., 2019; Vesala

124   et al., 2019), may have helped enable forest termite species to colonise and prosper in savanna

125   environments. This thermoregulation of nests could be particularly important for fungus-growing

126   termites, the subfamily Macroterminae within the termitids, which farm fungus from the genus

127   *Termitomyces* (Wood and Thomas, 1989). Maintaining ideal growing conditions for their fungus

128   symbionts would increase colony fitness, so the adaptation of nest thermoregulatory properties

129   would be vital for the success of Macrotermitinae species (Korb and Linsenmair, 2000; Korb, 2003).

130   While nest thermoregulation is likely to be important in facilitating the movement from forest to

131   savanna, termites forage outside the controlled environment of their nest, often on the surface,

132   risking exposure to extreme environmental conditions (Legendre et al., 2008; Traniello and Leuthold,

133   2000). One additional key mechanism facilitating the expansion of termites into savanna is the

134   evolution of wider physiological tolerances. Interspecific variation in thermal limits has been shown

135   to occur across different latitudes in other invertebrate lineages (Diptera, *Drosophila* - Rajpurohit,

136   Parkash and Ramniwas, 2008; Kellermann *et al.*, 2012; various, but dominated by Coleoptera,

137   Hymenoptera and Odonata - Sunday *et al.*, 2014) and with exposure to higher temperatures

138   (Diptera, *Drosophila* - Parkash, Rajpurohit and Ramniwas, 2008; Hymenoptera, Formicidae - Kaspari

139   *et al.*, 2015) with closely related species demonstrating significantly different thermal tolerances.

140   The extension of termite physiological tolerances may have enabled them to withstand the more

141   variable conditions and colonise savannas. However, few studies have documented the physiological

142   limits of soil insects, including termites (but see, Woon et al., 2018), so the patterns observed in

143   other studies may not hold across all insect orders.

144   In recent years, an increased focus on the thermal niche of species (Gvoždík, 2018; Kearney et al.,

145   2010; Porter and Kearney, 2009; Sunday et al., 2014), has produced hypotheses to explain thermal

146   performance, particularly given climate change concerns (Buckley et al., 2013; Clusella-Trullas et al.,

147   2011; Huey et al., 2012; Kearney and Porter, 2009; Sunday et al., 2011). These studies and

148   hypotheses have contributed to developing the Thermal Adaptation Hypothesis (Angilletta et al.,

149   2002; Angilletta, 2009; Huey and Kingsolver, 1989; Kaspari et al., 2015; Kingsolver and Gomulkiewicz,

150   2003), which states that species should be adapted to the thermal niche of their environment,

151   therefore suggesting that species found in thermally more variable environments should have wider

152   thermal ranges (Angilletta, 2009). In addition, the thermal adaptation hypothesis suggests that

153   species in more thermally stable environments, as well as having narrower thermal ranges, should

154   be operating closer to their thermal optimum (Angilletta, 2009). In the context of our study system,

155   tropical forests have much more stable environmental conditions, whereas savannas have more

156   extreme limits and more variation, so we would expect savanna species to have wider and more

157   extreme physiological limits to adapt to their environment.

158   Here, we test the hypothesis that savanna termite species have wider physiological limits, which are

159   likely to have facilitated their colonisation and speciation within savanna ecosystems. We quantify

160   the thermal limits (critical thermal minima [CT_{min}] and critical thermal maxima [CT_{max}]) of the most

161   abundant mound-building termite species across tropical forest and savanna areas in Ghana, to test

162   whether savanna species have more extreme physiological limits than forest species. We assess

163   these data and discuss the applicability of the thermal adaptation hypothesis.

164   We predict from our hypothesis that (1) termite species from savannas will have higher CT_{max} values

165   than forest species, and that (2) they will have lower CT_{min} values. We correlated the physiological

166   tolerances with climatic factors that change across the environmental gradient (from forest to

167   savanna), temperature, rainfall and canopy cover, to determine which, if any, may be more strongly

168   associated with physiological limits.

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170

171   **Materials and Methods**

172   **Sampling Locations**

173   Termites were sampled from four locations in Ghana across two different biomes: tropical rainforest

174   and Guinea savanna. The three forest locations were: Bobiri Forest Reserve, a moist semi-deciduous

175   forest in the Ashanti Region, a matrix of forest patches that have been, or currently are, logged (all

176   colonies sampled from fragments that have not been logged for at least 20 years); the Forestry

177   Research Institute of Ghana (FoRIG) Campus, a moist semi-deciduous forest patch located on the

178   campus at Fumesua, near Kumasi, in the Ashanti Region; and the Assin-Attandanso Resource

179   Reserve side of the Kakum Conservation Area, a moist evergreen tropical forest that has been

180   unlogged since 1990 (Wiafe, 2016), in the Central Region. Termites were sampled from a single

181   savanna site, Mole National Park, a large unfenced protected area in the Savannah Region, between

182   June and July 2019. Sampling in all locations was conducted during the end of the dry season and the

183   start of the wet season. Termites were sampled during the end of the dry season and start of the

184   wet season at all sites: between January and March 2019 for the three forest sites, and June and July

185   2019 for the savanna site (Table 1).

