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**Title: Termites mitigate the effects of drought in tropical rainforest**

**One Sentence Summary:** Termites maintain litter decomposition, soil moisture, soil nutrient heterogeneity and increase seedling survival during drought.

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**Abstract:** Termites perform key ecological functions in tropical ecosystems, are strongly affected by variation in rainfall, and respond negatively to habitat disturbance.

27 However, it is not known how the projected increase in frequency and severity of  
28 droughts in tropical rainforests will alter termite communities and the maintenance of  
29 ecosystem processes. Using a large-scale termite suppression experiment, we found  
30 that termites increased in activity/abundance during drought in a Bornean forest. This  
31 increase in termites resulted in accelerated litter decomposition, elevated soil moisture,  
32 soil nutrient heterogeneity, and seedling survival rates during the extreme El Niño  
33 drought of 2015-2016. Our work shows how an invertebrate group enhances ecosystem  
34 resistance to drought, providing evidence that the dual stressors of climate change and  
35 anthropogenic shifts in biotic communities will have multiple, negative consequences for  
36 the maintenance of rainforest ecosystems.

37

38 **Main text:**

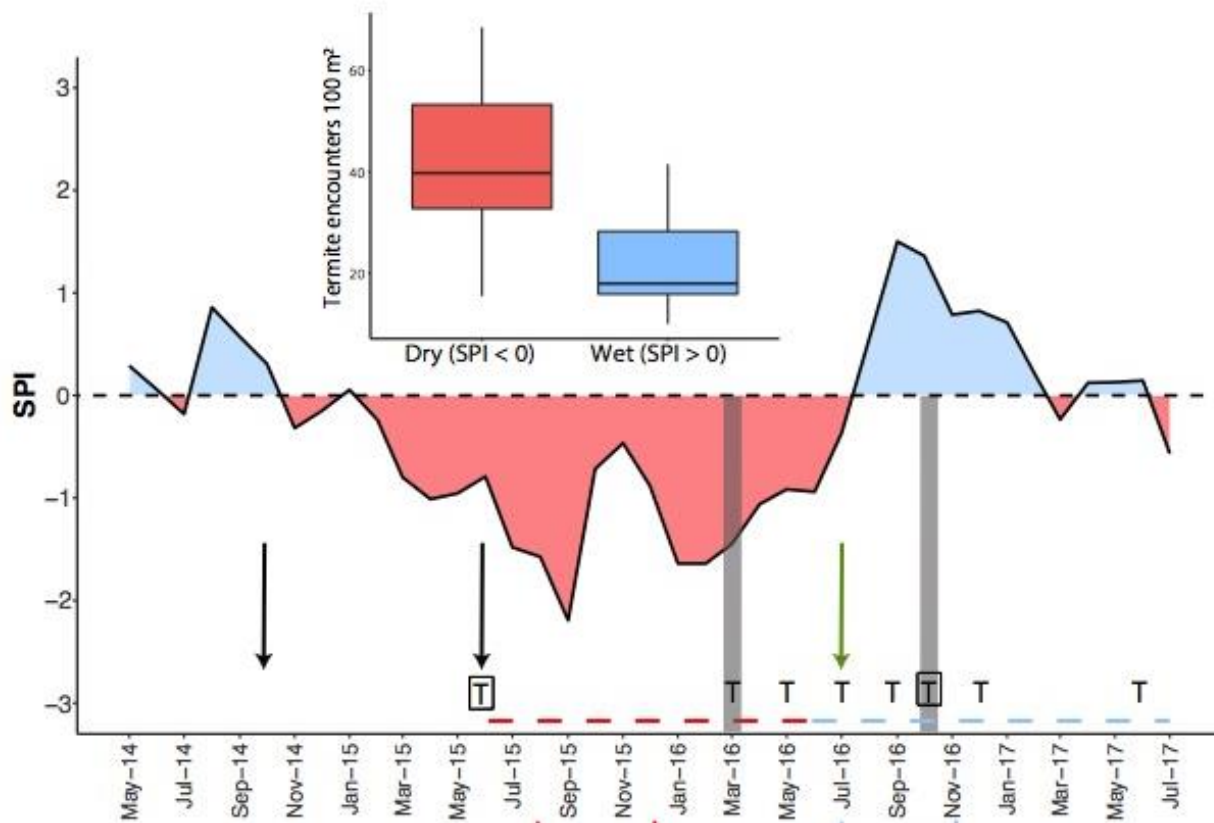
39 Tropical forests have the highest productivity and biodiversity of any terrestrial system  
40 (1). Climate change poses a threat to these ecosystems, with the frequency and  
41 intensity of droughts predicted to increase in coming decades (2, 3). Research has  
42 shown that extreme droughts cause increased tree mortality (4), with implications for  
43 forest structure and functioning. Microbial decomposition and the movement of nutrients  
44 through the soil are also thought to decrease during droughts because dry conditions  
45 reduce activity of microorganisms (5). Together, these results suggest ecosystem-wide  
46 effects of increasing drought frequency and severity. However, we know little about how  
47 drought-mediated changes in invertebrate communities affect the maintenance of  
48 functioning ecosystems during periods of environmental stress.

