Imperial College London

Investigating the resilience of termite communities to selective logging and climatic changes in Malaysian Borneo

Joel Woon

September 2016

A thesis submitted for the partial fulfillment of the requirements for the degree of Master of Science/Research at Imperial College London

Formatted in the journal style of Biotripica

Submitted for the MRes in Tropical Forest Ecology

DECLARATION

All experiments undertaken in this project were set up by myself, and I collected all data between February and June 2016. All experiments were conceived by myself and Michael Boyle (Department of Life Sciences, Imperial College London). All data analyses were undertaken by myself. All termite identification was done by myself at the Natural History Museum, with help from Dr Paul Eggleton (Natural History Museum, London) using identification keys present in the library.

1   **ABSTRACT**

2   Termites are extremely important for tropical forest ecosystems, but there are large

3   decreases in termite abundance and diversity in disturbed forest. This is likely due to

4   changes in microclimatic conditions that occur in selectively logged forests. The thermal

5   adaptation hypothesis states that tropical species should have a constrained thermal

6   tolerance, and that increases in temperature could cause extinctions of these species.

7   Furthermore, due to the stability of the tropics it has been suggested that the thermal

8   tolerance of creatures, particularly small ectotherms, will not be adaptable. Despite

9   termite importance, and their hypothesised susceptibility to climatic changes, termite

10   tolerances to climatic factors have not been studied. Thermal and desiccation tolerances

11   were recorded for various termite genera, and the significance of a number of life

12   history and physiological traits on these tolerances were tested. The thermal tolerance

13   of termites was higher than expected, with desiccation tolerance being fairly low. Hard

14   bodied termites had a higher thermal and desiccation tolerance than soft bodied

15   termites. Mound nesting genera had the lowest thermal tolerance of all the nesting

16   types, with wood nesting genera having the highest. In addition, deadwood feeders from

17   feeding group I had the highest thermal tolerance, which decreased down the

18   humification gradient to soil feeders which had the lowest. The study also showed that

19   one species of termite, *Macrotermes gilvus*, had phylogenetic variation in its thermal

20   tolerance, with assemblages from oil palm plantations having a significantly higher

21   thermal tolerance than assemblages found in primary forest. The results suggest that

22   the *thermal adaptation* hypothesis is too simple when predicting distributions of

23   termites, and potentially other small ectotherms. Furthermore, evidence of plasticity in

24   thermal tolerance refutes recent studies that suggest that small ectotherms will not be

25   able to adapt to the changing climate.

TROPICAL FORESTS ARE HOME TO AN EXTRAORDINARY DIVERSITY OF FLORA AND FAUNA (Connell

29   1978, Basset *et al.* 2012, Hubbell 2013). Despite this, and the forests' socio-economic

30   benefits, they are under increasing pressures from human activities (Koh & Wilcove

31   2008, Lewis *et al.* 2015). In SE Asia, an area with some of the oldest and most diverse

32   forests, selective logging and the oil palm industry are disturbing forest ecosystems

33   (Sodhi *et al.* 2004, 2010). How species react to these pressures is one of the most

34   important and frequently asked questions in ecology (Heydon & Bulloh 1996, Asner *et*

35   *al.* 2005, Broadbent *et al.* 2008, Ewers *et al.* 2015, Drescher *et al.* 2016).

36   When a forest is selectively logged, a large number of microclimatic conditions

37   change (Hardwick *et al.* 2015). As the canopy cover is reduced, a larger proportion of

38   sunlight reaches the understory, which increases the temperature and decreases the

39   humidity (Hardwick *et al.* 2015). Temperature regulation and water retention are two

40   mechanisms of homeostasis that are required by all living organisms. Any stress on

41   these processes will divert energy and resources, reducing fitness. This could be a big

42   problem for ectotherms, because they have fewer mechanisms to mitigate

43   environmental changes (Paaijmans *et al.* 2013, Sgrò *et al.* 2016). Furthermore, the

44   *thermal adaptation hypothesis* postulates that in the hot, aseasonal tropics, species will

45   not have a wide thermal range to which they are adapted (Angilletta 2009). The lack of

46   genetic diversity in thermal tolerance, and a limited ability to control their own

47   thermoregulation, could cause widespread extinctions of ectotherms in altered forests

48   (Huey *et al.* 2012).

49   A number of features also make small ectotherms extremely susceptible to

50   changes in humidity (Chown *et al.* 2011). A large surface-area to volume ratio, high

51   metabolic rate, and relatively high fat levels (Gibbs *et al.* 1997, Hoffmann & Harshman

52   1999), mean that water loss is increased in drier environments. Theoretically, with the

53   tropics being a stable environment for thousands of years, species would have faced less

54   selective pressure on desiccation resistant traits. The drop in humidity in selectively

55   logged forest, coupled with the generally low level of desiccation tolerance, could be a

56   decisive interaction in determining distributions of small ectotherms after disturbance.

57   Furthermore, with drought events predicted to increase in both frequency and severity

58   (Fu 2015), desiccation stress could increase in primary forests, thus altering ectotherm

59   distributions in all forest types.

60   When a forest is selectively logged many of the species are retained (Berry *et al.*

61   2010, Edwards *et al.* 2011), however, the disturbance puts stresses on the remaining

62   species (Osazuwa-Peters *et al.* 2015), with insects often being strongly affected (Ewers

63   *et al.* 2015). Insects are the main drivers of many processes within tropical forests,

64   from controlling plant growth by seed predation, pollination, and herbivory (Janzen

65   1971, Coley & Barone 1996) to providing a plentiful and reliable food source for other

66   species (Didham *et al.* 1996).

67   One of the most important insect-mediated ecosystem functions is

68   decomposition (Didham *et al.* 1996). The majority of insect driven decomposition is

69   conducted by termites (Bignell & Eggleton 2000). They break down plant matter across

70   the whole humification gradient, which ranges from recently fallen deadwood to soil

71   (Donovan *et al.* 2001), and provide other vital ecological services such as nutrient

72   cycling and soil turnover (Holt & Coventry 1990, Holt & Lepage 2000). Studies have

73   shown that in selectively logged forests, termite diversity and abundance drops (Lee

74   2012, Luke *et al.* 2014, Ewers *et al.* 2015). Luke *et al.* (2014) showed that both wood

75   and soil feeding termites drop in abundance in logged forest, with soil feeders dropping

4

more substantially. Given the functional redundancy within ecosystems, decomposition rates do not drop as much. However, the rate is still significantly lower than in primary forest (Ewers *et al.* 2015).