186   *Table 1 here.*

187   **Termite and Environmental Sampling**

188   We sampled termites directly from termite mounds, identified to genus level (based on their

189   diagnostic mound structures), which we located using directed searching, using the knowledge and

190   experience of the field assistants. Two mounds were sampled per day, typically between 07h00 and

191   09h00. Target mounds were broken open and we collected termites, as well as some mound

192   material, and placed them into a cool box to protect the termites from external conditions and

193   reduce stress that could affect their thermal tolerances while being transported to the laboratory.

194   The sample from each colony was placed in a separate container to prevent interaction between the

195   two colonies. Where possible, both worker and soldier castes were sampled. The time between

196   sampling and experimentation was reduced as much as possible (mean = 122.6 mins, sd = ±81.4

197   min). The large standard deviation is attributed to having a single collection, but running two

198   experiments, per day. The same colonies that were sampled were used in two experiments, one

199   testing thermal maximum and one testing thermal minimum (the order of which was decided

200   randomly); hence, the individuals used in the second experiment were kept inside the cool box

201   (which was out of direct sunlight) while the first experiment took place.

202   We photographed each mound to assist with species identification. Canopy cover above each

203   sampled mound was quantified using a hemispherical fish-eye lens (Canon EOS 70D camera, Sigma

204   4.5mm f/1:2.8 Circular Fisheye Lens). For large mounds the image was taken directly above the apex

205   of the mound, but with small mounds (<75 cm in height) the image was taken above the mound at a

206   height of 75 cm due to the height of the stabilising monopod. Due to variable light conditions when

207   the images were taken, we did not standardise ISO, shutter-speed or aperture, although variation in

208   these settings were reduced as much as possible. Variable light conditions and camera settings were

209   corrected using Gap Light Analyzer software (GLA; Frazer et al., 1999). The approximate leaf-area

210   index above each mound was then calculated as a measure of canopy cover. Leaf-area index is a

211   measurement of the quantity of leaf area in a canopy per unit area of ground, and ranges from 0 (no

212   leaf cover) to 6 (complete leaf cover).

213

214   **Thermal Tolerance Experiments**

215   We used similar methods to those outlined in Bishop et al. (2017) to estimate the thermal tolerance

216   of the termites. Fourteen individuals from each of two colonies (28 in total) were tested per

217   experimental run. Only individuals of the helper castes, workers and soldiers, were used in the

218   experiments Each termite was placed into a separate microcentrifuge tube. The tubes were then

219   placed into a dry heat bath (Tropicooler 260014-2, Boekel Scientific, Feasterville, PA, USA;

220   temperature range -19°C to 69°C and an accuracy of ±1°C). The heat bath contained two aluminium

221   inserts with each consisting of 14 wells, each of which held a single microcentrifuge tube. Individuals

222   from two colonies and different castes were randomly allocated to different wells to remove

223   potential equipment bias. The two colonies sampled each day were used in each experimental run

224   (CT_{max} and CT_{min}) and each colony was tested for both CT_{max} and CT_{min}; however, each individual

225   termite was only used in one experiment.

226   The temperature within each microcentrifuge tube was acclimated for 15 minutes. CT_{max}

227   experiments had an acclimation temperature of 30°C, and CT_{min} had an acclimation temperature of

228   24°C. After the acclimation period, the temperature was changed by 1°C (raised for a CT_{max}

229   experiment, and lowered for CT_{min}), and maintained at each new temperature for a further three

230   minutes. Following this three-minute period, we checked each termite for loss of muscle co-

231   ordination (CT_{max}) or lack of movement (CT_{min}) by flicking the microcentrifuge tube. If we noticed the

232   termite lost muscle co-ordination (CT_{max}) or had stopped moving (CT_{min}) the temperature was taken

233   as the thermal limit of that individual termite. The experimental run was ended when the thermal

234   limit of all 28 termites was recorded.

235   **Termite Identification**

236   Termite colonies were identified to genus level in the field based on their mound structure. All

237   termites used in experimental runs were preserved in 70% ethanol and brought to the UK. We took

238   an individual from each colony and DNA was extracted from each sample. The *COII* mitochondrial

239   gene was amplified and sequenced using Sanger Sequencing at the Natural History Museum,

240   London. Each sequence was matched with the most closely related sequence on NCBI using BLAST

241   (Johnson et al., 2008). If the sequences had a unique high likelihood identity match (>98%) with a

242   single species described on the NCBI database, that sample, and therefore the colony it was sampled

243   from, was considered identified as that species. If there was not a unique high likelihood identity

244   match, the sequences (and therefore the colonies from which each sample was taken) were grouped

245   and labelled as an unspecified species within a genus (for example, *Cubitermes sp. A,* Fig. 1*)*. After

246   identification, species that did not have at least three replicates per sampling location were removed

247   from the dataset (19 colonies removed, present in online dataset). Since the genetic identification

248   was conducted, the genus *Cubitermes* was split into several genera (Hellemans et al., 2020).