49

50 Termites are an important macroinvertebrate group for ecosystem function (6), with a  
51 wide tropical and sub-tropical distribution, from 50° north to 45° south (7). All termite  
52 groups have mutualistic relationships with microbes (i.e. groups of bacteria, archaea,  
53 protists and/or fungi), enabling digestion of cellulose (8). These mutualistic relationships  
54 have helped termites become dominant invertebrate leaf litter and dead wood  
55 decomposers. Termites are major ecosystem engineers (6, 8), changing the soil  
56 physical environment through bioturbation, decomposing soil organic matter, wood and  
57 leaf litter (9), and facilitating nutrient cycling (8), but their precise contributions to these  
58 ecosystem functions have not yet been experimentally quantified. Termites also  
59 regulate soil moisture (and hence the movement of nutrients through mass flow) by  
60 transporting water upwards through the soil and decreasing transpiration with their  
61 'sheeting' (temporary above-ground protective structures) (10). These processes are  
62 likely to have important effects on plant communities, especially during drought,  
63 because soil nutrient availability and heterogeneity influence plant growth and  
64 community structure (11) and promote species diversity (12). Moreover, soil moisture is  
65 a key factor determining the magnitude of water stress experienced by plants, directly  
66 influencing plant mortality (13). Termites are sensitive to changes in soil moisture and,  
67 counter-intuitively, they may be more active and abundant in rainforests during droughts  
68 (14). Given their key role in modifying soil environments, an increase in termite activity  
69 during extended dry periods could act to maintain soil moisture and soil nutrient flow  
70 and have indirect consequences for plant survival. Termites could therefore mitigate the  
71 ecological effects of drought in rainforest systems, as has been shown theoretically for  
72 drylands (15).

73

74 To investigate this, we carried out a large scale *in-situ* manipulation (16) of termite  
75 communities. We suppressed termite activity in old-growth tropical rainforest in  
76 Malaysian Borneo, during and after the El Niño drought of 2015-2016 (Fig. 1 and, Fig.  
77 S1), and monitored termite communities in control plots. This experimental approach  
78 allowed us to assess the relative contribution of termites to ecosystem functioning in  
79 drought versus post-drought conditions. Termite suppression was achieved through a  
80 targeted approach within quarter-hectare plots by physically removing termite mounds  
81 and using poisoned cellulose baits. The suppression reduced termite feeding activity on  
82 suppression plots by 45% ( $\Delta AIC = 59$ ; Table S2; Fig. S3 B and S4)) and significantly  
83 altered termite community composition (Monte Carlo permutation test within an RDA:  
84  $pseudoF = 23.6$ ,  $P = 0.001$ ; Fig. S5) by reducing the activity of large wood-feeding  
85 termites (Fig. S6) over two years (see Methods (17)). The targeted suppression did not,  
86 however, affect other ecosystem components (Table S1, Fig. S3 A, Fig. S7, Fig S9).  
87 This experimental manipulation us to partition the effects of termites from those of other  
88 organisms, and test the hypothesis that termites play a crucial role in maintaining  
89 ecosystem processes in rainforests during periods of drought.



90

91 **Fig. 1:** Three-month Standardised Precipitation Index (SPI) calculated using rainfall data from  
 92 Danum Valley Conservation area for one year preceding, and the two-year duration of the study  
 93 (2014 – 2017). SPI is climatic proxy used to quantify and monitor drought; negative values  
 94 indicate drier than average conditions, while positive values are wetter than average. See  
 95 Figure S1 for a 20-year SPI plot of the region. Brackets below the x-axis show the duration of  
 96 the litter decomposition experiments in the drought (red) and post-drought (blue), which were in  
 97 place for 4 months during the drought and post-drought period; the horizontal dashed lines  
 98 show the duration of the seedling survival assessment periods during the drought (red line) and  
 99 post-drought (blue line) periods; “T” symbols show repeated termite transect sampling events on  
 100 the control plots only to assess the effect of drought on termite communities, “T” symbols  
 101 encased in boxes represent termite transects that were carried out on control as well as the  
 102 termite suppression plots to assess the effect of our manipulation experiment on termite