To access the whole humification gradient, termites are highly diverse and specifically adapted. It is possible that a number of these adaptations are thermal or desiccation traits, which increase their tolerance to variable microclimatic factors. Many species are hard bodied, and tend to forage on the surface. The higher level of sclerotisation could allow them to withstand the harsh conditions of high temperatures and low humidity experienced during foraging, which wouldn't be experienced by the subterranean or tunnel building species. The higher sclerotisation will reduce gaseous exchange with the environment, allowing them to function in drier environments (Rajpurohit *et al.* 2008b, Schimpf *et al.* 2009).

Termites also have a number of nesting strategies. They nest in different strati of the forest to exploit different niches (Li *et al.* 2015), which will change the conditions they experience. Furthermore, there is a large amount of variation in nest building, which ranges from nesting within their food source, soil or wood, to built structures, carton or mound nests. These will all offer varying levels of environmental buffering, which could vary thermal tolerance.

Despite the importance of termites within tropical forests, their tolerances to changing microclimatic conditions have not been studied. This study will provide an insight into these tolerances. The upper boundary for thermal tolerance (CT_{max}) of all available termite genera will be documented, and the applicability of the *thermal adaptation hypothesis* will be tested. In addition, this study will test a number of life history and physiological traits to examine whether these traits significantly alter

100   thermal tolerance. First, feeding strategies will be tested. The strategies vary the

101   amount of contact with the ambient conditions and this may cause variation in thermal

102   tolerance. It is expected that the feeding groups that feed on soil will have less contact

103   with the ambient conditions and should have a lower thermal tolerance than the groups

104   that feed on plant matter higher up the humification gradient, such as deadwood and

105   leaf litter. Body sclerotisation will also be studied, testing whether the higher

106   sclerotised surface foragers have a higher thermal tolerance than the soft bodied

107   termites.

108   Another life history trait that will be examined is nesting strategy. Termites that

109   nest in the canopy will be exposed to higher temperatures (Smith 1973, Kaspari *et al.*

110   2015), and so they should have a higher thermal tolerance, compared to terrestrial or

111   subterranean nesting termites which wouldn't experience such harsh temperatures.

112   The four nest types will all offer varying amounts of buffering capacity against the

113   environmental conditions. Mound nests would offer the largest buffer, with thick mud

114   or clay walls, which would cause the nesting species to have the lowest thermal

115   tolerance. Carton nests, made of thin walls (Noirot & Darlington 2000), offer the least

116   protection from environmental conditions, and so these species can be expected to have

117   the highest thermal tolerance.

118   Finally, caste will be studied to determine whether the role within a colony can

119   alter thermal tolerance. Soldiers have to defend their colony from predators, which

120   would lead to them interacting with the ambient conditions more regularly than the

121   worker caste, and so they should have a higher thermal tolerance.

122   The specific thermal tolerances of one species of termite, *Macrotermes gilvus*, will

123   also be studied. *M.gilvus* is one of the few termites that thrives across the entire logging

6

124 gradient, from primary forest to oil palm plantations (Luke *et al.* 2014). The

125 environmental conditions within oil palm plantations are among the most extreme in

126 tropical regions, with a higher temperature range than any other forest type (Hardwick

127 *et al.* 2015). Despite these conditions, *M. gilvus* survives well. This could be due to

128 phenotypic plasticity, with certain assemblages having higher thermal tolerance. The

129 thermal tolerance of primary forest *M. gilvus* colonies will be compared to those found

130 within an oil palm plantation, to test whether intraspecific variation will cause thermal

131 tolerance to be higher in the assemblages found in oil palm, and how variable the

132 tolerance within a single species can be.

133   Finally, the desiccation tolerances of termite genera will also be tested. Other

134 groups of insects have been shown to have specific adaptations to increase their

135 desiccation resistance (Gibbs *et al.* 1997), one such being a highly sclerotised body

136 (Appel & Tanley 1999, Singh *et al.* 2009). This study will analyse whether the degree of

137 body sclerotisation has a significant effect in reducing water loss in desiccated

138 environments, with the highly sclerotised surface foragers expected to be more tolerant.

139

140 **METHODS**

141

142 SAMPLING AREA

143 All sampling occurred within Sabah, in East Malaysia, on the island of Borneo, between

144 February and June 2016. A major El Niño event occurred during this sampling period

145 and this may have affected the results and the generalisability of the findings. The great

146 majority, 91%, of samples were collected from the Maliau Basin Conservation Area

147   (4.85° N, 116.84° E), an area of primary mixed dipterocarp forest. The remaining 9% of

148   samples were collected within the SAFE project (Stability of Altered Forest Ecosystems)

149   experimental area (Ewers *et al.* 2011), in an oil palm plantation owned by Sabah

150   Softwoods.

151   TERMITE COLLECTION

152   Termite colonies were located within mounds or deadwood using random searching

153   methods in randomly chosen locations within the forest and plantation. (Soil pits were

154   also dug, but no soil termites were detected during the whole sampling period. This

155   absence of soil-feeders may have been due to the El Niño event). Once a colony was

156   located a portion of the colony structure containing termites was removed, and placed

157   in a cool-box, to maintain environmental conditions, and transported to the lab. Time

158   between sampling and the beginning of the experiment was minimised (averaging 30

159   +/- 18 minutes in Maliau, and 5 +/- 2 minutes in the oil palm plantation), to reduce

160   stress to the termites. Where possible, new genera were sampled to obtain the highest

161   taxonomic coverage.