249   However, there were limited sequence data for the new classifications so we have treated all the

250   new genera as *Cubitermes sensu lato*.

251   **Climate Data**

252   Climate data was sourced from the WorldClim2 dataset (Fick and Hijmans, 2017) using the 'raster'

253   package (Hijmans et al., 2020) in the R statistical software version 3.6.2 (R Core Team, 2019).

254   WorldClim2 gets average measurements of climatic variables each month, based on an interpolated

255   dataset between 1970 and 2000. We extracted measurements of average monthly rainfall, average

256   monthly maximum temperature, and average monthly minimum temperature to the highest

257   resolution possible (30 arc seconds, equivalent to approximately 1km^2) for each mound we sampled.

258   From these data we obtained average daily rainfall, highest average maximum temperature and

259   lowest average minimum temperature for the area around each colony centre.

260

261   **Statistical Analysis**

262   After genetic identification, eight species had a sample size of three colonies and were included in

263   the statistical analyses. Three of those species were sampled from the two savanna locations (Mole

264   North, Mole South, Table 1), and six species were sampled from the forest locations (FoRIG, Bobiri,

265   Kakum Forest and Kakum Farmland, Table 1). One species, *Macrotermes bellicosus*, was sampled in

266   both savanna and forest locations, but it was only found in the forest environment that was heavily

267   disturbed, Kakum Farmland (Table 1).

268   All statistical analyses used the R statistical package version 3.6.2 (R Core Team, 2019). We

269   calculated the estimated colony CT_{max} and CT_{min} by taking the average of the thermal tolerance of

270   each termite within that colony that was used in an experimental run. Initially, basic Welch's two-

271   sample t-tests were run to compare the thermal tolerances of species assemblages sampled in forest

272   and savanna environments (termites sampled from Kakum Farmland were not included, Table 1). A

273   t-test was also used to compare *Macrotermes bellicosus* thermal tolerances in two different

274   environment types (farmland and savanna), and a one-way analysis of variance test was used to

275   compare the thermal tolerances of the three *Cubitermes* species sampled. Tukey's HSD post-hoc

276   statistics were used for pairwise comparisons of the species thermal tolerances.

277   To test whether environmental variables affect termite colony thermal limits, mixed effects models

278   were fitted using the R package 'lme4' (Bates et al., 2019), with a separate model for CT_{max} and CT_{min}.

279   Maximal models tested the interactive effects of canopy cover, average daily rainfall (which was

280   rescaled from annual rainfall) at the mound, and temperature at the mound (maximum temperature

281   for the CT_{max} model, and minimum temperature for the CT_{min} model). A single random effect of

282   colony location (as listed in Table 1, Fig. S1) was used to account for additional unmeasured

283   environmental differences. Species was not included as a random effect (crossed or nested) because

284   there was little overlap in species composition between sampling locations, and so both site and

285   species would therefore explain the same variation, and so there was not enough data to prevent

286   non-convergence.

287   To understand which of the fixed effects and their interactions best explained the variation in

288   termite thermal tolerances, two lists of candidate models were generated (one for CT_{max} and one for

289   CT_{min}) using the 'dredge' function from the 'MuMIn' package (Bartoń, 2019). This takes the maximal

290   model and systematically removes variables and/ or interactions until all possible combinations have

291   been tested, and compared these complete lists of models using the package 'AICcmodavg'

292   (Mazerolle and Linden, 2019). The model with the lowest corrected AIC (AICc) value was obtained,

293   and the other models with a difference in AICc (ΔAICc) of less than two were retained to inform the

294   final 'full' model (Table S1 and Table S2; Burnham and Anderson, 2002). Model averaging, using the

295   candidate lists of the model with the lowest AICc value and all those with ΔAICc < 2, was used to

296   identify the best predictor variables across the models. The relative importance of these predictors

297   was calculated as the sum of their relative Akaike weights from all models in which they appear;

298   thus, models with lower AICc values contribute more to the final 'full' model. A series of *F* tests was

299   also conducted to verify the significance of the retained parameters on the thermal limits of the

300   termite species tested in the final models. This process was conducted for two separate model sets,

301   one testing CT_{min} and the other CT_{max}, generating two 'full' models.