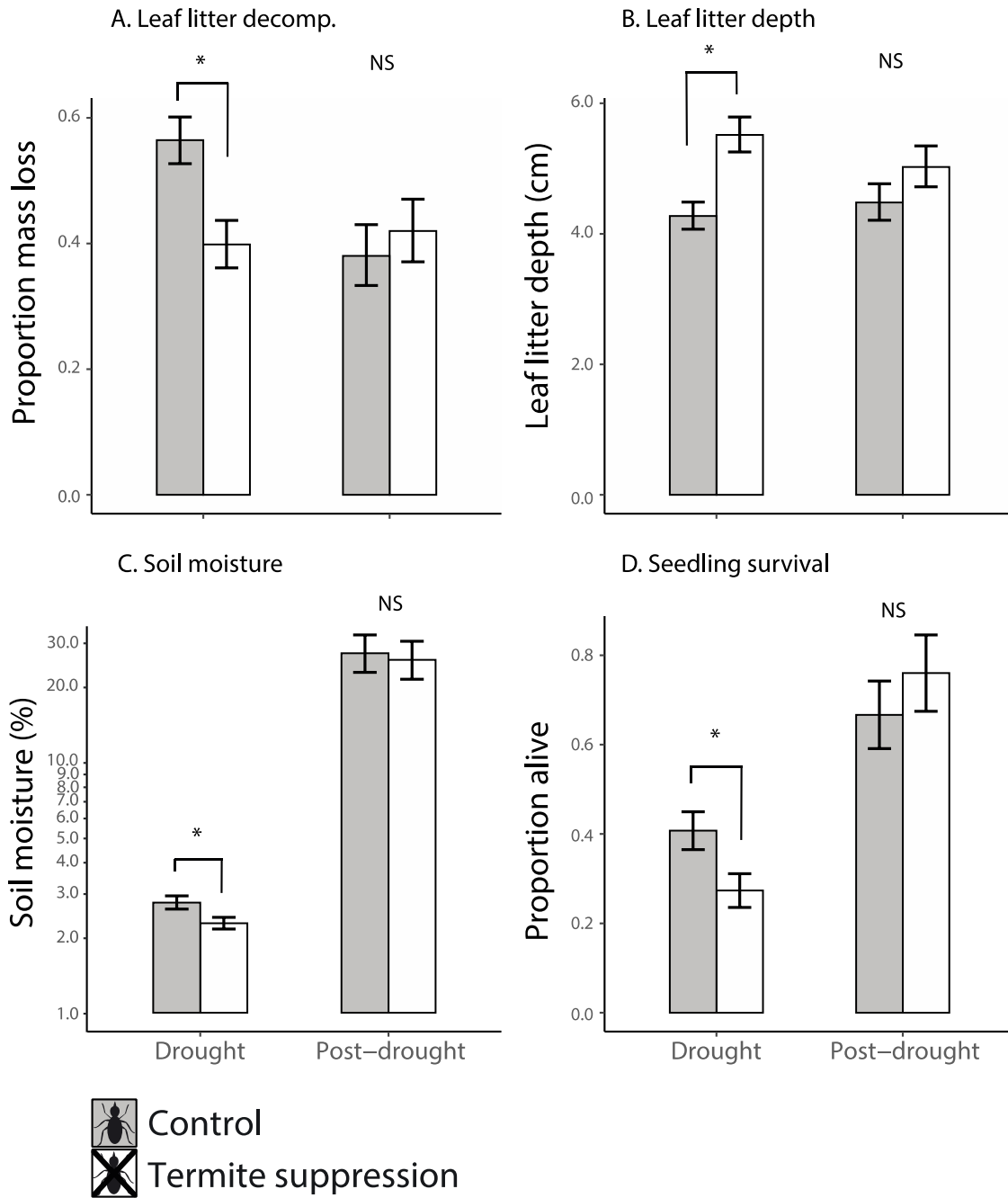
103 communities; the arrows indicate non-target invertebrate sampling: pre-drought and pre termite  
104 suppression (2014), during the drought and suppression (2015) and post-drought, during the  
105 suppression (2016); the green arrow represents the collection of soil and leaf material for  
106 pesticide residue analysis; the grey vertical lines indicate the soil moisture, soil nutrient analysis  
107 and leaf litter depth sampling events; inset, shows the higher termite encounter rate (median  
108 plus interquartile range) during the dry period (SPI < 0) compared with the wet period (SPI > 0)  
109 (assessed using termites transects, which provide relative abundance data).

110  
111 Termite abundance in standardised survey transects (18) in control plots was more than  
112 100% higher during drought compared with post-drought conditions (inset Fig. 1). This  
113 drought-induced change in termite abundance influenced a number of key ecosystem  
114 processes and properties, resulting in higher leaf litter decomposition rates, soil nutrient  
115 heterogeneity and soil moisture. Termites were responsible for all of the measured  
116 macroinvertebrate-driven leaf litter decomposition (See Table S3 and Fig. S3C for a  
117 detailed breakdown of microbial, macroinvertebrate and termite contributions to litter  
118 decomposition): no other invertebrate group compensated to maintain litter  
119 decomposition on the termite suppression plots (Fig. S8).