162   TEMPERATURE STUDY

163   The initial study tested the thermal tolerance of different termite genera, for which the

164   upper critical temperature (CT_{max}) beyond which termites were unable to survive was

165   experimentally determined. To do this, termites were removed from the substrate in the

166   lab. This was done carefully to prevent injuries. Up to 20 termites were individually

167   placed into separate glass tubes, which were then sealed. Individuals belonging to the

168   worker and soldier castes were treated separately, and if possible each caste was

169   sampled in equal numbers. If equal numbers were not achievable, every individual of

170   the less populous caste was used.

171   The experimental methods followed the standard protocol set out by Terblanche

172   *et al.* (2011). The tubes were submerged in a water bath at room temperature. The

173   water temperature was then increased to 34°C and held constant for approximately 5

174   minutes until the air temperature within each tube had equilibrated with the water

175   temperature. The holding period varied in length based on the original temperature of

176   the water. After equilibrating, the temperature of the water was increased at a ramping

177   rate of 0.2°C per minute. This chosen rate is a trade-off between getting as accurate

178   readings as possible, and the cause of death being the temperature increase. The rate of

179   increase was fast enough so that the termite deaths were not due to another reason,

180   such as desiccation. A higher rate of increase in temperature would cause a temperature

181   lag, which occurs when the temperature of the water is higher than the temperature

182   within the tube. This would result in CT_{max} estimates that would be higher than the true

183   value. At every increase of 2°C there was a two-minute pause, to further reduce any

184   temperature lag. The ramping continued until all 20 termites had died, and the

185   temperature at which each individual died was recorded. This process was repeated

186   twice daily, with individuals collected from a new colony for each experiment.

187   Physiological and life history trait data was taken from the current literature and

188   collected from the field. Feeding groups were categorised using the guilds outlined by

189   Donovan *et al.* (2001), which splits termites into one of four groups based on their

190   family, and feeding preference along the humification gradient (see table 1). Nesting

191   strategies were recorded in the field, and corroborated using Inward *et al.* (2007). Four

192   categories were used, soil, wood, carton or mound nests. Body sclerotisation was

193   recorded during identification, in a binary system of either hard or soft bodied. A

194   termite was considered soft bodied if the gut was visible through the abdomen.

ADAPTATION STUDY

196 To study the amount of phenotypic plasticity in thermal tolerance, *Macrotermes gilvus*

197 was sampled in two habitat types, primary forest and an oil palm plantation. The

198 plantation consisted of a grid of equidistant *Elaeis guineensis*, the most common palm oil

199 species. The sampling and experimental protocol was identical to the temperature

200 experiment described above. Individuals of all other genera were collected solely from

201 the primary forest.

202 DESICCATION STUDY

203 The final study quantified the desiccation tolerance of termites – which is the ability to

204 control water loss in low humidity environments – by measuring the rate of water loss

205 in a desiccated environment. The experiment focussed on four genera (*Macrotermes*,

206 *Hospitalitermes*, *Microcerotermes,* and *Dicuspiditermes*), chosen because they were all

207 abundant in primary forest, but they span a wide range of thermal tolerances and have

208 varying responses to selective logging (Luke *et al.* 2014).

209 Workers of one genus were collected from the field at a time, and 20 groups of

210 termites were weighed for each genus. Group size varied between 5 and 15 individuals

211 depending on the weight of each individual termite, and the quantity of termites

212 sampled. Where possible, all 20 groups were standardised to the same size. Once the

213 termite groups had been weighed they were placed into one of two tube types, a

214 treatment or a control tube. The treatment tube contained 5 g of silica gel which

215 reduced the humidity to $30\pm4.5\%$. The humidity within the control tubes was $76\pm8\%$.

216 The humidity of the tubes was measured using a humidity probe before the termites

217 were placed into the tube. The treatment tube also contained a small cardboard barrier,

218 to prevent termites from coming into contact with the silica gel. All 20 tubes were

219 placed in a water bath which was set to a constant 30°C. This temperature was chosen

220 as it was the coolest temperature that would be reliably hotter than room temperature.

221 At each of five time points (10, 30, 60, 120, and 180 minutes) four tubes were removed

222 for analysis: three treatment tubes and a single control. The weight of each termite

223 group and the number of dead termites within each tube was recorded. Weight change

224 was assumed to be due to water loss.

225 Samples containing approximately 50 termites were weighed and placed in a

226 drying oven for 24h at 60°C, and then weighed again. This was done for all four genera

227 and all weight change was attributed to water loss. This was taken as total water

228 content, and compared against weight loss values in the desiccation study to calculate

229 total body water loss.

230 STATISTICAL ANALYSIS

231 All data were analysed using the R statistical package version 3.2.2 (Team 2013). For all

232 three studied linear mixed effects models (package lme4, were fitted to the data and

233 simplified until the minimal adequate model was reached. Tukey's *post-hoc* tests were

234 used to determine differences between levels of categorical factors (package multcomp,

235 Horthorn *et al.* 2009).

236 The temperature analysis modelled thermal tolerance against five explanatory

237 variables – body sclerotisation, feeding group, nesting strategy, nesting layer, and caste.

238 These data were collected using the latest literature and observations in the field. The

239 model underwent a stepwise simplification process using likelihood ratio tests. Caste

240 and nesting layer were removed from the model during this process. The model used

241 colony identity as the random effect, as the different nests within each genus could still

242 explain differences in thermal tolerance. Tukey's *post-hoc* tests were then undertaken to

243 determine significant differences between factor levels within the explanatory

244 variables.

245   The adaptation study modelled thermal tolerance against a single explanatory

246 variable, forest type. The only random effect used was colony identity. Tukey's *post-hoc*

247 test was used to compare the two forest types.

248   Lastly, for the humidity study, the total body water lost was modelled against

249 three fixed effects; time, treatment, and body sclerotisation, with nest included as a

250 random effect. Fixed effects were modelled as two-way interactions. Profile confidence

251 intervals were calculated to determine the significance of the explanatory variables and

252 their interactions.

253

254 **RESULTS**

255 TEMPERATURE

256 Thermal tolerance varied by 5.25°C between termite genera (Fig. 1a), with body

257 sclerotisation, feeding group and nesting strategy all explaining a statistically significant

258 part of the variation.