302

303

304   **Results**

305   A total of 2042 termite specimens from 71 colonies and eight species were used in the final analyses

306   (1022 termites for CT_{max} experiments, 1020 termites for CT_{min} experiments). There was a large

307   amount of interspecific variation in thermal tolerance, with species averages varying by 4.86°C for

308   their CT_{max} and 2.96°C for their CT_{min} (Fig. 1). Savanna species had significantly higher CT_{max} values on

309   average than forest species ($p < 0.001$, t = -17.309, df = 52.37, Fig. 1A), and significantly lower CT_{min}

310   values on average than forest species ($p < 0.001$, t = 8.7035, df = 53.84, Fig. 1B); as a result, savanna

311   species had wider thermal limits than forest species. The three *Cubitermes* species tested had

312   significantly different CT_{max} values ($p < 0.001$, $F_{2,26} = 1424$, Fig. 1A) and CT_{min} values ($p < 0.001$, $F_{2,26} =$

313   29.24, Fig. 1B), with all species having significantly different thermal niches from one another

314   (Tukey's HSD; Fig. S2 & Fig. S3). *Macrotermes bellicosus* from multiple environments was tested

315   (farmland in the forest zone and savanna), but CT_{max} did not differ among the two habitats ($p =$

316   0.805, t = 0.255, df = 7.775, Fig. 1A). *M. bellicosus* did, however, have significantly different CT_{min}

317   values (p = 0.008, t = 3.132, df = 12.266, Fig. 1B), with savanna colonies having lower CT_{min}.

318   *Fig 1A and B here.*

319   **Critical thermal maximum**

320   *Fig 2 here.*

321   The full model retained all three fixed effects (canopy cover, maximum temperature and average

322   daily rainfall; Table 2), but the interaction between the terms were removed during the model

323   selection process. Of the three remaining variables, only canopy cover had a significant negative

324   correlation with colony CT_{max} (z = 3.138, p = 0.001, df = 63.470; Fig. 1A; Table 2), suggesting that as

325   the canopy cover above termite mounds increases, the average critical thermal maximum of the

326   termite colony decreases (Fig. 2). Despite being retained in the full model, neither maximum

327   temperature (z = 1.215, p = 0.358, df = 3.900; Table 2) nor rainfall (z = 0.068, p = 0.964, df = 3.689;

328   Table 2) showed a significant correlation with colony CT_{max}. The single random effect of colony

329   location (Table 1) explained 48.6% of the variation in the model.

330   *Table 2 here.*

331   **Critical thermal minimum**

332   *Fig 3 here.*

333   The full critical thermal minimum model retained two fixed effects (canopy cover and average daily

334   rainfall; Table 3), and it also removed all interactions between the variables. Unlike in the CT_{max}

335   model, canopy cover was not significantly correlated with CT_{min} of termite colonies (z = 0.269, p =

336   0.788, df = 59.671; Fig. 1B; Table 3); however, average daily rainfall was significantly positively

337   correlated with CT_{min} (z = 2.679, p = 0.007, df = 4.504; Fig. 1B; Table 3). Colony location (Table 1)

338   explained 39.6% of variation in the model.

339   *Table 3 here.*

340

341   **Discussion**

342   Our findings support the hypothesis that savanna termite species have more extreme physiological

343   tolerances, and developing these tolerances is likely to have been a key mechanism that has allowed

344   termites to colonise savanna environments. As predicted, savanna species had a significantly higher

345   CT_{max} than forest species. In addition, CT_{max} had a significant negative correlation with canopy cover.

346   As the canopy cover decreases the amount of sunlight reaching the soil surface and the surface of

347   the mound increases, which will increase the temperature of the air, soil surface, and potentially

348   within the mound and foraging areas (Hardwick et al., 2015). Canopy cover in our savanna

349   environments (average 26.6 ± 5.8%) was much lower than that found in tropical forests (84.7 ±

350   3.1%). To cope with higher day temperatures in savannas, the termites will have had to develop

351   mechanisms such as increased thermal tolerance. Our data support this idea, not only due to the

352   positive correlation between canopy openness and CT_{max}, but also among closely related species

353   (e.g., of *Cubitermes*) in which species in the more open and extreme savanna habitat had more

354   extreme thermal limits (Fig. 1A & Fig. 1B). *Cubitermes* are soil feeding termites, so do not need to

355   leave the protection of the soil to forage for food and so have a reduced interaction with ambient

356   conditions (when compared to other species), yet they have significantly different thermal

357   tolerances between species from the two environments. If these species had developed extensive

358   mound thermoregulatory mechanisms such that the environmental conditions experienced by the

359   termites were similar, we would expect closely related (i.e., congeneric) species to have similar

360   thermal tolerances, irrespective of the location they were sampled from; this is not the case with

361   *Cubitermes*, as closely related species have significantly different thermal tolerances.

362   Surprisingly, despite savanna species having a significantly lower CT_{min} than forest species, CT_{min} was

363   not significantly correlated with canopy cover. We expected that lower canopy cover in savannas

364   would allow the ground surface to cool more rapidly at night, and result in lower temperatures.