120  
121 Contrary to previous findings (19), which have focused on microbial decay, we found  
122 that leaf litter decomposition rates of a locally abundant species (*Shorea johorensis*  
123 (Dipterocarpaceae)) increased, rather than decreased, during the drought on our control  
124 plots (Fig. 2A). We attribute this higher litter decomposition rate to the increased  
125 abundance/activity of termites during the drought. We found a 41% higher leaf litter  
126 decomposition rate on the control vs. the suppression plots during drought conditions,

127 with termite suppression contributing substantially to model fit ( $\Delta AIC = 6$ ), whereas  
128 termite suppression did not influence model fit under post-drought conditions ( $\Delta AIC < 2$ ;  
129 Fig. 2A; Table S3D and Fig. S8). Microorganisms are typically assumed to be the main  
130 drivers of litter decomposition (20), perhaps due to a temperate bias in ecology, where  
131 termites are usually absent. Additionally, there is generally a microbial focus in tropical  
132 studies where termite effects are not considered (21, 22); when termites have been  
133 included they have not been well discriminated from other non-termite  
134 macroinvertebrates (23). Here, we show that termites are important decomposers in  
135 tropical rainforest systems and can actually accelerate litter decomposition during dry  
136 periods.

137



138

139 **Fig. 2:** The effect of drought and termite suppression on: A. proportion mass loss from open-  
 140 mesh leaf litter decomposition bags (assessed after remaining on the forest floor for four  
 141 months); B. forest floor leaf litter depth; C. soil moisture; D. probability of seedling survival. Grey  
 142 bars are control plots, white bars are termite suppression plots and all bars display mean values  
 143  $\pm$  SE. Asterisks denote significant differences between values (see Table S3 and S4 for model



144 outputs). Data presented are back-transformed mean predicted values from mixed effects  
145 model outputs and error bars are the back-transformed model estimates. Soil moisture (panel  
146 C) is presented on a  $\log_{10}$  scale for ease of interpretation.

147  
148 As might be predicted from the observed increase in decomposition rates during the  
149 drought period, leaf litter depth was lower, by 22%, on the control plots (where intact  
150 termite communities were present) compared with suppression plots (Fig. 2B.; Table  
151 S4A and Figure S3D.). This greater accumulation of leaf litter on suppression vs control  
152 plots during the drought (suppression effect model,  $\Delta AIC = 7$ ) but not during post-  
153 drought conditions (suppression effect model,  $\Delta AIC < 2$ ) (Fig. 2B.) shows an immediate  
154 ecosystem-level consequence of the change in termite activity.

155  
156 This observed increase in litter cycling represents a previously unmeasured and  
157 potentially large contribution by termites to terrestrial carbon flux during drought  
158 conditions. Evidence from the 2015-16 El Niño drought showed a net increase in  
159 tropical forest carbon flux compared with post-drought conditions (24), indicating that  
160 the increased termite-mediated carbon cycling is not offset by increased carbon uptake  
161 from plants. We estimate that termite-driven decomposition of leaf litter could contribute  
162 up to 1 MgC/ha/yr during drought periods (17). These findings suggest that present  
163 models may underestimate future carbon flux from tropical rainforests (25, 26). Given  
164 that termites have also been shown to contribute significantly to decomposition in the  
165 New World tropics (27), these results point to termites acting as major components of  
166 carbon cycling globally.