259   Feeding group was significantly correlated with termite thermal tolerances

260 (likelihood ratio test, χ^2 = 12.04, P = 0.007, df = 3), with maximum thermal tolerance

261 being highest in feeding group I and sequentially decreasing along the humification

262 gradient (table 1, Fig. 1b), with a 2.70 ± 0.90°C difference between the highest and

263 lowest groups (generalised linear hypothesis test, z = -2.991, P = 0.013).

264   Body sclerotisation was also correlated with termite thermal tolerances

265 (likelihood ratio test, χ^2 = 8.64, P = 0.003, df = 1), with the thermal tolerance of hard

266 bodied termites being 1.29 ± 0.45°C higher than soft bodied termites (Fig. 1c, glht , z = -

267 2.846, P = 0.004).

268   Nesting type was significantly correlated with termite thermal tolerances

269 (likelihood ratio test, χ^2 = 8.05, P = 0.045, df = 3). Termites that built mounds had the

270 lowest thermal tolerance and wood nesting termites the highest (Fig. 1d). However, the

271 *post-hoc* pairwise comparisons were not statistically significant (glht, z < 1.900, P >

272 0.208).

273   The random effect of colony identity also accounted for 54.7% of the explained

274 variation in the temperature model, with colony identity explaining a larger proportion

275 of the variation than the fixed explanatory variables.

276 ADAPTABILITY

277 When the thermal tolerance of *Macrotermes gilvus* was compared across the two for

278 habitat types, it was found that *M. gilvus* in oil palm had a 1.95 ± 0.72°C higher CT_{max}

279 than colonies found in primary forest (Fig. 3, glht, z = 2.721, P = 0.012).

280 HUMIDITY

281 Termites were shown to lose significantly more water in the desiccated environment

282 (see table 2). Because there was a huge variation in water loss in the soft bodied

283 termites, there was not a significant difference in total water loss between hard and soft

284 bodied termites (table 2). There was a difference in the rate of water loss between the

285 two body types, with soft bodied termites losing water significantly faster than hard

286 bodied termites (table 2). However, treatment type had a much larger effect on water

287 loss than body sclerotisation level (table 2). The random effect of colony identity also

288 accounted for 32.3% of the explained variation in the humidity model.

289

DISCUSSION

291 The different termite genera showed differing tolerances to both temperature and

292 desiccation, and various physiological and life history traits were shown to significantly

293 affect these tolerances. It is unknown whether these tolerances affect their distributions

294 in selectively logged forest, however, these results suggest they could play a major role.

295   Thermal tolerance was affected by a number of traits. Feeding group was shown

296 to have a significant effect on thermal tolerance. Both the most thermal tolerant genus,

297 *Coptotermes*, and the least tolerant, *Parrhinotermes*, are found in feeding group I. These

298 are both within the same family, *Rhinotermitidae*, which suggests that thermal tolerance

299 is not conserved at a family level. This is supported by the variation displayed in feeding

300 group II, all of which are in the *Termitidae* family. Feeding groups IIF and III (which

301 contain genera of the *Termitidae* family) had low thermal tolerances, significantly lower

302 than feeding group I. No genera from feeding group IV, the specialist soil consumers,

303 were present during sampling.

304   These results are alarming for selectively logged forest. If thermal tolerance is a

305 driver of species distributions, specific feeding groups will drop out of disturbed forest,

306 removing their ecosystem services. Specifically, feeding groups IIF, III and IV could

307 disappear from selectively logged forest, which will reduce soil decomposition and

308 nutrient cycling. If there is a lack of functional redundancy within these altered forests,

309 this could have a large damaging effect. Furthermore, typical decomposition studies

310 usually focus on leaf litter decomposition (Sundarapandian & Swamy 1999, Wieder *et*

311 *al.* 2009, Ewers *et al.* 2015)**,** but the effect of logging on the decomposition of other

312   levels of the humification gradient is largely unknown. If more studies were done

313   spanning the humification gradient, there would be a greater understanding of the

314   impacts of selective logging on decomposition, and the role of termites within that.

315   Hard bodied termites were shown to have a higher thermal tolerance than soft

316   bodied termites. It appears that the higher level of sclerotisation enables them to

317   withstand higher temperatures. Other insect studies show results to the converse of this

318   (Clusella Trullas *et al.* 2007, Kellermann *et al.* 2012), with higher levels of

319   sclerotisation typically correlating with a lower thermal tolerance. However, these

320   studies are done over altitudinal and latitudinal gradients, so they are not directly

321   comparable. Higher levels of sclerotisation also cause darker pigmentation, which is

322   likely an adaptation to increase solar radiation absorption, which would allow hard

323   bodied termites to function in low light levels (Willmer 1983). If this is the case, hard

324   bodied termites will require a higher thermal tolerance to withstand the absorption.

325   However, it remains unclear whether the higher tolerance is due to the higher

326   sclerotisation, or an additional adaptation to allow hard bodied termites to forage

327   terrestrially.

328   Of the two aspects to nesting strategy, only the nest type had a significant

329   correlation with thermal tolerance. Genera that nested in mounds did have the lowest

330   thermal tolerance, as expected. This is likely due to the thick walls providing a barrier

331   against the external conditions, keeping the internal nest cool. Additionally, other

332   species of mound-building termite, including African Savannah species of *Macrotermes*,

333   have complex ventilation systems that work to refresh and cool air inside the nest (Korb

334   2003). This aspect of nest building is unstudied in the SE Asian genera, but it could

335   explain this result. Contrary to what was predicted, carton nests did not have the

336 highest thermal tolerance; wood nesting species did. However, the result of

337 *Coptotermes*, which had the highest CT_{max}, being one of two wood nesting genera found

338 could be skewing the result, and the lack of repeats could make the result inaccurate.

339 Additionally, only two soil nesting genera were found, which is much lower than

340 expected in primary forests typically containing a large diversity of soil termites

341 (Eggleton *et al.* 1999, Luke *et al.* 2014). The lack of repeats within both the soil and

342 wood nesting types is likely the reason behind the lack of significance in the *post-hoc*

343 tests between the nesting types.