365   Consequently, we expected canopy cover to positively correlate with CT_{min}, as termites in locations

366   with lower canopy cover will experience lower temperatures at night. This is not what was found;

367   CT_{min} was significantly positively correlated with average daily rainfall. We are unsure about the

368   underlying process linking lower CT_{min} with reduced rainfall. The species from the savanna regions

369   had lower CT_{min} values, which has lower rainfall and therefore lower cloud cover, which would

370   increase heat loss and result in lower temperatures; however, minimum temperature was included

371   in the model and had no significant effect. More sampling is required, additional species from more

372   locations along the environmental gradient, including between the forest and savanna

373   environments, and further north of our savanna sites (in locations which would have higher day

374   temperatures, and lower night temperatures) to properly tease apart these relationships.

375   Canopy cover was expected to have a significant relationship with CT_{min} because some termite

376   species forage during cool parts of the day, including night time, which would put pressure on the

377   CT_{min} of foraging individuals, and that pressure would be greater in areas with low canopy cover

378   where the less heat would be retained overnight. For example, the specialist savanna grass-feeder,

379   *Trinervitermes*, typically forages at dusk, dawn or during the night (Adam et al., 2008). Our data

380   support this: *Trinervitermes germinatus* had the lowest CT_{min}, which would be expected for coping

381   with the lower temperatures experienced during foraging at night. Other studies have shown that

382   some savanna species (e.g. *Macrotermes* sp.; Darlington, 1982) forage during cooler parts of the day

383   or when overcast (Evans and Gleeson, 2001; Parr pers obs); however, these studies are few in

384   number and do not cover the species studied here. In general, behavioural avoidance of one thermal

385   extreme (e.g., in the case of *Trinervitermes*, hot conditions) may reduce selection pressures on the

386   physiological tolerance of that extreme (e.g. CT_{max}), but not necessarily the opposite extreme. This

387   interplay between behavioural and physiological adaptations represents an important avenue for

388   future study.

389   Mean site temperature did not have a significant effect on thermal tolerance at maximum or

390   minimum temperatures. This may be because the temperature data used in both models was

391   interpolated temperature of air (Fick and Hijmans, 2017), which is unlikely to be the best measure of

392   the conditions that termites would experience. Due to their small size, terrestrially foraging termites

393   forage in the thermal boundary layer, immediately above a surface of, in this case, the ground. The

394   thermal boundary layer has very different conditions from the recorded air temperature, both

395   during the day (where it is likely to be super-heated) and at night (retaining more heat due to

396   proximity to soil). Boundary layer temperature, or ground surface temperature, would be a more

397   accurate representation of the true thermal conditions that termites experience, but unfortunately

398   these data were not available at a fine-enough spatial scale. So, while it is likely that air temperature

399   and ground temperature are correlated, and lack of ground temperature does not invalidate these

400   results, the model would be improved by access to these data.

401   There was more intraspecific variation in CT_{min} than CT_{max} possibly associated with measurement

402   error. The protocol for recording CT_{min} used for other insects, such as ants (Bishop et al., 2018;

403   Kaspari et al., 2015), involves recording the temperature at which all movement ceases. However,

404   termites are much less mobile than ants, making it extremely difficult to tell the difference between

405   the onset of a chill coma (Hazell and Bale, 2011) and the true CT_{min}. Therefore, whereas the values

406   described here are biologically relevant, as termite fitness would be severely negatively affected if

407   temperatures were to drop to near these recorded "CT_{min}" values, the values recorded likely contain

408   measurement error. An additional method to test for signs of life in other insects is to shine a laser

409   pen into the eye of the individual in an attempt to elicit a head-movement response. This method is

410   not possible with termites, as the helper castes of almost all species lack eyes, so the only stimulus

411   that could be used was flicking the test tube. Another source of error is that a 'no movement'

412   reaction in a living individual is impossible to distinguish visually from a dead individual.

413   Consequently, these measurements may slightly underestimate true CT_{min}, resulting in greater

414   intraspecific variation than the true range. However, the measurement errors are likely to be

415   random, rather than systematically correlated with environmental variables. Moreover, despite the

416   measurement inaccuracies, CT_{min} correlated significantly with rainfall, and the differences in CT_{min}

417   between the species were pronounced.

418   Although we think it unlikely that there are mound thermoregulatory mechanisms in the *Cubitermes*

419   species we sampled because of their very different thermal limits, our data are equivocal as to

420   whether there is mound thermoregulation in *Macrotermes bellicosus* mounds. This is a topic of

421   much debate (Korb, 2003; Jones and Oldroyd, 2006; Gouttefarde et al., 2017; Scott Turner, 1994;

422   Turner, 2001). *Macrotermes bellicosus* had the same CT_{max} in all locations sampled despite

423   environmental conditions varying among habitats; this suggests that there may be thermoregulatory

424   mechanisms within their mounds, likely to maintain ideal growing conditions for their fungus

425   symbionts (Korb and Linsenmair, 2000; Korb, 2003). We sampled them from their native region

426   (savanna) and further south of their ancestral distribution, areas which have less extreme

427   environmental conditions, particularly a much lower maximum temperature, which would not put

428   any additional pressure on their thermal limits. Improved knowledge of likely thermoregulation in

429   *Macrotermes* mounds could come from comparisons of thermal tolerances of *M. bellicosus* from

430   multiple savanna environments, with varying climatic conditions (e.g. further north from where we

431   sampled, with a hotter and drier climate).