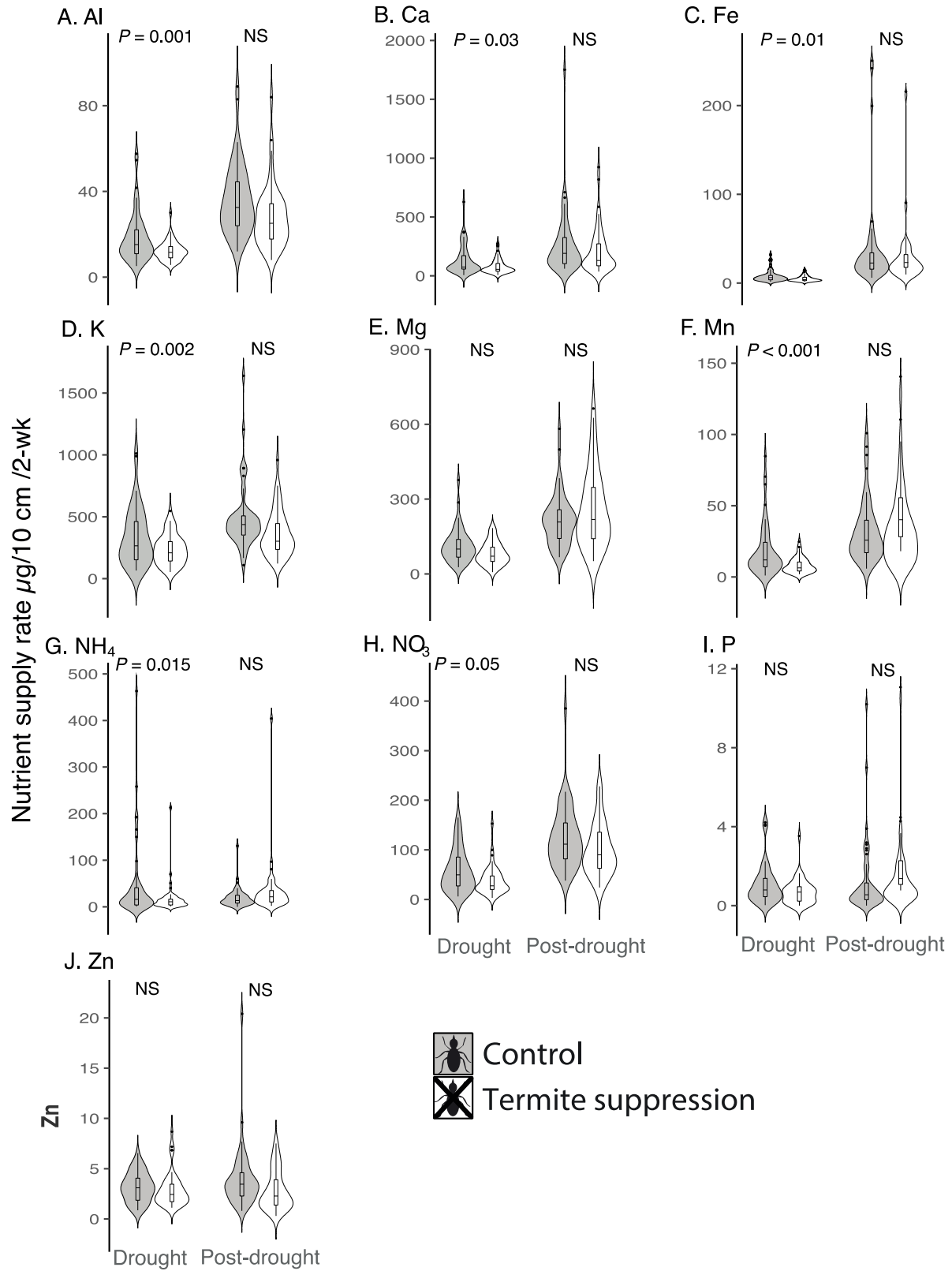
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168 As expected, soil moisture was lower on all plots during the drought compared with  
169 post-drought conditions. However, the presence of termites contributed substantially to  
170 soil moisture retention during the drought. Control plots displayed 36% greater soil  
171 moisture than the termite suppression plots at 5 cm (a depth relevant for shallow rooted  
172 plants and seedlings) during the drought ( $\Delta AIC = 3$ ), but not under post-drought  
173 conditions ( $\Delta AIC < 2$ ; Fig. 2C; Table S4B and Fig. S3D). These termite-driven increases  
174 in soil moisture are more than double the effect size reported by previous investigations  
175 into the influence of invertebrates on soil processes during drought (28).

176  
177 Soil nutrient availability (29, 30) and heterogeneity (12) contribute to plant productivity,  
178 distribution and diversity in rainforest ecosystems. By measuring plant available soil  
179 nutrients from multiple sub-samples across each plot in the drought and post-drought  
180 periods, we show that an increase in termite activity also had consequences for the  
181 spatial heterogeneity of soil nutrients (although not for mean plot-level nutrient  
182 concentrations, which did not differ significantly between control vs suppression plots  
183 under either drought or post-drought conditions, Fig. 3). In the drought, soil nutrient  
184 heterogeneity was significantly lower in the termite suppression plots compared with the  
185 control plots for nitrate, ammonia, calcium, potassium, iron, manganese and aluminium  
186 (Fligner-Killeen test for heterogeneity of variances; Fig. 3). Under post-drought  
187 conditions, the suppression of termites did not influence heterogeneity of any of the soil  
188 nutrients. This could be a direct effect of the movement of organic material, or an  
189 indirect effect of termite activity increasing soil moisture content (or both). These data  
190 imply that termites facilitate the movement of soil nutrients when soil moisture is very

191 low (ca 2.1 %  $\pm$  0.1 during drought compared with ca 25.2 %  $\pm$  0.8 under post-drought  
192 conditions, Fig. 2C), leading to a more heterogeneous soil environment.

193  
194 Seeding survival is often negatively affected by drought and soil desiccation (31). The  
195 positive impacts of termites on soil moisture and nutrient heterogeneity could therefore  
196 have positive effects for seedling survival. We investigated this using a transplant  
197 experiment to quantify the survival of liana seedlings (*Agelaea borneensis* (Fabaceae))  
198 on our plots during and after the drought. During the drought year, we found 51% higher  
199 seedling survival on the control, compared with the termite suppression plots, with the  
200 termite suppression treatment contributing substantially to model fit ( $\Delta$ AIC = 3). Termite  
201 suppression had no effect on model fit under post-drought conditions ( $\Delta$ AIC < 2; Fig.  
202 2D; Table S4C and Fig. S3D). Our findings show that termites may buffer seedlings  
203 against the negative effects of drought by enhancing soil moisture content and nutrient  
204 heterogeneity. Given that droughts are projected to become more frequent and severe  
205 with climate change (3), these results suggest that termites will play an increasingly  
206 important role in structuring tropical plant communities and maintaining plant  
207 productivity and diversity in the future.