344   Interestingly, nesting layer was not significantly correlated with thermal

345 tolerance, suggesting that foraging and nest location are more important in altering

346 thermal tolerance. The only other variable that did not have a significant effect was

347 caste. This suggests that across a colony, thermal tolerance is equal. However, juveniles

348 and queens were not tested, which are two castes vital for the survival of the colony

349 (Roisin 2000). If either of these castes has a significantly lower thermal tolerance than

350 the soldier or worker castes, it could determine where a genus can persist.

351   A large proportion of the variation in thermal tolerance was explained by the

352 random effects of colony differences. This suggests that within genus, there are large

353 nest-to-nest differences in thermal tolerances. Due to the coarse taxonomic scale, these

354 differences could be explained by species differences, and thermal tolerance may not be

355 conserved at genus level. Nest location could also influence the variation in thermal

356 tolerance. Nests located in particular areas, such as treefall gaps, could select for higher

357 levels of thermal tolerance.

358   All genera have a thermal tolerance that is significantly higher than any

359 temperature that they might experience in primary tropical forest. The average highest

360   daily temperature in the primary forest study zone was 26°C (Hardwick *et al.* 2015). So

361   why do these small ectotherms have such a high upper thermal limit? The *thermal*

362   *adaptation hypothesis* posits that it should be much closer to the temperatures

363   experienced in the forest (Angilletta 2009), but it is clearly not the case here.

364   Although ambient temperature has been an effective prediction variable for

365   altering species distributions in the past (Root *et al.* 2003, Parmesan & Yohe 2003), this

366   study, and a number of other recent studies (Clusella-Trullas *et al.* 2011, Kellermann *et*

367   *al.* 2012), suggest it may not be the best measure to use for ectotherms, particularly

368   small insects. Clusella-Trullas *et al.* (2011) suggest that temperature variation and

369   precipitation play a larger role than average ambient temperature in determining the

370   CT_{max} of larger ectotherms. Furthermore, the interaction between precipitation and

371   temperature has been shown to have an effect on insect thermal tolerance (Kellermann

372   *et al.* 2012). This suggests that the impacts of microclimate change on ectotherms will

373   not be as simple as the temperature rising, and ambient temperature cannot be the only

374   predictor variable used in future studies, as there are far too many changing conditions

375   to single out one.

376   Selective logging changes wind patterns (Laurance *et al.* 1998), light

377   concentration in the understory (Laurance & Williamson 2001), humidity (Shukla *et al.*

378   1990), and rainfall (Salati & Vose 1984), all of which could alter ectotherm distributions

379   over small or large scales. More study should be directed into these climate variables to

380   understand what dictates distribution changes, other than simply ambient temperature.

381   It certainly cannot be assumed that the thermal range of tropical ectotherms, and

382   termites specifically, is as narrow as the *thermal adaptation hypothesis* suggests

383   (Angilletta 2009, Huey *et al.* 2012). However, to provide full evidence, thermal

384 performance curves would have to be generated, which require critical minimum

385 temperature values. If this information was available, thermal optimums for all the

386 genera tested could be produced, which would allow for a greater insight into the

387 impacts of temperature changes on termite fitness.

388   The adaptation study showed that *Macrotermes gilvus* assemblages did have

389 different thermal tolerances in different forest types. As expected, the *M. gilvus*

390 assemblage from the oil palm plantation had a significantly higher thermal tolerance,

391 and this is likely due to phenotypic plasticity. This result supports the hypothesis that

392 the variation between colonies could be due to nest placement. Theoretical climate

393 change models suggest that phenotypic plasticity could allow for the persistence of

394 species despite the changing climatic conditions (Phillips *et al.* 2006, Mokany & Ferrier

395 2011, Bellard *et al.* 2012, Sgrò *et al.* 2016), and this result provides evidence that this is

396 possible. This opposes current thinking, that the upper thermal limits of small

397 ectotherms are constrained (Hoffmann *et al.* 2003, Hoffmann 2010, Kellermann *et al.*

398 2012, Huey *et al.* 2012), and this sort of result has not been shown in other insect

399 studies. If upper thermal limits are plastic, it could dramatically change the predicted

400 view of insect distributions in disturbed systems.

401   Still, it is unclear whether changes in temperature drive the observed changes in

402 selectively logged forest. Humidity could play a large role in dictating termite

403 distributions. The results show that hard bodied termites are more desiccation tolerant

404 than soft bodied termites, a result that is supported by recent studies (Parkash *et al.*

405 2008, Rajpurohit *et al.* 2008a). The lack of significance in total water loss between the

406 two body types can be attributed to the variation in both groups, however, after three

407 hours hard bodied termites had lost an average of 24.16% less total body water than

408 soft bodied termites. Furthermore, because the rate of water loss was faster in soft

409 bodied termites, it can be concluded that they are more desiccation sensitive. The only

410 hard bodied genus that was tested was *Hosptitalitermes*, as it is the only common hard

411 bodied genus. This means that although it appears hard bodied termites are more

412 desiccation tolerant, it could be specifically *Hosptitalitermes* that is highly desiccation

413 tolerant. More hard bodied genera would have to be tested to increase confidence in

414 the results. The soft bodied genus that lost the least amount of water was *Macrotermes*,

415 which could provide an additional insight into why they can persist in oil palm

416 plantations. Interestingly, *Hosptitalitermes* are not found in oil palm plantations (Luke *et*

417 *al.* 2014), however, because they are highly specialised this is likely due to habitat and

418 food loss (Jones & Gathorne-Hardy 1995). The other two soft bodied genera,

419 *Dicuspiditermes* and *Microcerotermes*, lost considerably more water, and they are both

420 heavily affected by selective logging and the forest conversion into oil palm (Luke *et al.*

421 2014). Additional data could be collected to improve the model, such as body size,

422 which is known to alter desiccation tolerance (Hoffmann & Harshman 1999). Smaller

423 creatures have a larger surface-area to volume ratio which suggests that larger termites

424 should be found in more desiccated environments.