432   As predicted by the thermal adaptation hypothesis, the forest species had much narrower thermal

433   limits than the savanna species (Angilletta, 2009). Forests have more stable temperatures (less

434   diurnal and annual variation), so the theory posits that the termite species found there should have

435   narrower thermal limits than the savanna species. This prediction of the thermal adaptation

436   hypothesis holds true, and it is likely that the stability, and lower extremes, of forest environments

437   have contributed to narrower thermal limits (and therefore thermal niches) of forest termite

438   species. How close the current temperatures are to termite thermal limits is not known, however,

439   due to the imprecise nature of the temperature data. Obtaining more accurate temperate data,

440   which measures surface temperature or boundary layer temperature, over a finer spatial scale, and

441   recorded from a more recent time period would allow us to make a more accurate prediction of the

442   resilience of termite assemblages to a warming climate. Understanding how close the thermal

443   conditions that termites experience are to their thermal limits, and to thermal optima, is vital in

444   making this prediction.

445   Our results suggest that for termites, the most important soil macroinvertebrates in savanna

446   environments (Davies et al., 2016a; Jouquet et al., 2016), a key mechanism that has facilitated their

447   colonisation of the seasonal, climatically extreme environments of savannas from forests is the

448   widening of their thermal tolerances. However, temperature is not the only variable that changes

449   along an environmental gradient from forest to savanna. Food type, food availability, soil mineral

450   content (and pH), humidity, predator diversity and abundance are a few of the factors that could

451   change along the gradient, and therefore influence termite species distributions. Some of these

452   would contribute to the large proportion of variation that is explained by the random effect of

453   sampling location in both models, making them promising avenues for future research. For example,

454   we have shown previously that desiccation tolerance is low in Bornean forest termites (Woon et al.,

455   2018), so quantifying the desiccation tolerance of African species, and comparing these tolerances

456   between environment types could provide additional information on how certain species are able to

457   survive in savannas.

458   Understanding how termite physiology and behaviour changes across environmental gradients such

459   as this one is particularly important in the context of climate change. The thermal adaptation

460   hypothesis predicts that species in more stable environments will be more heavily impacted by

461   warming conditions, due to those species operating closer to their thermal maximum (Angilletta,

462   2009), and be more susceptible to extinction. This suggests the forest species here may be more

463   vulnerable to rising temperatures associated with climate change, but more research is needed to

464   understand the complexities of physiological change, how it affects termite distributions, and how

465   they might be altered by the changing climate.

466   Our data suggest that the widening of termite thermal tolerances has occurred in species that have

467   established in areas of more extreme climatic conditions, and that is likely a large factor in allowing

468   termites to persist, speciate, and become ecologically dominant in arid, tropical environments.

469   Whether the widening of these physiological limits will make them more resilient to climate change

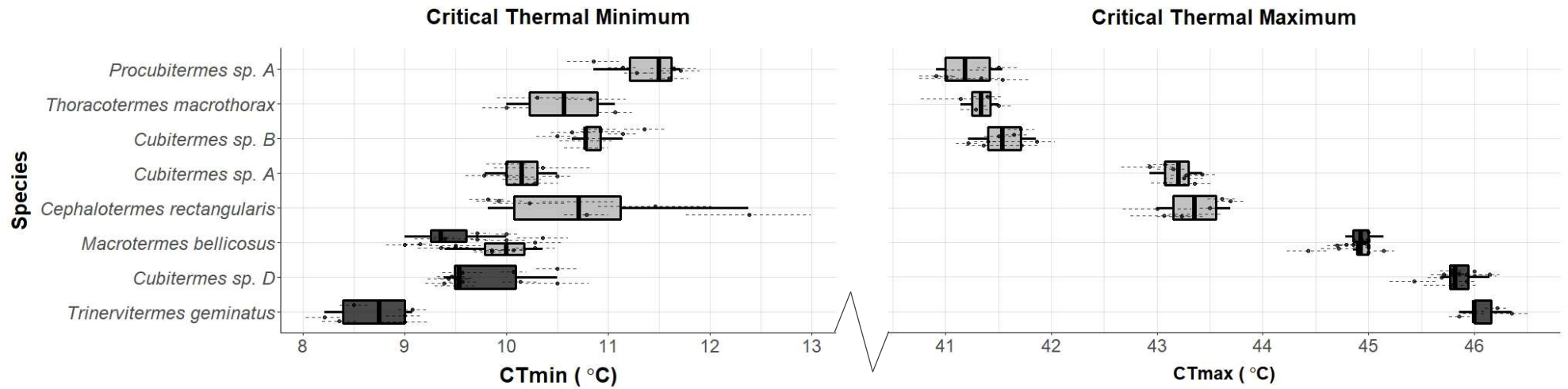470   is a question that remains to be answered.