209 **Fig. 3:** Extent of variability in A. Al; B. Ca; C. Fe; D. K; E. Mg; F. Mn; G. NH<sub>4</sub>; H. NO<sub>3</sub>; I. P; J. Zn  
210 soil nutrient supply over a 2-week period in control (grey violins) and termite suppression plots  
211 (white violins) during drought and post-drought conditions. Plots display (i) density of data  
212 estimated by kernel method (shaded areas); (ii) median values (horizontal line in the centre of  
213 the boxplots); and (iii) interquartile range (between the top and bottom of the box). Differences  
214 in heterogeneity between treatments were assessed using Flinger-Killen test of homogeneity of  
215 Variances carried out on the residuals from linear mixed effects models. *P* values denote  
216 significant differences between values.

217  
218 This study shows that termite activity increases in rainforests during dry conditions and  
219 that termites buffer important soil processes with consequences for seedling survival  
220 during these periods. Moreover, the buffering effect that we measured is likely to be a  
221 conservative estimate of the total effect as we were not able to exclude all termites in  
222 our experimental plots. Common large-bodied wood feeding termites, e.g. *Bulbitermes*-  
223 group, *Macrotermes*, and *Prohamitermes*, were most affected by our suppression and  
224 appear to be the main drivers of the termite-mediated ecosystem processes presented  
225 here. Although soil feeding termites and other groups that were not targeted by our  
226 suppression may also be important in maintaining ecosystem function, these occurred  
227 less frequently and contributed considerably less biomass to the overall termite  
228 community (Fig. S6). Mechanisms driving the increase in termite activity during  
229 droughts are yet to be established, but possible explanations could include favourable  
230 environmental conditions for tunnelling (e.g. drier, less waterlogged ground), increased  
231 foraging ability above ground in the absence of heavy rain and/or reduced predation  
232 pressure from ants. This increase in termite activity is contrary to the prevailing

233 perception that biota and ecological processes in tropical rainforests are negatively  
234 affected by drought (e.g. (4)). We show that termites form an essential link between  
235 dead plant material and the rest of the ecosystem during dry periods, and no other  
236 decomposer group compensates for the functions they perform.

237

238 This study is constrained by a relatively short temporal duration and we must consider  
239 the possibility that legacy effects in system recovery following the severe drought (e.g.  
240 32) could have influenced the post-drought patterns we observed. However, pre-  
241 drought abundances of non-termite invertebrates were comparable to post-drought  
242 abundances (Fig, S7), which provides evidence that our post-drought data are likely to  
243 be representative of the non-drought stressed system. To more definitively explore this,  
244 future investigations could expand the manipulative termite suppression approach to  
245 include multifactorial environmental manipulations (e.g. drought and litter addition  
246 experiments) and monitoring of ecosystem functioning and recovery over longer-term  
247 annual cycles. This would allow us to disentangle the role of termites in ecosystem  
248 processes following periods of system stress from other confounding environmental  
249 factors.

250

251 While there have been small-scale manipulative experiments showing the importance of  
252 invertebrates in alleviating the effects of drought (28), our large-scale data show that a  
253 major invertebrate group maintains ecosystem functioning during periods of drought,  
254 with potentially cascading consequences for plant survival during. Forest disturbance is  
255 known to reduce termite abundance and diversity (33, 34) and globally, more than 50 %

256 of tropical rainforests have been modified by humans: an area of over 10 million square  
257 kilometres (35). Tropical landscapes that are heavily modified by human disturbance  
258 are likely to be less resistant to drought, because of a reduction in termite-mediated  
259 buffering of ecosystem processes. Our findings suggest that climate change, along with  
260 human disturbance to invertebrate communities, will have negative and interacting (36)  
261 consequences for the maintenance of functioning rainforest ecosystems. Biodiversity is  
262 positively associated ecosystem functioning and stability (36, 37). This study provides  
263 further evidence of the importance of conserving natural ecosystems by showing that  
264 intact biological communities can safeguard ecosystem processes in a time of rapid  
265 environmental change.