425   Despite these results showing that various physiological and life history traits

426 have significant effects on tolerances to changing conditions, these are only laboratory

427 tests. The next stage would be to do some extensive field tests across a logging gradient.

428 There would be an expected drop off of soft bodied termites, as well as genera from

429 feeding group III, from primary forest through to oil palm. All genera should be tested

430 across the gradient, to try and assess whether phenotypic plasticity is present in all

431 genera. The El Niño event could have had a significant effect on both temperature and

432 desiccation tolerances by either increasing stress, and reducing fitness, thus lowering

19

433   the values, or it could have caused a selection pressure so the only persisting colonies

434   had higher than expected tolerances. This study should be repeated out of a drought

435   season to see what, if any, affect El Niño had on tolerances.

436   Termites have an extremely varied response to both temperature and

437   desiccation pressures, which a number of life history and physiological traits appear to

438   influence. However, how these traits influence tolerance is not known due to the lack of

439   knowledge from the field. Despite this, the results make it clear that the *thermal*

440   *adaptation hypothesis* is far too simple when describing small ectotherms, and a large

441   number of additional climatic variables must be considered before predicting

442   distribution changes based on selective logging and the changing climate.

443

Bibliography

ANGILLETTA, M.J., 2009. *THERMAL ADAPTATION: A THEORETICAL AND EMPIRICAL SYNTHESIS* ILLUSTRATED, REPRINT., OUP OXFORD.

APPEL, A.., AND M.. TANLEY, 1999. Water composition and loss by body color and form mutants of the German cockroach (Dictyoptera: Blattellidae). Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 122: p.415–420.

ASNER, G.P., D.E. KNAPP, E.N. BROADBENT, P.J.C. OLIVEIRA, M. KELLER, AND J.N. SILVA, 2005. Selective logging in the Brazilian Amazon. Science 310: p.480–482.

BASSET, Y. *ET AL.* , 2012. Arthropod diversity in a tropical forest. Science 338: p.1481– 1484.

BATES, D., M. MÄCHLER, B. BOLKER, AND S. WALKER, 2014. Fitting Linear Mixed-Effects Models using lme4. Available at: http://arxiv.org/abs/1406.5823.

BELLARD, C., C. BERTELSMEIER, P. LEADLEY, W. THUILLER, AND F. COURCHAMP, 2012. Impacts of climate change on the future of biodiversity. Ecol Lett 15: p.365–377.

BERRY, N.J., O.L. PHILLIPS, S.L. LEWIS, J.K. HILL, D.P. EDWARDS, N.B. TAWATAO, N. AHMAD, D. MAGINTAN, C.V. KHEN, M. MARYATI, R.C. ONG, AND K.C. HAMER, 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodivers Conserv 19: p.985–997.

BIGNELL, D.E., AND P. EGGLETON, 2000. Termites in Ecosystems. *I*n T. Abe, D. E. Bignell, and M. Higashi (Eds.) Termites: Evolution, Sociality, Symbioses, Ecology. pp. 363– 387, Dordrecht: Springer Netherlands.

BROADBENT, E., G. ASNER, M. KELLER, D. KNAPP, P. OLIVEIRA, AND J. SILVA, 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141: p.1745–1757.

CHOWN, S.L., J.G. SØRENSEN, AND J.S. TERBLANCHE, 2011. Water loss in insects: an environmental change perspective. J Insect Physiol 57: p.1070–1084.

CLUSELLA TRULLAS, S., J.H. VAN WYK, AND J.R. SPOTILA, 2007. Thermal melanism in ectotherms. J Therm Biol 32: p.235–245.

CLUSELLA-TRULLAS, S., T.M. BLACKBURN, AND S.L. CHOWN, 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. Am Nat 177: p.738–751.

COLEY, P., AND J. BARONE, 1996. Herbivory and Plant Defenses in Tropical Forests. Annual Review of Ecology and Systematics 27: p.305–335.

CONNELL, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199: p.1302–1310.

DIDHAM, R.K., J. GHAZOUL, N.E. STORK, AND A.J. DAVIS, 1996. Insects in fragmented forests: a functional approach. Trends Ecol Evol (Amst) 11: p.255–260.

DONOVAN, S.E., P. EGGLETON, AND D.E. BIGNELL, 2001. Gut content analysis and a new feeding group classification of termites. Ecol Entomol 26: p.356–366.

DRESCHER, J. *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: .

EDWARDS, D.P., T.H. LARSEN, T.D.S. DOCHERTY, F.A. ANSELL, W.W. HSU, M.A. DERHÉ, K.C. HAMER, AND D.S. WILCOVE, 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Proc Biol Sci 278: p.82–90.

EGGLETON, P., R. HOMATHEVI, D.T. JONES, J.A. MACDONALD, D. JEEVA, D.E. BIGNELL, R.G. DAVIES, AND M. MARYATI, 1999. Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. Philos Trans R Soc Lond, B, Biol Sci 354: p.1791–1802.

EWERS, R.M. *ET AL.* , 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. Nat Commun 6: p.6836.

EWERS, R.M., R.K. DIDHAM, L. FAHRIG, G. FERRAZ, A. HECTOR, R.D. HOLT, V. KAPOS, G. REYNOLDS, W. SINUN, J.L. SNADDON, AND E.C. TURNER, 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philos Trans R Soc Lond, B, Biol Sci 366: p.3292–3302.

FU, R., 2015. Global warming-accelerated drying in the tropics. Proc Natl Acad Sci U S A 112: p.3593–3594.

GIBBS, A.G., A.K. CHIPPINDALE, AND M.R. ROSE, 1997. Physiological mechanisms of evolved desiccation resistance in Drosophila melanogaster. J Exp Biol 200: p.1821–1832.

HARDWICK, S.R., R. TOUMI, M. PFEIFER, E.C. TURNER, R. NILUS, AND R.M. EWERS, 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. Agricultural and Forest Meteorology 201: p.187–195.

HEYDON, M.J., AND P. BULLOH, 1996. The impact of selective logging on sympatric civet species in Borneo. Oryx 30: p.31.