Fig. 1 – *Relationship between termite species thermal limits and the habitat they were sampled from. Species are ordered from lowest CTmax (top) to highest CTmax (bottom). Colour of the boxplot denotes the location the termites were sampled, dark-grey from savanna and light-grey from forest. Macrotermes bellicosus was sampled from both savanna and forest environments, and so it has distinct boxplots for each community. The points represent the estimated thermal limit of a unique termite colony, and the dotted lines represent the standard error around the colony average. Central thick line of the boxplot represents the species median thermal limit, the box represents the interquartile range, and the whiskers the upper and lower adjacent values.*
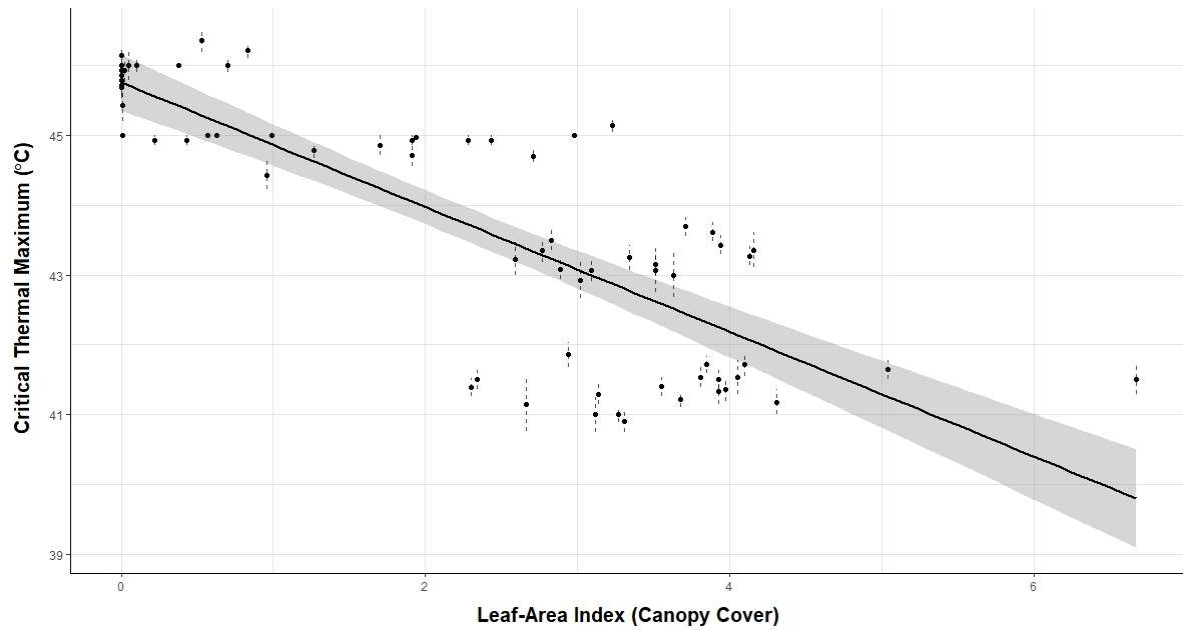
484   *Fig. 2 – Significant negative correlation between the estimated critical thermal maximum of termite*

485   *colonies and the canopy cover above the colony centre (p = 0.001), as predicted by a linear mixed*

486   *effects model (with sampling location as the random effect). Leaf-area index is the measurement of*

487   *canopy cover used, with higher leaf-area index representing higher canopy cover above the mound.*

488   *Each point represents the estimated thermal maximum of a unique termite colony across all*

489   *locations sampled, the thermal maximum is averaged from each individual termite that was used in*

490   *the experiment, and the dotted line represents the standard error around this mean. The solid black*

491   *line represents predicted relationship based on the model, with the shaded grey area representing*