266

## 267 **References and notes:**

- 268 1. R. M. May, Tropical Arthropod Species, More or Less? *Science* **329**, 41-42 (2010).
- 269 2. W. Cai *et al.*, Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat.*  
270 *Clim. Change*. **4**, 111-116 (2014).
- 271 3. A. Dai, Increasing drought under global warming in observations and models. *Nat. Clim. Change*  
272 **3**, 52-58 (2013).
- 273 4. D. Bonal, B. Burban, C. Stahl, F. Wagner, B. Hérault, The response of tropical rainforests to  
274 drought—lessons from recent research and future prospects. *Ann For Sci* **73**, 27-44 (2016).
- 275 5. J. B. Yavitt, S. J. Wright, R. K. Wieder, Seasonal drought and dry-season irrigation influence leaf-  
276 litter nutrients and soil enzymes in a moist, lowland forest in Panama. *Austral Ecol.* **29**, 177-188  
277 (2004).
- 278 6. P. Jouquet, S. Traoré, C. Choosai, C. Hartmann, D. Bignell, Influence of termites on ecosystem  
279 functioning. Ecosystem services provided by termites. *Eur J Soil Biol* **47**, 215-222 (2011).
- 280 7. P. Eggleton, in *Termites: evolution, sociality, symbioses, ecology*. (Springer, 2000), pp. 25-51.
- 281 8. T. Abe, D. E. Bignell, M. Higashi, T. Higashi, *Termites: evolution, sociality, symbioses, ecology*.  
282 (Springer Science & Business Media, 2000).
- 283 9. M. D. Ulyshen, Wood decomposition as influenced by invertebrates. *Biological Reviews* **91**, 70-  
284 85 (2016).
- 285 10. B. K. Gautam, G. Henderson, Water Transport by *Coptotermes formosanus* (Isoptera:  
286 Rhinotermitidae). *Environ. Entomol.* **43**, 1399-1405 (2014).
- 287 11. D. K. Wijesinghe, E. A. John, M. J. Hutchings, Does pattern of soil resource heterogeneity  
288 determine plant community structure? An experimental investigation. *J. Ecol.* **93**, 99-112 (2005).
- 289 12. W. Xu *et al.*, Soil phosphorus heterogeneity promotes tree species diversity and phylogenetic  
290 clustering in a tropical seasonal rainforest. *Ecol. Evol.* **6**, 8719-8726 (2016).

- 291 13. N. McDowell *et al.*, Mechanisms of plant survival and mortality during drought: why do some  
 292 plants survive while others succumb to drought? *New Phytol.* **178**, 719-739 (2008).
- 293 14. L. Dibog, P. Eggleton, F. Forzi, Seasonality of soil termites in a humid tropical forest, Mbalmayo,  
 294 southern Cameroon. *J. Trop. Ecol.* **14**, 841-850 (1998).
- 295 15. J. A. Bonachela *et al.*, Termite mounds can increase the robustness of dryland ecosystems to  
 296 climatic change. *Science* **347**, 651-655 (2015).
- 297 16. T. M. Fayle *et al.*, Whole-ecosystem experimental manipulations of tropical forests. *Trends Ecol.*  
 298 *Evol.* **30**, 334-346 (2015).
- 299 17. L. A. Ashton *et al.*, Supplementary materials for: Termites mitigate the ecosystem-wide effects  
 300 of drought in tropical rainforest. *Science*, (2018).
- 301 18. D. T. Jones, P. Eggleton, Sampling termite assemblages in tropical forests: testing a rapid  
 302 biodiversity assessment protocol. *J. Appl. Ecol.* **37**, 191-203 (2000).
- 303 19. M. E. Crockatt, D. P. Bebber, Edge effects on moisture reduce wood decomposition rate in a  
 304 temperate forest. *Global Change Biol.* **21**, 698-707 (2015).
- 305 20. M. J. Swift, O. W. Heal, J. M. Anderson, *Decomposition in terrestrial ecosystems*. (Univ of  
 306 California Press, 1979), vol. 5.
- 307 21. F. Xuluc-Tolosa, H. Vester, N. Ramirez-Marcial, J. Castellanos-Albores, D. Lawrence, Leaf litter  
 308 decomposition of tree species in three successional phases of tropical dry secondary forest in  
 309 Campeche, Mexico. *For. Ecol. Manage.* **174**, 401-412 (2003).
- 310 22. K. L. Yeong, G. Reynolds, J. K. Hill, Leaf litter decomposition rates in degraded and fragmented  
 311 tropical rain forests of Borneo. *Biotropica* **48**, 443-452 (2016).
- 312 23. G. Liu *et al.*, Termites amplify the effects of wood traits on decomposition rates among multiple  
 313 bamboo and dicot woody species. *J. Ecol.* **103**, 1214-1223 (2015).
- 314 24. C. S. O'Connell, L. Ruan, W. L. Silver, Drought drives rapid shifts in tropical rainforest soil  
 315 biogeochemistry and greenhouse gas emissions. *Nat. Commun.* **9**, 1348 (2018).
- 316 25. W. K. Cornwell *et al.*, Plant traits and wood fates across the globe: rotted, burned, or consumed?  
 317 *Global Change Biol.* **15**, 2431-2449 (2009).
- 318 26. S. Luysaert *et al.*, CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from a global  
 319 database. *Global Change Biol.* **13**, 2509-2537 (2007).
- 320 27. M. Kaspari, N. A. Clay, D. A. Donoso, S. P. Yanoviak, Sodium fertilization increases termites and  
 321 enhances decomposition in an Amazonian forest. *Ecology* **95**, 795-800 (2014).
- 322 28. S. N. Johnson *et al.*, An insect ecosystem engineer alleviates drought stress in plants without  
 323 increasing plant susceptibility to an above-ground herbivore. *Funct. Ecol.* **30**, 894-902 (2016).
- 324 29. R. John *et al.*, Soil nutrients influence spatial distributions of tropical tree species. *PNAS* **104**,  
 325 864-869 (2007).
- 326 30. G. D. Paoli, L. M. Curran, D. R. Zak, Soil nutrients and beta diversity in the Bornean  
 327 Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *J. Ecol.* **94**, 157-  
 328 170 (2006).
- 329 31. F. Padilla, F. Pugnaire, Rooting depth and soil moisture control Mediterranean woody seedling  
 330 survival during drought. *Funct. Ecol.* **21**, 489-495 (2007).
- 331 32. W. R. L. Anderegg *et al.*, Pervasive drought legacies in forest ecosystems and their implications  
 332 for carbon cycle models. *Science* **349**, 528-532 (2015).
- 333 33. S. H. Luke, T. M. Fayle, P. Eggleton, E. C. Turner, R. G. Davies, Functional structure of ant and  
 334 termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian  
 335 Borneo. *Biodivers. Conserv.* **23**, 2817-2832 (2014).
- 336 34. P. Eggleton *et al.*, Termite diversity across an anthropogenic disturbance gradient in the humid  
 337 forest zone of West Africa. *Agric., Ecosyst. Environ.* **90**, 189-202 (2002).