HOFFMANN, A.A., 2010. Physiological climatic limits in Drosophila: patterns and implications. J Exp Biol 213: p.870–880.

HOFFMANN, A.A., R.J. HALLAS, J.A. DEAN, AND M. SCHIFFER, 2003. Low potential for climatic stress adaptation in a rainforest Drosophila species. Science 301: p.100–102.

HOFFMANN, A.A., AND L.G. HARSHMAN, 1999. Desiccation and starvation resistance in Drosophila: patterns of variation at the species, population and intrapopulation levels. Heredity 83 (Pt 6): p.637–643.

HOLT, J., AND R. COVENTRY, 1990. Nutrient Cycling in Australian Savannas. J Biogeography 17: p.427–432.

HOLT, J.A., AND M. LEPAGE, 2000. Termites and Soil Properties. *In* T. Abe, D. E. Bignell, and M. Higashi (Eds.) Termites: Evolution, Sociality, Symbioses, Ecology. pp. 389–407, Dordrecht: Springer Netherlands.

HOTHORN, T., F. BRETZ, AND P. WESTFALL, 2008. Simultaneous inference in general parametric models. Biom J 50: p.346–363.

HUBBELL, S.P., 2013. Tropical rain forest conservation and the twin challenges of diversity and rarity. Ecol Evol 3: p.3263–3274.

HUEY, R.B., M.R. KEARNEY, A. KROCKENBERGER, J.A.M. HOLTUM, M. JESS, AND S.E. WILLIAMS, 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos Trans R Soc Lond, B, Biol Sci 367: p.1665–1679.

INWARD, D.J.G., A.P. VOGLER, AND P. EGGLETON, 2007. A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. Mol Phylogenet Evol 44: p.953–967.

JANZEN, D.H., 1971. Seed Predation by Animals. Annu Rev Ecol Syst 2: p.465–492.

JONES, D.T., AND F. GATHORNE-HARDY, 1995. Foraging activity of the processional termiteHospitalitermes hospitalis (Termitidae: Nasutitermitinae) in the rain forest of Brunei, north-west Borneo. Insectes Soc 42: p.359–369.

KASPARI, M., N.A. CLAY, J. LUCAS, S.P. YANOVIAK, AND A. KAY, 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Global change biology 21: p.1092–1102.

KELLERMANN, V., J. OVERGAARD, A.A. HOFFMANN, C. FLØJGAARD, J.-C. SVENNING, AND V. LOESCHCKE, 2012. Upper thermal limits of Drosophila are linked to species distributions and strongly constrained phylogenetically. Proc Natl Acad Sci U S A 109: p.16228–16233.

KOH, L.P., AND D.S. WILCOVE, 2008. Is oil palm agriculture really destroying tropical biodiversity? Conservation letters 1: p.60–64.

KORB, J., 2003. Thermoregulation and ventilation of termite mounds. Naturwissenschaften 90: p.212–219.

LAURANCE, W.F., L.V. FERREIRA, RANKIN-DE MERONA, JUDY M., AND S.G. LAURANCE, 1998. RAIN Forest Fragmentation and the Dynamics of Amazonian Tree Communities. Ecology.

LAURANCE, W.F., AND G.B. WILLIAMSON, 2001. Positive Feedbacks among Forest Fragmentation, Drought, and Climate Change in the Amazon. Conserv Biol 15: p.1529–1535.

LEE, S.-H., 2012. Effects of environmental perturbation on the territory size of subterranean termites: A simulation study. J Asia Pac Entomol 15: p.457–463.

LEWIS, S.L., D.P. EDWARDS, AND D. GALBRAITH, 2015. Increasing human dominance of tropical forests. Science 349: p.827–832.

LI, H.-F., Y.-C. LAN, I. FUJISAKI, N. KANZAKI, H.-J. LEE, AND N.-Y. SU, 2015. Termite Assemblage Pattern and Niche Partitioning in a Tropical Forest Ecosystem. Environ Entomol 44: p.546–556.

LUKE, S.H., T.M. FAYLE, P. EGGLETON, E.C. TURNER, AND R.G. DAVIES, 2014. Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. Biodivers Conserv 23: p.2817–2832.

MOKANY, K., AND S. FERRIER, 2011. Predicting impacts of climate change on biodiversity: a role for semi-mechanistic community-level modelling. Diversity and Distributions 17: p.374–380.

NOIROT, C., AND J.P.E.C. DARLINGTON, 2000. Termite Nests: Architecture, Regulation and Defence. *In* T. Abe, D. E. Bignell, and M. Higashi (Eds.) Termites: Evolution, Sociality, Symbioses, Ecology. pp. 121–139, Dordrecht: Springer Netherlands.

OSAZUWA-PETERS, O.L., I. JIMÉNEZ, B. OBERLE, C.A. CHAPMAN, AND A.E. ZANNE, 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 Manage 357: p.10–21.

P<small>AAIJMANS</small>, K.P., R.L. H<small>EINIG</small>, R.A. S<small>ELIGA</small>, J.I. B<small>LANFORD</small>, S. B<small>LANFORD</small>, C.C. M<small>URDOCK</small>, <small>AND</small> M.B. T<small>HOMAS</small>, 2013. Temperature variation makes ectotherms more sensitive to climate change. Global change biology 19: p.2373–2380.

P<small>ARKASH</small>, R., S. R<small>AJPUROHIT</small>, <small>AND</small> S. R<small>AMNIWAS</small>, 2008. Changes in body melanisation and desiccation resistance in highland vs. lowland populations of D. melanogaster. J Insect Physiol 54: p.1050–1056.

P<small>ARMESAN</small>, C., <small>AND</small> G. Y<small>OHE</small>, 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: p.37–42.

P<small>HILLIPS</small>, S.J., R.P. A<small>NDERSON</small>, <small>AND</small> R.E. S<small>CHAPIRE</small>, 2006. Maximum entropy modeling of species geographic distributions. Ecol Modell 190: p.231–259.