492   *the uncertainty around these predictions.*

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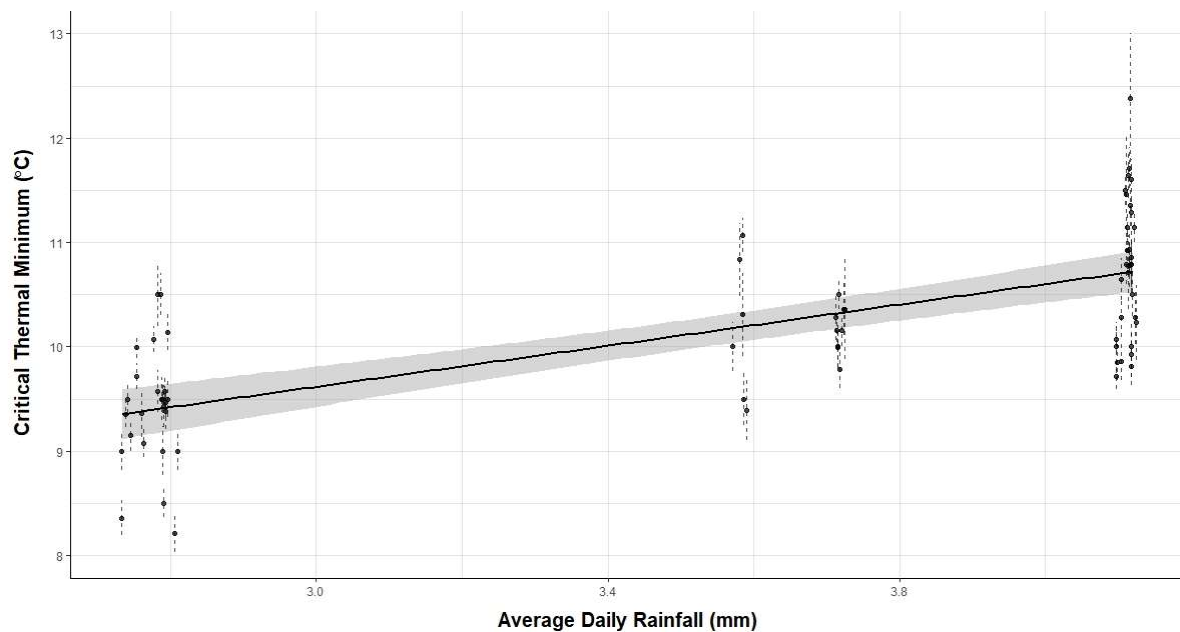
494   ***Fig. 3 - S****ignificant positive correlation between average daily rainfall at the mound (data obtained*

495   *from WorldClim2, Fick and Hijmans, 2017), and the estimated critical thermal minimum of termite*

496   *colonies (p = 0.007), as predicted by a linear mixed effects model (with sampling location as the*

497   *random effect). Each point represents the estimated thermal minimum of a unique termite colony*

498   *across all locations sampled, the thermal minimum is averaged from each individual termite that was*

499   *used in the experiment, and the dotted line represents the standard error around this mean. The solid*

500   *black line represents predicted relationship based on the model, with the shaded grey area*

501   *representing the uncertainty around these predictions.*

502   **Table 1** – *Summary statistics of the different sampling sites, with their locations and climatic*

503   *conditions. The GPS co-ordinates are a representative location, at the approximate centre of the*

504   *sampling location. Climate data sourced from WorldClim 2 (Fick and Hijmans, 2017).*

Location	Vegetation type	GPS Co-ordinates	Mean Maximum Temperature	Mean Minimum Temperature	Mean Annual Rainfall
Bobiri Forest Reserve	Rainforest	6.689 N, 1.342 W	31.3°C	18.5°C	1306 mm
Forestry Research Institute of Ghana (FoRIG)	Rainforest	6.716 N, 1.529 W	31.4°C	19°C	1357 mm
Kakum Farmland	Farmland (formerly forest)	5.568 N, 1.388 W	31°C	19.8°C	1504 mm
Kakum National Park	Rainforest	5.573 N, 1.379 W	30.9°C	19.7°C	1502 mm
Mole North	Savanna	9.334 N, 1.868 W	35.2°C	19.3°C	1018 mm
Mole South	Savanna	9.286 N, 1.847 W	35.2°C	19.3°C	1025 mm

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518 **Table 2** – *'Full' averaged model coefficients and their significance as produced by the 'AICcmodavg'*

519 *package (Mazerolle and Linden, 2019) modelling termite CT_{max} change as a function of environmental*

520 *factors. The full model fitted the following fixed effects and a single random effect of sampling*

521 *location to predict the critical thermal maximum of termite colonies. Asterisks indicate level of*

522 *significance.*

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Model Parameter	Full model-averaged coefficient	Lower CI	Upper CI	z-value	p-value
Intercept	31.984	13.772	50.196	1.756	0.079
Leaf-Area Index	-0.367	-0.483	-0.250	3.138	0.001 **
Maximum Temperature	0.385	-0.034	0.804	0.919	0.358
Average Daily Rainfall	0.063	-1.340	1.466	0.045	0.964

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530 **Table 3** – *'Full' averaged model coefficients and their significance as produced by the 'AICcmodavg'*

531 *package (Mazerolle and Linden, 2019) modelling termite CT_{min} change as a function of environmental*

532 *factors. The full model fitted the following fixed effects and a single random effect of sampling*

533 *location to predict the critical thermal minimum of termite colonies. Asterisks indicate level of*

534 *significance.*

Model Parameter	Full model-averaged coefficient	Lower CI	Upper CI	z-value	p-value
Intercept	6.878	5.714	8.042	5.910	$2e^{-16}$ ***
Average Daily Rainfall	0.885	0.555	1.216	2.679	0.007 **
Leaf-Area Index	0.011	-0.030	0.052	0.269	0.788

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