- 338 35. W. F. Laurance, J. Sayer, K. G. Cassman, Agricultural expansion and its impacts on tropical  
339 nature. *Trends Ecol. Evol.* **29**, 107-116 (2014).
- 340 36. I. M. Côté, E. S. Darling, C. J. Brown, Interactions among ecosystem stressors and their  
341 importance in conservation. *Philos. Trans. Royal Soc. B.* **283**, 20152592 (2016).
- 342 37. B. J. Cardinale *et al.*, Biodiversity loss and its impact on humanity. *Nature* **486**, 59 (2012).
- 343 38. Ashton, L.A., Griffiths, H.M., Evans, T.A., Parr, C.L., Eggleton, P., Termite abundance and  
344 ecosystem processes in Maliau Basin, 2015-2016. NERC Environmental Information Data Centre,  
345 10.5285/1e9993ae-add7-497a-b54b-745b0fc6a7ca (2018)
- 346 39. T. A. Evans, T. Z. Dawes, P. R. Ward, N. Lo, Ants and termites increase crop yield in a dry climate.  
347 *Nature communications* **2**, 262 (2011).
- 348 40. A. B. Davies, P. Eggleton, B. J. van Rensburg, C. L. Parr, Assessing the relative efficiency of  
349 termite sampling methods along a rainfall gradient in African savannas. *Biotropica* **45**, 474-479  
350 (2013).
- 351 41. N. Iqbal, T. Evans, Evaluation of fipronil and imidacloprid as bait active ingredients against  
352 fungus-growing termites (Blattodea: Termitidae: Macrotermitinae). *Bull. Entomol. Res.* **108**, 14-  
353 22 (2018).
- 354 42. A. Brune, Symbiotic digestion of lignocellulose in termite guts. *Nature Reviews Microbiology* **12**,  
355 168 (2014).
- 356 43. D. K. Aanen, P. Eggleton, Symbiogenesis: Beyond the endosymbiosis theory? *J. Theor. Biol.* **434**,  
357 99-103 (2017).
- 358 44. J. French, P. Robinson, Baits for aggregating large numbers of subterranean termites. *Aust. J.*  
359 *Entomol.* **20**, 75-76 (1981).
- 360 45. S. M. Vicente-Serrano, S. Beguería, J. I. López-Moreno, A multiscalar drought index sensitive to  
361 global warming: the standardized precipitation evapotranspiration index. *J. Clim.* **23**, 1696-1718  
362 (2010).
- 363 46. S. Both, D. M. O. Elias, U. H. Kritzler, N. J. Ostle, D. Johnson, Land use not litter quality is a  
364 stronger driver of decomposition in hyperdiverse tropical forest. *Ecology and Evolution* **7**, 9307-  
365 9318 (2017).
- 366 47. A. M. Stoklosa *et al.*, Effects of mesh bag enclosure and termites on fine woody debris  
367 decomposition in a subtropical forest. *Basic Appl. Ecol.* **17**, 463-470 (2016).
- 368 48. J. M. Cohen, M. J. Lajeunesse, J. R. Rohr, A global synthesis of animal phenological responses to  
369 climate change. *Nature Climate Change* **8**, 224 (2018).
- 370 49. R Development Core Team. (R Foundation for Statistical Computing, Vienna, 2016).
- 371 50. T. Riutta *et al.*, Logging disturbance shifts net primary productivity and its allocation in Bornean  
372 tropical forests. *Global Change Biol.* **24**, 2913–2928 (2018).

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### **Supplementary Materials:**

### **Materials and Methods**

**Fig S1-S9**

**Tables S1-S5**

**Graphical abstract**