R<small>AJPUROHIT</small>, S., R. P<small>ARKASH</small>, S. R<small>AMNIWAS</small>, <small>AND</small> S. S<small>INGH</small>, 2008a. Body melanization and its adaptive role in thermoregulation and tolerance against desiccating conditions in drosophilids. Entomological research 38: p.49–60.

R<small>AJPUROHIT</small>, S., R. P<small>ARKASH</small>, S. R<small>AMNIWAS</small>, <small>AND</small> S. S<small>INGH</small>, 2008b. Variations in body melanisation, ovariole number and fecundity in highland and lowland populations of*Drosophila melanogaster* from the Indian subcontinent. Insect Science 15: p.553–561.

R<small>OISIN</small>, Y., 2000. Diversity and Evolution of Caste Patterns. *In* T. Abe, D. E. Bignell, and M. Higashi (Eds.) Termites: Evolution, Sociality, Symbioses, Ecology. pp. 95–119, Dordrecht: Springer Netherlands.

R<small>OOT</small>, T.L., J.T. P<small>RICE</small>, K.R. H<small>ALL</small>, S.H. S<small>CHNEIDER</small>, C. R<small>OSENZWEIG</small>, <small>AND</small> J.A. P<small>OUNDS</small>, 2003. Fingerprints of global warming on wild animals and plants. Nature 421: p.57–60.

SALATI, E., AND P.B. VOSE, 1984. Amazon basin: a system in equilibrium. Science 225: p.129–138.

SCHIMPF, N.G., P.G.D. MATTHEWS, R.S. WILSON, AND C.R. WHITE, 2009. Cockroaches breathe discontinuously to reduce respiratory water loss. J Exp Biol 212: p.2773–2780.

SGRÒ, C.M., J.S. TERBLANCHE, AND A.A. HOFFMANN, 2016. What Can Plasticity Contribute to Insect Responses to Climate Change? Annu Rev Entomol 61: p.433–451.

SHUKLA, J., C. NOBRE, AND P. SELLERS, 1990. Amazon deforestation and climate change. Science 247: p.1322–1325.

SINGH, S., S. RAMNIWAS, AND R. PARKASH, 2009. Fitness consequences of body melanization inDrosophila immigrans from montane habitats. Entomological research 39: p.182–191.

SMITH, A.P., 1973. Stratification of Temperature and Tropical Forests. Am Nat 107: p.671–683.

SODHI, N.S., L.P. KOH, B.W. BROOK, AND P.K.L. Ng, 2004. Southeast Asian biodiversity: an impending disaster. Trends Ecol Evol (Amst) 19: p.654–660.

SODHI, N.S., L.P. KOH, R. CLEMENTS, T.C. WANGER, J.K. HILL, K.C. HAMER, Y. CLOUGH, T. TSCHARNTKE, M.R.C. POSA, AND T.M. LEE, 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. Biological Conservation 143: p.2375–2384.

SUNDARAPANDIAN, S.M., AND P.S. SWAMY, 1999. Litter production and leaf-litter decomposition of selected tree species in tropical forests at Kodayar in the Western Ghats, India. Forest Ecology and Management 123: p.231–244.

TEAM, R., 2013. R: A language and environment for statistical computing. Available at: http://cran.fiocruz.br/web/packages/dplR/vignettes/timeseries-dplR.pdf.

TERBLANCHE, J.S., A.A. HOFFMANN, K.A. MITCHELL, L. RAKO, P.C. LE ROUX, AND S.L. CHOWN, 2011. Ecologically relevant measures of tolerance to potentially lethal temperatures. J Exp Biol 214: p.3713–3725.

WIEDER, W.R., C.C. CLEVELAND, AND A.R. TOWNSEND, 2009. Controls over leaf litter decomposition in wet tropical forests. Ecology 90: p.3333–3341.

WILLMER, P.G., 1983. Thermal constraints on activity patterns in nectar-feeding insects. Ecol Entomol 8: p.455–469.

Table 1. *A breakdown of the termite feeding groups as categorised by Donovan et al. (2001).*

Feeding Group	Families	Food
I	Lower termites (including *Kaleotermitidae* and *Rhinotermitidae*)	Deadwood and Grass
II	*Termitidae*	Deadwood, Grass, Leaf-litter, Micro-epiphytes
IIF	*Termitidae*	Fungal comb growers (otherwise equivalent to group II)
III	*Termitidae*	Organic upper-layers of soil
IV	*Termitidae*	Mineral soil

Table 2. *Results of the linear mixed effects model, analysing water loss in hard and soft bodied termites in a desiccated and control environment. All effects are presented no matter the significance, and generated using a generalised linear hypothesis* post-hoc *test. Confidence intervals* WERE CALCULATED *using the profile method.*

Effect	Estimate	t value	2.5% CI	97.5% CI
Intercept	0.694	0.140	-9.356	10.713
Soft Bodied	-1.630	-0.297	-12.759	9.654
Desiccated	13.466	3.795	6.476	20.460
Time	-0.007	-0.247	-0.060	0.047
Soft Bodied: Desiccated	12.553	3.680	5.833	19.275
Soft Bodied: Time	0.072	2.916	0.023	0.121
Desiccated: Time	0.218	9.175	0.171	0.265

Figure 1a. A boxplot of each genera's CT_{max}. All outliers were attributed to injured individuals. The numerals within the parentheses correspond to the feeding group of each genus. 1b. A comparison of the CT_{max} of the four feeding groups that were found. They sequentially decrease through the humification gradient from the higher wood feeders in group I, to the wood, grass and leaf litter feeders in group II and IIF, to the soil feeders in group III. None of the true soil feeders of group IV were found. 1c. A comparison of the CT_{max} of hard and soft bodied termites. 1d. A comparison of the CT_{max} of the four nesting strategies found. Nesting strategy was classified using the most recent literature, and observations in the field (Inward et al. 2007).

Figure 2. The water loss in hard and soft bodied termites through time. Solid lines and triangular points indicate a desiccated environment whereas the dashed line and circular points are control. Black symbols and lines are hard bodied termites, whereas the red symbols and lines are soft bodied termites. Negative values were attributed to water absorption from the tube environment, and measurement error.

Figure 1a-d.

Figure 2